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Conserving low-intensity farming is key to halting the declines of migratory passerines in their tropical wintering grounds

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Abstract

Half of all migratory bird species have declined over the past 30 years, with intercontinental migrants declining faster than their short-distance migratory counterparts. One potential cause of these declines is habitat loss and degradation on tropical wintering grounds, where agricultural conversion of natural habitats and intensification of traditional, low-intensity agricultural systems are frequently occurring. Although the broad patterns of wintering migrant abundance are well understood along most flyways, how species' habitat associations vary across disturbance gradients in agricultural landscapes remains a key question, with implications for landscape-level farm management and restoration activities. We used 328 point count locations and associated habitat assessments targeted at a cohort of eight severely declining Afro-Palaearctic migratory passerines in the Guineo–Congolian transition zone of Western Africa to model the probability of the presence of migrants within grass, shrub, forb and forest-covered areas. We found support for the widespread use of early successional habitats retained within traditionally managed farmland by migrants. Most species utilize scrubland on fallows within the agricultural mosaic, especially Spotted Flycatcher, Garden Warbler, Melodious Warbler, Whinchat and Common Nightingale. Only Pied Flycatcher relied upon mature forested areas. The avoidance of mature forested habitats by most species suggests that habitat requirements of severely declining migrant birds must be explicitly considered within conservation and restoration schemes, via mechanisms to retain low-intensity farming, especially short-term abandoned fallows that regenerate scrubby areas within the agricultural matrix. Any habitat management within the agricultural matrix should be considered in the context of the needs of local communities.

Introduction

An estimated 50 billion birds, the majority of which are passerines, undertake migration twice annually (Berthold, 1993; Kirby *et al*., 2008; Newton & Brockie, 2007). They do so to take advantage of seasonal abundances in food and avoid extreme climates. Yet this mass movement is in peril, with over half of migratory bird species declining over the past 30 years (Runge *et al*., 2015), some catastrophically. Most at risk appear to be long-distance intercontinental migrants, which have displayed far more severe declines than their resident or short-distance migratory counterparts (Sanderson *et al*., 2006; Faaborg *et al*., 2010; Vickery *et al*., 2014). For example, Whinchat *Saxicola rubetra* and Common Nightingale *Luscinia megarhynchos* populations in mainland Europe and the UK declined by 67% and 63%, respectively, in 30 years (Vickery *et al*., 2014).

Our understanding of the drivers of declines in migratory birds is biased towards breeding grounds (Terborgh, 1989; Vickery *et al*., 2014; Li Yong *et al*., 2015), where agricultural land-use change and forest fragmentation (Donald, Green, & Heath, 2001; Benton, Vickery, & Wilson, 2003) have been identified as the largest pressures causing declines (UNEP, 2014). However, the source of population declines in long-distance migrants is often attributed to their reliance on multiple geographical locations, such as stopover sites (Bayly *et al*., 2017; Xu *et al*., 2019; Schmaljohann, Eikenaar, & Sapir, 2022), and their dependence on tropical wintering grounds (Confer & Holmes, 1995; Sherry & Holmes, 1995; Kirby *et al*., 2008; Vickery *et al*., 2014). This is because these passerine populations have performed so much worse than short-distance migrants (Sanderson *et al*., 2006; Sanderson *et al*., 2016) and the fact that long-distance migratory passerines spend the majority of their lifecycle in tropical wintering grounds (Faaborg *et al*., 2010). Yet the specific causes of their declines remain unknown (Vickery *et al*., 2014; Li Yong *et al*., 2015).

Land-use change has accelerated rapidly in the tropics over the past three decades, with the highest rates of deforestation and degradation globally (Hansen *et al*., 2013; Vancutsem *et al*., 2021), and increasing conversion of low-intensity farmland and shifting agriculture to permanent, more-intensive farming systems (Tilman *et al*., 2001). Given that just 9% of migratory birds are adequately covered by protected areas (Runge *et al*., 2015), we require detailed knowledge of migrant habitat use to pinpoint the effects of land-use change and develop adequate conservation initiatives for migrants (Dänhardt *et al*., 2010; Li Yong *et al*., 2015; Cresswell, Nanchin, & Patchett, 2020). Yet, such understanding is hindered by the relative paucity of quantitative studies conducted on the wintering grounds (Salewski & Jones, 2006; Faaborg *et al*., 2010; Li Yong *et al*., 2015), partly as a result of limited conservation resources (Vickery *et al*., 2014; Li Yong *et al*., 2015), although this situation is improving (Vickery *et al*., 2023).

Occupation of low-intensity farmed areas is emerging as a general pattern for wintering migrants (Jones *et al*., 1996; Atkinson *et al*., 2014; Elsen *et al*., 2017). For instance, during the winter in the Himalayas, bird species richness and abundance (of local to longer-distance migrants) were higher in low-intensity farmland than primary forest, with 80% of primary forest species having equal to greater abundances in low-intensity farmland (Elsen *et al*., 2017). Similarly, in the Neotropics, shade coffee and cacao provide important habitat for long-distance migratory birds (Wunderle & Latta, 1996; Petit *et al*., 1999; Tejeda-Cruz & Sutherland, 2004), with many conservation initiatives developed to protect these habitats. However, although Afro-Palaearctic (AP) migrants may be robust to habitat degradation (Jones *et al*., 1996; Wilson & Cresswell, 2006; Cresswell *et al*., 2007; Ivande & Cresswell, 2016), the potential importance of low-intensity farmland and the mechanisms of habitat use within farmlands for AP migrants has only been quantified for a few species (Wood Warbler *Phylloscopus sibilatrix*, Mallord *et al*., 2016; Whinchat *Saxicola rubetra*, Hulme & Cresswell, 2012; Whitethroat *Curruca communis*, Stoate, 1997; Tapia-Harris & Cresswell, 2022; Vickery *et al*., 1999; Northern Wheatear *Oenanthe oenanthe*, Wilson & Cresswell, 2010b), which hampers the development of conservation plans for long-distance migrants more broadly.

In this study, we investigate the importance of low-intensity farmland for eight AP migratory passerine species that overwinter throughout the Guineo–Congolian transition zone of Western Africa (Morrison *et al*., 2013; Vickery *et al*., 2014). This AP migrant cohort has suffered considerable recent population declines (Brlík *et al*., 2021) and represents a substantial subset of the potential AP migrant passerine community overwintering in the region. In addition, such a cohort represents each major passerine feeding guild and includes species with wide-ranging life histories. We tackle two key objectives: (1) determine the use of low-intensity farmland versus natural forest; and (2) identify which habitat features within low-intensity farmland are used. In providing a unique assessment of the habitat-occupancy patterns for eight severely declining long-distance migrant species, our study is integral to guiding conservation efforts of threatened migrants.

Materials and methods

Study area

Data were collected in sites within the Guineo–Congolian to Sudanian transition zone in Ghana, Togo, Benin and Burkina-Faso (Fig. 1). The more southern Guineo–Congolian region comprises areas of wet and semi-deciduous forests, transitional forests and secondary grassland, while the more northern Sudanian region constitutes drier woodland and more open savannah vegetation types (Julier *et al*., 2018). Due to deforestation and agricultural conversion, estimates suggest the Guineo–Congolian region lost around 80% of its original forest cover through the 20th century, producing a complex mosaic of anthropogenically degraded shrublands, agriculture and forested fragments (Braimoh & Vlek, 2005; Norris *et al*., 2010; Sugihara *et al*., 2014). This region lies within the non-breeding ranges of many migrant species (Fishpool & Evans, 2001), and agricultural production is of high economic importance (Faulkner & Mackie, 2013).

Focal species

Eight declining migratory species known to spend the non-breeding season throughout the study area were investigated (European population trend, 1980–2019, given in parentheses (Brlík *et al*., 2021)): Nightingale *Luscinia megarhynchos* (−68%); Tree Pipit *Anthus trivialis* (−57%); Whinchat (−89%); Spotted Flycatcher *Muscicapa striata* (−58%); Pied Flycatcher *Ficedula hypoleuca* (−25%); Wood Warbler (−39%); Garden Warbler *Sylvia borin* (−17%) and Melodious Warbler *Hippolais polyglotta* (−16%).

Migrant sampling

Fieldwork was conducted from October to February annually throughout 2010–14, comprising the initial data collection block, with an additional field season conducted through

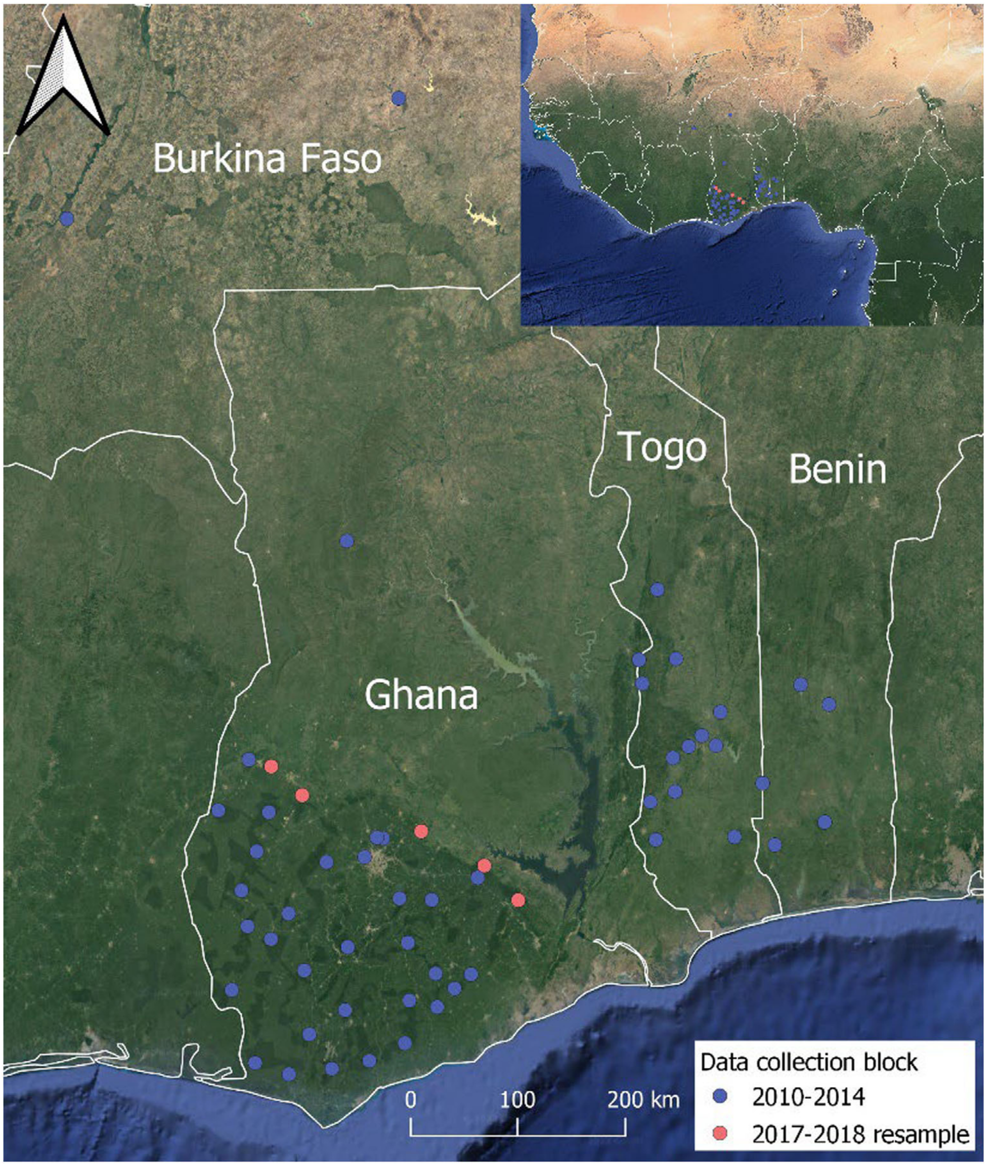

Figure 1 Map showing the location of survey sites coloured by data collection block.

2017–18 centred on resampling five sites towards the northern margin of Guineo–Congolian region, a region identified as being particularly important for our target community. Avian migrants were sampled using both visual and vocal detection within 50-m radius (Warren-Thomas *et al*., 2019; Borah *et al*., 2022), 5-minute duration point counts. Point counts were conducted between 05:45 and 11:00, avoiding conditions of rain, high winds or poor visibility. A full list of avian species detected during point counts is presented in Table S1. Fifty-eight sites were sampled, each being separated by at least 6 km (Fig. 1). Every site contained between one to six transects, each constituting 3–20 points spaced ≥200 m apart (Hill & Hamer, 2004), totalling 328 point count locations. Transects were on average placed 6 km apart, located along roads and tracks to allow for greatest access to landscapes. This includes access roads into forested areas and narrow tracks used by farmers to access their land. Most point counts were visited only once, but a subset of 141 had a second visit later in the year or the following year, and at one intensively sampled site (Pepease) some points were visited up to 10 times, at least 2 weeks apart throughout the 2010–2014 data collection site (sampled this frequently to monitor seasonal changes in Wood Warbler abundance; Mallord *et al*., 2017a; Mallord *et al*., 2017b).

Point counts during 2017/18 were recorded using an Olympus LS11 linear recorder (Olympus, Shinjuku, Tokyo, Japan), to allow for later identification of unknown or missed vocalizations using online reference material (www.xeno-canto.org). Initial surveys (2010–2014) were part of a wider study targeting Wood Warblers, therefore, in addition to point counts, 1-min duration playback surveys followed by a 1-min response period were conducted at each point, using a FOXPRO NX4 MP3 player (FOXPRO Inc, Lewiston, PA, USA). Since statistical comparisons between species are not analysed in this study, any inflated detection rates for Wood Warbler do not impact the habitat-use analysis.

Vegetation cover assessments

Vegetation cover assessments were performed within a week of the first point count and repeated each field season. Habitat measurements were recorded within a 25 m-radius buffer centred on each point. Habitat variables measured included those considered most likely to be important to migrants (Dowsett-Lemaire & Dowsett, 2014). As the vegetation types of interest often overlap in plant height, vegetation cover types are instead defined by other characteristics. Shrubs were defined as woody vegetation below 3 m in height; forbs were defined as herbaceous, non-grassy vegetation, including weeds, herbs and shoots; and grassland, which often included areas of low-lying herbaceous vegetation interspersed with *Chromolaena*. During vegetation cover assessments, shrub, forb, grass and tree canopy cover percentages were estimated. To account for collector bias, cover percentages were classified into the following categories: 0%, 1–4%, 5–15%, 16–40%, 40–65% and >65%. In addition, to capture information on the presence of current anthropogenic land use, point buffer areas were categorized as being either managed or natural. Point buffers are classified as natural composed primary forest and natural grassland, thus contained no anthropogenic disturbance or land-use change. Point buffers classified as managed showed evidence of anthropogenic land use change, including currently used farmland and fallow.

Statistical analysis

All modelling was performed in R v4.2.2 (R Core Team, 2023), with QGIS v3.18.0 (QGIS Development Team, 2023) used for initial exploratory spatial analysis. Species-specific generalized linear mixed effect models, with Binomial distributions, were implemented using the *lme4* package (Bates *et al.*, 2015). We included a Point ID random effect to account for variation in the number of visits, as well as temporal pseudo-replication. Additionally, this Point ID random effect was nested within Transect ID, which was nested within Site ID, to account for spatial pseudo-replication. Multicollinearity was assessed using both diagnostic plotting (*corrplot* package; Taiyun & Viliam, 2017) and variance inflation factors (*CAR* package; Fox & Weisberg, 2011). No predictor variables exceeded a variance inflation factor of five. The same diagnostics were checked for all models presented. Plotted confidence intervals were generated using 100 000 bootstrap replicates of predicted intervals.

To quantify the effect of anthropogenic land use on the presence of migrants, the discrete managed and natural land-cover type categorizations were modelled as predictor variables, with each species' presence used as the response variable. Likelihood Ratio Tests were then used to test for model significance.

The effect of vegetation type cover on species presence was modelled with the presence of each species as the response variable and the midpoint of each vegetation cover type as predictor variables. To decrease model selection uncertainty and increase the robustness of parameter estimates, model averaging was performed using an information theoretical approach by computing averaged parameter estimates from the best-selected models with ΔAICc < 5 (Burnham, Anderson, & Huyvaert, 2011; Grueber *et al.*, 2011), using the package *MuMIn* (Barton, 2012). Relative variable importance (RVI) was calculated as the sum of AICc weights over the most parsimonious models including a given predictor (Burnham, Anderson, & Huyvaert, 2011; Barton, 2012). An analysis investigating the relationship between vegetation cover types across different agricultural landscape types is presented in Figure S1 and Table S2.

Results

A total of 820 point counts (spanning 328 point count locations) were conducted. A total of 369 Wood Warblers, 331 Nightingales, 115 Pied Flycatchers, 162 Melodious Warblers, 65 Spotted Flycatchers, 33 Whinchats, 52 Tree Pipits and 28 Garden Warblers were recorded.

Migrant use of natural habitat versus farmland

In total, 416 point counts were classed as managed and 404 were classified as natural. Three species showed a significant trend in the probability of presence when comparing natural and managed areas (Table 1). Both Melodious Warbler (Fig. 2a) and Common Nightingale preferred managed areas (Fig. 2b), while Wood Warbler (Fig. 2c) preferred natural areas. Melodious Warbler was present at 66 point counts classified as managed and 22 classified as natural. Common Nightingale was present at 99 point counts classified as managed and 49 classified as natural. Wood Warbler was present at 105 point counts classified as managed and 68 classified as natural. Garden Warbler, Pied Flycatcher, Whinchat, Spotted Flycatcher and Tree Pipit all showed non-significant trends (Table 1).

Table 1 Summary statistics of natural habitat versus farmland models for each species.

Species	Chi-squared (χ^2)	*P*-value (*P*)
Wood Warbler	17.22	3.33×10^{-5}[a]
Pied Flycatcher	0.63	0.42
Tree Pipit	0.05	0.82
Garden Warbler	1.06	0.30
Whinchat	0.01	0.87
Melodious Warbler	4.42	0.036[a]
Common Nightingale	4.46	0.034[a]
Spotted Flycatcher	0.10	0.75

[a] Indicates a statistically significant model.

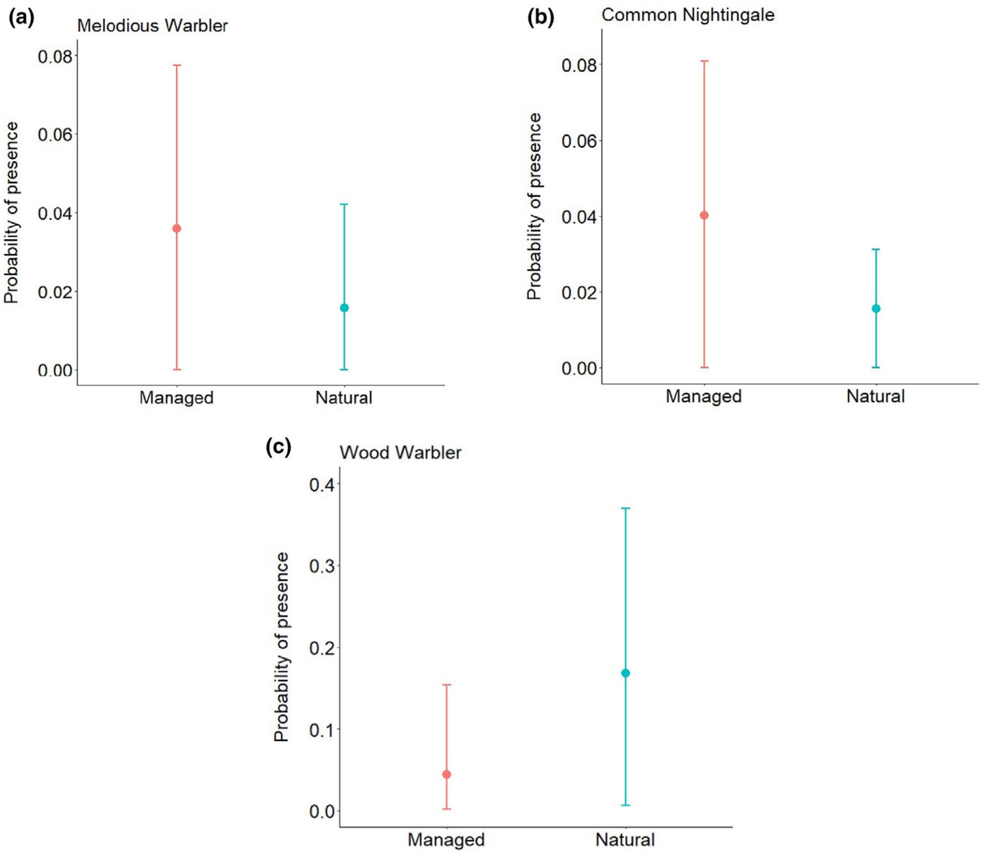

Figure 2 The probability of the presence of Melodious warbler (a), Common Nightingale (b), Wood Warbler (c), in both managed and natural areas. Error bars denote 95% CIs.

Migrant use of habitat features within low-intensity farmland

Shrub cover was the habitat feature most commonly driving impacts on species probability of presence, doing so for five species. Wood Warbler probability of presence was negatively correlated with increasing shrub cover, while Common Nightingale, Melodious Warbler, Whinchat and Garden Warbler all responded positively to increasing shrub cover. Forb cover influenced the probability of presence for four species. Wood Warbler responded negatively to increasing forb cover, while Common Nightingale, Spotted Flycatcher and Whinchat all responded positively to increasing forb cover. Both grass cover and tree cover influenced the probability of presence for three species. Increasing grass cover negatively influenced the probability of presence of both Wood Warbler and Tree Pipit, while positively influencing the probability of the presence of Common Nightingale. Increasing tree cover negatively influenced the probability of the presence of both Common Nightingale and Melodious Warbler, while increasing the probability of the presence of Pied Flycatcher (Fig. 3).

Relative variable importance (RVI), calculated as the sum of AICc weights over the most parsimonious models including a given predictor, for each vegetation cover type for each species is presented in Table 2. Species-specific candidate models can be found in Table S3. Conditional and marginal *R*-squared values for each candidate model are presented in Table S4.

Discussion

We investigated the importance of low-intensity farmland for eight species of declining AP migrants, revealing widespread use of early successional habitats dominated by shrub and forb. Areas dominated by forbs and shrublands supported higher probabilities of the presence of migrant species than forest areas. These results highlight the importance of preserving low-intensity farmland and suggest the need for migrant habitat requirements to be explicitly considered within landscape-level conservation and restoration schemes.

Farmland versus natural habitat

Native dense forests were avoided by two of our eight study species. Pied Flycatcher was the only species whose probability of presence increased with increasing tree cover, suggesting the species favours areas of woodland. However, although it is found in both closed and cleared forests (Morel & Morel, 1992; Thorup *et al.*, 2019), the species is

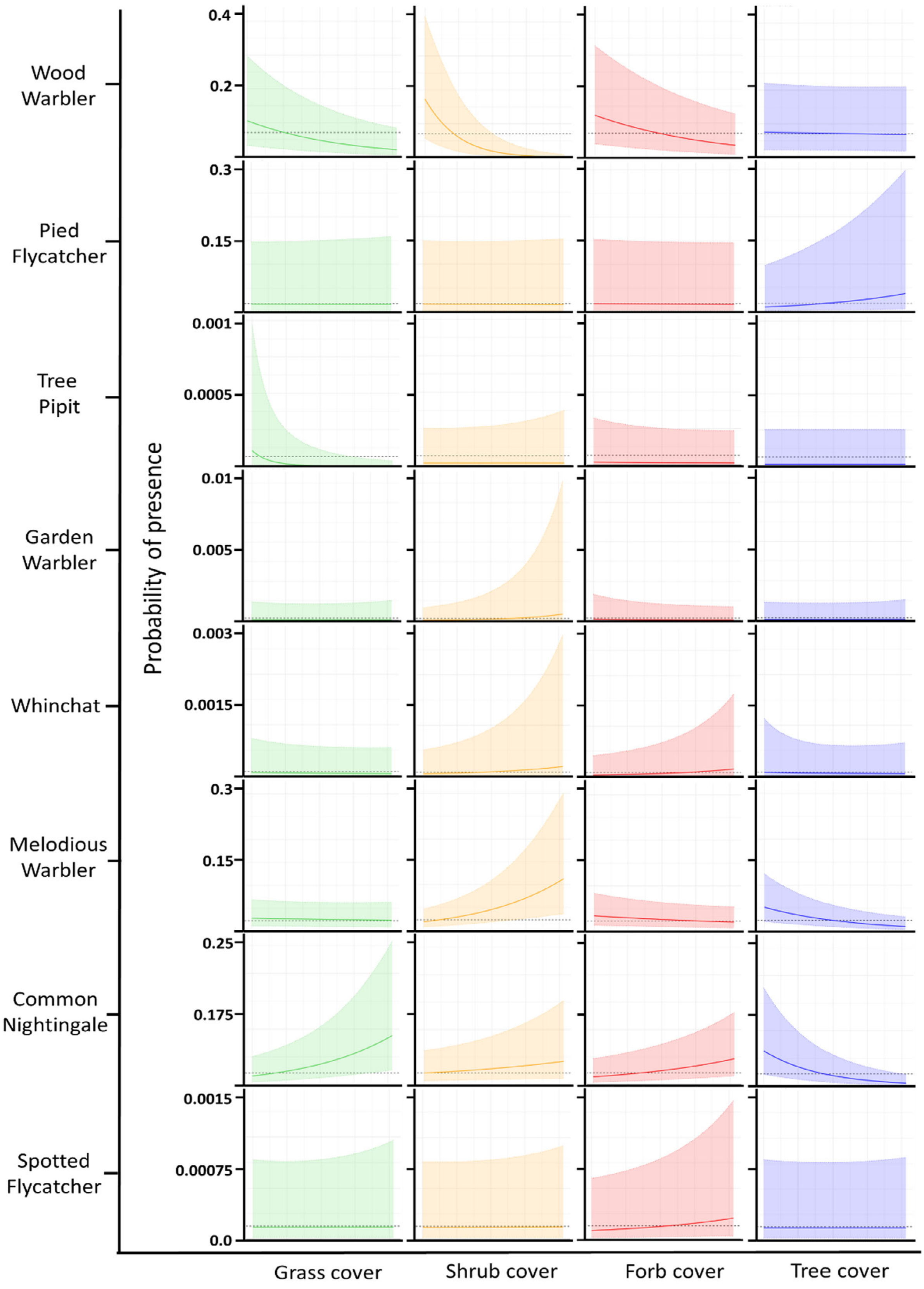
Wood Warbler
Pied Flycatcher
Tree Pipit
Garden Warbler
Whinchat
Melodious Warbler
Common Nightingale
Spotted Flycatcher
Probability of presence
0.4
0.2
0.3
0.15
0.001
0.0005
0.01
0.005
0.003
0.0015
0.3
0.15
0.25
0.175
0.0015
0.00075
0.0
Grass cover
Shrub cover
Forb cover
Tree cover

Figure 3 The influence of vegetation cover on the probability of presence of each species. Probability of presence is scaled within species. *X*-axis units increase from 0 to 82.5 representing vegetation percentage cover. Coloured ribbons present 95% CIs. Where not indicated lower *Y*-axis ticks indicate 0. Plotted grey horizontal lines present null model trends.

often found in more open woodland than forests with more complete canopy cover (Salewski, Bairlein, & Leisler, 2002; Salewski, Falk, Bairlein, & Leisler, 2002), defending individual territories with both high inter- and intra-annual site fidelity (Salewski, Bairlein, & Leisler, 2002; Willemoes *et al*., 2017; Thorup *et al*., 2019).

There is evidence of prolific land-cover change in sub-Saharan Africa, with a loss of natural forest and grassland habitats through conversion to agriculture (Brink & Eva, 2009). However, our results suggest that this may not necessarily impact negatively on AP migrants, depending on how the cultivated land is managed. Whereas open-country species are more likely to be able to cope with increasing cultivation (Blackburn & Cresswell, 2016), even those species more reliant on trees can be resilient to the loss of densely forested habitats (e.g. Wood Warblers; Buchanan *et al*., 2020; Mallord *et al*., 2017a; Mallord *et al*., 2017b). It is worth noting that these habitat use patterns are consistent throughout migratory cycles, with most AP migrants utilizing open woodlands and low-intensity farmland on their breeding grounds (Hewson & Noble, 2009). Unfortunately, this consistency extends to their vulnerability to agricultural intensification, posing a significant threat to breeding AP migrants. The avoidance of native forest by most migrant species on their wintering sites in this study, suggests that the focus of many carbon-based payments for ecosystem service schemes (e.g. the United Nations' Reducing Emissions from Deforestation and Forest Degradation programme, also known as REDD+) on reducing deforestation and forest degradation may not benefit these severely declining species.

Important low-intensity farmland habitats

The historical conversion of natural areas to low-intensity farmland would have shifted community composition in those areas. This would have benefitted species able to utilize degraded areas while harming species more reliant on natural structurally complex habitats (Cresswell *et al*., 2007). While AP migrants may have benefitted from the historical conversion of natural habitats to low-intensity farming, there is now evidence that this community of long-distance migrants is experiencing significant declines (Brlík *et al*., 2021).

Table 2 The relative variable importance (RVI) of each vegetation cover type explanatory variable per species

Species	Grasscover	Shrubcover	Forbcover	Treecover
Wood Warbler	1	1	1	0.5
Pied Flycatcher	0.42	0.42	0.29	1
Tree Pipit	1	0.5	0.5	0
Garden Warbler	0.36	0.63	0.54	0.27
Whinchat	0.54	0.54	0.63	0.36
Melodious Warbler	0.5	1	0.5	1
Common Nightingale	1	0.5	1	1
Spotted Flycatcher	0.37	0.37	0.62	0.25

With most AP migrants displaying tolerance to certain levels of habitat degradation (Jones *et al*., 1996; Wilson & Cresswell, 2006; Cresswell *et al*., 2007; Ivande & Cresswell, 2016), continued agricultural intensification could push many AP migrants past their tolerance threshold (Cresswell *et al*., 2007; Morrison *et al*., 2013). Actively farmed agricultural land and areas devoid of natural features show little use by AP migrants (Wilson & Cresswell, 2006; Cresswell *et al*., 2007). However, our results highlight the importance of maintaining a mosaic of semi-natural habitats and early successional vegetation types to continually support suitable habitat availabilities for AP migrants.

Scrubland consisting of both forbs and shrubs held the largest number of migrants. This included ground-feeding Tree Pipit, which on the breeding grounds prefers shrubbier areas than other sympatric congeners (Kumstátová *et al*., 2004), and whose negative relationship with early-successional grasslands reported here may have been due to a lack of bare ground (Burton, 2007). Another open-country species, Whinchat, requires the presence of 'viewpoints' (posts or shrubs) from which to hunt (Hulme & Cresswell, 2012; Blackburn & Cresswell, 2015). Garden Warbler and Melodious Warbler both occur in scrubby habitats, such as hedgerows and bramble thickets, on the breeding grounds (Mason, 1976; Hinsley *et al*., 1995; Pons *et al*., 2008), while occurring in a variety of habitats in the non-breeding season, including disturbed cultivated areas (Iwajomo, Ottosson, & Thorup, 2016; Thorup *et al*., 2019). Greater scrubland cover also led to a higher abundance of Spotted Flycatcher which, like many migrants, occupy a variety of habitats on the non-breeding grounds, such as scrub, thickets and secondary growth (Pearson & Lack, 1992).

Grassland and scrubby forb covered areas were important for Common Nightingales, which perhaps reflects the species' more generalist habitat preferences, being found in the dense understorey of woodlands, scrub, fallow fields with shrub regrowth and the edges of heavily cultivated farmland (Boano, Bonardi, & Silvano, 2004; Hewson & Noble, 2009; Reif *et al*., 2018). The greater structural complexity of scrubland, compared to grassland and cultivated land, is likely the driver of a higher abundance of migrants in this habitat (Leisler, 1992; Salewski, 2000). Migrants utilize open habitats to a greater extent than ecologically similar resident species, exploiting ephemeral and locally abundant food sources, which are more frequently found in open habitats (Leisler, 1992; Sherry & Holmes, 1995; Ivande & Cresswell, 2016).

Although Wood Warblers are considered one of the few AP migrant species to utilize tropical forests (Morel & Morel, 1992), they are more a species of well-wooded farmland (Mallord *et al*., 2016; Lerche-Jørgensen *et al*., 2019), preferring areas with moderate tree cover (~50%; Buchanan *et al*., 2020; Mallord *et al*., 2016), a habitat type that may be increasing within the species wintering range in West Africa due to agricultural expansion and forest degradation (Buchanan *et al*., 2020). Tree cover thus need not be extensive, and this would likely benefit many West African resident savannah species that also utilize isolated and scattered trees (Wilson & Cresswell, 2006; Zwarts, Bijlsma, & Kamp, 2018). Niche partitioning and competitive exclusion by resident species (Salewski, Bairlein, & Leisler, 2003; Ivande & Cresswell, 2016) are additional factors that may affect the types of habitats AP migrants are able to utilize.

Conservation implications and conclusions

Despite substantial sampling effort, we found AP migrant passerines to be uncommon in our study area across West African landscapes. With many AP migrants showing high levels of population spread and low migratory connectivity in their non-breeding sites (Cresswell, 2014; Finch *et al*., 2017; Patchett, Finch, & Cresswell, 2018), small-scale and site-based conservation measures are likely to be of limited value, except for a few habitat specialists (e.g. Aquatic Warbler *Acrocephalus paludicola* and Ortolan Bunting *Emberiza hortulana*; Vickery *et al*., 2023). This instead points to the need for larger-scale retention of low-intensity farmland. However, the importance of low-intensity farmland for migratory passerines could generate conflict with meeting rising agricultural demand, conserving pristine natural habitats favoured by many resident species (Phalan *et al*., 2011), and global goals for restoration. Indeed, landscape-level restoration schemes and carbon-funding mechanisms, such as REDD+, often focus on the protection or restoration of large patches or blocks of native forest.

Agricultural intensification is a major threat to both migrant and resident species (Wilson & Cresswell, 2006; Atkinson *et al*., 2014). With agricultural intensification affecting both generalist species able to utilize low-intensity farming and specialist species who require undegraded natural habitats, agricultural intensification creates a lose-lose scenario for both resident and migratory species (Kupsch *et al*., 2019; Jarrett *et al*., 2021; Yilangai *et al*., 2023). Resident species generally utilize more complex and dense habitats than their AP migrant counterparts (Cresswell *et al*., 2007), necessitating the preservation or restoration of undegraded habitats within protected areas. However, current agricultural practices need to maintain or (re)establish longer fallow periods to ensure the persistence of declining long-range migrants outside of the protected area networks. This could be via a three-compartment 'land-sparing' system that combines the protection of spared natural habitat and high-nature value, low-intensity farming with the intensification of remaining farmland needed to meet rising demand for food (Feniuk, Balmford, & Green, 2019). In spared low-intensity farmland, the maintenance of adequate fallow periods to regenerate shrubby habitats within the farmland matrix could provide suitable habitat for a number of grassland and shrubland species.

This potential will be determined by both local human and regional environmental factors (Gleave, 1996). The objective of several large- and small-scale Aid and Development initiatives is to improve livelihoods and/or increase resilience to climate change by growing native trees and shrubs (e.g. Bizikova *et al*., 2015). Similarly, the emergence of Forest and Landscape Restoration (FLR) targets under the Bonn Challenge initiative may provide a basis for the recovery of migrant-friendly landscapes via the addition of trees into farmland. The African Forest Landscape Restoration Initiative (AFR100) has received 128 million hectares of commitments to bring land under restoration by 2030 in sub-Saharan Africa. However, only a small proportion of tree species are actually favoured by birds (Zwarts *et al*., 2015), suggesting the need for the careful selection of tree species for these planting schemes to maximize their biodiversity potential.

While there is potential for restoration and REDD+ schemes to cost-effectively support migratory species via tree protection or recovery within farmland (US\$2.49 to US \$6.45 t^{-1} CO_2; Davies *et al*., 2021) – generating income for local landowners in the process – their potential to deliver retention of low-intensity farmland features favoured by declining long-distance migrants is more complicated. Blanket tree promotion would threaten the habitat suitability of several migrant species, with the use of plantation versus natural habitat recovery reducing potential benefits for biodiversity and a range of ecosystem services (Hua *et al*., 2022). Extending from a 2- to 3-year fallow cycle or reintroducing a 3-year fallow cycle to create more shrubby habitat were both expensive in unwooded farmland, but the former becomes more competitively priced when combined with tree protection (US\$4.67–US\$10.24 t^{-1} CO_2) (Davies *et al*., 2021). Funding for carbon protection and landscape restoration would thus likely need to be supplemented by additional support from governments or conservation organizations to promote such agri-environment-like programmes.

In conclusion, features associated with low-intensity farming provide a key habitat for several long-distance AP migrant birds wintering in West Africa. The conservation of these species requires a landscape-level approach that embodies multi-functionality (Staver, Archibold, & Levin, 2011; Brancalion & Chazdon, 2017). It points to complex trade-offs between competing conservation (i.e. forest resident vs. migrant species) priorities, challenges in working at sufficient spatial scales given the high levels of population spread and low migratory connectivity of AP migrants across their non-breeding grounds (Cresswell *et al*., 2007; Wilson & Cresswell, 2010a; Finch *et al*., 2017; Patchett, Finch, & Cresswell, 2018), the need to balance conservation with development and increased food production, and economic difficulties in raising sufficient resources to fund conservation programmes.

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Author contributions

D.P.E, J.M, C.A and C.B conceived the study idea. R.S and C.O discussed and further developed the study idea. L.N, A.D, K.B, J.R and G.S collected the data. C.A and M.M analysed the data and produced all figures. C.A wrote the first draft of the paper, with all coauthors contributing edits.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Full list of both resident and migratory species detected during the course of fieldwork, including both common and Latin names.

Table S3. Candidate models explaining the probability of the presence for each species in vegetation cover types. Null models within grey rows were not used in the averaged models, but are presented for comparison.

Table S4. Coefficient of determination (R^2) for each candidate model.

Figure S1. The predicted probabilities a vegetation cover type level arises within an agricultural landscape type.

Table S2. Multinomial logistic regression summary statistics presenting the coefficients, standard errors and p-values of each vegetation cover variable within different agricultural types, as compared to the High Permanent reference level.