Effects on Birds of the Conversion of Savannah to Farmland in the Sahel: Habitats are Lost, But Not Everywhere and Not For All Species

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Effects on birds of the conversion of savannah to farmland in the Sahel: habitats are lost, but not everywhere and not for all species

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Many migratory bird species, several of which are in severe decline, and African residents spend the northern winter in the Sahel, by nature a huge savannah, half of which has been converted into farmland. We analyse the impact of such large-scale changes on birds. On average, woody cover is 38% lower on farmland than on savannah. More critically, farmers have drastically changed the vegetation communities of their farmland. In the arid and semi-arid zone, they partly removed bird-rich trees such as Umbrella Thorn *Acacia tortilis* and Desert Date *Balanites aegyptiaca*, yet further south they created a richer bird habitat by replacing the original woody species by Winter Thorn *Faidherbia albida*, a preferred tree species for Afro-Palearctic migrants (but less so for Afro-tropical residents). Still further south, two bird-poor trees, Shea Tree *Vitellaria paradoxa* and African Locust Bean Tree *Parkia biglobosa*, dominate farmland, causing birds, mainly Afro-tropical residents, to lose habitat. As a consequence of farming, arboreal migrants are confronted with habitat degradation in the northern arid zone and in the southern humid zone, but face more favourable wintering conditions in the sub-humid central zone. Ground-foraging birds are more abundant on savannah than on farmland; 24 bird species from this group, including three wheatear species and many residents, are more than twice as abundant on savannah. Conversion of savannah into farmland has mixed outcomes for ground-foraging birds, but were generally negative except for five species (including Western Yellow Wagtail *Motacilla flava*) which were more than twice as abundant on farmland than on savannah. Thus, the conversion of savannah into farmland represents a loss for many but not all bird species.

Key words: Sahel, savannah, farmland, *Faidherbia albida*, *Acacia tortilis*, Shea Tree

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Savannahs, covering about 20% of the land surface worldwide and up to 40% of the African continent (White 1983, Scholes & Walker 1993), are found in the tropics, mainly in two wide bands at about 8°–20°N and 8°–20°S. These bands may be considered as a transition zone between treeless deserts and equatorial rainforest, an ecotone where wood cover gradually increases towards the equatorial region. In Africa, barren desert turns into savannah grassland with shrubs and isolated trees where annual rainfall ranges from 100 to 200 mm. Woody cover increases with increasing rainfall. At 600–700 mm, woody savannah becomes woodland (Sankaran *et al.* 2005). Wooded savannah and humid forests were important habitats for early man, whose imprint on the ecosystem gradually increased through the millennia. The impact of human occupation on savannah ecosystems gained momentum in the 20th century when the huge numbers of wild herbivores roaming the savannah south of the Sahara in the 19th century were eradicated and replaced by several hundred million domestic livestock (Spinage 1968, www.faostat3.fao.org). Despite the vast number of cattle, sheep and goats, the region can still be characterised as an extensive savannah with thorny shrubs and scattered trees. The short rainy season boosts an explosive growth of dense herbaceous vegetation and the subsequent seed production forms the staple food for insects, birds and rodents during the ensuing long dry season (Bille 1974, Morel & Morel 1974, 1978).

The recent ecological changes include the conversion of savannah into cropland, which is usually associated with tree loss and reduced seed production (Photo 1). Farmers growing rice in the floodplains of the Inner Niger Delta (Mali) removed trees on a large scale, as has happened in rice polders in the Senegal Valley, in the agricultural zone of 'Office du Niger' in central Mali and in the vast, fertile plains in southeast Sudan. However, such large-scale tree removal is rather exceptional. In the drylands of the Sahel, farmers grow crops beneath scattered trees. At present, the woody cover on farmland and on savannah is about the same (Brandt *et al.* 2018). The visual impression of farmland in the Sahel, described as agroforestry parkland (Boffa 1999), does not differ much from that of woody savannah. Farmers in the Sahel often use a crop-fallow rotation system to allow soil fertility to recover. Fields are temporarily left uncultivated, and these are covered with a dense vegetation of seed-producing grasses and forbs not unlike savannah vegetation. After the harvest, agricultural land is intensively grazed by livestock during the dry season.

It remains poorly known in which way and to what extent the conversion of savannah into farmland has affected the bird community in the Sahel. Our surveys suggest a negative impact on arboreal and granivorous ground-foraging birds (Zwarts *et al.* 2023d,e), but many variations on this theme are possible. In Burkina Faso, for example, bird density on farmland and savannahs varied with soil type and the duration of farmland left fallow, but the differences were insignificant when savannah and farmland had the same soil type (Söderström *et al.* 2003). However, the effects were large in West Africa for raptors and other large bird species (Thiollay 2006); the encounter rate with larger raptors in agricultural land was 97% lower than in pastoral land and savannahs and 30% lower for smaller raptor species. A similar significant difference was found for raptors and other bird species in Cameroon (Buij *et al.* 2013), Uganda (Bolwig *et al.* 2006, Shaw *et al.* 2019) and South Africa (Malan & Benn 1999). In Zimbabwe, Pringle *et al.* (2019) recorded a decline of larger bird species (>150 g), but an increase of the

Photo 1. Farmland with millet and small *Guiera senegalensis* shrubs bordering savannah with Umbrella Thorn *Acacia tortilis*. Picture taken in Niger (13.983°N, 7.302°E) during the dry season (10 December 2016). Note the bare ground in the millet field and the low, but dense vegetation in the savannah.

smaller ones, after savannah-like, large-scale rangeland was converted into smallholder farmed land. The bird density in the Serengeti savannah (Tanzania) was more than twice as high as in adjacent former savannah converted into agriculture, and the difference was still larger in ground-foraging seedeaters and insectivores (Sinclair *et al.* 2002). In contrast, Whinchats *Saxicola rubetra* in the Central African Republic were exclusively recorded in the sparse agricultural plots amidst vast woody savannahs in December 2017 (own unpubl. data); this species was in Nigeria most common in intensely used farmland (Hulme & Cresswell 2012).

The potential impact of land use changes on birds may be especially large in the Sahel, where 50% of the millions of km^2 of savannah in the 300–1200 mm annual rainfall zone has been converted into farmland. Rainfed farming is not possible in the arid zone. Farmland is therefore scarce (4%) in the 100–200 mm rainfall zone, increasing to 22% at 200–300 mm, 46% at 300–400 mm and 54% at 400–1200 mm rainfall (Figure S46 in Zwarts *et al.* 2023a). The savannah zone is the wintering ground of many millions of Afro-Palearctic migrants and much larger numbers of resident Afro-tropical birds. Among the ground-foraging migrants, three granivorous and ten insectivorous species are almost entirely dependent on this zone (Figure 13A and 14A in Zwarts *et al.* 2023a), as are 13 arboreal migratory species (Figure 5A in Zwarts *et al.* 2023b). The widespread creation of farmland throughout savannahs across the 300–1200 mm annual rainfall zone has drastically changed the wintering habitat of these 26 migratory species, several of which are in steep decline, such as Tawny Pipit *Anthus campestris*, European Turtle Dove *Streptopelia turtur*, Northern Wheatear *Oenanthe oenanthe* and Whinchat (van Turnhout 2005, Eraud *et al.* 2009, Zwarts *et al.* 2009, Vickery *et al.* 2014). These species are known to have faced serious habitat loss and habitat degradation on their breeding grounds (e.g. Brown & Aebischer 2004, Fay *et al.* 2021), but the large-scale changes in land use in their African wintering quarters presents them with double jeopardy, simply because they spend half their lives in the sub-Sahara.

Ideally, in order to address the impact of changing land use in Africa on birds, we should compare bird densities before and after the conversion of savannah vegetation into farmland. Because such data are lacking, we had to adopt the alternative approach of comparing bird densities of Afro-Palearctic migrants and Afro-tropical species between savannah and farmland. This paper focuses on two questions: (1) how many arboreal birds and ground-feeding birds of which species forage on farmland and savannah in the Sahel, and (2) what might have been the impact – in terms of species composition and abundance of birds – of the conversion of savannah into farmland?

METHODS

We refer to Zwarts & Bijlsma (2015) for a description of the methods used to count birds and woody plants and to Zwarts *et al.* (2023a,b,c) for a description of the dataset used in this paper. All 2144 study sites (each usually 4.5 ha) were situated between 7 and 22°N and between 17°W and 42°E. The analysis is based on sites across the entire width of the Sahel, but we excluded Ethiopian sites as being too different from the rest of our study area. In the strictest sense, the Sahel is the climate zone where the annual rainfall varies between 100 and 600 mm (Figure 5 in Zwarts *et al.* 2023a), but we use the term more loosely as including the full transition zone between Sahara in the north and the humid forests in the south. From the dataset, we selected sites where bird counts had been performed in random plots in the period 20 November – 10 March 2011–2019. Most of these counts were done in January and February two to four months after the crops had been harvested.

The sites were assigned to one of three main habitats: woodland, farmland or savannah. Farmland included fallow land, but savannah encompassed a wider range of habitats including bare desert, rangeland, scrubland and woody savannah. Savannah was heavily grazed by livestock, as was farmland after the harvest, resulting in bare soils after December (Figure 1 in Zwarts *et al.* 2023d). All crops and herbaceous vegetation not yet grazed by November had usually become withered by the time of our surveys. Overall, farmland was often so bare that we sometimes had to search for subtle traces like plough tracks to identify a site as farmland. Since most bird counts used in this paper were from January–February, we sometimes were in doubt whether land was in fallow or had been cultivated some months before, and, if cultivated, what crop the farmers had grown (which shows to what extent farmland is sometimes stripped of leftovers after harvest, both by farmers and by pastoralists passing through with cattle and goats/sheep). The sites not always exclusively consisted of woody vegetation, savannah or farmland. When mixed, the category with the highest coverage was noted. Woodland sites were excluded, as well as stony sites (sandstones, laterite soils, rocks). At first, we only noted Afro-Palearctic birds (from now on called migrants), but in later years also Afro-tropical species (from now on called residents). The number of sites used for the analyses of migrants (675 sites on farmland and 717 sites on savannah) is therefore larger than that for arboreal residents (529 sites on farmland and 633 sites on savannah), and ground-foraging residents (294 sites on farmland and 596 sites on savannah).

The land cover map (Figure 1A) and field data (Figure 1B) agree that half of the surface area in the 300–1000 mm rainfall zone is farmland, but the regional differences that we found are large. A comparison between our 2144 ground-truthing study plots and the land cover classification identified from remote sensing data shows that the satellite-based map slightly overestimated the coverage of farmland, mainly in the zones where the rainfall is less than 500 mm/year. Three older land use maps underestimated the extent of farmland and were less accurate (Table 1 in Zwarts *et al.* 2023a).

Between 13 and 16°N, nearly 100% of the area in W Senegal (13–17°W), N Nigeria, S Niger (4–11°E) and SE Sudan (30–36°E) comprises farmland, but much less so in E Senegal, W Mali (8–14°W) and in Chad (15–25°E). This variation is largely explained by soil characteristics, which are excellent for agriculture in W Senegal (fine sand) but poor in E Senegal and W Mali (laterite soils; Figure 1C). In less populous Chad, however, large parts of the zones that receive between 300 and 1200 mm of rainfall and are suitable for cultivation remain free of farming. To compare the average density of arboreal birds between farmland and savannah, we selected all sites where the annual rainfall was >300 mm, representing an area where half of the savannah had been modified into farmland.

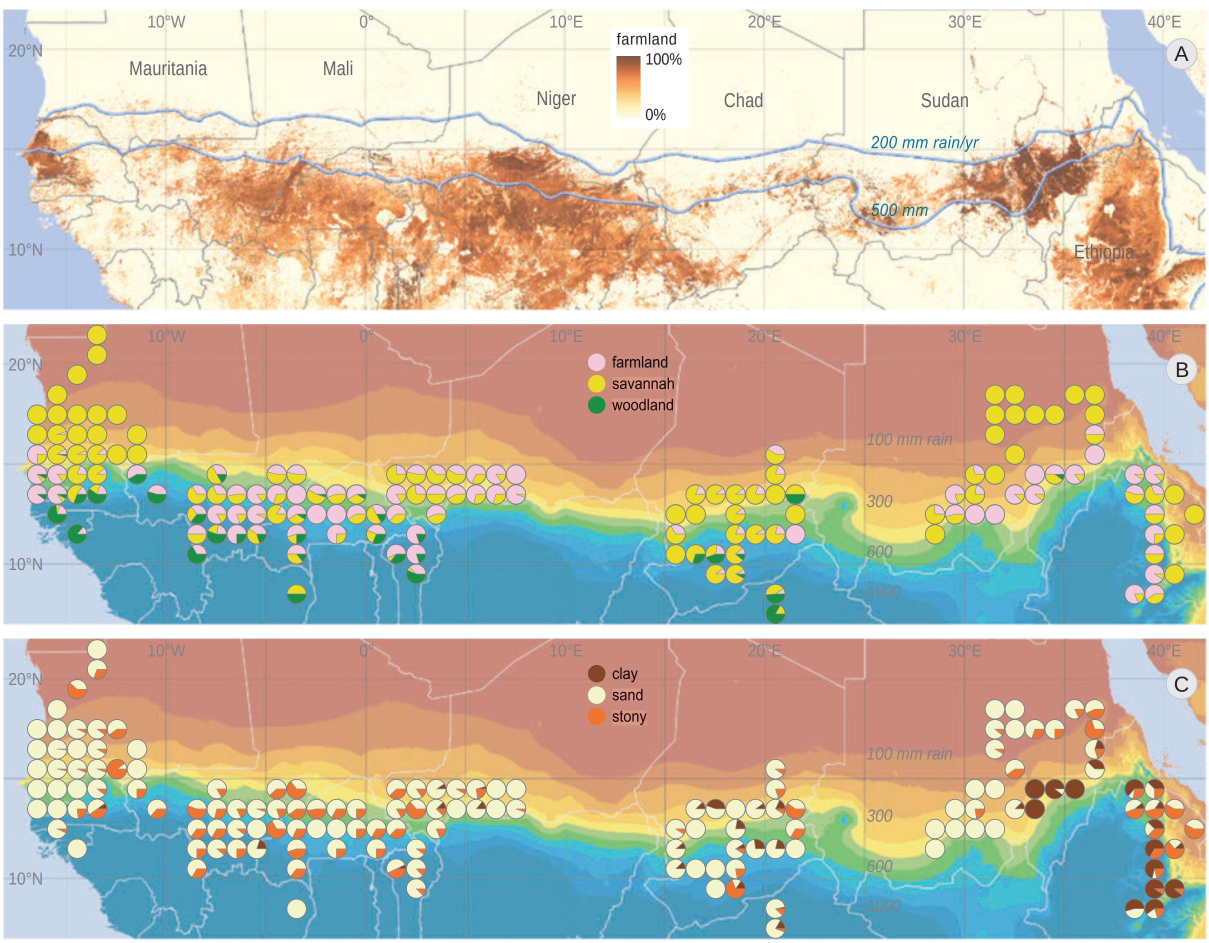

Figure 1. (A) Percent farmland in 2015 expressed per 100×100 m based on remote sensing data (source: Buchhorn *et al.* 2020), (B) percentage of study sites (n = 2144) categorised as farmland, savannah or woodland, averaged for 150 1° latitude × 1° longitude grid cells with annual rainfall as background (source: Hijmans *et al.* 2005), (C) percentage of the study sites in 150 grid cells classified as having a clayish, sandy or rocky soil.

RESULTS

Woody vegetation

Woody cover on farmland and savannah increased significantly with rainfall (Figure 2A) but, on average, woody cover on farmland was significantly lower (38%) than on savannah. Fewer woody species were expected on farmland due to selective felling, but this effect was recorded only in the humid zone (>800 mm rain; Figure 2B). In drier habitats the number of woody species on farmland was similar to that on savannah (Figure 2B).

The reduced woody vegetation on farmland might imply habitat loss for arboreal bird species, but actually does so only when tree loss occurred in bird-preferred woody species. Four tree species stand out because they attract many birds and are also common (Zwarts *et al.* 2023c). The most important woody species for birds was Umbrella Thorn *Acacia tortilis*, common and widespread in the savannah in the 100–500 mm/year rainfall zone, but far less so on farmland (Figure 3A). Desert Date *Balanites aegyptiaca* also attracted many birds, occurring across the wider rainfall range of 100–600 mm and in Chad even including the subhumid rainfall zone of 600–900 mm. Overall, *Balanites* was less common on farmland than on savannah (Figure 3B). Red Acacia *Acacia seyal* was typically confined to floodplains and clayish soils (Figure 3C). Winter Thorn *Faidherbia* (=*Acacia*) *albida* was found almost exclusively on farmland in the 300–700 mm rainfall zone (Figure 3D).

Of the widespread tree species usually avoided by arboreal birds (Zwarts *et al.* 2023c), *Guiera senegalensis* was a very common shrub in the 400–700 mm rainfall zones (Figure 4A). Farmers frequently removed *Guiera* shrubs, and the remaining shrubs were mostly 1 m high, their woody cover on farmland being half that for savannah (Figure 4A). *Combretum glutinosum* can become a large tree on the savannah in the 500–1000 mm rainfall zone, but on farmland most were removed, any remaining trees being small (Figure 4B). As an economically important tree, Shea Tree *Vitellaria paradoxa* (Figure 4C) was treated with care by farmers and was often the dominant tree species on farmland in southern Mali and Burkina Faso (annual rainfall >700 mm). This tree species was rarely found in woodland or savannah. African Locust Bean Tree *Parkia biglobosa* was characteristic of farmland in the humid zone, but almost completely absent on savannah except where annual rainfall exceeded 1000 mm (Figure 4D).

Very few woody species were common on both farmland and savannah. Most were either common on savannah and rare on farmland or vice versa (Figure 5A). *Faidherbia albida* and several fruit-bearing trees, such as Mango *Mangifera indica*, were not found beyond farmland. Common savannah species such as camel's foot *Piliostigma* spp., *Combretum* spp. and tallow tree *Detarium* spp. were common on farmland, but rarely as large trees because of frequent cutting; total woody cover therefore remained low.

Arboreal birds

Shea Tree *Vitellaria paradoxa* was poor in birds (Figure 5B), and would have held even fewer birds were it not for the large-scale presence of the parasite *Tapinanthus* spp. which attracted birds taking their berries and,

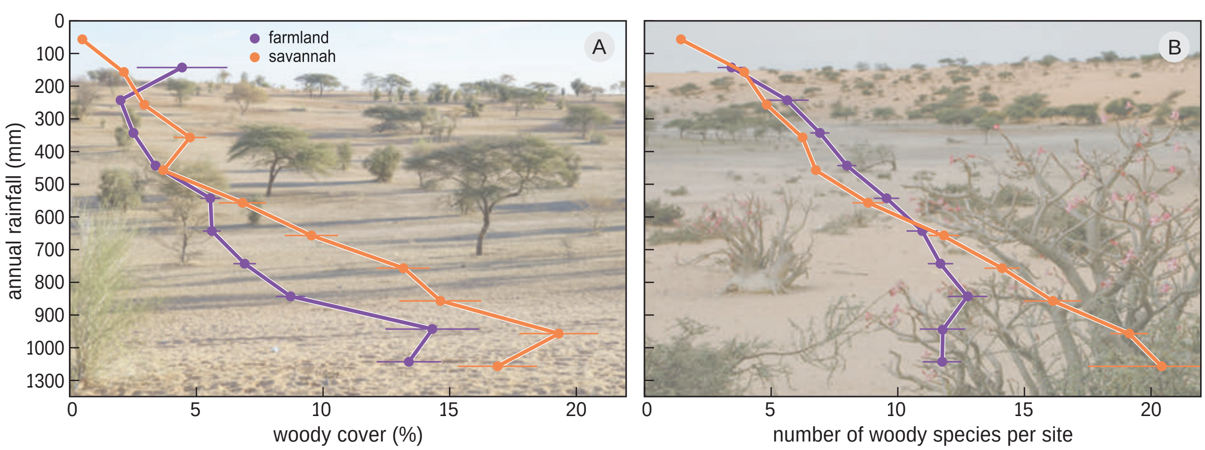

Figure 2. (A) Average woody cover (%) ± SE and (B) number of woody species ± SE on farmland and savannah in 11 annual rainfall zones. Woody cover and number of woody species differ significantly for land use (2 classes), rainfall (11 classes) and the interaction term (two-way ANOVA for A: $r^2 = 0.39$, $n = 1392$, $P < 0.001$ and for B: $r^2 = 0.44$, $n = 1392$, $P < 0.001$). Photos show dunes and valleys in southern Mauritania, with (A) mainly Umbrella Thorn *Acacia tortilis* and (B) Desert Rose *Adenium obosum*.

when flowering, sunbirds (73% of *Vitellaria* in Chad were infested with this parasite, in Burkina Faso up to 95% (Lamien *et al.* 2006, Kanika *et al.* 2020). The expansion of *Vitellaria* parkland must have inevitably had a negative impact on arboreal birds in the humid zone where this woody species is widespread. On the other hand, farmers in the sub-humid zone have created a bird-rich agroforestry parkland dominated by *Faidherbia*. The conversion of savannah into farmland again has had a negative impact yet farther north in the semi-arid zone where bird-rich tree species such as *A. tortilis* and *Balanites* were partly removed from farmland.

The species composition of the woody vegetation on farmland differed substantially from that on savannah (Figure 5), with far-reaching consequences for birds. Because farmers removed bird-rich trees in the semi-arid zone (especially *A. tortilis* & *Balanites*), fewer arboreal migrants were found on farmland than on savannah in the 100–400 mm rainfall zone (Figure 6A). In contrast, farmland in the 400–700 mm rainfall zone, where bird-rich *Faidherbia* (Figure 5B) was most abundant (Figure 3D), was highly attractive to arboreal migrants. The more humid zone held few migrants (Figure 6A) on farmland or savannah, but insectivorous residents were more abundant, albeit at much lower densities on farmland than on savannah (Figure 6B), as was also the case for nectarivorous residents (Figure 6C) and frugivorous residents (Figure 6D).

Ground-foraging birds

Insectivorous ground-foraging migrants were most abundant in the drier zones. In the zone with 100–300 mm rainfall/year, their density was on farmland twice as high as on savannah. On the contrary, there were fewer birds on farmland than on savannah in the more humid zones (Figure 7A). For ground-foraging residents taking insects (Figure 7B) or seeds (Figure 7C), bird densities increased with rainfall in both farmland

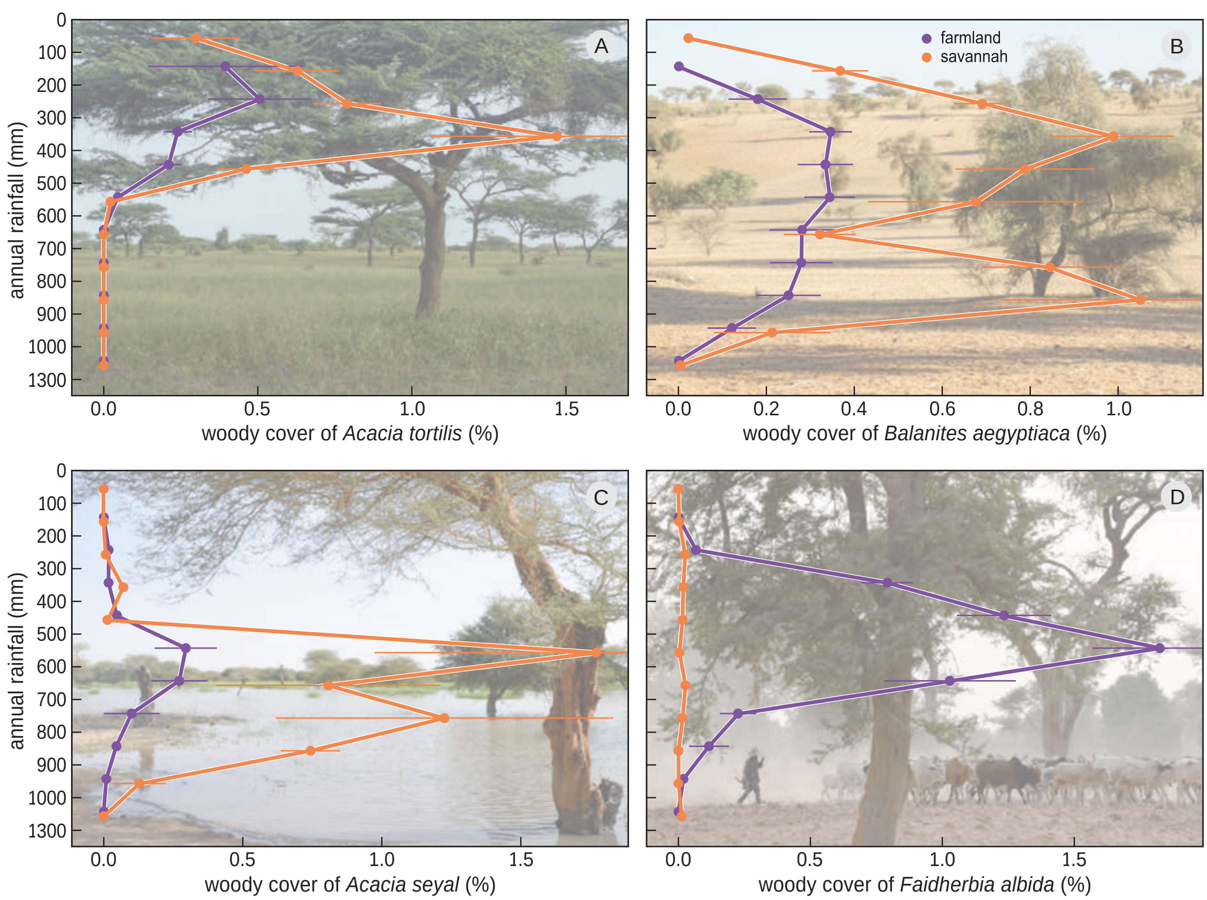

Figure 3. Average woody cover (%) ± SE of four bird-rich woody species on farmland and savannah in 11 annual rainfall zones. Woody cover in the four tree species differs significantly for land use, rainfall and the interaction term ($P < 0.001$), but $P < 0.01$ for the interaction term in *A. tortilis* and *Balanites* and not significant for land use in *A. tortilis* (two-way ANOVA; n =1392 in the four tree species; A: r^2 = 0.05, B: r^2 = 0.09, C: r^2 = 0.05, D: r^2 = 0.18).

and savannah but there were no perceivable differences in bird density between these two land uses.

The overall densities of ground-foraging birds were quite similar when comparing farmland and savannah (Figure 7). However, at the species level distinct variations were evident (Table 2). Bird densities for eight migratory species were higher on savannah (significant for the three wheatear species), while in two other migratory species densities were higher (non-significant) on farmland, namely Woodchat Shrike *Lanius senator* and Western Yellow Wagtail *Motacilla flava*, the latter associating with farmland near wetlands. Residents were also found in higher densities on savannah (36 species, 9 significant) than on farmland (10 species, 1 significant). The fraction of granivorous species occurring in higher densities on savannah (76%, 25 out of 33 species) was similar to the fraction of insectivorous species (79%, 19 out of 24 species). Bird densities on farmland and savannah differed significantly in 14 of the 57 ground-foraging species, of which only one species, Laughing Dove *Spilopelia senegalensis*, reached a higher density on farmland; in 13 other species densities were higher on savannah.

DISCUSSION

Most bird species (63%, 57 of 90) were recorded in a higher density on savannah than on farmland (Table 1 and 2). The densities of arboreal birds differed significantly between savannah and farmland in 36% of the bird species overall, ranging from 42% of insectivorous ground-feeding birds to 12% of the granivorous bird species (Table 1). This does not necessarily mean that conversion into farmland had a smaller impact on granivores. Granivorous birds often feed in flocks and recorded densities were therefore more variable (Figure 12 in Zwarts *et al.* 2023a). An extreme example is the

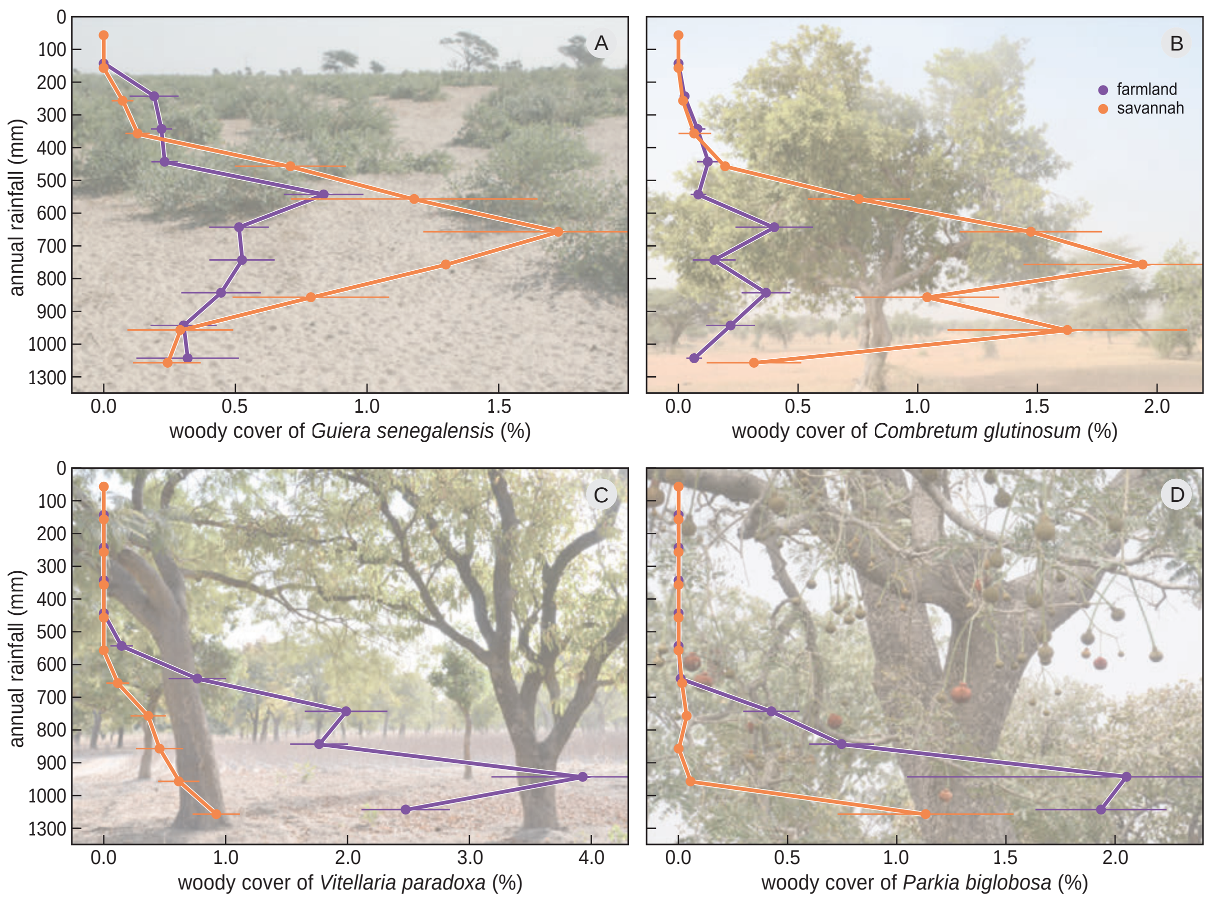

Figure 4. Average woody cover (%) ± SE of four most common woody species on farmland and savannah in 11 annual rainfall zones. Woody cover in the four woody species differs significantly for land use, rainfall and the interaction term ($P < 0.001$), but $P < 0.01$ for land use and interaction term in *Guiera* (two-way ANOVA; $n = 1392$ in the four tree species; A: $r^2 = 0.06$, B: $r^2 = 0.12$, C: $r^2 = 0.28$, D: $r^2 = 0.15$).

European Turtle Dove observed in only four savannah sites (0.6%), once in a flock of 28 birds. We saw none on our farmland sites, nor in the agricultural west of Senegal where van Tuijl (2018) found a large concentration of European Turtle Doves. To obtain reliable data for flock-feeding granivorous bird species more or larger counting sites are necessary.

Even when excluding Ethiopia, as we did in the face of its divergent habitats, regional and local variations in bird densities remained large (Zwarts *et al.* 2023a,b). Furthermore, we inevitably enlarged the variation by lumping all farmland habitats into a single category. Bird densities not only differ between fallow and recently cultivated land (Söderström *et al.* 2003) but also between the various crops (e.g. millet, sorghum, fonio, peanuts, bissap and cotton). The highest densities were recorded in well-tended and watered vegetable gardens. Even though we excluded sites with stony soil, sites categorised as savannah also consisted of a wide range of different sub-habitats, such as bare sandflats, grassland, scrubland and areas with few or many trees. Seasonal variation was to some extent reduced by selecting bird counts performed between 20 November and 10 March, corresponding with the middle of the dry season. Bird counts were always performed after harvest, the latter usually in September and October.

Savannah and farmland may sometimes look the same in the dry season, but the difference is substantial when it comes to the presence and identity of woody species, especially concerning trees either highly or rarely preferred by birds. On average, arboreal migrants on the savannah reached peak densities between the 100-mm and 400-mm rainfall zones. The conversion of savannah into farmland in this rainfall zone reduced the woody cover of bird-rich trees such as *A. tortilis* and *Balanites* (Figures 3A and 3B), leading to a reduction of bird densities on farmland by 34% compared to the original savannah (Figure 6A). However, further south, in the 400–600 mm rainfall zone *Faidherbia* was retained and protected by farmers (Figure 3D); the density of arboreal birds in this zone was 71% higher than on savannah (Figure 6A). To quantify the overall gain for arboreal migrants in the *Faidherbia* agroforestry zone and the losses following removal of preferred trees in the *Acacia* belt in the north, we calculated total bird numbers per rainfall zone and habitat. Bird densities on savannah and farmland (Figures 6 and 7) were multiplied by their respective total surface areas within the region covered (Figure 8A; see also Supplementary Material 1 in Zwarts *et al.* 2023a), while accounting for the percentage coverage of farmland and savannah (Figure S46 in Zwarts *et al.* 2023a;

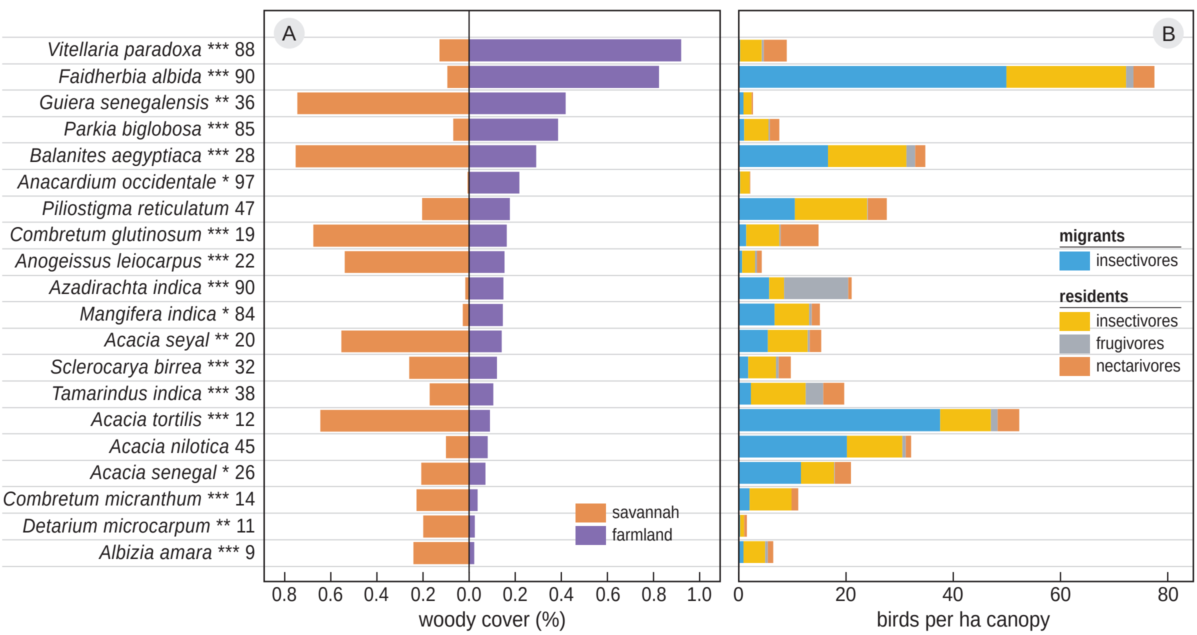

Figure 5. (A) Woody cover (%) of twenty common woody species on farmland and savannah. A selection is made for sites in the rainfall zones of >300 mm/year (n = 406 for savannah and n = 681 for farmland). Seventeen of the 20 woody species occurred significantly more often on either savannah or farmland (one-way ANOVA; $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$). Occurrence on farmland (relative to occurrence on farmland + savannah), varying between 2 and 98% of the total woody cover, is shown along the vertical axis next to the tree name. (B) Average bird density per ha of canopy (data from Figure 3 in Zwarts *et al.* 2023c).

Figure 8B). We omitted the farmlands and savannahs of Ethiopia. The estimate arrived at a total of 145 million arboreal migrants using farmland and savannah between Senegal and Sudan as a wintering site in the 2010s: of that total 72 million arboreal migrants used farmland and 73 million savannah (Figure 8C).

The historical numbers of arboreal birds per rainfall zone could be derived on the assumptions that all existing farmlands in the zone under study had originally been savannah and that it had held the same bird densities per rainfall zone as calculated for the 2010s (Figure 8C). In the absence of farmland in the continuous savannah vegetation of the past, we back-calculated that the region must have harboured an estimated 141 million arboreal migrants, some 4 million fewer than in the present situation. This suggests that arboreal migrants have not suffered from the conversion of savannah to farmland. However, the extent to which numbers were gained or lost are species-specific. Bird species abundant in *Faidherbia*, such as Western Olivaceous Warbler *Iduna pallida* (up by 53% in the current situation compared to the theoretical situation without farmland), Western Bonelli's Warbler (+33%) and Rüppell's Warbler *Curruca ruppeli* (+23%) profited from the conversion of savannah into farmland (because of the increase of *Faidherbia*), but Western Orphean Warbler *Curruca hortensis*, which concentrates in the northern Sahel and is largely dependent on *Acacia tortilis* (a typical savannah tree), would be down by 39%. For several other Palearctic passerines, occurring in a wide range of rainfall zones, changes in fortunes as a result of the conversion were probably minor, such as for Subalpine Warbler *Curruca iberiae* + *C. subalpina* + *C. cantillans* –5%, Lesser Whitethroat *Curruca curruca* +2% and Common Redstart *Phoenicurus phoenicurus* +6%.

Because arboreal migrants are less common in the more humid zones within the studied region, the

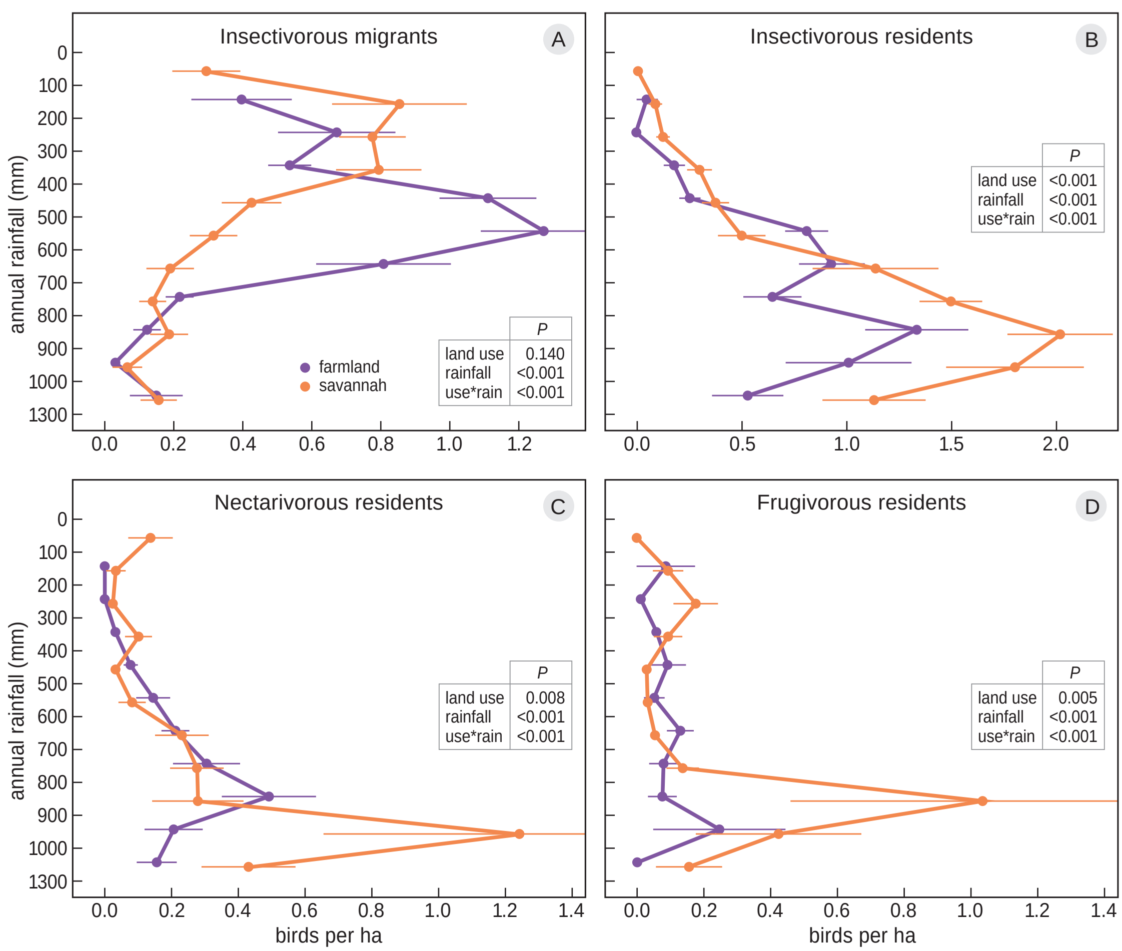

Figure 6. Bird densities per ha ± SE of four categories of arboreal birds on farmland and savannah, in 11 rainfall zones. The significance of the statistics comparing between land uses, rainfall values and their interaction term are given (two-way ANOVA).

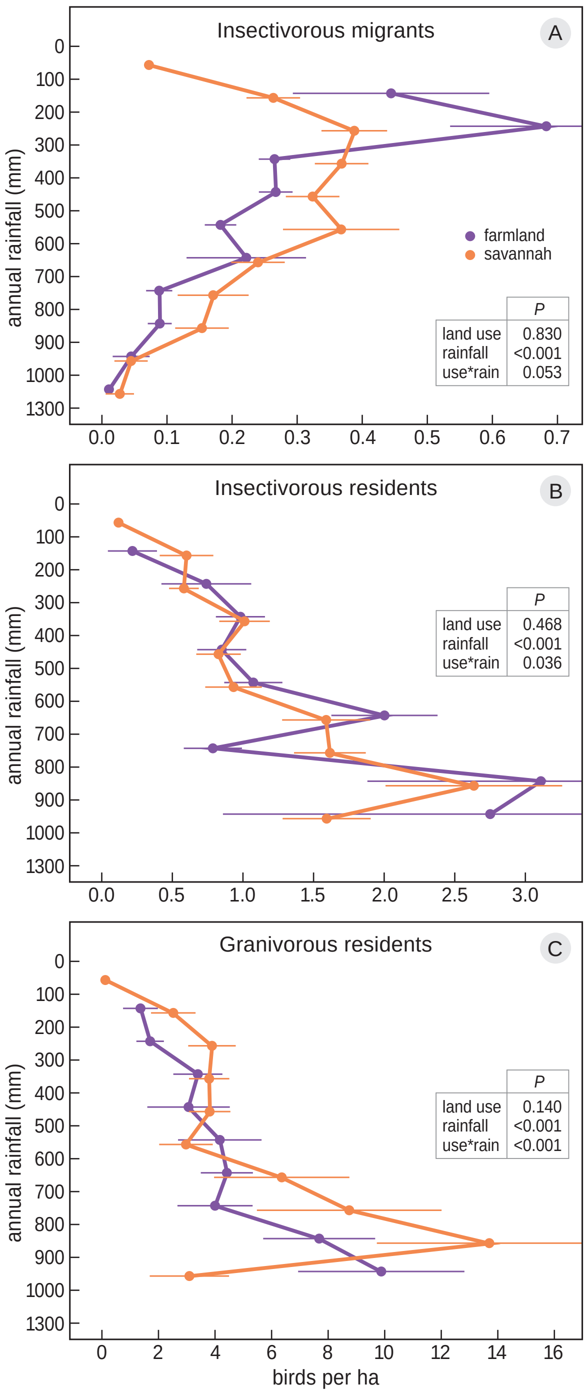

Figure 7. Densities of three categories of ground-foraging birds per ha ± SE on farmland and savannah in 11 annual rainfall zones. The statistical significance of the differences in bird densities between land uses, rainfall values and their interaction term are given (two-way ANOVA).

conversion of woodland savannah into *Vitellaria* parkland (which is almost completely devoid of arboreal migrants) is not likely to have had a significant impact on their total population (Figure 8C). However, in that part of the humid zone which mainly lies south of our study area's southern limit (7°N), species like Willow Warbler *Phylloscopus trochilus*, Wood Warbler *Phylloscopus sibilatrix*, Melodious Warbler *Hippolais polyglotta* and European Pied Flycatcher *Ficedula hypoleuca* might have suffered from the conversion of woody savannah into parkland dominated by *Vitellaria* and *Parkia*. The post-conversion losses must have been especially large for the many arboreal residents that are common in this rainfall zone (Figure 6).

During the dry season, the ground of farmland and savannah is typically largely bare in the northern Sahel region, but food supply for ground-foraging birds at this time of year potentially differs between the two habitats. In the rainy season savannah is covered by a dense vegetation of annual grasses in the arid part of the Sahel and by perennial grasses in the humid zone, which to a lesser degree also may be covered by forbs. Seed production, except in drought years, was in pre-conversion times sufficiently high to constitute a reliable food resource for the many ground-foraging granivorous birds during the long dry season (Zwarts *et al.* 2023e). On farmland, however, weeds are actively removed by farmers, as are crops during harvest. Consequently, food supply for ground-foraging birds has become much more reduced on farmland than on savannah, as evident from the higher numbers of granivores (+36%) and insectivores (+33%) on savannah during the dry season (Table 2). The difference is even larger for seven dove species (but not for Laughing Dove) and for three wheatear species.

We were unable to determine bird densities separately for cropped and fallow fields. Both field types were therefore merged into a single 'farmland' class. In the long run, fallow land will turn again into savannah and may until that time be considered as an intermediate stage between farmland and savannah. Farmers keep their land under fallow for an average of 4 to 6 years, and as a result 63% of the farmland in the Sahel is under fallow (Tong *et al.* 2020). In the dry season, the soil of farmland in China was found to contain between 90% (Hu *et al.* 2015) and 71% (Li *et al.* 2017) fewer seeds than on savannah; intermediate values applied for mixed land use. The same goes for insects. Kaiser *et al.* (2015), for example, found more ants (an important prey for birds, especially in arid regions (Dean & Milton 2018), more in fallow fields than on farmland. Hence, we suspect that a negative impact of

Table 1. Average density (*n*/ha) on farmland and on savannah of 33 arboreal bird species, excluding Ethiopia, stony sites, and sites where the average rainfall was less than 300 mm/year. **Food**: ins = insect, nec = nectar; **r-m**: r = residents, m = migrants; **rain** : average annual rainfall (mm) in the distribution area of the bird species, marked light blue <500 mm and dark blue >800 mm. **Farmland** is marked light green when density on farmland was higher than on savannah and dark green when it was twice as high; **savannah** is marked light yellow when density on savannah was higher than on farmland and dark yellow when it was twice as high. $n = 1392$ (migrants) or 1162 (residents); *P*: statistical significance of the difference between farmland and savannah: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$ (one-way ANOVA).

Bird species		Food	r-m	Rain	Farmland		Savannah		*P*
					Mean	SE	Mean	SE	
Blue-naped Mousebird	*Urocolius macrourus*	fruit	r	519	0.027	0.011	0.086	0.011	
Green Woodhoopoe	*Phoeniculus purpureus*	ins	r	589	0.024	0.010	0.007	0.010	
African Grey Hornbill	*Lophoceros nasutus*	ins	r	673	0.014	0.004	0.018	0.004	
Vieillot's Barbet	*Lybius vieilloti*	fruit	r	658	0.014	0.004	0.016	0.004	
African Grey Woodpecker	*Dendropicos goertae*	ins	r	562	0.009	0.003	0.009	0.003	
Rose-ringed Parakeet	*Psittacula krameri*	fruit	r	710	0.014	0.006	0.015	0.006	
Senegal Batis	*Batis senegalensis*	ins	r	668	0.000	0.000	0.017	0.000	*
Yellow-crowned Gonolek	*Laniarius barbarus*	ins	r	706	0.009	0.004	0.015	0.004	
Black-headed Gonolek	*Laniarius erythrogaster*	ins	r	888	0.004	0.001	0.015	0.001	*
Brubru	*Nilaus afer*	ins	r	718	0.005	0.002	0.014	0.002	
Sennar Penduline Tit	*Anthoscopus punctifrons*	ins	r	517	0.002	0.001	0.018	0.003	***
Common Bulbul	*Pycnonotus barbatus*	fruit	r	885	0.018	0.003	0.020	0.003	
Northern Crombec	*Sylvietta brachyura*	ins	r	643	0.020	0.005	0.050	0.005	**
Western Bonelli's Warbler	*Phylloscopus bonelli*	ins	m	450	0.237	0.025	0.054	0.025	***
Common Chiffchaff	*Phylloscopus collybita*	ins	m	586	0.008	0.005	0.019	0.005	
Eastern Olivaceous Warbler	*Iduna pallida*	ins	m	468	0.017	0.003	0.011	0.003	*
Western Olivaceous Warbler	*Iduna opaca*	ins	m	534	0.057	0.004	0.008	0.003	***
Tawny-flanked Prinia	*Prinia subflava*	ins	r	727	0.148	0.013	0.237	0.013	**
Green-backed Camaroptera	*Camaroptera brachyura*	ins	r	752	0.090	0.011	0.172	0.011	***
Yellow-bellied Eremomela	*Eremomela icteropygialis*	ins	r	493	0.004	0.002	0.016	0.002	*
Senegal Eremomela	*Eremomela pusilla*	ins	r	775	0.058	0.011	0.066	0.011	
Lesser Whitethroat	*Curruca curruca*	ins	m	433	0.018	0.006	0.037	0.006	*
Western Orphean Warbler	*Curruca hortensis*	ins	m	287	0.012	0.003	0.021	0.003	
Subalpine Warbler	*Curruca cantillans*	ins	m	368	0.166	0.016	0.120	0.015	
Common Whitethroat	*Curruca communis*	ins	m	471	0.076	0.007	0.090	0.007	
Northern Yellow White-eye	*Zosterops senegalensis*	ins	r	1017	0.012	0.005	0.003	0.003	
European Pied Flycatcher	*Ficedula hypoleuca*	ins	m	1128	0.006	0.002	0.007	0.002	
Common Redstart	*Phoenicurus phoenicurus*	ins	m	616	0.035	0.006	0.037	0.006	
Pygmy Sunbird	*Hedydipna platura*	nect	r	699	0.092	0.013	0.127	0.013	
Scarlet-chested Sunbird	*Chalcomitra senegalensis*	nect	r	913	0.032	0.011	0.022	0.011	
Beautiful Sunbird	*Cinnyris pulchellus*	nect	r	838	0.028	0.005	0.028	0.005	
Variable Sunbird	*Cinnyris venustus*	nect	r	773	0.007	0.003	0.012	0.003	
Little Weaver	*Ploceus luteolus*	ins	r	591	0.154	0.018	0.076	0.018	**
TOTAL					1.421		1.467		

Table 2. Average density (n/ha) of 57 ground-foraging bird species on farmland and on savannah, excluding Ethiopia, stony sites and sites where average rainfall was less than 300 mm/year. **Food**: gran (incl. g+i, g+i+f) = granivores, ins (incl. i+f) = insectivores (g = grain, i = insect, f = fruit):, r-m: r = resident, m = migrant, rm = both; **rain**: average annual rainfall (mm) in the distribution area of the bird species, marked light blue <500 mm and dark blue >800 mm. **Farmland** is marked light green when density on farmland was higher than on savannah and dark green when it was twice as high; **savannah** is marked light yellow when density on savannah was higher than on farmland and dark yellow when it was twice as high. n = 1392 (migrants) or 890 (residents); P = statistical significance of the difference between farmland and savannah: $^{*}P$ <0.05, $^{**}P$ < 0.01, $^{***}P$ < 0.001 (one-way ANOVA).

Bird species		Food	r-m	Rain	Farmland		Savannah		P
					Mean	SE	Mean	SE	
Double-spurred Spurfowl	*Pternistis bicalcaratus*	gran	r	570	0.001	0.001	0.017	0.004	*
Speckled Pigeon	*Columba guinea*	gran	r	708	0.003	0.001	0.012	0.001	
European Turtle Dove	*Streptopelia turtur*	gran	m	407	0.000	0.000	0.016	0.000	
African Collared Dove	*Streptopelia roseogrisea*	gran	r	507	0.022	0.009	0.065	0.009	**
Mourning Collared Dove	*Streptopelia decipiens*	gran	r	770	0.019	0.003	0.031	0.003	
Vinaceous Dove	*Streptopelia vinacea*	gran	r	754	0.128	0.018	0.159	0.018	
Laughing Dove	*Spilopelia senegalensis*	gran	r	537	0.252	0.046	0.107	0.046	**
Black-billed Wood Dove	*Turtur abyssinicus*	gran	r	825	0.030	0.003	0.048	0.003	
Namaqua Dove	*Oena capensis*	gran	r	432	0.082	0.013	0.245	0.013	**
Black-headed Lapwing	*Vanellus tectus*	ins	r	494	0.017	0.006	0.050	0.006	*
Eurasian Hoopoe	*Upupa epops*	ins	rm	484	0.011	0.002	0.017	0.003	
Northern Red-billed Hornbill	*Tockus erythrorhynchus*	ins	r	663	0.080	0.015	0.130	0.012	
Abyssinian Roller	*Coracias abyssinicus*	ins	r	647	0.025	0.003	0.022	0.003	
Black-crowned Tchagra	*Tchagra senegalus*	ins	r	622	0.011	0.004	0.028	0.004	*
Yellow-billed Shrike	*Corvinella corvina*	ins	r	820	0.020	0.009	0.028	0.009	
Great Grey Shrike	*Lanius excubitor*	car	r	308	0.013	0.003	0.025	0.003	**
Woodchat Shrike	*Lanius senator*	ins	m	426	0.043	0.004	0.033	0.004	
Piapiac	*Ptilostomus afer*	g+i+f	r	635	0.021	0.013	0.001	0.013	
Black-crowned Sparrow-Lark	*Eremopterix nigriceps*	gran	r	297	0.067	0.029	0.149	0.029	
Chestnut-backed Sparrow-Lark	*Eremopterix leucotis*	gran	r	502	0.138	0.026	0.139	0.026	
Singing Bush Lark	*Mirafra cantillans*	ins	r	438	0.022	0.005	0.032	0.007	
Greater Short-toed Lark	*Calandrella brachydactyla*	ins	m	180	0.002	0.052	0.019	0.052	
Red-pate Cisticola	*Cisticola ruficeps*	ins	r	664	0.024	0.004	0.059	0.004	**
Cricket Warbler	*Spiloptila clamans*	ins	r	323	0.044	0.008	0.057	0.008	
Brown Babbler	*Turdoides plebejus*	ins	r	835	0.013	0.007	0.050	0.007	*
Greater Blue-eared Starling	*Lamprotornis chalybaeus*	i+f	r	866	0.054	0.004	0.070	0.004	
Purple Starling	*Lamprotornis purpureus*	i+f	r	811	0.090	0.019	0.046	0.019	
Long-tailed Glossy Starling	*Lamprotornis caudatus*	i+f	r	743	0.044	0.014	0.049	0.014	
Chestnut-bellied Starling	*Lamprotornis pulcher*	ins	r	382	0.235	0.037	0.181	0.037	
Black Scrub Robin	*Cercotrichas podobe*	ins	r	429	0.019	0.004	0.067	0.004	***
Rufous-tailed Scrub Robin	*Cercotrichas galactotes*	ins	rm	557	0.019	0.003	0.049	0.004	***
Northern Wheatear	*Oenanthe oenanthe*	ins	m	450	0.041	0.004	0.071	0.004	***
Isabelline Wheatear	*Oenanthe isabellina*	ins	m	463	0.017	0.004	0.041	0.004	*
Black-eared Wheatear	*Oenanthe hispanica*	ins	m	335	0.003	0.001	0.012	0.001	***
Sahel Bush Sparrow	*Gymnoris dentata*	g+i	r	869	0.017	0.006	0.035	0.005	
North. Grey-headed Sparrow	*Passer griseus*	gran	r	555	0.395	0.094	0.313	0.034	
House Sparrow	*Passer domesticus*	gran	r	322	0.025	0.009	0.010	0.009	
Sudan Golden Sparrow	*Passer luteus*	gran	r	369	1.243	0.201	1.414	0.201	
White-billed Buffalo Weaver	*Dinemellia dinemelli*	g+i	r	442	0.170	0.048	0.097	0.023	
Chestnut-cr. Sparrow-Weaver	*Plocepasser superciliosus*	gran	r	815	0.002	0.001	0.012	0.002	
Speckle-fronted Weaver	*Sporopipes frontalis*	gran	r	530	0.248	0.029	0.277	0.029	
Vitelline Masked Weaver	*Ploceus vitellinus*	g+i	r	623	0.106	0.030	0.113	0.030	

Table 2. Continued.

Bird species		Food	r-m	Rain	Farmland		Savannah		*P*
					Mean	SE	Mean	SE	
Village Weaver	*Ploceus cucullatus*	gran	r	841	0.002	0.000	0.009	0.000	
Red-billed Quelea	*Red-billed Quelea*	gran	r	696	0.151	0.413	1.009	0.413	
Northern Red Bishop	*Euplectes franciscanus*	gran	r	908	0.040	0.001	0.130	0.063	
African Silverbill	*Euodice cantans*	gran	r	364	0.174	0.044	0.088	0.044	
Black-rumped Waxbill	*Estrilda troglodytes*	gran	r	682	0.090	0.022	0.102	0.022	
Cut-throat Finch	*Amadina fasciata*	gran	r	600	0.019	0.005	0.087	0.005	
Red-cheeked Cordon-bleu	*Uraeginthus bengalus*	gran	r	717	0.454	0.063	0.688	0.059	
Green-winged Pytilia	*Pytilia melba*	gran	r	615	0.017	0.005	0.032	0.005	
Red-billed Firefinch	*Lagonosticta senegala*	gran	r	669	0.066	0.019	0.047	0.019	
Sahel Paradise Whydah	*Vidua orientalis*	gran	r	668	0.002	0.001	0.011	0.001	
Western Yellow Wagtail	*Motacilla flava*	ins	m	593	0.024	0.014	0.011	0.014	
Tawny Pipit	*Anthus campestris*	ins	m	362	0.008	0.003	0.015	0.003	
White-rumped Seedeater	*Crithagra leucopygia*	gran	r	669	0.050	0.009	0.022	0.009	
Gosling's Bunting	*Emberiza goslingi*	gran	r	742	0.002	0.001	0.009	0.002	
Golden-breasted Bunting	*Emberiza flaviventris*	gran	r	675	0.008	0.002	0.013	0.002	
TOTAL					4.924		6.667		

Photo 2. Two pictures taken by G. Gray Tappan (U.S. Geological Survey, EROS Center, USA) from exactly the same spot in central Senegal, south of Kaffrine, during the dry season in November 1994 (still savannah, shortly after a grass fire) and March 2010 (farmland with millet and peanut, after harvest).

Photo 3. When the landscape in the Sahel has some relief, farming is usually restricted to the valleys (here Sourou Valley in E. Mali in the early dry season; photo by Richard Julia), where the sediment is slightly more clayey and more resistant to water runoff than on sandy hill slopes with shallow soils or rocky outcrops (in the background).

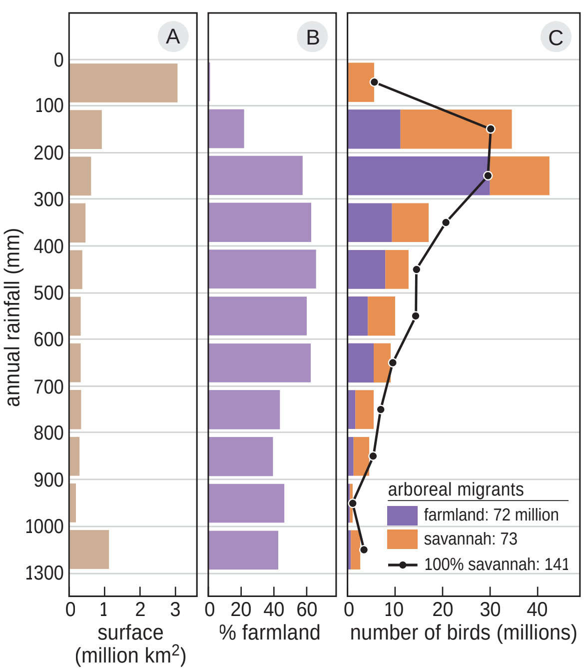

Figure 8. (A) Surface (million km^2) of farmland + savannah in 11 rainfall zones between 7 and 22°N (excluding Ethiopia). (B) Percent farmland relative to farmland + savannah (excluding woodland and Ethiopia). (C) Estimated number of insectivorous arboreal migrants feeding in woody vegetation. The black line gives the predicted numbers if the original savannah had not been partly converted to farmland.

farming on granivorous and insectivorous birds was not evident in our data because so much farmland was under fallow.

There are two reasons to assume that the actual impact of the conversion of natural savannah to farmland is larger than our bird counts indicate. First, Pringle *et al.* (2019) in Zimbabwe found an increase in small (<150 g) bird species, but a decline in larger bird species after savannah was turned into farmland (see also Thiollay 2006). Our data seem at variance, but it should be noted that all bird species listed in Table 1 and 2 are small because large bird species either had already disappeared or had become very rare by the time we started our fieldwork. Second, we compared

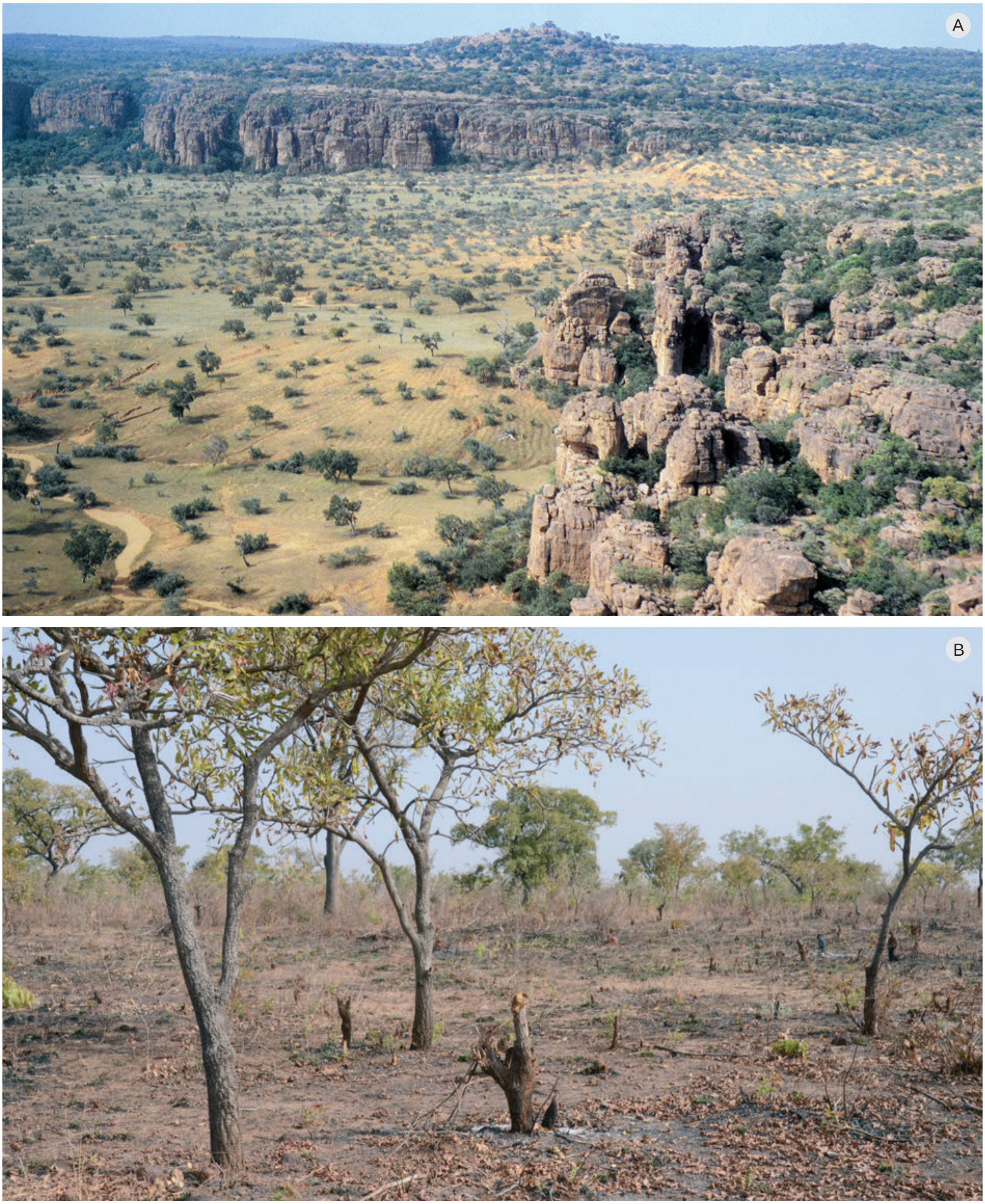

Photo 4. (A) Semi-arid savannah in eastern Mali near the Bandiagara escarpment has been mainly converted into agricultural land (see plow tracks), but tree density is about the same as on the remaining savannah (photo G. Gray Tappan, U.S. Geological Survey, EROS Center, USA) (B) To facilitate agriculture in the woody humid zone, farmers cut down and burn the woody vegetation to create a more open landscape (S. Mali; 11.42°N, 6.73°W). Note that the few remaining woody plants are Shea trees *Vittelaria paradoxa*. In the humid zone the conversion of savannah into agro-forestry parkland has a larger negative impact on arboreal birds than in the arid zone (Figure 6).

bird densities between existing savannah and farmland and not densities before and after conversion of the land; the latter comparison might have yielded bigger losses. To make a fair comparison between farmland and savannah, we excluded stony sites (5.0% and 21.2% of the sites with farmland and savannah, respectively), but other differences in soil composition between farmland and savannah remained, particularly for sandy/clayey soils. For example, conversion of savannah into farmland is often deployed in topographic depressions where the soil is relatively fine-grained, rather than on hillsides which comprise coarse, sandy soil (Photo 3). Also, farmland established in seasonal floodplains or near water courses always attracts many birds. The savannah nearby will most likely have poor soils less conducive to farming (e.g. Hiernaux *et al.* 2009). This difference in productivity is further exacerbated by enriching arable land with manure collected from nearby savannah used as rangeland.

The shift in food supply following the conversion of savannah into farmland has a bearing on the respective bird communities (though needs better quantification where food resources are considered), but it is probably not the sole explanation. Many more changes have taken place in the wake of increasingly intensive human exploitation: more people, houses, tracks, dogs, chickens and other livestock can be found on farmland than on savannah. This may have had an additional effect on birds (Pringle *et al.* 2019). Our savannah sites were indeed more remote than our farmland sites. The average distance to the nearest house was 1273 ± 1523 m (±SD, n = 846) for savannah sites and 697 ± 1069 m (n = 879) for farmland sites, excluding the sites in the <200 m rainfall zone (using the data from Figure S47 in Zwarts *et al.* 2023a).

The rate at which farmland in the Sahel and neighbouring vegetation zones has expanded since the 1960s varied locally between 0.7% per year in Senegal (Tappan *et al.* 2004), 2% in SW Niger (Hiernaux *et al.* 2009) and 3.9% in SW Burkina Faso (Augusseau *et al.* 2006). For West Africa overall it is estimated at 2% (CILSS 2016). Agricultural expansion has levelled off in areas where nearly all suitable land is under cultivation, but is unabated in 'empty' quarters, for example in Senegal in the most northern semi-arid regions and in the humid southern parts of the country (Tappan *et al.* 2004, CILSS 2016). Expansion of farmland in the semi-arid zone signifies loss of wintering habitat for arboreal Palearctic birds like Western Orphean Warblers, and similarly in the south for residents and for such migrants as Willow Warblers.

Half of the arboreal migrants (Figure 8C) and 37% of the ground-foraging migrants spend the northern winter in the Sahel on farmland. The future of more than twenty Eurasian species depends on how farmers in the Sahel continue to manage their agricultural parkland. The expansion of farmland has not yet been accompanied with serious intensification of agricultural practices. However, the increasing shortage of suitable arable land has resulted in shorter fallow cycles in the crop-fallow rotation system (e.g. Augusseau *et al.* 2006, Hiernaux *et al.* 2009), with possible negative impacts on birds. In Europe, it was not the expansion of agricultural land as such that caused substantial declines in birds, but rather the large-scale changes of agricultural practices in the second half of the 20th century (Newton 2017). This may yet happen in Africa.

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SAMENVATTING

Tientallen trekvogelsoorten, waarvan er vele sterk zijn afgenomen, overwinteren in de Sahel, van nature een uitgestrekte savanne die inmiddels voor de helft is omgevormd tot landbouwgrond. Welk effect heeft deze grootschalige verandering in landgebruik gehad op de vogels voor wie het gebied tijdelijk of permanent het leefgebied is? Zou de achteruitgang misschien deels kunnen worden verklaard door die conversie, gezien ook de afhankelijkheid van bomen als bron van voedsel voor de meeste trekvogels? Op boerenland staan namelijk minder bomen dan op de savanne, gemiddeld zelfs 38% minder. Nog belangrijker dan een afname van bomen sec bij de omzetting van savanne in akkerland is het feit dat de boeren bepaalde boomsoorten systematisch hebben weggehaald en andere hebben laten staan of hebben aangeplant. In de aride en semiaride zone hebben zij voor vogels aantrekkelijke bomen als *Acacia tortilis* en Woestijndadel *Balanites aegyptiaca* gedeeltelijk verwijderd. Meer naar het zuiden hebben de boeren echter een rijk vogelhabitat gecreëerd door de oorspronkelijke bomen te vervangen door *Faidherbia albida*, een acaciasoort die favoriet is bij trekvogels (en in mindere mate ook bij lokale vogels). Nog verder naar het zuiden, in de meer humide zone, is vooral de Karitéboom *Vitellaria paradoxa* in het boerenland gaan overheersen, een bij uitstek voor vogels onaantrekkelijke boomsoort; deze omslag heeft veel leefgebied, hoofdzakelijk van lokale vogelsoorten, verloren doen gaan. Al deze veranderingen hebben ertoe geleid dat boom- en struikbewonende vogelsoorten in de noordelijke aride zone en in de zuidelijke humide zone aanzienlijk terrein hebben verloren, maar in de tussenliggende sub-humide zone vooralsnog hebben geprofiteerd van de omzetting. Voor de vogels die op de grond foerageren, liggen de zaken anders. Die zijn talrijker op de savanne dan op landbouwgrond: 24 vogelsoorten (waaronder drie tapuitensoorten) waren meer dan tweemaal zo talrijk op de savanne als op landbouwgrond. Vijf soorten echter (waaronder de Gele Kwikstaart *Motacilla flava*) waren meer dan tweemaal zo talrijk op landbouwgrond als op de savanne (met de kanttekening: mits in de buurt van water). Per saldo kan de omzetting van savanne in landbouwgrond als habitatverlies voor vogels worden aangemerkt, maar dat geldt dus niet voor alle soorten. Bedenk daarbij dat de landbouw in Afrika nog betrekkelijk extensief is; intensivering onder invloed van stijgende bevolking kan de zaken op den duur drastisch negatiever laten uitpakken.

RÉSUMÉ

Des dizaines d'espèces d'oiseaux migrateurs, dont beaucoup ont fortement décliné, hivernent au Sahel. Cette vaste zone était originellement une savane, mais la moitié a déjà été convertie en terres agricoles. Quel effet ce changement à grande échelle de l'utilisation des terres a-t-il eu sur les oiseaux qui l'habitent en permanence ou temporairement ? Leur déclin pourrait-il s'expliquer en partie par cette conversion, compte tenu de la dépendance de la plupart de ces espèces à des habitats arborés ou arbustifs ? En moyenne, les terres agricoles accueillent en effet 38% d'arbres en moins que la savane et, plus préjudiciable encore, les agriculteurs ont systématiquement éliminé certaines essences et les ont remplacées par d'autres. Dans la zone semiaride, notamment, ce sont des arbres très attractifs pour les oiseaux comme l'Acacia faux-gommier *Acacia tortilis* et le Dattier du désert *Balanites aegyptiaca* qui en ont fait les frais. A l'opposé, plus au Sud, les agriculteurs ont créé un habitat favorable en remplaçant les essences indigènes par *Faidherbia albida*, une espèce d'acacia appréciée des oiseaux migrateurs et dans une moindre mesure des oiseaux locaux. Plus au Sud encore, dans la zone plus humide, le Karité *Vitellaria paradoxa*, peu attractif pour les oiseaux, est devenu dominant dans les zones cultivées. Ce changement a entraîné d'importantes pertes d'habitats, principalement pour les espèces locales. En raison de ces changements, les espèces arboricoles ont perdu de grandes surfaces d'habitat au Sahel dans la zone septentrionale aride et dans la zone méridionale humide. Au contraire, dans la zone intermédiaire subhumide, elles en ont pour le moment bénéficié. La situation est différente pour les espèces qui se nourrissent au sol : vingt-quatre des espèces étudiées, dont trois de traquets, étaient plus de deux fois plus abondantes sur les savanes que sur les terres agricoles, alors que seulement cinq espèces (dont la Bergeronnette printanière *Motacilla flava*) étaient plus de deux fois plus abondantes sur les terres agricoles que sur les savanes. Dans l'ensemble, la conversion de la savane en terres agricoles entraîne donc une perte d'habitat pour les oiseaux, mais pas pour toutes les espèces.

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