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2 Running head: Habitat generalism in migrants

3 **Temperate migrants and resident species in Afro-tropical
4 savannahs show similar levels of ecological generalism**

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9 How specific an animal's habitat requirements are will determine its ability to deal with
10 anthropogenic climate and habitat change. Migratory birds are observed as being particularly
11 vulnerable to such change, but theory predicts that they should be largely generalist. This
12 prediction was tested with the aim to confirm whether migratory Palearctic birds wintering in
13 the savannah biome of Africa were relatively generalist compared to taxonomically and
14 ecologically similar Afrotropical resident species in terms of habitat use. The degree of
15 specialization of these species groups to certain habitat characteristics was assessed and
16 compared by calculating the relative occurrence of the species along habitat gradients, where
17 wide occurrence would indicate generalism and narrow occurrence implies specialism.
18 Palearctic migrants as a group could not be clearly distinguished as generalists relative to
19 Afrotropical residents with respect to habitat attributes. The only indication of greater
20 flexibility in Palearctic migrants was a significant tendency to utilize habitats over a larger
21 latitudinal range. The results probably confirm that migrants are generalists but not
22 particularly more so than taxonomically similar resident species that also occur over a wide
23 range of habitat types within the savannah biome. Availability of specific habitat
24 requirements on the wintering grounds in Africa is therefore unlikely to be a primary limiting
25 factor for many migrant bird species.

26 **Key-words:** habitat specialization, generalists, Palearctic migrants, Afrotropics, migration,
27 habitat use, distribution

28 **Introduction**

29 Understanding habitat specificity in organisms is important in explaining and predicting how
30 they may respond to environmental change. Species may be closely associated with one or
31 more habitats or habitat characteristics and are often described as specialists or generalists
32 depending on the range of such habitats that they are able to exploit and their capability and
33 efficiency at using each one (MacArthur 1972, Julliard, *et al.* 2006). Whereas specialists may
34 only occupy relatively small niches (i.e. exploit only a small subset of habitat characteristics)
35 but utilise them very efficiently, generalist species may alternatively occupy larger niches,
36 exploiting a wider range of resources but sometimes with relatively lower efficiency
37 (MacArthur 1972, Wilson and Yoshimura 1994). Generally, habitat specialists, which are
38 also associated with lower dispersal ability, are thought to be more negatively affected by
39 environmental stochasticity. They are also thought to respond more to local ecological and
40 habitat processes in contrast to generalist species which generally have broader geographic
41 distributions as well as good dispersal and colonization abilities (Julliard, *et al.* 2006, Shubha,
42 *et al.* 2009, Clavel, *et al.* 2011, Sokolov, *et al.* 2012).

43 In environments where species' requirements may overlap, differences in habitat
44 specialization could provide a mechanism for the coexistence of potentially competing
45 species and thus have implications for the dynamics of such communities (Morris 1996). This
46 study investigates the relative degree and difference in habitat specialization patterns using an
47 avian community of migratory and resident species in an Afrotropical savannah zone where
48 this may potentially be important in fostering coexistence. Migratory species/individuals in
49 these communities have often been described as habitat generalists, thought to adopt
50 generalist strategies and exhibit ecological flexibility in order to 'fit in' with the 'superior and
51 dominant' resident communities where these migrants were also seen as 'visitors' or
52 'temporary invaders' (Herrera 1978, Sinclair 1978, Leisler 1992). Consequently, observations

53 of migrants' occurrences in more open and peripheral habitats, combined with their relatively
54 higher foraging speeds and a tendency to use a wider range of foraging tactics have largely
55 also been interpreted as evidence that migrants are flexible and generalists (Salewski, *et al.*
56 2002, Salewski, *et al.* 2003, Salewski and Jones 2006, Salewski, *et al.* 2007, Jones, *et al.*
57 2010). Furthermore, in a recent review, Cresswell (2014) argued that a generalist strategy is
58 the most likely to be selected for in migrants considering the potential for stochastic
59 processes to affect the initial selection of site at a large scale for an animal migrating for the
60 first time. The debate however remains as to whether these observed attributes and
61 distribution patterns are consequences or precursors for migration behaviour (Salewski and
62 Jones 2006).

63 As well as being of theoretical interest with respect to the evolution of migration and the
64 structuring of communities that contain migrants, the degree of habitat specialisation shown
65 by Palearctic migrants is relevant to their conservation. This is especially important given
66 reports of substantial declines in the populations of some Palearctic migrant species. In many
67 cases, connections have been made between these declines and the changing habitat and
68 climatic conditions in their wintering quarters (Ockendon, *et al.* 2012, Ockendon, *et al.* 2014,
69 Vickery, *et al.* 2014) which appear to be related to the degree to which the concerned
70 migratory species or populations are specific in their use of these habitats. For instance,
71 population declines in the 1970s were greatest in species that specifically utilise the dry
72 woodland and scrub habitats of the Sahel during the winter periods (Baillie and Peach 1992,
73 Walther, *et al.* 2011, Atkinson, *et al.* 2014). In recent years however, greater declines have
74 largely been observed for trans-Saharan migrant species utilising the more humid
75 Afrotropical Guinea savannah habitats (Vickery, *et al.* 2014). Investigating habitat specificity
76 in migrants is therefore not only important to help understand the underlying mechanisms of
77 these declines and how this may be related to the degree of specificity in habitat use, but

78 could also be vital in informing appropriate management strategy and policy necessary for
79 the successful conservation of these species.

80 This study explores at a landscape scale, the relative distribution and habitat use of Palearctic
81 migrants and Afrotropical resident species in the Guinea and Derived savannah habitats in
82 Nigeria, West Africa. The degree of specialization of these two species' groups to habitat
83 characteristics in this area are evaluated and compared, testing the hypothesis that migrants
84 will to a greater degree be more generalist – use a wider range of the habitats within the
85 savannah - than taxonomically similar residents in the Afrotropics. We adopt a relatively
86 straightforward approach to test this hypothesis where we compare the occurrence across
87 habitat gradients of migrant species versus taxonomically and ecologically similar resident
88 species. We use all possible species that provided sufficient records to allow statistical
89 testing, and test whether there were any significant biases due to not considering rarer species
90 and due to potential detectability differences between migrants and resident species.

91 **Materials and methods**

92 **Study area**

93 This study was carried out in the Guinea and Derived savannahs in Nigeria, West Africa. The
94 Guinea savannah is located between the mainly arid and open Sudan and Sahel savannahs to
95 the north and the more humid and densely vegetated rainforests to the south. Together with
96 the Derived savannah (which is essentially cleared and logged portions on the northern edge
97 of the rainforest and representing an extension of the savannah into the rainforest), the
98 Guinea savannah covers about 50% of the Nigerian landscape and forms an ecological and
99 transitional belt of vegetation across the middle regions of Nigeria. Vegetation in this
100 ecological zone is dominated by broad-leaved and short-boled trees up to 15m high, with a
101 heterogeneous mosaic of habitats ranging from isolated gallery and riparian forests, open
102 wood/shrublands and open grasslands. Anthropogenic and climatic effects are severe: fierce

103 annual fires in the dry season have allowed fire-resistant species to predominate while
104 continuous clearing for agricultural lands and intense grazing continues to reduce and
105 fragment this area (Adegbola and Onayinka 1976, FORMECU 1998, Abbas 2009). Survey
106 areas (habitats) were selected to represent the entire range of habitats available in terrestrial
107 Guinea savannah from highly anthropogenic habitats such as cleared farmland through to
108 relatively pristine Guinea savannah woodland with high densities of natural vegetation (e.g.
109 see the variation illustrated in Fig. A1 supplementary material).

110 **Field survey**

111 Bird surveys and habitat characterization were conducted during the northern winters of
112 2011/2012 and 2012/2013. The point transects method was used to record birds and involved
113 counts of birds from several points which were located at regular intervals along a given
114 transect. A total of about 630 points were surveyed, spread across 12 survey sites which were
115 distributed over a 4 degree latitudinal range (6 – 10°N) in the Guinea savannah (Figure 1,
116 Supplementary material Table A1). There were at least 3 survey sites per latitude and at least
117 3 transects spread across different habitat types within a survey site. Eighteen point transects
118 spread across six survey sites were surveyed once every month in the first winter period from
119 February – May 2012. Three surveys were conducted during the second winter; one survey in
120 each period of September-December 2012, January – February 2013, and March - April 2013
121 across 24 transects in 8 survey sites (3 out of 6 of the first winter sites plus 5 new sites).
122 Presence and absence of birds were recorded for 5 minutes at each point which had a radius
123 of 50m and these were located at 100m intervals along the transects of between 1.5 – 2 km in
124 length. All bird counts were conducted during the early hours of the day just after dawn,
125 usually from about 06:00 hours for about three hours. For every sighted bird, the distance
126 from the observer who was at the centre of the point was recorded using a Nikon 550 laser
127 range finder. The geographical coordinates was recorded at the centre of each point count
128 location and the distance between points was checked with a Garmin 62 GPS. Environmental

129 variables characterizing the vegetation density/cover, structure/height profile, anthropogenic
130 impact/disturbance and latitudinal/geographical distribution of habitats were also recorded at
131 each point location (Supplementary material Table A2) during every survey visit. Vegetation
132 sampling during every survey visit allowed for any changes in the characteristics of the
133 vegetation with season to also be recorded. For example a point that was visited early in the
134 season with a dense grass cover could eventually have very low to no grass cover later in the
135 season especially in areas where the vegetation is seasonally burnt.

136 **Data analysis**

137 All statistical procedures and tests were conducted in R version 3.1.0 statistical software (R
138 Development Core Team 2014). All migratory passerine species as well as taxonomically-
139 related and ecologically similar Afrotropical resident species were selected from all recorded
140 species for the purpose of comparison and analysis. An initial total of 35 species from five
141 families were considered for this analysis including 11 Palearctic species recorded during
142 point count surveys and 24 Afrotropical species from the same families, with similar sizes,
143 from similar foraging guilds and/or with similar foraging strategies as the Palearctic species.
144 Ten of these 35 species (fully listed in Supplementary material Table A3) had very limited
145 occurrence and were recorded from less than 10 points (i.e. less than 2% of the total surveyed
146 points and less than 15% of the survey points at a site) throughout the study area and period.
147 These were excluded to give a second set of 25 species (Supplementary material Table A3 &
148 Table 1). This selection did not alter the abundance/occurrence ratio between migrants and
149 residents: a *t*-test indicated that the difference in abundance/occurrence ratio of migrants and
150 resident birds before and after the exclusion was not statistically significant (with the group
151 of 35 species - Abundance: $t = 1.4$, d.f. = 14.1, $P = 0.19$ and Occurrence: $t = -1.4$, d.f. = 12.7,
152 $P = 0.18$ and with the group of 25 species - Abundance: $t = -1.6$, d.f. = 10.7, $P = 0.13$ and
153 Occurrence: $t = -1.7$, d.f. = 9.1, $P = 0.13$). Consequently, a total of 25 species from five
154 families recorded from at least 10 different points were considered to have provided

155 sufficient records to allow statistical testing and were used for this analysis (note that
156 analyses using all 35 species are largely the same species i.e. no significant differences in
157 habitat specialization save for differences in latitudinal distribution). This consisted of 8
158 Palearctic migrant and 17 Afrotropical resident species. These Afrotropical species were from
159 the same taxonomic families and foraging guilds and have similar foraging strategies as the
160 recorded Palearctic species (Fry, *et al.* 2000, Urban, *et al.* 1992, Urban, *et al.* 1997).

161 We tested whether there were detectability differences between the migrant and resident
162 groups by comparing the frequency distribution of distances that each species was recorded
163 during a point count, with species classified into the two groups. A Generalized Linear Mixed
164 effects Model (GLMM) was carried out using the library lme4 in R with the model structure
165 of: distance recorded (<50m) = migratory status (resident or migrant) + year + species
166 identity (as a random effect). There was no significant difference in detectability (distance at
167 which a bird was recorded) by migratory status for either the 35 species data set, or the
168 reduced 25 species data set used in subsequent analyses (migratory status: -0.63 +/- 1.3 SE
169 for residents, $\chi^2 = 0.3$, P = 0.58, N = 1414; or -0.31 +/- 1.2 SE for residents, $\chi^2 = 0.1$, P =
170 0.74, N = 1261, respectively). The models were very robust to violation of assumptions with
171 a reasonable normal distribution of residuals, no evidence of heteroscedasticity or outliers;
172 truncation to <50m only reduced sample sizes by 11% for both models and only <1% and c.
173 5% of variance for fixed and random effects respectively was accounted for in both models.
174 Therefore there was no evidence of any likely confounding effects from variable
175 detectability: migrants and resident species had similar recorded distances.

176 We adopted a simple definition of specialists as species utilizing a narrow range of resources
177 and generalists as those that use a wide range of resources. Therefore, specialists would use
178 and be associated with only a small and specific range of the habitat characteristics measured
179 and hence will show little variability for these habitat variables. The reverse would be the
180 case for a generalist species i.e. associated with a relatively higher variation in measured

181 habitat variables. A Habitat Specialization score (HS score) was calculated based on the
182 degree of variation (represented by the standard deviations) observed in the range of habitat
183 characteristics from points where each species was recorded. This involved, in the first
184 instance, a Principal Component Analysis (PCA) using the prcomp function and a varimax
185 rotation to summarise all recorded 13 habitat variables across all points surveyed into three
186 composite variables i.e. the top three components from the PCA (Supplementary material
187 Table A4). Bartlett's test of sphericity, which tested the overall significance of all the
188 correlations within the correlation matrix of the habitat variables indicated that it was
189 appropriate to summarise the dataset in a PCA (Bartlett's test: $\chi^2 (78) = 2170.4$, $P < 0.001$).
190 The Kaiser-Meyer-Olkin (KMO) measure of sampling adequacy further indicated sufficient
191 relationships among these variables (KMO criterion = 0.75) to proceed with the analysis.

192 For each species, PCA scores for all points where it was recorded (i.e. its presence points)
193 were then extracted and the standard deviations (sd) calculated to give a measure of its
194 variability in habitat use with respect to the composite variable. This sd value was divided by
195 an overall standard deviation of all habitat scores from every point that had been surveyed to
196 obtain a proportion of the variability in that habitat characteristic associated with the
197 occurrence of that species. These proportions were then scaled between 0 and 1 to give a
198 habitat specialization score for each of the three principal components and for each species. A
199 zero HS score represents the most specialized species in the group with the least specialized
200 species i.e. a generalist, showing greatest habitat flexibility with a score of 1 (i.e. occurred in
201 all habitats). Habitat specialization scores of migrants and Afro-tropical residents for all three
202 principal components were compared for significant differences using a *t*-test.

203 In a second approach, HS scores were derived following a similar process as above but using
204 the values of the 13 unsummarized habitat variables instead of the scores for the composite
205 variables derived from a PCA. We analysed the individual variable values as well as the
206 composite scores to better understand the biological significance of the habitat variation. All

values were also compared with a t-test between resident and migratory birds for each of these 13 unsummarised habitat variables. A Bonferroni multiple-comparison correction was carried out by dividing each p - value by the total number of tests (i.e. there were 13 t -tests, so $0.05/13$) to set a new significant threshold value (0.004) to account for the probability of increasing the Type I error rate.

Results

Relative habitat specialization

The top three principal components (PCs) accounted for 57 % of the variance (see Supplementary material Table A4 for details of the loadings and correlation of habitat variables and principal components). Some of the highest loading habitat variables are plotted with principal components and are shown in Supplementary material Figure A1 to facilitate interpretation. The first principal component shows positive relationships with tree density, diversity and height: habitat characteristics that could serve as proxies for habitat quality/structure (i.e. higher scores indicating forests or denser woodlands). The latitude of habitats and the index for bush fires loaded positively on principal component 2 whereas shrub density/height, ground vegetation cover, and tree height all showed an inverse relationship with principal component 2. These relationships appear to reflect the latitudinal gradient that is characteristic of the Afrotropical environment i.e. shorter and sparser vegetation associated also with a higher frequency of bush fires in the open and usually more arid savannah habitats which occur at higher and more northern latitudes. Grass height and the presence of livestock dung showed positive and inverse relationships with principal component 3 respectively. There was also a weak positive relationship of lopped trees with principal component 3. These relationships appear to represent habitat disturbance i.e. areas with short grass also associated with higher levels of grazing and with more lopped trees - an additional activity associated with grazing. Thus principal components 1, 2 and 3 were taken

232 as indices to represent the structure/quality, latitude/geographical distribution and level of
233 anthropogenic disturbance of habitats respectively.

234 Habitat specialization scores calculated from the PCA scores for all species are shown in
235 Table 1. The differences in HS scores derived from principal component 1 and principal
236 component 3 (i.e. average habitat specialization scores for structure/quality and level of
237 anthropogenic disturbance of habitats) between Palearctic migrant and Afrotropical resident
238 species were not statistically significant (mean PC1 HS score for migrants 0.56 and residents
239 0.57, *t*-test: $t = 0.1$, d.f. = 17.4, $P = 0.92$ and mean PC3 HS score for migrants 0.67 and
240 residents 0.54, *t*-test: $t = -1.3$, d.f. = 15.4, $P = 0.21$). Palearctic migrants however had a
241 significantly higher HS score for principal component 2 i.e. were more generalist and
242 occupied a relatively larger latitudinal range compared to the Afrotropical resident species
243 (mean PC2 HS score for migrants 0.64 and residents 0.37; *t*-test: $t = -2.4$, d.f. = 11.1, $P =$
244 0.03). Relative distributions of the HS scores for all species in both residency groups are
245 shown in Figure 2.

246 The HS scores derived from the 13 unsummarised habitat variables were also not
247 significantly different between resident and migratory birds except for Latitude (Table 2)
248 where migratory birds had significantly higher scores (i.e. were generalists and occurred over
249 a wider latitudinal range) compared to Afrotropical resident birds ($t = -3.3$, d.f. = 16.5, $P =$
250 0.005); note however that this P - value is just above the new threshold value after a
251 Bonferroni correction is applied (i.e. $0.05/13 = 0.004$).

252 **Discussion**

253 Our results suggest that Palearctic migrants and Afrotropical resident species in the Guinea
254 savannah in Nigeria are similar in their degree of generalism or specialization with respect to
255 habitat quality/structure (principal component 1) and disturbance (principal component 3).
256 However, there was some evidence of greater flexibility due to a significant tendency for the

257 Palearctic migrants to occupy habitats over a significantly wider latitudinal range (principal
258 component 2) in the study area compared to their Afro-tropical resident counterparts.
259 Although the PCA model only explained 57% of variance, the analysis of individual variables
260 also confirmed that there was no strong evidence for differences in breadth of habitat
261 occupancy across almost all of the gradients considered apart from latitude. Our results are
262 unlikely to be confounded by detectability differences between the two groups because
263 species in the two groups, on average, were recorded at similar distances and so it seems
264 reasonable to conclude that migrants and residents occupy habitats in a broadly similar way.

265 The observations in this study of habitat overlaps and similarity in habitat occupancy provide
266 additional evidence for the emergent view of Palearctic migrants as integral, rather than
267 marginal or peripheral components of the tropical avian communities (Salewski and Jones
268 2006). Earlier studies tackling the question of coexistence between migrants and resident
269 species with the aim to find evidence for greater flexibility and generalism in the migratory
270 species/individuals often ascribed a great significance to the role of competitive interactions
271 between these groups in shaping these communities (Herrera 1978, Sinclair 1978, Leisler
272 1992). This assumption greatly influenced the description of migrants as ‘invading’, ‘less-
273 dominant and flexible’ members in Afro-tropical avian communities, further promoting the
274 idea that migrants also resorted to using more open and diverse habitats in marginal and
275 peripheral parts of the vegetation in order to coexist with the more ‘dominant’ resident
276 species (Salewski and Jones 2006). However, most of these studies investigating the impacts
277 of competitive interactions on the dynamics of coexistence of these species, as in this study
278 also, have tended to report significant overlaps in habitat occupancy and with little evidence
279 of direct interspecific competition (Leisler 1992, Salewski, *et al.* 2003, Salewski, *et al.* 2007,
280 Wilson and Cresswell 2007, Jones, *et al.* 2010, Wilson and Cresswell 2010). It seems
281 therefore that any impacts of competition in shaping these avian communities may have
282 occurred in the evolutionary past, such that its current influences might thus be relatively

283 negligible and less detectable (Salewski and Jones 2006). Furthermore, reported evidence of
284 migrants using the presence of temperate resident species as cues in selecting profitable
285 breeding sites rather than avoiding them (Forsman, *et al.* 2002, Mönkkönen, *et al.* 2004,
286 Forsman, *et al.* 2009) suggest that habitat overlaps between migrants and ecologically similar
287 resident species in the tropics should perhaps also be expected. The possibility of
288 heterospecific attraction for migrants in influencing community structures in the tropics is
289 thus well worth investigating.

290 Despite the similarities in habitat occupancy, the observed tendency for Palearctic migrants to
291 occupy these habitats over a significantly wider latitudinal range compared to their
292 Afrotropical resident counterparts does fit with the expectation of generalism and ecological
293 flexibility for migratory species. This may be related to their dispersal capabilities which
294 often also means that they tend to respond mainly to spatial and other factors related to patch
295 dynamics and usually at larger scales than more specialized species (Morris 1996, Shubha, *et*
296 *al.* 2009).

297 The utilization of relatively larger ranges by generalist species is also sometimes explained
298 with the suggestion that coexistence with competitors may be fostered by their exploitation of
299 margins and underutilised conditions in-between habitats already occupied by multiple
300 specialized competitors (Morris 1996, Sinclair 1978). The ability of migrants to
301 opportunistically track temporary insect abundance brought about by the initial localised
302 rainstorms during the short rainy season in Central-East Africa (a strategy not used by most
303 of their resident counterparts) may be an example of this. However, overlaps in habitat use
304 between residents and migrants have also been reported in this region from areas of
305 superabundance of food resources (Sinclair 1978). Furthermore, in West Africa, migrants
306 arrive at the end of the rains when the general conditions progressively get drier, particularly
307 in more northern areas (Nicholson, *et al.* 1990, Schneider, *et al.* 2014). There is thus an
308 important contrast in the ecological conditions between the regions with the opportunity for

309 opportunistic niches and increased food supply arising only in East Africa – yet Palearctic
310 migrants coexist and occupy both regions to similar degrees.

311 Other factors besides competitive interactions may give rise to generalist traits in migrants
312 and explain the tendency for migrants to occupy relatively larger ranges. Some authors
313 (Levey and Stiles 1992, Salewski and Jones 2006, Cresswell 2014) have argued that the
314 ecological flexibility often expected (and that is strongly suggested in this study) for migrants
315 could actually be a fundamental requirement for the evolution and maintenance of migration
316 in the first place. Cresswell (2014), for example, suggests that stochastic events when an
317 individual migrates for the first time could lead to the spread of passage and wintering sites
318 over wide areas, across suitable and not so suitable habitats. If this is the case, then ecological
319 flexibility and generalism would be vital in promoting survival of these naive young birds
320 that would not have prior knowledge of the location of localised habitats on their initial
321 arrival in the savannah zone of Africa. In line with this argument, one may draw parallels to
322 introduced or invading species where similar generalist traits and mechanisms have been
323 shown to significantly contribute to the successful establishment of such organisms to novel
324 environments (Martin and Fitzgerald 2005, Wright, *et al.* 2010).

325 In conclusion, our observation of the presence/absence of migrants and ecologically similar
326 residents across habitats in a tropical savannah in Nigeria mainly indicate that migrants and
327 residents occupied similar habitat types although migrants had a tendency to occupy habitats
328 over larger spatial scales. This suggests that migrants are probably generalists in the breadth
329 of habitats that they occupy, but not particularly more so than taxonomically similar resident
330 species. Our use of presence/absence data only allowed us to report overlaps and similarities
331 in habitat occupancy between these species groups. A better understanding of the underlying
332 mechanisms of their coexistence will however require investigation also of the interactions
333 between these species, their relative densities in areas of overlaps, foraging behaviour and
334 even the fitness consequences of co-occupancy or habitat segregation. But regardless of the

335 mechanism, generalism itself in migrants has implications for their population dynamics. As
336 generalists, migrants may be expected to show some resilience especially in dealing with
337 local and small scale changes on their wintering grounds such that these are unlikely to be the
338 primary limiting factor in their population dynamics for many migrant species. This
339 conclusion is particularly relevant considering the widespread and ongoing declines in the
340 populations of Palearctic migrants (Vickery, *et al.* 2014). Put simply – our study provides
341 additional evidence that habitat availability in Africa may not be limiting for many migrant
342 species.

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352 **References**

- 353 **Abbas, I.I. (2009)** An overview of land cover changes in Nigeria, 1975 - 2005. *Journal of*
 354 *Geography and Regional Planning* **2:** 062-065.
- 355 **Adegbola, A.A. & Onayinka, E.A.O. (1976)** A review of range management problems in
 356 the southern Guinea and derived savanna zones of Nigeria. *Tropical Grasslands* **10:**
 357 41-51.
- 358 **Atkinson, P.W., Adams, W.M., Brouwer, J., Buchanan, G., Cheke, R.A., Cresswell, W.,**
 359 **Hewson, C.M., Hulme, M.F., Manvell, A., Sheehan, D.K., Small, R.D.S.,**
 360 **Sutherland, W.J. & Vickery, J.A. (2014)** Defining the key wintering habitats in the
 361 Sahel for declining African-Eurasian migrants using expert assessment. *Bird*
 362 *Conservation International* **24:** 477 - 491.
- 363 **Baillie, S. & Peach, W. (1992)** Population limitation in Palaearctic-African migrant
 364 passerines. *Ibis* **134:** 120 - 132.
- 365 **Clavel, J., Julliard, R. & Devictor, V. (2011)** Worldwide decline of specialist species:
 366 toward a global functional homogenization? *Frontiers in Ecology and the*
 367 *Environment* **9:** 222-228.
- 368 **Cresswell, W. (2014)** Migratory connectivity of Palaearctic–African migratory birds and
 369 their responses to environmental change: the serial residency hypothesis. *Ibis* **156:**
 370 493-510.
- 371 **FORMECU (1998)** Assessment of Vegetation and Land Use Changes in Nigeria between
 372 1978 and 1993. Geomatics International Inc., Beak Consultants Limited of Canada and
 373 Unilag Consults Nigeria, Federal Department of Forestry, Abuja, Nigeria.
- 374 **Forsman, J.T., Hjernquist, M.B. & Gustafsson, L. (2009)** Experimental evidence for the
 375 use of density based interspecific social information in forest birds. *Ecography* **32:**
 376 539 - 545.
- 377 **Forsman, J.T., Seppänen, J.T. & Mönkkönen, M. (2002)** Positive Fitness Consequences of
 378 Interspecific Interaction with a Potential Competitor. *Proceedings: Biological*
 379 *Sciences* **269:** 1619-1623.
- 380 **Fry, C.H., Keith, S. & Urban, E.K. (2000)** *The Birds of Africa*. Academic Press, London,
 381 UK.
- 382 **Herrera, C.M. (1978)** Ecological Correlates of Residence and Non-Residence in a
 383 Mediterranean Passerine Bird Community. *Journal of Animal Ecology* **47:** 871-890.
- 384 **Jones, P., Salewski, V., Vickery, J. & Mapaure, I. (2010)** Habitat use and densities of co-
 385 existing migrant Willow Warblers *Phylloscopus trochilus* and resident eremomelas
 386 *Eremomela* spp. in Zimbabwe. *Bird Study* **57:** 44-55.
- 387 **Julliard, R., Clavel, J., Devictor, V., Jiguet, F. & Couvet, D. (2006)** Spatial segregation of
 388 specialists and generalists in bird communities. *Ecol. Lett.* **9:** 1237-1244.
- 389 **Leisler, B. (1992)** Habitat selection and coexistence of migrants and Afrotropical residents.
 390 *Ibis* **134:** 77-82.

- 391 **Levey, D.J. & Stiles, F.G.** (1992) Evolutionary precursors of long-distance migration-
392 resource availability and movement patterns in Neotropical landbirds. *American
393 Naturalist* **140**: 447-476.
- 394 **MacArthur, R.H.** (1972) *Geographical Ecology*. Harper & Row Publishers Inc., New York,
395 USA.
- 396 **Martin, L.B. & Fitzgerald, L.** (2005) A taste for novelty in invading house sparrows, *Passer
397 domesticus*. *Behavioral Ecology* **16**: 702-707.
- 398 **Mönkkönen, M., Forsman, J.T. & Thomson, R.L.** (2004) Qualitative geographical
399 variation in interspecific interactions. *Ecography* **27**: 112 - 118.
- 400 **Morris, D.W.** (1996) Coexistence of Specialist and Generalist Rodents Via Habitat
401 Selection. *Ecology* **77**: 2352-2364.
- 402 **Nicholson, S.E., Davenport, M.L. & Malo, A.R.** (1990) A comparison of the vegetation
403 response to rainfall in the Sahel and East Africa, using Normalized Difference
404 Vegetation Index from NOAA AVHRR. *Climate change* **17**: 209-241.
- 405 **Ockendon, N., Hewson, C.M., Johnston, A. & Atkinson, P.W.** (2012) Declines in British-
406 breeding populations of Afro-Palaearctic migrant birds are linked to bioclimatic
407 wintering zone in Africa, possibly via constraints on arrival time advancement. *Bird
408 Study* **59**: 111-125.
- 409 **Ockendon, N., Johnston, A. & Baillie, S.R.** (2014) Rainfall on wintering grounds affects
410 population change in many species of Afro-Palaearctic migrants. *Journal of
411 Ornithology* **155**: 905917.
- 412 **Salewski, V., Almasi, B., Heuman, A., Thoma, M. & Schlageter, A.** (2007) Agonistic
413 behaviour of Palaearctic passerine migrants at a stopover site suggests interference
414 competition. *Ostrich* **78**: 349-355.
- 415 **Salewski, V., Bairlein, F. & Leisler, B.** (2002) Different wintering strategies of two
416 Palearctic migrants in West Africa - a consequence of foraging strategies? *Ibis* **144**:
417 85 - 93.
- 418 **Salewski, V., Bairlein, F. & Leisler, B.** (2003) Niche partitioning of two Palearctic
419 passerine migrants with Afrotropical residents in their West African winter quarters.
420 *Behavioral Ecology* **14**: 493-502.
- 421 **Salewski, V. & Jones, P.** (2006) Palearctic passers in Afrotropical environments: a
422 review. *Journal of Ornithology* **147**: 192-201.
- 423 **Schneider, T., Bischoff, T. & Haug, G.H.** (2014) Migrations and dynamics of the
424 intertropical convergence zone. *Nature* **513**: 45-53.
- 425 **Shubha, N.P., Jurek, K. & Karl, C.** (2009) Contrasts between habitat generalists and
426 specialists: an empirical extension to the basic metacommunity framework. *Ecology*
427 **90**: 2253-2262.
- 428 **Sinclair, A.R.E.** (1978) Factors affecting the food supply and breeding season of resident
429 birds and movements of Palaearctic migrants in a tropical African savannah. *Ibis* **120**:
430 480-497.
- 431 **Sokolov, V., Ehrlich, D., Yoccoz, N.G., Sokolov, A. & Lecomte, N.** (2012) Bird
432 communities of the arctic shrub tundra of Yamal: habitat specialists and generalists.
433 *PLoS One* **7**: e50335.
- 434 **Urban, E.K., Fry, C.H. & Keith, S.** (1992) *The Birds of Africa*. Academic Press, London,
435 UK.

- 436 **Urban, E.K., Fry, C.H. & Keith, S.** (1997) *The Birds of Africa*. Academic Press.
- 437 **Vickery, J.A., Erwin, R.S., Smith, K.W., Pain, D.J., Bairlein, F., Škorpi洛va, J. &**
- 438 **Gregory, R.D.** (2014) The decline of Afro-Palaearctic migrants and an assessment of
- 439 potential causes. *Ibis* **156**: 1 - 22.
- 440 **Walther, B.A., Van Niekerk, A. & Rahbek, C.** (2011) Long-term population declines of
- 441 Palearctic passerine migrant birds: a signal from the Sahel? *BOU Proceedings – The*
- 442 *Ecology & Conservation of Migratory Birds*; [http://www.bou.org.uk/bouproc-](http://www.bou.org.uk/bouproc-net/migratory-birds/walther-etal.pdf)
- 443 [net/migratory-birds/walther-etal.pdf](http://www.bou.org.uk/bouproc-net/migratory-birds/walther-etal.pdf)
- 444 **Wilson, D.S. & Yoshimura, J.** (1994) On the Coexistence of Specialists and Generalists.
- 445 *Am. Nat.* **144**: 692-707.
- 446 **Wilson, J.M. & Cresswell, W.** (2010) Densities of Palearctic warblers and Afrotropical
- 447 species within the same guild in Sahelian West Africa. *Ostrich* **81**: 225-232.
- 448 **Wilson, J.M. & Cresswell, W.R.L.** (2007) Identification of potentially competing
- 449 Afrotropical and Palaearctic bird species in the Sahel. *Ostrich*, **78**: 363-368.
- 450 **Wright, T.F., Eberhard, J.R. & Hobson, E.A.** (2010) Behavioral flexibility and species
- 451 invasions: the adaptive flexibility hypothesis. *Ethology Ecology & Evolution* **22**: 393-
- 452 404.
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456 **SUPPORTING INFORMATION**

457 Additional supporting information may be found in the supplementary materials and include:

458 **Table A1.** A list of all surveyed sites and transects with geographical coordinates arranged
459 and listed from North to South (top to bottom) along with their survey dates.

460 **Table A2.** A description of all vegetation and habitat quality and geographical variables
461 collected at each point along every transect at each survey site.

462 **Table A3.** A list of all 35 species of both Afrotropical resident and Palearctic migrant species
463 recorded and initially considered for analysis with information about the number of points
464 and transects from where they were observed as well as average abundance and migratory
465 status.

466 **Table A4.** Habitat variable loadings on the top three principal components after the principal
467 components analysis

468 **Figure A1.** Illustration of the relationship of some of the top loading habitat variables on the
469 first three principal components.

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474 **Table 1.** All 25 species included in the analysis showing habitat specialization scores (HS
 475 scores) derived from each of the three principal components (PC 1 – 3 i.e. habitat quality,
 476 distribution and disturbance) and their residency status (R=Afrotropical Resident,
 477 M=Palearctic migrant). See Supplementary material Table A3 for scientific names.

Common name	HSS (PC1)	HSS (PC2)	HSS (PC3)	Migratory status
<i>Pipits and likes</i>				
Tree Pipit	1.0	0.6	0.7	M
Plain-back Pipit	0.0	0.3	0.7	R
Yellow Wagtail	0.4	0.8	0.8	M
Yellow-throated Longclaw	0.2	0.2	0.2	R
<i>Chats and likes</i>				
African Thrush	0.7	0.5	0.6	R
Snowy-crowned Robin-chat	0.8	0.2	0.2	R
Whinchat	0.6	0.6	0.6	M
African Stonechat	0.1	0.3	0.0	R
Familiar Chat	0.7	0.3	0.5	R
<i>Warblers and likes</i>				
Garden Warbler	0.3	0.9	0.7	M
Common Whitethroat	0.6	0.0	0.3	M
Willow Warbler	0.8	0.8	1.0	M
Senegal Eremomela	0.7	0.4	0.9	R
Northern Crombec	0.8	1.0	0.4	R
Grey-backed Camaroptera	0.7	0.4	0.8	R
Tawny-flanked Prinia	1.0	0.4	0.7	R
Dorst's Cisticola	0.6	0.4	0.6	R
Rock-loving Cisticola	0.1	0.0	0.3	R
<i>Flycatchers and likes</i>				
Northern Black Flycatcher	0.5	0.1	0.6	R
Spotted Flycatcher	0.4	0.7	0.4	M
Pale Flycatcher	0.7	0.5	0.4	R
Pied Flycatcher	0.5	0.8	0.8	M
African Paradise Flycatcher	0.7	0.4	0.8	R
Senegal Batis	0.7	0.4	0.8	R
Yellow-billed Shrike	0.7	0.4	0.8	R

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481 **Table 2.** Average Habitat Specialization scores derived from the 13
 482 unsummarised habitat variables of Afrotropical and Palearctic migratory birds
 483 with results of tests of differences between the residency groups for each variable.

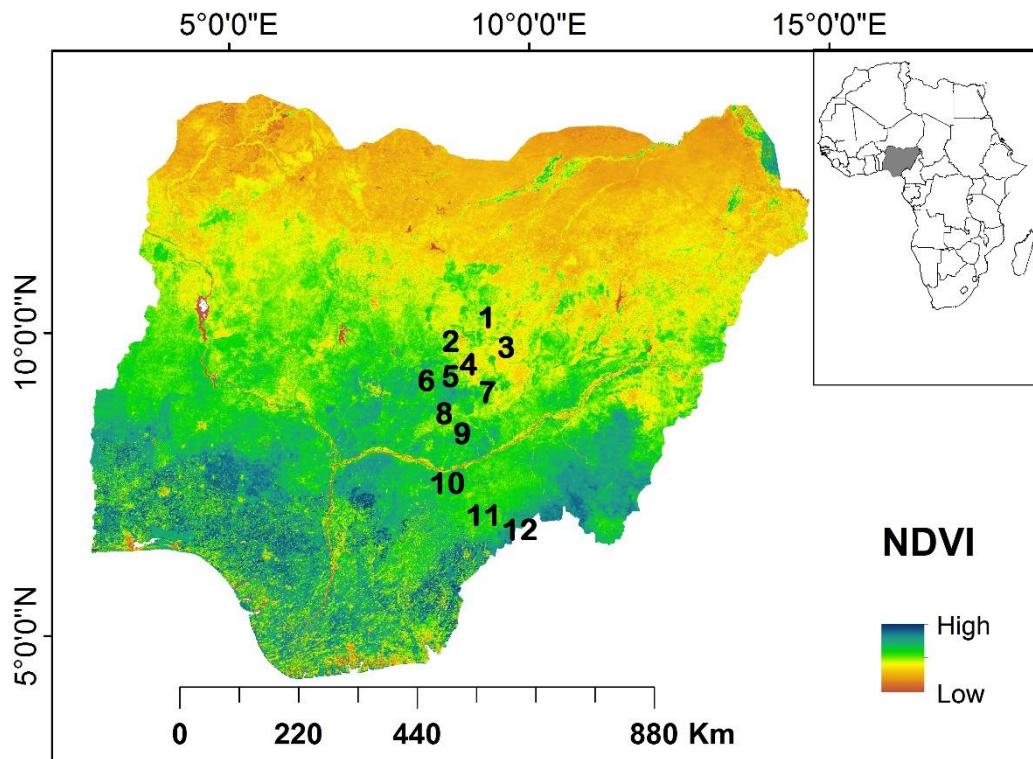
Habitat Variable	Mean HS score		<i>t</i> -value	d.f.	P
	Afrotropical species	Palearctic migrants			
Vegetation cover					
Number of trees	0.5	0.5	-0.2	14.3	0.82
Tree species richness	0.6	0.5	0.7	21.9	0.51
Number of shrubs	0.2	0.3	-1.3	8.2	0.23
Ground vegetation cover	0.5	0.6	-1.8	16.2	0.10
Vegetation height profile & structure					
Dominant vegetation layer	0.5	0.5	-0.1	21.9	0.89
Tree height	0.5	0.6	-1.7	18.6	0.11
Shrub height	0.5	0.6	-1.4	15.4	0.18
Grass height	0.7	0.5	1.3	11.7	0.22
Habitat disturbance					
Number of loped trees	0.4	0.3	0.7	15.6	0.51
Cattle dung (grazing)	0.6	0.6	-0.1	13.4	0.92
Number of tree stumps	0.2	0.1	1.4	22.9	0.19
Bush burning	0.8	0.8	0.2	20.9	0.86
Habitat location					
Latitude	0.5	0.8	-3.3	16.5	*0.005

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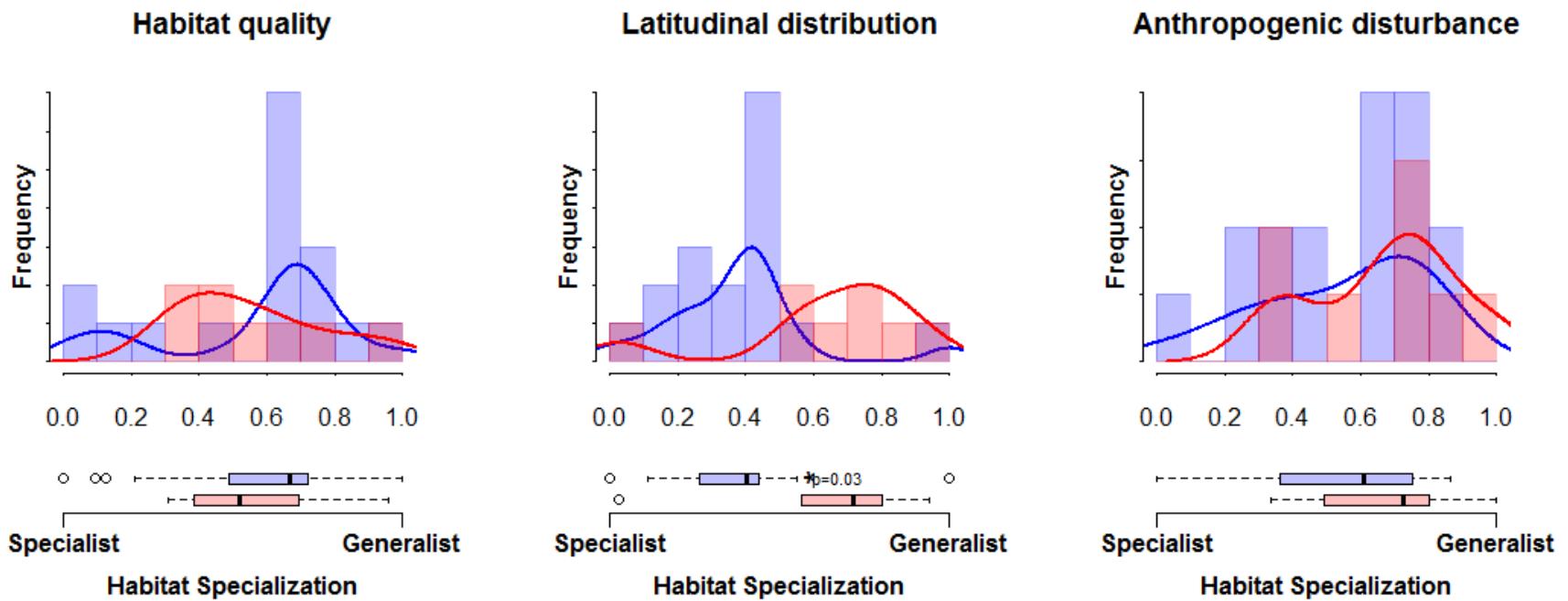
*The critical P value after Bonferroni correction (α / n) is 0.004.

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490 **Figure 1.** An NDVI map of Nigeria at the end of the rainy season (November-December
491 2012) showing location of survey sites. Numbers on map correspond to site number shown in
492 Table 1. A map of Africa is shown as an inset at the top right corner of the figure to show the
493 location of Nigeria within Africa.



494

495 **Figure 2.** Histograms, probability density functions and boxplots of HS scores of the top three principal components. Bars and lines in blue show
 496 distribution of HS scores for Afro-tropical resident species while red bars and lines are for Palearctic migrants. Some overlaps can be seen for
 497 instances where scores are similar and not statistically different (far left and right plots) for HS scores (habitat quality & anthropogenic
 498 disturbance). There is less overlap in the distribution of scores for latitudinal distribution with more migrants clustering to the generalist (high score)
 499 end of the scale (middle plot)

Table A1. List of all surveyed sites and transects with geographical coordinates arranged and listed from North to South (top to bottom) and survey dates. Winter 1 = Feb – May 2012; Winter 2 = Oct 2012 – Mar 2013; Winter 3 = Oct 2013 – Feb 2014.

Site No.	Site	Transect number	Latitude (°N)	Longitude (°E)	Survey Dates	
					Winter 1 2011/12	Winter 2 2012/13
1	+Jos	1	9.8794	8.9759	9 Feb, 6 Mar, 6 Apr, 1 May	8 Oct, 10 Dec, 7 Feb, 11 Mar
		2	9.8587	8.9910	10 Feb, 7 Mar, 7 Apr, 2 May	9 Oct, 11 Dec, 8 Feb, 12 Mar
		3	9.8359	8.9762	11 Feb, 8 Mar, 9 Apr, 3 May	10 Oct, 13 Dec, 9 Feb, 13 Mar
		4	9.8170	8.9046	-	11 Feb, 14 March
2	+Kagoro	1	9.5694	8.3703	20 Feb, 21 Mar, 18 Apr, 11 May	5 Oct, 4 Feb, 15 Mar
		2	9.5641	8.3593	21 Feb, 22 Mar, 19 Apr, 12 May	6 Oct, 5 Feb, 16 Mar
		3	9.5280	8.3706	22 Feb, 23 Mar, 20 Apr, 13 May	7 Oct, 6 Feb, 17 Mar
3	*Aboro	1	9.4875	8.5914	17 Feb, 18 Mar, 15 Apr, 8 May	-
		2	9.4841	8.5844	18 Feb, 19 Mar, 16 Apr, 9 May	-
		3	9.4825	8.5979	19 Feb, 20 Mar, 17 Apr, 10 May	-
4	*Pankshin	1	9.3900	9.2963	6 Feb, 3 Mar, 3 Apr, 27 Apr	-
		2	9.3683	9.5308	7 Feb, 4 Mar, 4 Apr, 28 Apr	-
		3	9.3513	9.4311	8 Feb, 5 Mar, 29 Apr,	-
5	*Farin Ruwa	1	9.1078	8.7380	14 Feb, 15 Mar, 12 Apr, 5 May	-
		2	9.1029	8.7254	15 Feb, 16 Mar, 13 Apr, 6 May	-
		3	9.0976	8.7405	16 Feb, 17 Mar, 14 Apr, 7 May	-
6	†Endehu	1	8.8415	8.4592	8 Dec, 1 Feb, 18 Mar	-
		2	8.8375	8.4855	9 Dec, 2 Feb, 19 Mar	-
		3	8.8302	8.4518	- , 3 Feb, 20 Mar	-
7	+Pandam	1	8.6494	8.9746	2 Feb, 29 Feb, 31 Mar, 24 Apr	31 Oct, 29 Jan, 21 Feb
		2	8.6342	8.9256	3 Feb, 1 Mar, 1 Apr, 25 Apr	1 Nov, 30 Jan, 22 Feb
		3	8.6209	8.9652	4 Feb, 2 Mar, 2 Apr, 26 Apr	2 Nov, 31 Jan, 23 Feb
8	†Akanga	1	8.3016	8.5606	-	3 Nov
		2	8.3008	8.5629	-	4 Nov, 28 Jan
9	†Makurdi	1	7.9686	8.5678	-	6 Nov, 25 Jan, 25 Mar
		2	7.8045	8.6168	-	7 Nov, 26 Jan, 26 Mar
		3	7.4605	8.5851	-	8 Nov, 27 Jan, 27 Mar
10	†Ushongo	1	7.1521	8.8408	-	29 Nov, 22 Jan, 28 Mar
		2	7.1517	8.8368	-	30 Nov, 23 Jan, 29 Mar
		3	7.1503	8.8386	-	1 Dec, 24 Jan, 30 Mar
		4	7.1369	8.8409	-	2 Dec
11	†Obudu2	1	6.6221	9.3549	-	3 Dec, 19 Jan, 31 Mar
		2	6.6189	9.3391	-	4 Dec, 20 Jan, 1 Apr
		3	6.4991	9.4280	-	5 Dec, 21 Jan, 2 Apr
12	†Obudu	1	6.3815	9.3769	-	10 Nov, 16 Jan, 3 Apr
		2	6.3754	9.3751	-	11 Nov, 17 Jan, 4 Apr
		3	6.3703	9.3945	-	12 Nov, 18 Jan, 5 Apr

+ Sites surveyed during both winter seasons

* Sites surveyed in the first winter season only

† Sites surveyed in the second winter season only

Table A2. All vegetation and habitat quality and geographical variables collected at each point along every transect at each survey site

Variables	Description
Tree density	Number of trees (plants >1m height and diameter at breast height >10cm)within a 25 m radius circular plot centred at the points where bird counts had been recorded
Tree species richness	Number of different species of trees present in the plot
Dominant vegetation layer	A score of 1 – 4 if dominant vegetation layer in the 25m circular plot was bare or dominated by grasses, shrubs or trees respectively
Tree height	Scored between 1 – 4 if height of trees within a 25 m radius of the point ranged between <3m, 3-7m, 7-14m, >14m respectively
Shrub height	Scores of 1 – 4 if height of shrubs within a 25 m radius of the point ranged between <0.5m, 0.5-3m, 3-5m, >5m respectively
Grass height	Scores of 1 – 4 if height of grass within a 25 m radius of the observer mostly ranged between <0.03-0.3m, 0.3-1m, 3m, >3m respectively
Lopped trees	The number of trees with evidence of lopping to provide fodder for livestock
Canopy cover	A percentage estimate of the circular view obscured by the vegetation canopy as viewed through the reverse end of a binoculars
Shrubs	The number of shrubs (plants with multiple stems from the ground surface or with main boles small enough to be grabbed by one hand) in the circular plot
Habitat type	Classified as Woodland (no evidence of farming and closed canopy), Open Woodland (no evidence of farming but little to no canopy cover), Wooded Farmland (farmland with retained trees and canopy and hedge vegetation) or Open Farmland (no trees and canopy cover)
Ground vegetation cover	1 minus the proportion of bare ground visible within the circular plot
NDVI	Normalised Difference Vegetation Index extracted at the coordinates of each point, derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor at 250m spatial resolution, every 16 days and downloaded from the International Research Institute for Climate and Society, Earth Institute, Colombia University website http://iri.columbia.edu/ . NDVI was extracted for the 16 day period closest to the survey date of the point.
Stumps	The number of tree stumps after tree or shrub felling, counted within the 25 m circular plot

Burn status	Scored as 0 or 1 if there was any evidence of burning of the ground and shrub vegetation within 25 m radius of point
Grazing/Livestock dung	Scored as 0 or 1 if there was any evidence of livestock dung
Latitude	Obtained at each point in decimal degrees from the Garmin 62 GPS

Table A3. List of all 35 species of both Afrotropical resident and Palearctic migrant species recorded and initially considered for analysis. (Migratory status: R=Afrotropical resident, M=Palearctic migrant). Species not included in analysis are in italics.

Common name	Scientific name	Number of points where seen	Average count over survey period ¹	Migratory status	Number of transects where seen
<i>Common Sandpiper</i>	<i>Actitis hypoleucus</i>	5	10	M	2
Tree Pipit	<i>Anthus trivialis</i>	40	77	M	8
Plain-backed Pipit	<i>Anthus leucophrys</i>	15	27	R	7
Yellow Wagtail	<i>Motacilla flava</i>	14	99	M	4
Yellow-throated Longclaw	<i>Macronyx croceus</i>	17	27	R	4
African thrush	<i>Turdus pelios</i>	81	126	R	12
Snowy-crowned Robin Chat	<i>Cossypha niveicapilla</i>	11	19	R	4
Whinchat	<i>Saxicola rubetra</i>	158	312	M	11
African Stonechat	<i>Saxicola torquatus</i>	22	38	R	1
Familiar chat	<i>Cercomel afamiliaris</i>	22	32	R	6
<i>Cliff Chat</i>	<i>Myrmecocichla cinnamomeiventris</i>	2	4	R	1
<i>Northern Anteater Chat</i>	<i>Myrmecocichla aethiops</i>	8	16	R	2
Garden Warbler	<i>Sylvia borin</i>	16	22	M	5

Common Whitethroat	<i>Sylvia communis</i>	67	92	M	5
Wood Warbler	<i>Phylloscopus sibilatrix</i>	8	9	M	4
Willow Warbler	<i>Phylloscopus trochilus</i>	82	108	M	11
Senegal Eremomela	<i>Eremomela pusilla</i>	101	265	R	10
Northern Crombec	<i>Sylvietta brachyura</i>	14	17	R	6
Grey-backed Camaroptera	<i>Camaroptera brachyura</i>	52	60	R	10
Tawny-flanked Prinia	<i>Prinia subflava</i>	89	146	R	11
Red-winged Warbler	<i>Heliolais erythropterus</i>	9	16	R	6
Dorst's Cisticola	<i>Cisticola guinea</i>	29	43	R	8
Rock-loving Cisticola	<i>Cisticola aberrans</i>	12	16	R	2
Chubb's Cisticola	<i>Cisticola chubbi</i>	7	12	R	1
Northern Black Flycatcher	<i>Melaenornis edolioides</i>	39	97	R	7
Spotted Flycatcher	<i>Muscicapa striata</i>	67	149	M	9
Pale flycatcher	<i>Melaenornis pallidus</i>	40	76	R	8
Pied Flycatcher	<i>Ficedula hypoleuca</i>	124	152	M	10
African Paradise Flycatcher	<i>Terpsiphone viridis</i>	53	77	R	8
African Blue Flycatcher	<i>Elminia longicauda</i>	7	11	R	2

Senegal Batis	<i>Batis senegalensis</i>	42	70	R	8
Common Wattle-Eye	<i>Platysteira cyanea</i>	6	10	R	4
Woodchat Shrike	<i>Lanius senator</i>	2	6	M	1
Mackinnon's Shrike	<i>Lanius mackinnoni</i>	9	10	R	1
Yellow-billed Shrike	<i>Corvinella corvina</i>	26	68	R	10

¹ total count of individuals for each species over both winter seasons divided by 2

Table A4. Habitat variable loadings on the top three principal components after the principal components analysis

Habitat variables	Unrotated loadings			Varimax loadings		rotated
	PC1	PC2	PC3	PC1	PC2	
Tree density	0.36	-0.29	0.22	0.51		
Loped	0.24	0.11	-0.17			-0.36
Livestock dung	0.23	0.11	-0.58		-0.23	-0.58
Stump density	0.24	0.03	-0.02	0.16		-0.17
Burning	0.18	0.23	0.43	0.14	0.49	0.17
Shrub density	-0.01	-0.31	-0.33		-0.43	-0.13
Ground veg cover	-0.33	-0.33	-0.07		-0.38	0.28
Latitude	0.28	0.39	0.01		0.36	-0.32
Tree diversity	0.39	-0.27	0.24	0.52		
Dominant veg layer	0.38	-0.24	0.02	0.43		-0.12
Tree height	0.30	-0.33	0.06	0.43	-0.12	
Shrub height	-0.03	-0.44	-0.22	0.16	-0.47	
Grass height	-0.31	-0.22	0.43			0.56
Standard deviation	1.78	1.70	1.16			
Proportion of Variance	0.24	0.22	0.10	Proportion Variance	0.077	0.077
Cumulative Proportion	0.24	0.47	0.57	Cumulative Variance	0.077	0.154
						0.231

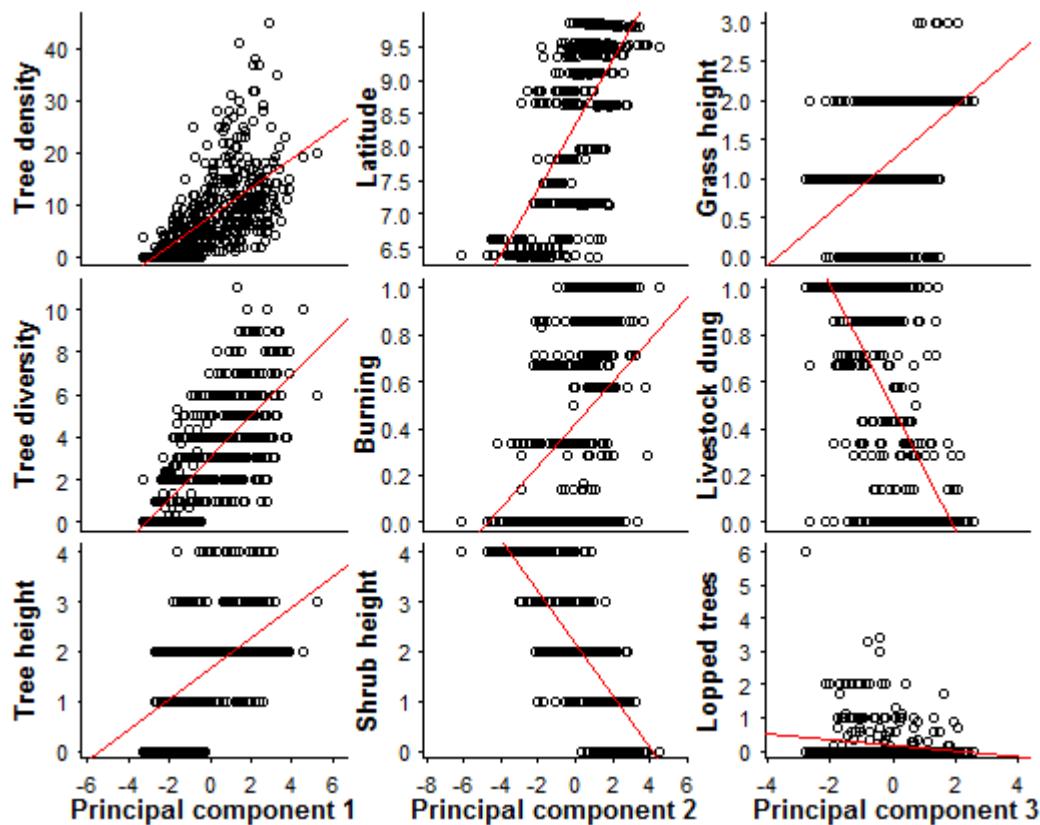


Figure A1. Relationship of some of the top loading habitat variables on the first three principal components. The first column of three plots show positive loadings of tree density, diversity and height (top-bottom respectively) on principal component 1. The three plots in the middle column show a positive loading of latitude and the index for bush burning and a negative loading of shrub height with principal component 2. In the last column, the three plots show positive loadings of grass height, and negative loadings of livestock dung and density of lopped trees with principal component 3.