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Large decline of birds in Sahelian rangelands due to loss of woody cover and soil seed bank

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A R T I C L E I N F O

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A B S T R A C T

The large and widespread decline of European migratory birds spending the northern winter in the Sahel suggests – on top of adverse changes in the breeding quarters – pivotal changes in African overwintering areas. This paper attempts to answer three questions related to the sub-Saharan region: (1) can a change in the woody vegetation explain the decline of migratory birds feeding in trees, (2) ditto for the ground vegetation and bird species searching for food on the ground, and (3) are African bird species also in decline? The analysis is confined to the western Sahel (annual rainfall 100–400 mm, 15.5–18°N and 14.7–16°W), a region intensively used as rangeland but too dry for agriculture. The woody cover, largely stable before 1970, declined in the driest zone by 90% between the 1960s and 2000s, and by 40% in the more humid zone where the woody cover was already low in the 1960s. The woody vegetation changed in many places from an Acacia savanna into an open savanna with scattered bushes and few trees, concomitant with a shift in species composition. These changes took place during a prolonged drought (1969–1992), and were aggravated by increased grazing pressure after the construction of boreholes as evident from the loss of woody cover close to boreholes. A comparison of bird composition and densities in grazed and ungrazed areas and in three study sites intermittently surveyed between 1960 and 1994, with our surveys in the same sites in 2014–2015, revealed about 80% losses for birds feeding on the ground. The increased grazing pressure of livestock must have caused a large reduction of the soil seed bank and most likely also of insects. Between 15 and 16°W an estimated 8 million arboreal birds, mainly migrants, and 30 million ground-feeding birds, mainly granivorous residents, lost their habitat. Assuming that this zone is representative for the Sahelian rangelands as a whole, 1.5–2.0 billion birds have lost their habitat in half a century.

1. Introduction

Billions of birds from the northern hemisphere spend the northern winter in the Sahel, where they face the outcome of highly variable rainfall in the months preceding their stay. Eurasian migrants arrive in September at the end of the short rainy season and find a habitat that gradually desiccates till their departure in March–April. Several long-distance migratory bird species are known to suffer high mortality during Sahelian droughts (reviewed in Zwarts et al., 2009). In general, less rainfall translates into less food, as annual grasses produce fewer seeds and trees fewer leaves and fruit (Bille, 1974; Poupon and Bille, 1974; Poupon, 1980; Grouzis, 1992), and consequently fewer arthropods (Gillon and Gillon, 1973) and rodents (Poulet, 1974).

The year-to-year variation in Sahelian rainfall cannot fully explain the population trends of migratory birds, since many species show, regardless of rainfall, a long-term decline. This may partly relate to habitat degradation on the European breeding grounds (e.g. Newton, 2017) or conditions *en route* during migration (e.g. Brochet et al. 2016), but the on average larger declines of European bird species wintering south of the Sahara, compared to those remaining the entire year in Europe (Sanderson et al., 2006), suggests that conditions in the African wintering quarters at large play a significant role. Since the decline is observed in birds wintering in various habitats (wetlands, open savanna, woody savanna) and across latitudinal zones (Zwarts et al., 2009), it is likely that an array of factors has adversely affected Sahelian bird habitats. As in Eurasian migrants, a distinct decline is also evident in large African bird species (Thiollay, 2006), but population trends of resident passerines are unknown.

In this paper, we aim to estimate what changes in the landscape explain the extensive decline of so many bird species by repeating bird counts and vegetation surveys carried out decades ago and comparing satellite photos and images from the last 50 years. We restrict our

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analysis to the savanna just south of the Sahara, grazed by livestock but without agriculture due to the limited rainfall (100–400 mm) and legislative measures. Of the experimental studies on grazing in the western Sahel, the one quantifying the impact of different grazing regimes on the vegetation over 27 years (Miehe et al., 2010) is particularly important to understand how the Sahel has changed, also in terms of bird habitat. Historical surveys of bird densities were used to detect and explain long-term bird trends, specifically those performed in the Ferlo (northern Senegal) in the 1960s (Morel, 1968), 1970s (Morel and Morel, 1978) and 1990s (Tréca et al., 1996). We repeated their pioneering surveys on birds and vegetation and analysed satellite photos and satellite images for their study areas over a range of years, to quantify changes in vegetation and in bird numbers - African and migratory - in the interim. By combining both sets of data, we set out to detect (1) what has changed in the woody vegetation to explain the decline of migratory birds feeding in trees, (2) what has changed on the ground to explain the decline of ground-dwelling bird species, and (3) is the large decline of migratory birds also evident in African bird species?

2. Methods

2.1. Study area

Our data (Table 1) were collected in SW Mauritania and in the Ferlo, NW Senegal, between 14.6 and 16°W and 15.25 and 18°N (Fig. 1A). The semi-arid Ferlo has an open, gently undulating countryside on red-brown sandy soils and ferruginous tropical sandy soils (Tappan et al., 2004), dotted with shrubs and trees (Fig. 1D + E). The landscape of SW Mauritania is quite similar, but the dunes are higher, usually forming long ridges, with wide valleys in between (Fig. 1B + C; Niang et al., 2008). The entire region is grazed with cattle, sheep and goats, in the north also with camels. Even when grazers are absent, the abundance of droppings and dung testifies to the intensity of grazing in the previous months. Grazing conditions vary seasonally, with herders traditionally moving northward during the rainy season and moving southward in the dry season as soon as the green vegetation has withered or has been depleted by grazing. In our study area, grazing used to be mostly restricted to the rainy season and early dry season as long as temporary ponds still held water. In the mid-1950s, when 50 boreholes were drilled across some 30,000 km^2 of the Ferlo, year-round grazing became feasible over a wider area (Fig. 1A; see also Barral, 1982; Juul, 1996; Lind et al., 2003; Vincke et al., 2010). Initially, grazing of livestock in the Ferlo was restricted to within 3 km of boreholes (Bourlière, 1972). Grazing expanded to within a 10-km radius of boreholes when livestock numbers increased in the early 1980s (Barral et al., 1983; Le Houérou, 1989) and further away in the late 1990s (Adriansen, 2008), with cattle staying within 10–15 km of wells, sheep and goats usually at smaller distances.

Table 1

Sources of information used in this study to quantify changes in woody vegetation and bird densities during the last half century: (1) sites visited in 2014–2015; (2) a fenced area where livestock has been excluded since 1981, visited in 2014; (3) three sites revisited by us where field work had been done between 1960 and 1994 (see Fig. 6 for timelines of visits); (4) circular plots where woody plants were counted and woody cover was measured using satellite photos from 1965 to 1972 and satellite images from 2013 to 2016; (5) 89 circular plots (as 4) where satellite imagery was available for 2002–2004 and 2014–2016.To study the ecological impact of man-made watering points, we selected 48 field sites and 97 circular plots within 1–20 km from the boreholes.

source	period	data	location
119 visits to 94 sites	2014–2015	birds, woody plants; field	Fig. 1A
grazing exclosure	2014	birds, woody plants; field	Fig. 1A
3 reference sites	1960–1994; 2014–2015	birds, woody plants; field	Fig. 1A
390 circular plots	1956–1972; 2013–2016	woody plants; satellite data	Fig. 8A
89 circular plots	2002–2004; 2014–2016	woody plants; satellite data	Fig. 8A

2.2. Sites

2.2.1. Recent sites (2014–2015)

The study area was visited four times: the sites between Richard-Toll and Widou (including the Widou Thiengoly exclosures) on 10–13 January 2014, those between Dahra and Richard-Toll (again including Widou Thiengoly) and in Mauritania on 11–20 December 2014, those southeast of Dagana (inclusive Fété-Olé) on 25 February-4 March 2015 and the sites between Dahra and Richard-Toll (without Widou Thiengoly) on 29–31 October 2015 (Fig. 1A). 25 sites were visited twice, the remaining 69 sites once. The exact position of the sites is given in Table S1.

We followed a stratified sampling regime, with study sites located at latitudes intersecting 16.000°N, 16.050°N and so on, or along a track at fixed distances (1, 2, 5, 10, 15 or 20 km) of a borehole, alternately to the left or right side of the track. All sites were situated in rangeland; the Senegal Valley with its irrigated cropland, flooded forests and wetlands was excluded.

Per site, we counted and identified all woody plants and birds in usually three transects of 300 × 50 m in a triangular configuration (Fig. 2). We surveyed 376 transects in 119 sites, covering 609 ha (Fig. 1A). Transects, and trees within transects, were located using a GPS and a laptop with GPS connection with on-screen borders of transects and georeferenced, high-resolution satellite images. This enabled *in situ* checks whether trees or bushes were within the boundaries of the transects (Fig. 2).

2.2.2. Comparing sites (1960–2015)

Apart from sites mentioned in 2.2.1., we also visited two sites where in the past much research had been done, Fété-Olé and Widou Thiengoly (Fig. 1A). In the late 1960s, the Fété-Olé study site (1 × 1 km) was chosen because of its isolated position relative to surrounding boreholes (see Fig. 1A). Its precise position was not indicated in the original papers, but detailed vegetation maps in Poupon (1980) enabled us to pinpoint the site (Fig. 3). We surveyed the entire southwestern quadrant (500 × 500 m) where in the past bird counts and most other field work had been done.

The fenced experimental site Widou Thiengoly (14 km^2 at 15.955°N and 15.296°W; Fig. 4) was studied in detail between 1981 and 2007 by Miehe et al. (2010). We counted birds and woody plants in the four exclosures (9, 9, 3.4 and 2.2 ha; numbered A to D in Fig. 4) during two visits. For comparison, we studied four sites (4.5 ha each) outside the fence at a distance of 100 m (January 2014) and four sites at a distance of 400 m (December 2014) from each exclosure. The fence of the Widou Thiengoly exclosures was still intact during our first visit in January 2014, but we found some droppings of sheep and goats in one exclosure and saw three goats in another. Clearly, grazing pressure was not nil, but certainly very low compared to the grazed areas outside the fence. During our second visit in December 2014, part of the fence had been breached some time previously; livestock was absent in the exclosures but the presence of dung indicated grazing in the preceding months.

Tréca et al. (1996) and Diouf et al. (2002) did their field work near Souilène, at present known as Keur Mor Abra, in a site of 1 ha at about 16.361°N and 15.428°W. Since we did not visit the site, we used a Google Earth satellite image of 14 February 2016 to determine the woody cover for circles with a radius of 100, 200 and 300 m from the given position. Within these circles we counted 16.2, 17.2 and 19.4 woody plants (of > 0.5 m diameter) per ha, respectively, with a total woody cover of 2.6, 1.9 and 1.8%. As for bird and vegetation counts, we selected all ten sites within 13 km from Souilène, of which two were visited in January 2014, four in December 2014 and four in October 2015 (total area surveyed 67.5 ha). The woody cover in these sites

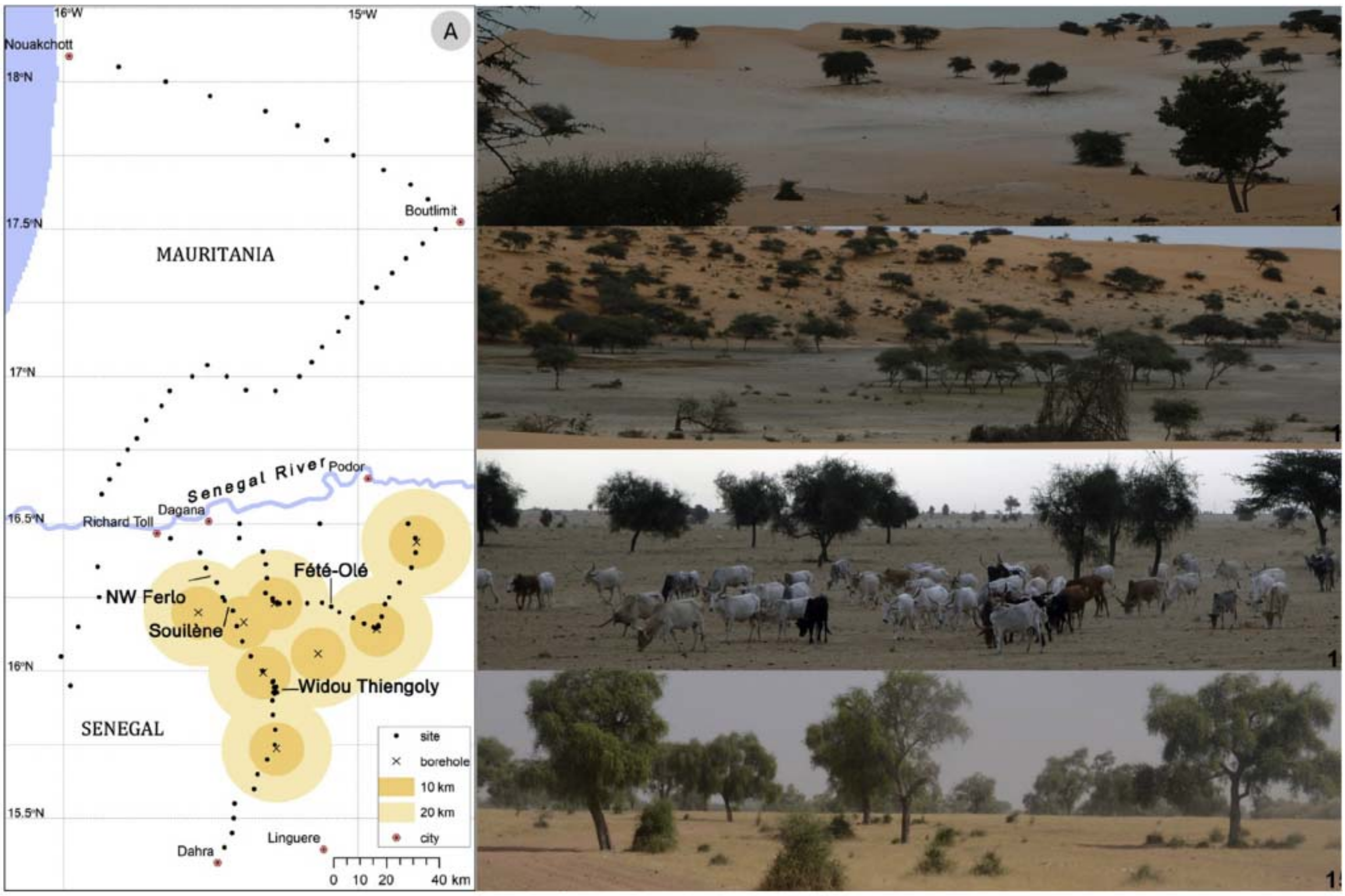

Fig. 1. (A) Study area with the location of sampling sites and boreholes, the latter encircled with radii of 10 and 20 km. Fété-Olé, Souilène, Widou Thiengoly and NW Ferlo are four study sites where in the past extensive field work has been done. The photos (from Jan. 2011 (B & C) and Feb. 2015 (D & E)) show the gradual change of the landscape going south between 18 and 15.5°N.

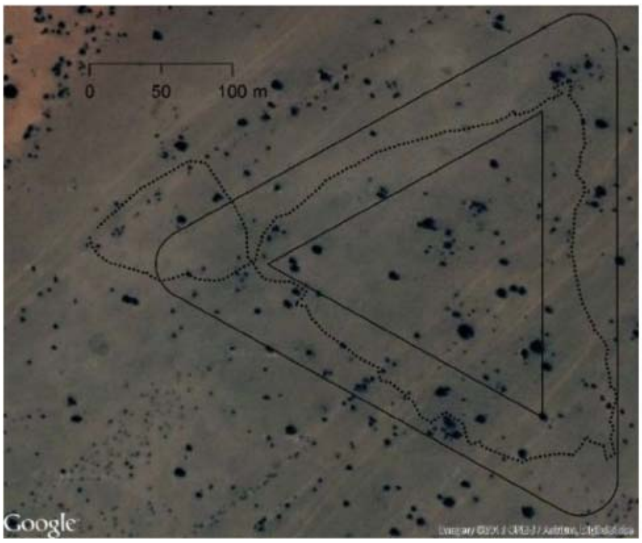

Fig. 2. An example of a satellite image as used in the field to survey sites (here #M48 in Mauritania). The three transects (legs of the triangle; each 300 × 50 m) are indicated as well as the GPS track of one of the three observers (dashed line), mostly along the midline of the three transects. *Balanites aegyptiaca* trees (canopy width of 4–9 m) are distinctly visible as black dots, but also the many *Leptadenia pyrotechnica* shrubs with a diameter of 1–2 m (small, grey dots; mainly SW of the transects). The site is situated in a valley (greenish grey) with sand dunes (salmon-pink) in the NW. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

amounted to 2.6% (range 0.2–4.7%), on average, similar as found for the approximate Souilène site on the satellite image.

In 1960–1962, Morel (1968) counted birds every month in a site of 25 ha in the northern Ferlo between Richard-Toll and Souilène. Since the exact position of his site is unknown, we compare his data with all 25 sites available from the same latitude (16.25–16.5°N) and longitude (14.8–15.8°W), surveyed in January and December 2014 and in February and October 2015. The proximate position of Morel's study site is indicated as 'NW Ferlo' on the map (Fig. 1A).

2.2.3. *Woody cover measured on satellite images*

Apart from the study sites where we collected field data, we selected 390 circular plots (radius 100 m, randomly distributed between 15 and 16°W and 15.25 and 18°N, excluding the Senegal valley; locations given in Fig. 8A) between 15 and 16°W, randomly distributed across the area shown in Fig. 1. These plots were used to quantify the woody cover on satellite photos (1965–1972) and satellite images from 2002 to 2004 and from 2013 to 2016 (see 2.3).

2.3. *Woody vegetation*

2.3.1. *Field data*

Our field work was always done by three persons. All trees and shrubs in the transects were identified (names followed Arbonnier, 2004). The height of each woody plant was measured with a laser rangefinder, but estimated by eye if $<$ 4 m. We counted and measured 48,880 individual woody plants of 39 species. Canopy width of each woody plant was estimated in the field by eye (using height as reference), and/or afterwards from photographs, as fraction of height

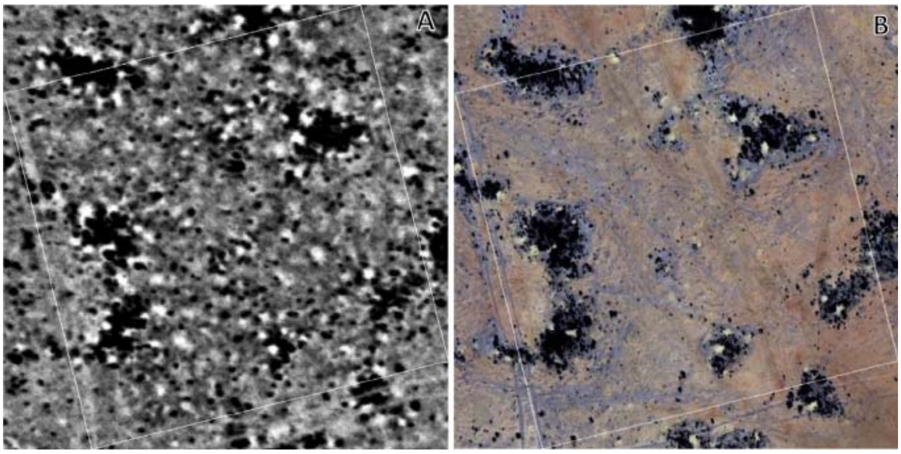

Fig. 3. Woody cover in the southwest quadrant of the Fété-Olé study site (500 × 500 m; white line) (A) in April 1972 (Corona satellite photo) and (B) in February 2013 (satellite image; © Bing Map Microsoft|Here). Total woody cover amounted to 10.4% in 1972 (for shrubs and trees > 4 m wide) and 3.7% in 2014 (all woody plants). In 2015, the pole indicating the southwestern corner of the site was still present (16.2160°N and 15.0926°W). Note the large decline of woody cover on low dunes (salmon-pink) compared to that in depressions (grey), even when the difference in altitude is less than 2–3 m. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(more details in Zwarts and Bijlsma, 2015). Canopy surface in a horizontal plane was calculated assuming that all tree crowns were circular. Woody cover (%) is defined as the sum of the canopy surface of all woody plants relative to the total surface of the site, the latter usually 4.5 ha.

2.3.2. Google Earth and Bing satellite images (2002–2016)

Within 390 circles (radius 100 m), we also measured the woody cover on Google Earth and Bing satellite images for the dry seasons of 2013–2016. Google Earth images from the period 2002–2004 were available for, in total, 87 of the 390 circular plots (see Fig. 8A). These images were compared with the most recent images (2014–2016) to check the change in woody cover during the 12 years in between.

On the images, woody plants are clearly outlined as separate, dark dots on a dry, sandy and usually bare underground during the dry season (Fig. 2). Woody plants can be automatically discriminated using object-based image analysis software, but we preferred to manually plot all individual woody plants using the Arc2Earth-extension in ArcGIS, with the image at a scale of 1:800 (Google Earth) or 1:1000 (Bing). Since the tree canopies are circular, each tree was marked with a circle with a different diameter (Suppl. Data: Fig. S3 and S4), allowing us to calculate the canopy surface per woody plant and thereby the total woody cover (being the sum of the canopy surfaces of all woody plants) within the site.

The number and canopy surface of woody plants calculated for the 390 circular plots on satellite images was ground-truthed with data collected in the field. For this exercise, we selected 28 field sites (106.5 ha) where 8470 woody plants with a total canopy of 50,752 m^2 had been measured. For the same 28 sites, the satellite images revealed a total of 3533 woody plants (41.9% relative to the numbers counted in the field) with a total canopy surface area of 42,721 m^2 (84.1% relative to the field measurements). There was a good fit for the number of woody plants > 2m wide, but on the images we missed more than half of the woody plants with a diameter of 2 m or less (Suppl. data: Fig. S1). Further inspection of our field data showed that we had overlooked much of the grassy (*Leptadenia pyrotechnica*) or herblike (*Calotropis procera*) woody vegetation on the satellite images but not the small *Boscia senegalensis* shrubs (having a dense foliage). Both overlooked plant species were recognizable on the satellite images as grey rather than black dots (Fig. 2). Taking this into account, the adjusted total woody cover as measured within the 390 circular plots on satellite images should approach the measurements in the field, although leafless woody plants, if small, will often remain unnoticed on current satellite images (mostly a resolution of 0.5 m).

2.3.3. Corona satellite photos (1965–1972)

Isolated desert and savanna trees can be detected on Corona satellite photos (Andersen, 2006; see also Fig. 3A and Suppl. data: Fig. S2). Corona photos, taken in the 1960s and 1970s from US spy satellites, were declassified in the 1990s and have since than been used in remote sensing studies to show historical changes in land cover and land use (e.g. Tappan et al., 2004; CILSS, 2016). We manually georeferenced all 43 Corona satellite photos (covering each 18 × 75 km of the earth surface) without clouds being available for the study area (http://earthexplorer.usgs.gov/), 19 from 26 December 1965, 21 from 31 January 1968 and 3 from 20 April 1972, using Google Earth or Bing Maps, with 10–50 reference points per photo (e.g. roads, buildings, hedges). The spatial error was 10–50 m for photos from Senegal, but, due to scarcity of reference points, 30–80 m for Mauritania. Corona photos from 1965 and 1968 were available for 48 of our circular plots, and from 1968 and 1972 for 19 field plots.

Woody plants are usually standing apart in deserts and savannas, hence are easy to distinguish individually on Corona photos taken during the dry season (Figs. 3 and 4, Suppl. data: Fig. S2-S4, S7). When the density of woody plants increases, however, they could still be distinguished individually on the coloured satellite imagery, but less so on the panchromatic Corona photos. Since trees are usually circular, the few oval-shaped black dots were considered to refer to two neighbouring circular woody plants.

We marked with circles the black dots recognized as trees on the Corona photos, in the same way as on satellite images, in order to measure the density of trees taking into account the variation in tree diameters. One problem with the Corona photos is their resolution, being 2.74 m for those from 1965 to 1968 and 1.83 m for those of 1972, restricting our measurements to woody plants with a diameter of at least 3 or 4 m. Another problem is that measurements constructed from Corona photos cannot be checked in the field, unlike those from recent satellite images (Fig. S1). The field work of Bille and Poupon (1972a) at Félé-Olé (25 ha), however, offers a unique possibility to validate to some degree the woody cover extracted from Corona photos. From the photo, we calculated a woody cover of 9.3% in 1968 and 10.4% in Félé-Olé in 1972 (Fig. 3A). Our photo analysis showed 776 woody plants, but Bille and Poupon (1972a) mentioned 3000 woody plants for the same site in 1969–1970. Assuming that all woody plants overlooked on the photos (below the resolution threshold) had an average diameter of 1 or 2 m, we underestimated the total woody cover in Félé-Olé by 0.3 or 2.8%. Consequently, total woody cover may have been 9.6–12.1% (1968) or 10.7–13.2% (1972). Morel and Morel (1978) gave for the same Fété-Olé site a woody cover of 9.6%, but as 13.4% of the trees died in the dry year 1972/1973 (Poupon and Bille, 1974), the woody cover in the preceding years may be estimated at 11.1%, i.e. in agreement with our estimates (9.6–13.2%) based on the Corona photos.

The reliability of our estimates from Corona photos may also be estimated by comparing the woody cover measured on photos from different dates. The woody cover in 48 circular plots was measured on Corona photos from 1965 and 1968, and in 19 circular plots from 1965

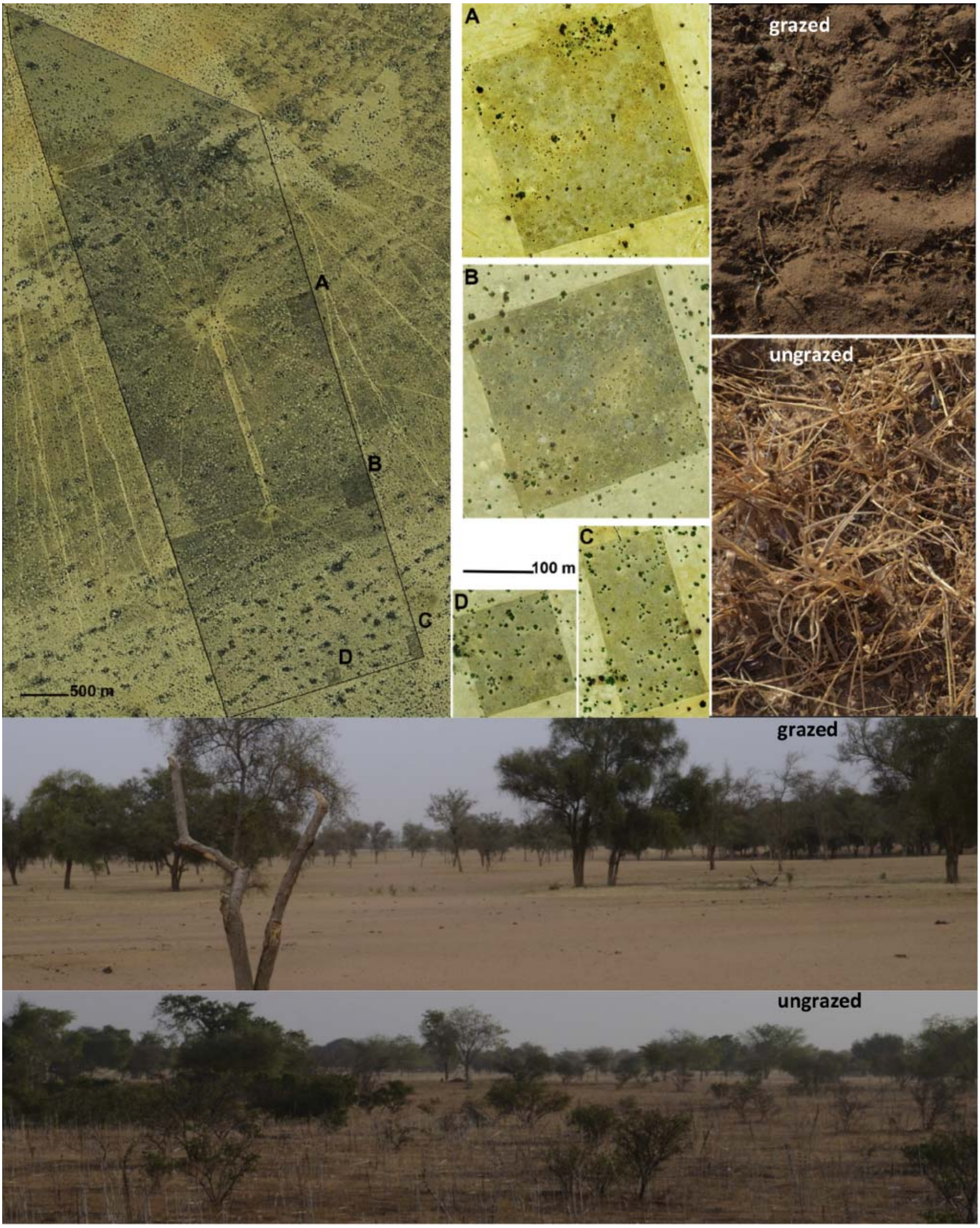

Fig. 4. Satellite image of the Widou Thiengoly experimental study site (April 2013; © Bing Map Microsoft|Here). The grazing pressure was controlled at a low level in the fenced area, with no grazing in the exclosures A – D (shown also at a larger scale); woody plants are clearly visible as black dots. The photos (December 2014) illustrate how the vegetation and the landscape look like with, and without, livestock. The discrepancy in colour between grazed and ungrazed areas is obvious on photos as well as satellite images. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

and 1972. The measured woody cover in the 1968-plots was 7% lower as in 1965 (5.3 vs. 5.7%, on average, for 48 plots) and 18% lower as in 1972 (6.1 vs. 7.2%, on average, for 19 plots). This discrepancy must be due to differences in quality of the images, being on average better for 1972 than for 1968, although Corona photos from 1968 were excellent for Mauritania, while those from 1965 and 1972 were poor and not used. Hence the woody cover may be measured on most, but not all, Corona photos, albeit not very accurate.

2.4. Birds

All birds in the study sites were identified and counted, as were all trees. Birds feeding in trees were recorded separately per individual tree. This enabled the calculation of bird density per tree species (expressed as birds per ha canopy). Birds, especially migratory species, are highly selective in their tree choice, and ignore most of the woody species in West Africa (Zwarts et al., 2015). As bird density is, on average, four times higher in acacias and other thorny tree species than in non-thorny tree species, woody cover is calculated separately for thorny and non-thorny woody species.

Our bird counts were absolute, i.e. each tree was searched for as long as necessary to detect all birds present (Zwarts and Bijlsma, 2015). A direct comparison with earlier counts of arboreal birds is complicated, as our labour-intensive bird counts are likely to have produced higher bird densities than earlier, less intensive surveys. Tréca et al. (1996) spent 1 h to survey their 1-ha study site (woody cover 40%) whereas it would have taken us 1.6 h with 3 observers to detect all birds on such a site, including secretive species, such as *Sylvia* spec., which may be missed easily (Zwarts and Bijlsma, 2015). We expect that the underestimation of such bird species is still larger in the studies of Morel who had to survey 25 ha.

Birds feeding on the ground were easy to count since the soil is bare during the dry season. Hence we are convinced that all birds present were detected, not only in our counts but also in those done by Morel and Tréca. The sites were too small to calculate an accurate density for aerial feeding birds and birds with large foraging ranges, such as swallows, bee-eaters and birds of prey; these birds, always few compared to the birds feeding on the ground or in trees, are excluded from the analysis.

In the study sites, we recorded a total of 3357 birds in 92 bird species. Bird names are according to del Hoyo et al. (2017); for a full list of all scientific names see Suppl. data: Table S4, S8, S9 and S11. The bird species are classified in three dichotomous categories (Suppl. data: Table S4, S8, S9 and S11):

(1) prey choice: insects or seeds,
(2) feeding habitat: in woody plants or on the ground,
(3) origin: migrants (breeding north of the Sahara, mainly in Europe and Asia), or residents (breeding south of the Sahara, thus including intra-tropical migrants).

This classification is based on Morel (1968), Morel and Morel (1978), and own observations. Note that doves, starlings and sparrows are categorized as ground-feeders since they collect all their food on the ground although they spend most of the day roosting in the shadow of tree foliage. The dichotomy is not always clear-cut. Many ground-feeding, granivorous birds also take insects, especially in the short rainy season (Morel, 1968), but since our data were collected in the dry season, nearly all ground-feeders are considered as granivorous birds. Many insectivorous birds will also take small fruit, but fruit-bearing trees, such as *Salvadora persica*, were rare in our study area. The bird densities of all species are given in the appendix, including some less common species not included in the applied categories, such as residents feeding in trees on fruit (mousebirds) or on nectar (sunbirds).

2.5. Rainfall

We calculated the average annual rainfall using the data from the rain gauges in Dagana, Podor, Dahra and Linguère (see Fig. 1A) and three stations nearby: Saint-Louis (16.65°N, 14.97°W), Louga (15.61°N, 16.23°W) and Matam (15.65°N, 13.25°W). We were unable to fully update the rainfall data for recent years, but since 1 January 2001, the NOAA's Climate Prediction Centre produces satellite-derived daily precipitation data for Africa in a 0.1° grid resolution (ftp://ftp.cpc.ncep.noaa.gov/fews/fewsdata/africa/rfe2/shp). These grid values highly correlated with the rainfall measured with rain gauges (Pierre et al., 2011), although partly because daily gauge measurements, if available, are used instantaneously to correct the satellite estimates. The correlation coefficient between rainfall and satellite-derived Rainfall Estimate (RFE) for the just mentioned rain stations varied between +0.936 and + 0.951; calculations based on monthly aggregated data (181 months between January 2001 and March 2016, of which gauge data were available for 163–172 months). The RFE is systematically lower than the rainfall on the just mentioned ground stations. To correct this bias, we used correction factors varying between 1.19 and 1.28 for the different rain stations. The corrected monthly rainfall estimates were substituted for the months lacking ground measurements.

Rainfall in 2013 and 2015 was close to normal compared to the rainfall since 2001, but 2014 was very dry (Fig. 5), although not yet as dry as some years in the 1970s and 1980s (Fig. 6). The decline of rainfall in the western Sahel since 1850 (when the measurements started in Saint-Louis) has turned into a slight increase during the past 30 years, with 2010 as the first wet year after 40 relatively dry years. The year-to-year variation in Sahelian rainfall is large, though. This has to be taken into account when a comparison is made with studies from different years (Fig. 6).

2.6. Statistics

SPSS-23.0 was used for statistical tests. We performed simple and multiple regression analyses and one-way analyses of variance to test the differences in woody cover and bird densities. Most statistics are given in the electronic appendix. The maps of the woody cover (Fig. 8) were derived from measurements on 390 circular plots, using a geostatistical procedure, kriging, within ArcGIS (spherical semivariogram model), to get interpolated values for the entire study area; the

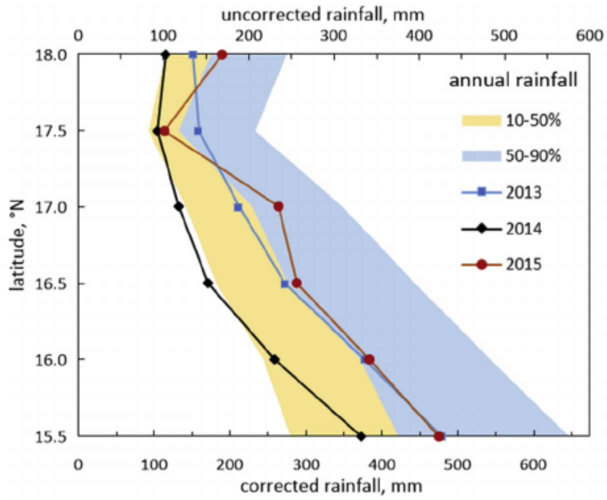

Fig. 5. Latitudinal variation in annual rainfall in the area delimited in Fig. 1A, averaged per 0.5° latitude (15.5°N = 15.25–15.75°N, etc.) in 2013–2015. The median and the 10–90% range refer to the period 2001–2015. The annual rainfall, based on satellite derived data (RFE2.0), is given without and with correction for a systematic bias (upper and lower horizontal axis, respectively).

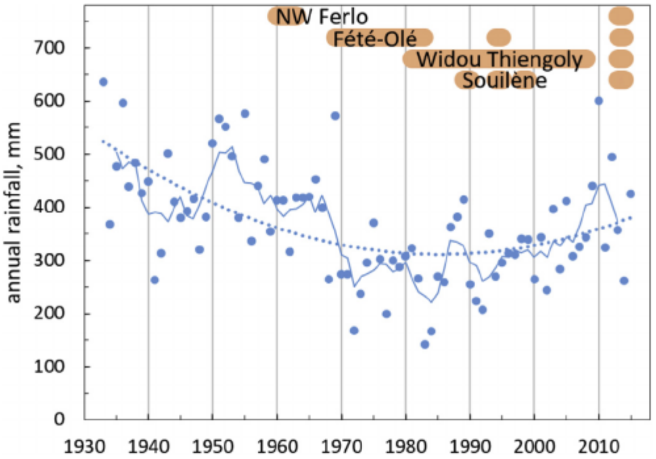

Fig. 6. Average annual rainfall in Northern Senegal at 16°N, calculated for 7 meteorological stations: Dagana, Podor, Dahra and Linguère (see Fig. 1A) and Saint-Louis, Louga and Matam. We substituted corrected, satellite-derived monthly rainfall estimates for lacking data in recent years (see text). Solid line: 5-year running mean; dashed line: second degree polynomial. The observation periods in four study sites are indicated.

interpolations were performed with a variable search radius to find the 12 nearest input sample points. The split-half method was used to test the reliability of the interpolated map and the average woody cover.

3. Results

3.1. Change of woody cover between 2003 and 2016

We used Google Earth and Bing images to count and measure the canopy size of woody plants within 87 circular plots (Fig. 8A), on a total surface area of 273 ha. We counted 62,649 woody plants in 2002–2004 (229/ha) and 32,252 in 2014–2016 (118/ha). Nearly all woody plants were small, having a canopy width of 1 or 2 m. Larger trees (up to 16 m wide) were much less common (Fig. 7A). Although the numerical density of woody plants declined by nearly 50% in the interim, the total woody cover increased by 20%, from 4.1 to 4.9%, on average (Fig. 7B). The explanation of this contrasting result is the decline of small, and the increase of tall trees. Individual woody plant species could mostly not be distinguished on the satellite images, but the small *Leptadenia* shrubs were recognizable as grey dots (Fig. 2). Comparing the satellite images revealed a large decline of *Leptadenia* shrubs (Suppl. data: Fig. S3) and the growth of other woody plants (Suppl. data: Fig. S4). Some trees disappeared, but this loss was more than compensated by the growth of the remaining trees (Suppl. data: Fig. S4).

For NW Senegal, we detected no latitudinal trend in the change of woody cover between 2003 and 2015, but in SW Mauritania the distinct increase of woody cover in the south (+100% at 16.5°N) gradually changed into a large decline further north (−50% at 17.8°N) (Suppl. data: Fig. S5).

3.2. Change of woody cover between 1965 and 2016

Using Google Earth and Bing satellite images from 2013 to 2016, we counted and measured 111,876 woody plants within 390 circular plots (1367 ha), but on the Corona photos from 1965 to 172 within the same plots only 31,662 woody plants. The relatively low number on the photos is partly due to the lower resolution of the Corona photos; woody plants of 1–2 m canopy width were impossible to detect, or partly overlooked (3–4 m). Woody plants > 5 m wide showed an average decline by 82% (Fig. 7C) between 1965-1972 and 2013–2016, and this decline was the same for all size classes. Very large trees (diameter 19–23 m) were rare in the 1960s, and absent 50 years later. Looking at smaller time scales, we found no decline in woody cover

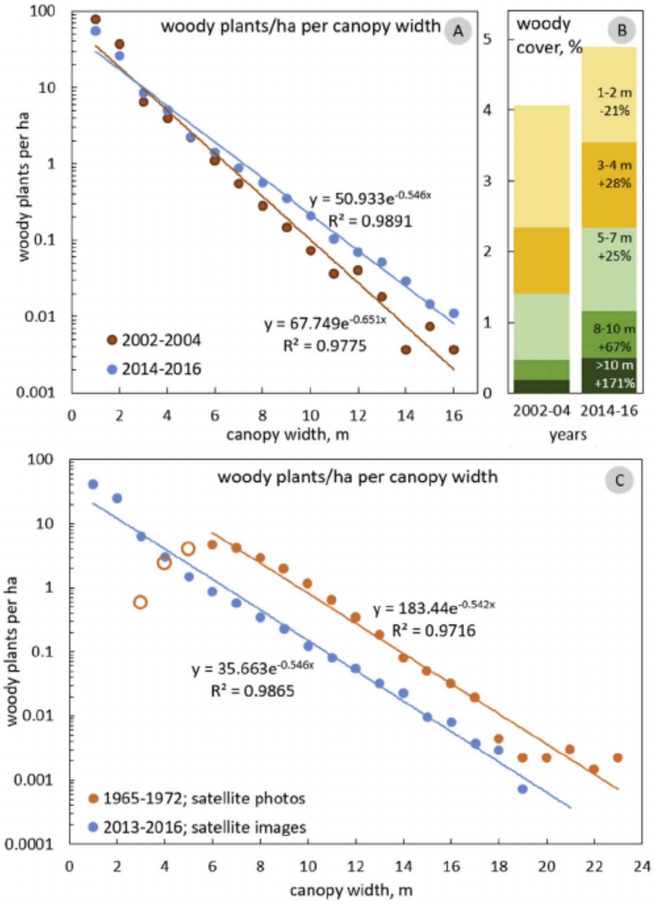

Fig. 7. (A) The frequency distribution of the canopy width (m) of woody plants (n per ha) in 87 circular plots (see Fig. 8A for their location), measured on Google Earth images from 2002 to 2004 and on Google Earth or Bing images from 2014 to 2016. Note log scale is used on Y-axis.
(B) The total woody cover (as % relative to the total surface), given separately for 5 size classes in 2002–04 and 2014–16, based on the same data as (A). The percentages in the right column refer to the change in woody cover for the 5 size classes in 12 years.
(C) The frequency distribution of the canopy width (m) of woody plants (n per ha) in 390 circular plots (see Fig. 8A for their location), measured on Corona satellite photos from 1965 to 1972 and on Google Earth or Bing images from 2013 to 2016. Note log scale on Y-axis. The image resolution is 0.5 m for the used Google Earth images, but 1.83 or 2.74 m for Corona photos, which explains why all woody plants having a diameter 1 or 2 m, nearly all of 3 m, and likely also part of 4 and 5 m, are not detected on the Corona photos; the regression line does not refer to woody plants of 3–5 m (open symbols).

between 1965 and 1972 (comparing Corona photos; see 2.3.3) and even an increase between 2003 and 2015 (Fig. 7B). This suggests that the actual decline of woody cover must have occurred in the dry years between 1973 and 2002 (Fig. 6).

Woody cover was not related to latitude (and by default: rainfall), neither in the 1960s, nor in the 2010s (Fig. 8). Between the 1960s and 2010s, woody cover across the entire region decreased substantially (Fig. 8), especially north of 16.75°N where the woody cover declined by 91%, but less so south of 15.75°N (minus 40%). The contrast is still larger for large trees (canopy width > 10 m), declining by 98% north of 16.75°N and by only 12% south of 15.75°N (Suppl. data: Table S2). The savanna, densely scattered with large Acacia trees at 17°N in the 1960s (Fig. S2A), has changed in later years into an open landscape with few trees (Fig. 1B and C, Suppl. data: Fig. S2B).

In the 2010s, trees and shrubs of ≤4 m dominated the woody vegetation north of 17.25°N (Fig. 7C). As small trees and shrubs are impossible to discern on Corona photos, their presence and abundance in the 1960s, when large trees were still present, remain uncertain. It might be that *Leptadenia* was absent in the woody savanna before the

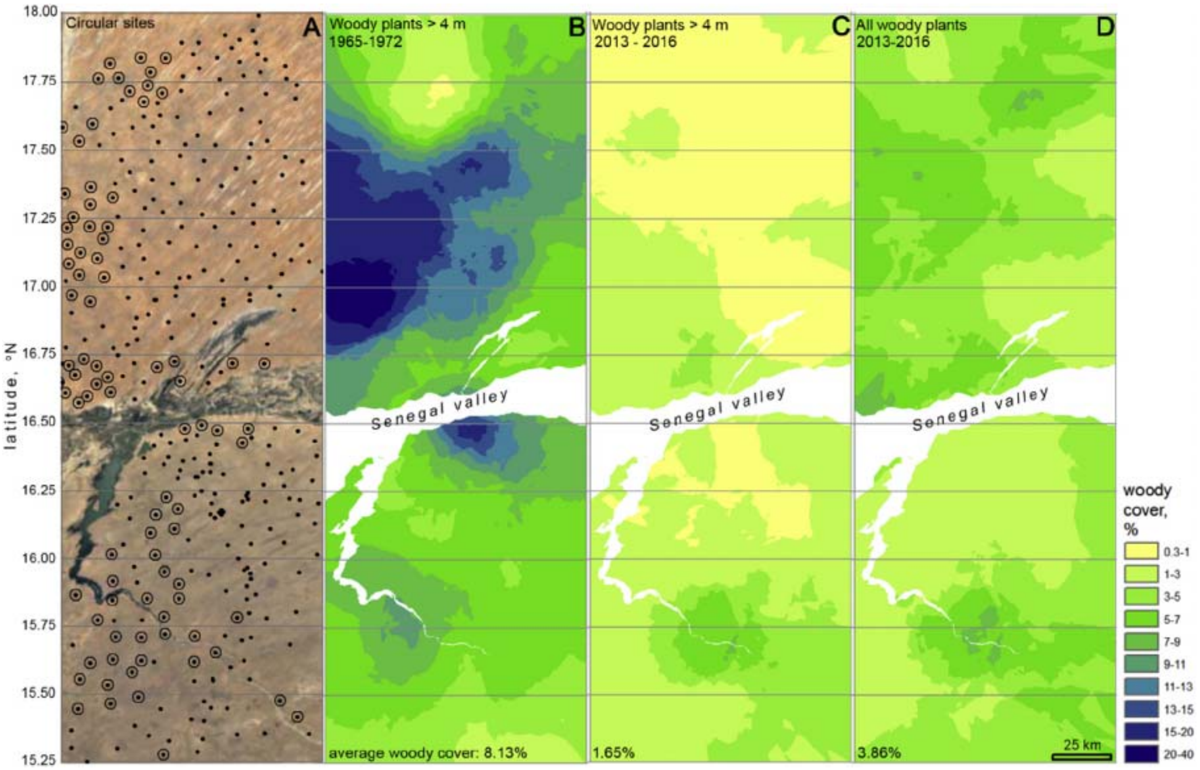

Fig. 8. An interpolated map of the woody cover between 15 and 16°W and 15.25 and 18°N, based on the 390 circular plots (black dots in panel A), using a kriging technique; the 87 plots surrounded by circles indicate plots where satellite images were available for 2013–2016 as well as for 2002–2004. Since the contribution of woody plants ≤4 m is unknown for 1965–1972 (B), woody cover in 2013–2016 is given without (C) and with (D) small woody plants. Similar maps produced with a split-half method (Suppl. data: Fig. S6) show that the three maps are reliable on a global scale, but not in detail.

1970s and colonised the bare ground after larger trees had disappeared.

3.3. Current latitudinal trends in woody cover and bird density

To describe the latitudinal variation, we selected data from December 2014, when we visited sites (a total of 59) across the entire range between 15 and 18°N. Woody cover, measured in the field, was not related to latitude within the study area (Fig. 10A), as found in the analysis of recent satellite images. The route taken in December 2014 passed through areas with a relatively high woody cover in most latitudinal bands. This explains why the woody cover measured in the field plots (Fig. 10A) is about twice as high as the average per latitudinal band calculated from the satellite images (Fig. 9). To check whether this large difference indeed reflected a biased selection of the field sites, rather than a systematic error in the measurements of woody cover either in the field or from satellite images, we compared the woody cover measured in the field with those interpolated for the same 59 plots using satellite measurements (Fig. 8D). The woody cover measured in the field plots hardly deviated (+8%) from the satellite measurements for the same plots, as expected from the good agreement in the measurements of tree canopies in the field and on satellite images (Suppl. data: Fig. S1). Hence, the woody cover shown in Fig. 10A is correct in itself, but not representative for the different latitudinal bands in the study area.

Within the 280-km wide latitudinal range, species composition of the woody vegetation varied, with *Sclerocarya birrea* occurring only in the south and the grassy shrub *Leptadenia pyrotechnica* only in the dry north (Fig. 10A). *Balanites aegyptiaca* and *Acacia tortilis* were distributed across the full range (Suppl. data: Table S3). The observed latitudinal shift in species composition was not due to selective planting of trees by people, with one exception: plantations of *Acacia senegal* at 15.5°N.

Since the landscapes of SW Mauritania and NW Senegal differ substantially, the 16.5°N band has been split according to country. The northern Ferlo (Senegal) is an open steppe with *Boscia senegalensis*, a low shrub with leathery leaves, and few, scattered trees, as compared to the woody savanna with thorny trees north of the Senegal River (Fig. 1C), mainly *Acacia senegal* in valleys and mainly *Acacia tortilis* on dunes. Within the 16.5°N band, the woody cover in the four available Mauritanian sites totalled 7.9% for thorny and 1% for non-thorny trees, on average, compared to 3.0% and 1.0% respectively for 25 Senegalese sites.

For the seven latitudinal bands, the density of birds feeding in trees (Fig. 10B) was highly positively correlated with woody cover (Fig. 10A) ($R = +0.88$; $N = 7$; $P = 0.006$). When calculated as birds per ha *canopy*, the density increased southwards from about 7 birds per ha canopy at 17.5–18°N to 30–35 birds per ha canopy at 15.5–16.4°N. This trend ($R = -0.90$; $N = 7$, $P = 0.003$) can be explained by the species composition of woody cover. The grassy shrub *Leptadenia pyrotechnica*, abundant at northern latitudes (Fig. 10A), hardly attracted any birds (1.1 migrants and 0.4 residents per ha canopy) and was responsible for the low overall density per ha canopy in the northern latitudes. When excluding *Leptadenia,* the latitudinal trend in birds/ha canopy was only weakly present ($R = -0.48$, $P = 0.14$).

Densities of ground-feeding birds were not related to latitude ($R = +0.06$), with the lowest density recorded at 16.4°N. Sudan Golden Sparrow *Passer luteus* was the most common species further north, and Namaqua Dove *Oena capensis* and Speckle-fronted Weaver *Sporopipes frontalis* abounded further south (see Suppl. data: Table S4 for densities per latitude for all bird species).

3.4. Distance from borehole

In the 1960s, woody cover in the Ferlo slightly increased with distance from boreholes from, on average, 4% at 0 km to 6% at 20 km,

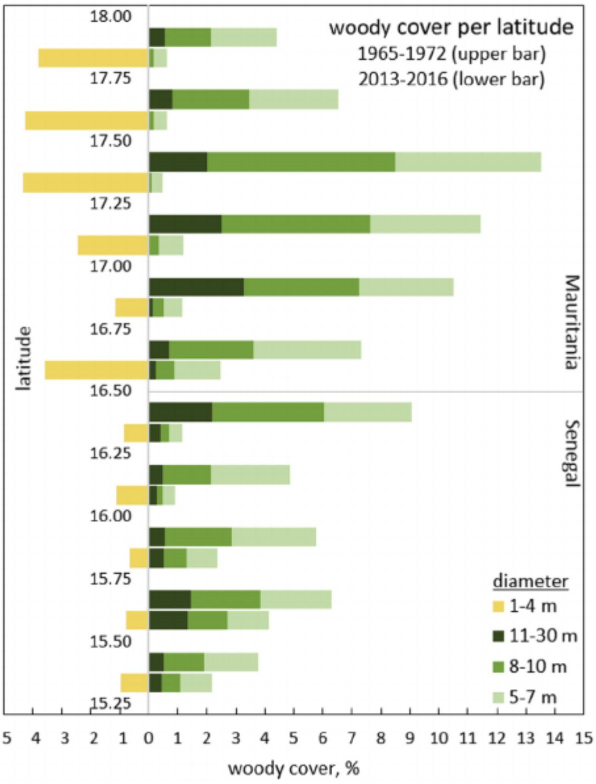

Fig. 9. Latitudinal change of average woody cover (% of total area) between 15 and 16°W in 1965–1968 (based on Corona satellite photos) and 2013–2016 (based on Google Earth and Bing images), for woody plants with different crown diameters; same data as Fig. 7. The resolution of Google Earth images is sufficiently high to record all woody plants ≥1 m wide. Corona photos have a lower resolution, consequently woody plants with ≤4 m canopy width (Fig. 7C) could not be detected. The latter category is therefore shown for recent images only. Further (statistical) details in Suppl. data: Table S2.

although the variation was large (Suppl. data: Fig. S7A; based on 97 circular plots on Corona photos). Fifty years later, the woody cover near boreholes had, on average, declined to 0.7% and at a distance of 20 km to 4.3% (Suppl. data: Fig. S7B; based on the same 97 circular plots on Google Earth or Bing satellite images). The woody cover within 5 km from boreholes had declined within this period by 80–90%. At larger distances, the average decline was 65% at 5–10 km and 45% at 10–20 km (Suppl. data: Fig. S7C). Boreholes in the Ferlo are intensively used by pastoralists (Suppl. data: Fig. S8) which explains why the woody savanna around boreholes has gradually changed into a more open landscape.

For our 48 sites at < 20 km of a borehole visited in 2014–2016, we also regressed woody cover per woody species against distance from the nearest borehole (Figs. 1A and 8A). All 19 woody species showed an increase of cover with distance, of which 4 significantly so (Suppl. data: Table S5). Including latitude as variable, the increase of woody cover with distance remained present for the different woody species (Suppl. data: Table S5). Only *Boscia senegalensis* and *Calotropis procera* declined (non-significantly) with distance from boreholes; both species are hardly, or not, palatable for livestock. The distance effect, as found in 1995 by Vincke et al. (2010), is therefore still present in 2014–2016.

The density of resident birds feeding on the ground was not related to the distance from the borehole, but contrasting trends were found in migrants (Suppl. data: Table S6). Bird density of migrants feeding in trees (combining counts in January and December 2014) increased with distance from the borehole. The same positive trend was found on the species level. In contrast, the density of migrants feeding on the ground was slightly higher near to the borehole, as found on the species level. From this we tentatively conclude that the landscape change due to the boreholes had an overall negative impact on arboreal migrants, but not on birds feeding on the ground.

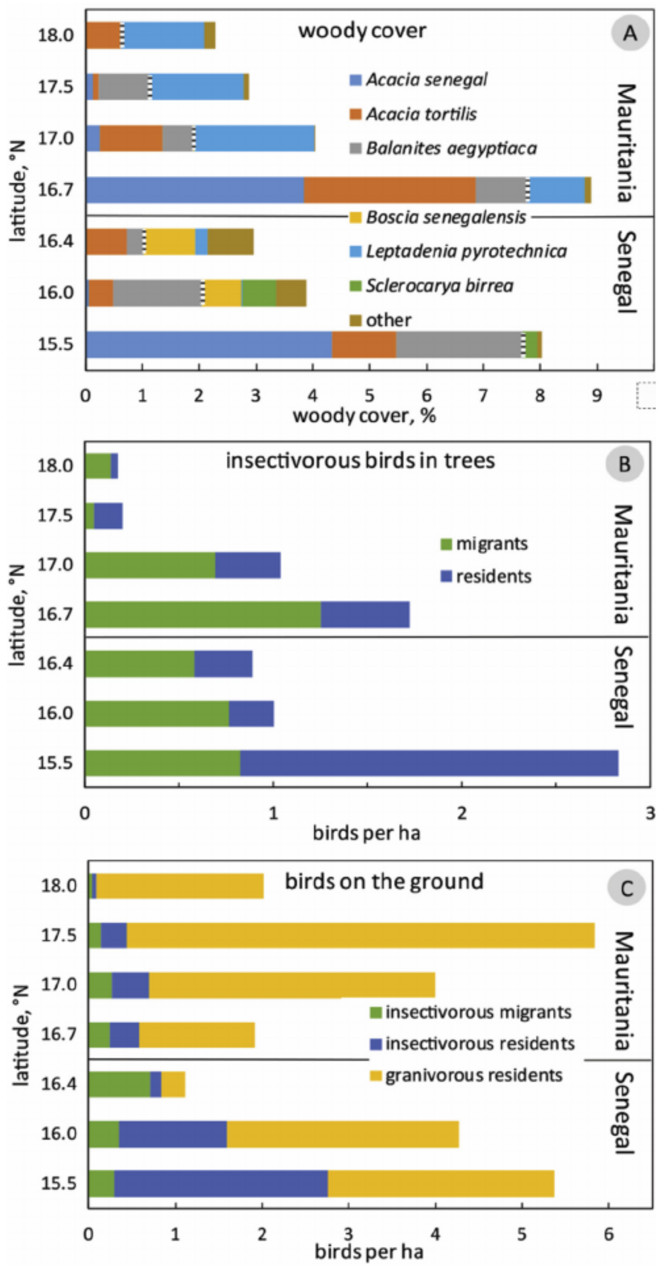

Fig. 10. (A) Woody cover (%) and density (n/ha) of birds feeding (B) in woody plants, (C) on the ground as a function of latitude, calculated for 59 sites visited in December 2014, without Widou Thiengoly exclosures. The data for the 16.5°N band were split for sites in Mauritania and Senegal. Woody species left of the broken line in panel A are preferred by birds feeding in trees.
Woody cover and bird density per species are given in Suppl. data: Table S2 and S2.

3.5. Souilène study site

We presume that Tréca et al. (1996) had specifically selected their 1-ha site because of its high woody cover (40% in 1989) as compared to the surroundings (see also Diouf et al., 2002). The Corona photo from 1965 shows that the woody cover of the area just north of Souilène varied locally between 10 and 40%. Despite the study site being protected by a fence until at least 1994 (Tréca and Tamba, 1997), woody cover declined to 23% in 1998 (Tréca et al., 1996; Diouf et al., 2002), and this decrease has continued since then (Fig. 11A). Woody cover of

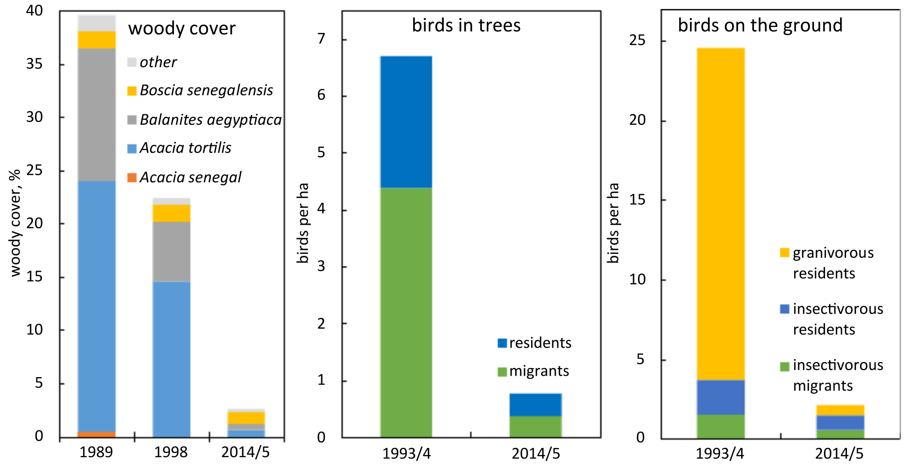

Fig. 11. (A) Woody cover (%) and (B) density (n/ha) of birds feeding in tree and shrubs, and (C) on the ground in Souilène during the dry season (October–January). Woody cover in 1989 and 1998 and bird densities in 1993/94 according to Tréca et al. (1996) and Diouf et al. (2002). The recent counts were done in October, December and January 2014/15. Woody species below the broken line in panel A are preferred by birds feeding in trees.

tree species preferred by birds declined by 97% (from 36.5% to 1.2%) between 1993/94 and 2014/15, more steeply than found for non-preferred trees (from 2.6% to 1.4%; −53%). The site used to be a woody savanna dominated by *Acacia tortilis* (Fig. 11A); see also photograph in Grouzis & Le Floc'h (2003, p. 123), but it has transformed into open grassland with *Boscia senegalensis* shrubs (89/ha), scattered *Balanites aegyptiaca* trees (4.5/ha) and very few *Acacia tortilis* (0.7/ha); eight other woody species have become rare (in total 0.5/ha) (details in Suppl. data: Table S7).

Tréca et al. (1996) counted birds four times per month in 1993/94. Numbers remained more or less constant from October through January. We compared their four-month average with the average density recorded in October–January in 2014/15 (Fig. 11B and C; for densities per bird species see Suppl. data: Table S7). Total bird density declined between 1993/94 and 2014/15 from 31.3 to 2.9 birds/ha. Losses were particularly large for birds feeding in trees, both migrants (−91%) and residents (−83%), not surprising given the 97% decline of woody cover in the intervening period (Fig. 11A). The decline of ground-feeding birds was also large, i.e. 64% for insectivorous migrants and 58% for insectivorous residents; the largest decline was found for granivorous residents (−97%).

3.6. NW Ferlo study site

The 25-ha study site of Morel (1968) was situated in the northwestern part of the Ferlo, NW of Souilène, but its precise position is not given. In 1960–1962, Morel recorded 58.2 trees (> 1m high) per ha, mostly *Boscia senegalensis* (19/ha) and *Acacia senegal* (14/ha) (Fig. 12A). The high density of *Acacia senegal* was related to specific protection for gum production (Morel, 1968). At the time, already a decline of large *Acacia tortilis* was evident (Morel, 1968). Between the 1960s and 2010s, the northern Ferlo changed from a woody savanna with thorny trees and *Guiera* and *Boscia* shrubs into grassland with very few trees but still many *Boscia* (12/ha), and as new species: *Calotropis procera* (28/ha) and *Leptadenia pyrotechnica* (11/ha) (Fig. 12A) (densities only of woody plants > 1 m high, to have a comparable data set with the survey of Morel (1968)). This shift in the species composition made the savanna much less attractive for birds feeding in trees due to the large decline of, for them attractive, thorny species and the increase of species which they largely avoid (*Boscia*, *Calotropis*, *Leptadenia*) (Zwarts et al., 2015).

The average bird density in October–February, calculated from ten counts between February 1960 and May 1962 in the 25-ha site, amounted to 3.82 birds/ha (Morel, 1968), among which 1.45 granivorous residents. These ground-feeding birds declined by 40% to 0.88 birds/ha in 2014/15 (Fig. 12C). Much larger was the decline of insectivorous birds feeding on the ground (91% in residents and 94% in migrants (Fig. 12C). Birds feeding in trees declined by 32% in migrants and 75% in residents (Fig. 12B), but the actual losses of arboreal birds must have been still larger given the assumed underestimation of these birds counted in the 1960s (see 2.4); (details in Suppl. data: Table S9).

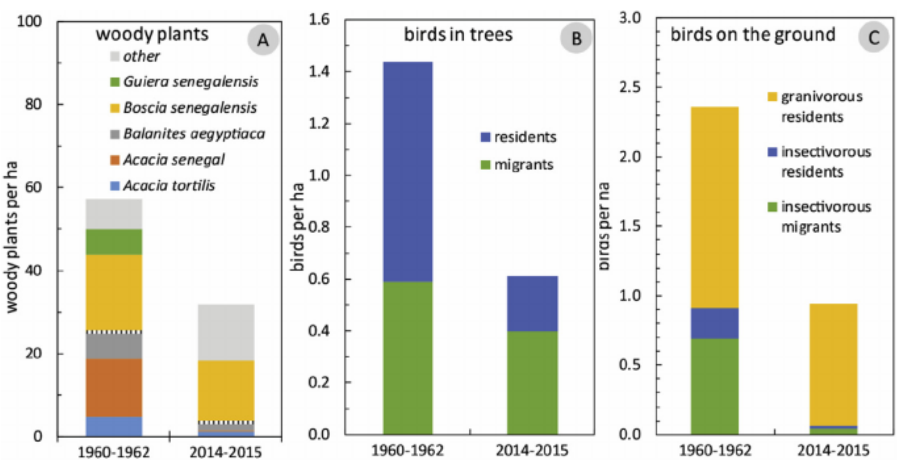

Fig. 12. Comparison of woody vegetation and bird density on a site of 25 ha in NW Ferlo in 1960–1962 (Morel, 1968) and on 25 sites in the surroundings in 2014–2015. (A) Number of woody plant (> 1 m high) per ha, (B) density (n/ha) of birds feeding in tree and shrubs, and (C) on the ground in October–February 1960–1962 and 2014–2015. Woody species below the broken line in panel A are preferred by birds feeding in trees.

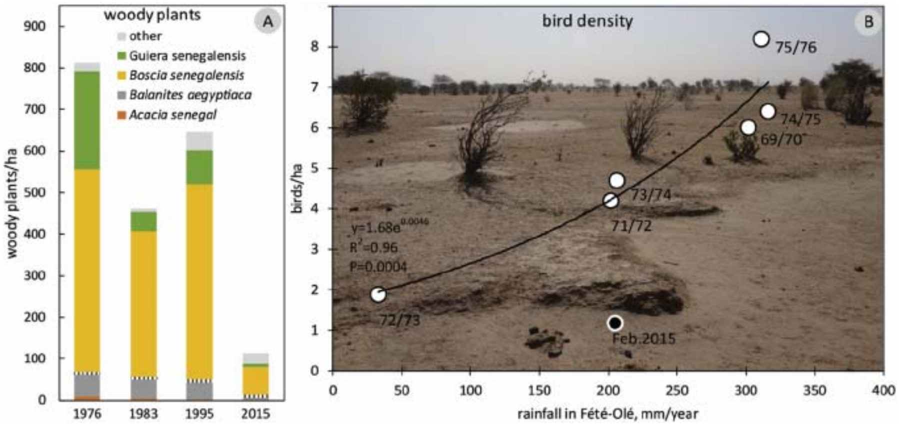

Fig. 13. (A) Number of woody plants per ha in Féte-Olé in 1976 (Poupon, 1980), 1983 and 1995 (Vincke et al., 2010) and 2015. Woody species below the broken line in panel A are preferred by birds foraging in trees. (B) Bird density in Fété-Olé in 1969/70–1975/76 (averaged for the period October–February; from Morel and Morel, 1978) and in February 2015 as a function of local annual rainfall (gauge in the 1970s after Morel and Morel, 1992; derived from RFE-2.0 for 2014/15). The regression line refers to the data collected in the 1970s.The photo shows how the area looked like in February 2015: bare sand with scattered (grazed) *Boscia* and some (still ungrazed) *Leptadenia* shrubs.

3.7. Fété-Olé site

In the early 1970s, woody cover of the Fété-Olé-site amounted to 9.6% (Morel and Morel, 1978; see also Fig. 3A), but had declined to 3.7% (of which 0.8% thorny trees) by February 2015 (Fig. 3B). The area changed from woody savanna, as shown on photos taken in 1969 and 1972 (Bille and Poupon, 1972a, 1972b; Bille, 1974) into a sandflat with scattered bushes (Fig. 13B) found in the shallow valleys (Fig. 3B). Species composition also changed between 1970 (Bille and Poupon, 1972a) and 2015, with a relative increase of *Calotropis procera* (from 0 to 17.5%), *Boscia senegalensis* (7–65%) *Balanites aegyptiaca* (7–9%) and substantial declines for *Guiera senegalensis* (from 53 to 7%), *Grewia bicolor* (10–0%), *Commiphera africana* (8–0%) and *Acacia senegal* (7–0%). The survey in 1995 indicated a small recovery of woody vegetation (Vincke et al., 2010), but our inventory shows that, despite improved rainfall since 1993, the decline of the woody vegetation in fact continued through 2015 (Fig. 13A).

In Fété-Olé, Morel and Morel (1978) recorded large seasonal and annual differences in bird densities. Total bird density was high in the rainy season and gradually declined during the dry season from October to May, with larger seasonal declines in years with less rain. The rainfall in 2014/2015 was well below average (Fig. 6), although not yet as low as in 1972/1973, the driest year during the study of Morel and Morel (1978). Given the close relationship between rainfall and bird density in the dry season during the 1970s (Fig. 13B), we expected, if nothing had changed in the intervening period of 40 years, about 4.5 birds/ha in February 2015, mainly ground-feeding granivorous residents; in fact, the density was 1.16, 74% lower than expected (Fig. 13B), mostly ground-feeding insectivorous residents (0.48/ha) and arboreal insectivorous birds (0.28 migrants/ha and 0.20 residents/ha). The density of ground-feeding granivorous birds was very low (0.16/ha), and Sudan Golden Sparrow, Black-crowned *Eremopterix nigriceps* and Chestnut-backed Sparrow Lark *Eremopterix leucotis*, species that were most common in the 1970s, were absent in 2015.

3.8. Widou Thiengoly exclosure

In Widou Thiengoly, the woody cover in the non-grazed exclosure (23.6 ha) and in the surrounding grazed area (76.5 ha) was about the same, but the species composition differed (Fig. 14A; for species list see Suppl. data: Table S10). In the exclosures, we found non-spiny species (*Combretum aculeatum*, *Commiphera africana*, *Feretia apodanthera* and *Grewia tenax*) which were lacking in the grazed area. *Acacia senegal* was more common in the ungrazed than in the grazed area.

Although the woody cover in the exclosures did not differ from the grazed area, with *Balanites* and *Boscia* being dominant everywhere, the respective landscapes were very different (see photos in Fig. 4). *Boscia* outside the fence was heavily browsed and stripped, but not so in the fenced area. The grazed area had bare, sandy soil with a low density of dead grass stalks. In contrast, the exclosures were covered by desiccated grass and herbs up to 10–20 cm high and stood out, even from a large distance, as brown squares in a salmon-pink setting, even on the satellite image (Fig. 4). We found very few seeds in the top layer of the soil in the grazed area, but many in the ungrazed area (not quantified). Despite some grazing in the non-grazed exclosures in the months preceding our second visit, the coverage of grasses and herbs was still dense (see Fig. 4 for a photo of the landscape made in December 2014).

Bird densities in the exclosures did not differ significantly for the two visits in January and December 2014 (Suppl. data: Table S11: ungrazed), nor in the grazed area nearby (Suppl. data: Table S11: grazed). The data of the two periods were pooled to compare grazed and ungrazed areas (Suppl. data: Table S11: ungrazed-grazed). The density of birds feeding in trees was only non-significantly higher in the grazed area than in the exclosure (Fig. 14B, Suppl. data: Table S11), as expected from the near-similar woody cover of preferred woody plants (Fig. 14A). In contrast, in the exclosure the density of ground-feeding birds was five times larger as in the grazed area (22.4 vs. 4.4. birds/ha), and six times larger in granivorous birds (18.3 vs. 2.9 birds/ha).

4. Discussion

4.1. Increasing human impact

The human population in the western and central Sahel (i.e. Mauritania, Senegal, Mali, Burkina Faso, Niger, Chad) increased from 8.7 million in 1900 (www.populstat.info) to 17 million in 1950 and 89 million people in 2015 (https://esa.un.org/unpd/wpp/). In the early 20th century, the Sahel was a relatively pristine woody savanna. The Ferlo still held antelopes, giraffes, elephants and large carnivores, but already before the 1950s this fauna had gone extinct (Barral, 1982).

In the late 1930s, some cattle grazed along large rivers and close to permanent lakes in the Sahel during the dry season (Bonnet-Dupeyron, 1945), and on savanna during the rainy season. The construction of a network of large boreholes, producing 10–30 m^3 of water per hour, permitted year-round cattle grazing in the Ferlo after the mid-1950s (Théboud, 1990; Ancey et al., 2008). It was the overture of a steep increase of cattle, from 1 per km^2 in 1950 to 4 and 12 per km^2 in 1955 and 1970, respectively (Barral, 1982; Santoir, 1983). In 1950, the Ferlo held on average about 3 goats and sheep per km^2. In the department of Linguère (SW Ferlo), their population became 4.3 times larger between 1955 and 1970 (Santoir, 1983). During the dry years 1970–1993, cattle numbers declined in Linguère by 28%, but sheep and goats continued to increase. In 1993, cattle numbers were 3 times larger than in 1945, the number of goats and sheep 10.3 times larger (Juul, 1996). We have no data on the increase of the grazing pressure in the Ferlo since 1993, but in Senegal the cattle population increased by 46% between 1993 and

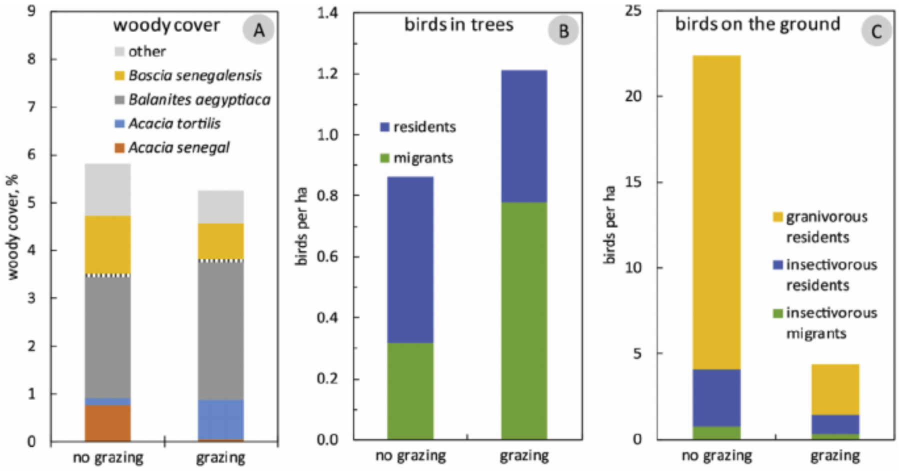

Fig. 14. (A) Woody cover (%) and density (n/ha) of birds feeding in trees and shrubs (B), and on the ground (C) in the non-grazed exclosures of Widou Thiengoly compared to the average calculated for the random grazed sites at the same latitude (16.5°N) in 2014. Woody species below the broken line in panel A are preferred by birds foraging in trees.

2014, whereas the number of goats and sheep became 4.25 times larger (source: www.faostat3.fao.org). Within the last 60 years, cattle numbers in the Ferlo must have likely increased 12–15 times, goats and sheep even about 50 times.

At first, pastoralists in the Ferlo herded their livestock in the vicinity of watering points, but this routine changed after the 1980s when people brought water to their livestock (rather than *vice versa*), using large rubber inner tubes (Juul, 1996) and 1000 l containers (own obs.) on donkey carts. This change was especially important for goats and sheep which need to quench their thirst closer to grazing grounds than cattle. As a consequence, a much larger part of the Ferlo became intensively grazed. This development was further favoured by the extermination of large carnivores in the 1950s (Barral, 1982) and the construction of new wells after 1990, mostly in the SW and NE of the Ferlo (nowadays > 200 large boreholes; Ancey et al., 2008; Touré et al., 2010).

In the 1940s, the density of cattle amounted to < 0.5 cows/ha at 17–18°N and 10–15 cows/ha at 16°N, but no such latitudinal increase was present in sheep and goats (Bonnet-Dupeyron, 1950). During the dry 1970s, the number of cows declined in Mauritania from 2.0 to 2.5 to 1.0–1.5 million, to increase again to nearly 2 million in the 2010s after rainfall improved. In contrast, goats and sheep steadily increased from 6 to 8 million in the 1960s and 1970s to 14 million in the 2010s (www.faostat3.fao.org). The ongoing increase of small ruminants must have had a large impact on the woody vegetation, since for sheep and goats browsing is more important than for cows which show only a partial shift from grazing to browsing during the dry season (*e.g.* Sanon et al. 2005).

4.2. Decline of woody cover

The maximal woody cover in African savannas linearly increases with rainfall, from 0% cover at an annual rainfall of < 100 mm to a maximum of 80% cover at 650 mm rainfall, although the actual woody cover is usually much lower than this maximum (Sankaran et al. 2005). Given the decline of annual Sahelian rainfall with latitude (Fig. 5), the maximal woody cover is expected to be a function of latitude (Fig. 15), but must have declined during the dry 1970s and 1980s when the rainfall was 53% lower than during the preceding 20 years (Fig. 6). As a consequence, the expected maximal woody cover would have declined by 70% at 17.5°N and by 44% at 15.5°N.

The actual woody cover in the 1960s was close to the expected maximum at 17–18°N, but this gradually declined to 15% of the expected maximum at 15.5°N. The decline of the actual woody cover after the prolonged drought was much larger than the shift downward of the

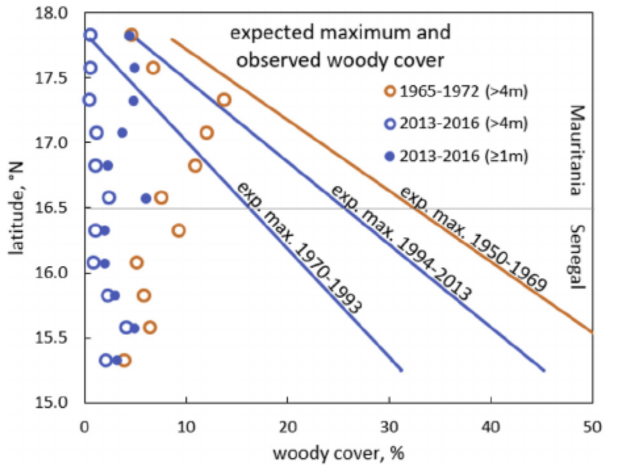

Fig. 15. The woody cover per latitude (data from Fig. 9) in 1965–1992 (canopy width > 4m) and 2013–2016 (canopy width > 4 m and ≥ 1m) compared to the expected maximum woody cover as a function of rainfall (Sankaran et al. 2005) and thereby latitude (Fig. 6). The expected maximum cover is given for recent years (1994–2013), the preceding dry period 1970–1993 (rainfall 34% lower than 1994–2013) and wet period 1950–1969 (rainfall 17% higher than 1994–2013).

expected maximum (Fig. 15), especially in the northern Ferlo (16–16.5°N). After the recovery of the rainfall since the early 1990s, the woody cover in southern Mauritania doubled (16.5°N), but there was, on average, no increase in northern Senegal (Suppl. data: Fig. S5). These data suggest that the decline of woody cover in Mauritania was mainly due to the prolonged drought in the 1970s and 1980s. However, the larger than expected (from drought alone) decline of woody cover in northern Senegal, and the lack of recovery in recent years, indicates that also processes other than rainfall, such as the construction of boreholes with its associated increase in grazing pressure (Suppl. data: Fig. S7), must be involved.

Comparing aerial photos from 1942, satellite photos from 1965 to 1968 and satellite imagery and field inventories from the 1980s and 1990s, Tappan et al. (2004) concluded that woody vegetation in the Ferlo covered 10–15% in 1942 and 1965, then declined to 5% in 1998. Comparing the same Corona satellite photos from the 1960s with satellite images 50 years later, we found an equally large decline of woody cover, being higher in the northern Ferlo (72% for woody plants > 4 m) than in the southern Ferlo (11%). Our data also confirm for SW Mauritania (Figs. 8 and 9) a large decline of woody vegetation as described by Niang et al. (2008) using aerial and satellite photographs taken in 1952, 1972 and 1992; see also the landcover map of Mauritania from 1975, 2000 and 2013 given in CILSS (2016).

Five, not mutually exclusive, processes can be put forward to explain the decline of woody cover and the compositional shift in the woody vegetation in Sahelian rangelands.

(1) Repeated bush fires may have had a negative impact. Corona photos show that large areas were still being burned in the study area in the 1960s, but this has become rare and localized in the 2010s (visible on the high-resolution satellite images available since 1993), because the woody cover is now too open to carry fire.
(2) Large trees were selectively cut (Morel, 1968; Diouf et al., 2002). This practice continues into the present (own obs.), perhaps the main explanation why larger trees have declined so much in the Sahel since at least the 1960s (Fig. 9, see also point 3).
(3) Mass mortality of trees due to drought occurred during the 1970s and 1980s. Tree loss in NW Senegal was estimated at 22% between 1954 and 1989 (Gonzalez, 2001). In Fété-Olé, 13.4% of the trees died in the first dry year, 1972 (Poupon and Bille, 1974). Tree mortality in 1972 amounted to 22% in Dahra (Senegal; 400 mm rain/year) in another site without grazing, but in a site with normal grazing pressure it was 48%. The grazing-related discrepancy in tree loss was even larger in Ndoli (Senegal; 560 mm rain/year), i.e. 41% in a grazed and 8% in an ungrazed site (Bille, 1992). Since ungrazed areas are extremely rare in the western Sahel, we may conclude that in 1972, the first dry year, nearly half of the trees died. In Fété-Olé, tree mortality was much higher in the dunes than in the depressions (Poupon and Bille, 1974; Vincke et al., 2010), resulting in larger spatial heterogeneity in woody cover after the 1970s and 1980s (Fig. 3A and B). This explains why inter-dune depressions in the Ferlo (only a few percent of the area) had an average woody cover of 10–40%, compared to 1–5% elsewhere (Tappan et al., 2004). Tree mortality also differed between woody species: typical Sahel-species, like *Acacia tortilis* and *Balanites aegyptica*, survived the dry years, but species from the more humid south mostly disappeared (Bille, 1992; Maranz, 2009). Drought-related mortality was higher for large than for small trees (Poupon and Bille, 1974), another explanation why large trees have become scarce in the Sahel.
(4) The boreholes and their surroundings are intensively used by pastoralists, causing a decline of woody vegetation (Suppl. data: Fig. S7, S8).
(5) The high grazing pressure near boreholes caused a shift in the species composition of the woody vegetation (Barral et al., 1983). In 1995, only woody species being less or not palatable for livestock (*Boscia senegalensis*, *Calotropis procera*) and thorny species resistant to intense browsing (*Balanites aegyptiaca*) survived near boreholes, while palatable, once common, species like *Acacia senegal*, *Commiphera africana* and *Grewia bicolor* disappeared (Vincke et al., 2010). At present, this spatial effect of boreholes is, as shown in this paper, still weakly present, suggesting a more uniformly high grazing pressure across the Ferlo. The present grazing pressure also prevents a recovery of the woody vegetation (Figs. 11A, 12A and 13A, Suppl. data: Fig. S5, S7) despite the improvement of rainfall since 1992 (Fig. 6), in contrast to what was found in the Gourma, Mali (Hiernaux et al., 2009) and in southern Mauritania (Suppl. data: Fig. S5).

4.3. Decline of arboreal birds

Between the 1970s and 2000s, the woody cover at 16–18°N has declined by 83% for woody plants > 4m wide (Fig. 9, Table S1). Migratory birds are highly selective in tree choice when foraging, with only a handful of tree species being important (listed in Suppl. data: Table S3, S5, S7). Tree species favoured by migratory birds were disproportionally affected in the past 50 years. The berry-bearing shrub *Salvadora persica*, a most attractive woody plant for birds (Zwarts et al., 2015), was still common in the 1960s in northern Senegal (Stancioff et al., 1986) and in southern Mauritania (ould Taleb, 1999), but has all but disappeared (except in the (brackish) surroundings of the Senegal Delta). Of the thorny species preferred by birds, *Acacia tortilis* and especially *Acacia senegal* have shown a large decline. In contrast, woody plants ignored by birds, as *Calotropis procera* and *Boscia senegalensis*, are still common or have increased. Preferred species as *Acacia tortilis* and *Balanites aegyptiaca* are still common and widespread, but the woody vegetation as a whole must have become less attractive for birds feeding in trees. The actual habitat loss between 16 and 18°N for these birds is likely larger than could be derived from the estimated decline of total woody cover by 83%.

Our quantitative information on the decline of woody plants is limited to trees with a canopy width of > 4m (Fig. 9). In the area between 16 and 18°N and 15 and 16°W, the cover of woody plants > 4m declined from 8.3% to 1.0% between 1965-1968 and 2013–2016 (Fig. 9; Suppl. data: Table S1), equivalent to a total loss of 0.17 million ha canopy. The bird density in woody plants > 4m for this latitudinal zone amounts to 50 individuals per ha canopy (data from Zwarts et al., 2015). Assuming that bird densities have not changed over these decades, these data suggest an estimated loss of habitat for some 8.4 million arboreal birds, of which 7.2 million migrants: 2.5 million Subalpine Warblers *Sylvia cantillans*, 2.2 million Bonelli's Warblers *Phylloscopus bonelli*, 0.7 million Orphean Warblers *Sylvia hortensis* and 1.8 million in 12 other migratory species. This may be less if birds would be able to (1) increase their density in the remaining trees, (2) switch to woody plants ≤ 4 m (assuming these have not declined as much as woody plants > 4 m, which is not known), or (3) switch to woody plants further south. For none of these scenarios has any evidence surfaced. Local survival of migratory birds, when forced to feed in much higher densities, probably declined, as suggested by the 91% decline of birds in Souilène concomitant with a 97% decline of the woody cover (Fig. 11A). Bird density in woody plants of 1 and 2 m wide was 2.5 times lower (19 and 23 birds/ha canopy, respectively) than in larger woody plants. Moreover, shrubs were mostly used by other bird species than those foraging in larger trees (Fig. 4 in Zwarts et al., 2015). For migratory birds wintering in the Sahel, a southward shift as compensation for habitat loss incurred in their wintering sites is unlikely given the (much) lower densities found for these species at more southerly latitudes (Zwarts et al., 2015). The overall conclusion, therefore, is that arboreal, insectivorous birds wintering in the Sahel have lost most of their habitat in the past 50–60 years. Their populations must have suffered huge losses, which largely escaped detection because most European bird species wintering in the Sahel breed in southern Europe, where monitoring schemes started only recently.

4.4. Loss of soil seed bank

In West African savannas during the dry season, most resident birds feed on grass seeds which they take from the ground (Morel, 1968; Morel and Morel, 1974, 1978, 1992). The annual production in Fété-Olé has been estimated at 2 seeds million per ha (Bille, 1974), of which 7–10% was consumed by birds (Morel and Morel, 1972a), 4–13% by Senegal Gerbils *Taterillus pygargy* (Poulet, 1974) and an unknown fraction by ants, termites and grasshoppers. In total 90% of the seeds disappeared during the dry season. Seed production varied from year to year, being higher in wet years (Bille, 1974). This may explain the close relationship between bird density and rainfall (Fig. 12B), although food supply was so large in the 1960s that even in a dry year not all seeds were consumed (Morel and Morel, 1974; Grouzis, 1992). Despite the latter conclusion, numbers of granivorous birds must have been constrained by food supply in dry years. First, less than 30% of the seeds can be found in the upper 1 cm of soil, the rest is more deeply buried (Carrière, 1989) and out of reach of the bill. Secondly, birds are highly selective. The poisonous seeds of *Cassia tora*, for example, are not eaten

(Gillon et al., 1983). The lower acceptance threshold for seeds increases with body mass, from 0.10 mg in Namaqua Dove (40 g) to 0.22 mg for Laughing Dove *Spilopelia senegalensis* (130 g) and 0.25 mg for Mourning Collared-dove *Streptopelia decipiens* (190 g) (Morel and Morel, 1972b). In wet years, all six studied dove species mostly fed on seeds of *Panicum laetum*, and, to a much lesser degree, on *Brachiaria hagerupii* and *Dactyloctenium aegyptium* (Morel and Morel, 1974). These grasses were rare in dry years, and, instead of switching to other grass species, doves started to forage on legumes (*Tribulus terrestris*, *Gisekia pharmacioides*, *Zornia glochidiata*). Seeds of some dominant grass species are probably difficult to handle or ingest by granivorous birds because the seeds have sharp awns (e.g. *Aristida*, *Andropogon*, *Schoenefeldia*) or spiny burrs (e.g. *Cenchrus biflorus*). Birds consumed 7–10% of the total annual seed bank in Fété-Olé, but depleted a much higher fraction of the selected species, as also found at Bandia (West Senegal, 570 mm rain/year) by Gillon et al. (1983). Poor rainfall, via a decline in preferred seeds, has been shown to promote intra-African dispersal, increase mortality and reduce reproductive output of granivorous residents (Morel and Morel, 1974, 1992).

4.5. Decline of ground-feeding birds

The large decline of granivorous birds in Souilène (Fig. 11C), NW Ferlo (Fig. 12C) and Fété-Olé (Fig. 13B), and their much higher density in ungrazed Widou Thiengoly sites compared to grazed surroundings (Fig. 14C), are related to the disparate feeding pressure on the available seed. First of all, the present intensive and year-round grazing in the Sahel impacts flowering and seeding of plants (Grouzis, 1992; Sternberg et al., 2003). At Widou Thiengoly, during 27 years of monitoring, high grazing pressure was found to cause a degradation of pastures, with fewer soil nutrients, reduced productivity and a vegetational shift towards arid-adapted grass species and fewer legumes (Miehe et al., 2010). Other studies also showed a shift in species composition depending on grazing pressure, for instance more *Cenchrus biflorus* and less *Schoenefeldia gracilis* in intensively grazed areas (Le Houérou, 1989; Bille, 1992). It is still unclear to what degree the latter shifts impacted food quality for granivorous birds.

At present, granivorous birds occur in an average density of 2.5 birds/ha between 16 and 18°N (Fig. 10C), but it used to be much higher. Their density declined by 96% in Fété-Olé (Fig. 13B), 97% in Souilène (Fig. 11C) and 40% in NW Ferlo (Fig. 12C), whereas the density in the grazed area was 84% lower as in the ungrazed area of Widou Thiengoly (Fig. 14C). At an average decline of 80%, some 24 million African granivorous birds have disappeared from rangelands between 15 and 16°W (2.4 million ha x 10 birds/ha). An even larger relative decline was recorded for a migratory granivore, European Turtle-dove *Streptopelia turtur* (Zwarts et al., 2009), although this species also suffers from adverse developments on the breeding grounds (Browne and Aebischer, 2005; Newton, 2017).

In a similar way, we calculated for the same 2.4 million ha of our study area that ground-feeding insectivorous residents declined by some 5 million birds (present overall density: 0.71/ha, assuming that it has been 4x as high in the past (loss in NW Ferlo 91%, Widou Thiengoly 83% and Souilène 48%)) and insectivorous migrants by some 1 million birds (present overall density: 0.30/ha, assuming that it has been 2.5 as high in the past (loss in NW Ferlo 94%, Souilène 64%, Widou Thiengoly 48%)).

A decline of tree cover, shrubs, herbs and grasses in the wake of increased grazing pressure may favour insectivorous ground-feeding birds, like Northern and Black-eared Wheatear, *Oenanthe oenanthe* and *O. hispanica*. However, densities of ground-feeding birds were higher in the past (Suppl. data: Table S8, S8) and also higher in the ungrazed Widou Thiengoly exclosures than in grazed land beyond the fence (Suppl. data: Table S11). Less vegetation not only translates into less seed, but also in fewer arthropods and fewer rodents (hence also fewer rodent-eating raptors (Morel and Morel, 1974)).

4.6. Extrapolation to all Sahelian rangelands?

The question is whether the losses we describe for NW Senegal and SW Mauritania are representative for the Sahelian rangelands at large. Watering points are found elsewhere in the Sahel and many have also been motorized since the 1960s, but nowhere in the Sahel is the network of large boreholes so dense as in the Ferlo. This enabled people to settle permanently and increase livestock numbers. For this reason, we may doubt whether the woody cover in the Sahelian rangelands has declined as much as in the Ferlo. On the other hand, the long drought in the 1970s and 1980s has caused high mortality of woody plants across the entire Sahel (e.g. Hiernaux et al., 2009; Maranz, 2009). Moreover, elsewhere grazing pressure has increased even more than in the Ferlo. Between 1984 and 2014, cattle numbers in Senegal have increased by 1.51%/year and sheep + goat by 2.42%/year. The relative increase was faster, however, for the western and central Sahel as a whole: 2.17%/year for cattle and 3.47%/year for sheep + goat (calculated for Mauritania, Senegal, Mali, Burkina Faso, Niger and Chad; source: www.faostat3.fao.org). It is therefore plausible that the changes described for the western Sahel between 15 and 16°W may apply for the rangelands throughout in the Sahel between 16°W and 35–40°E. If so, the Sahel may have lost 1.5–2 billion birds during the last 50 years, mainly granivorous residents, and 20% migrants.

5. Conclusions

In the past half century, the Sahelian rangelands have lost much of their bird population, for which two major explanations are put forward. Firstly, common granivorous residents have been decimated because grazing by livestock intensified, resulting in near-complete loss of their food resources. Secondly, woody cover of trees (diameter > 4 m) has declined by more than 80% during the dry years between 1972 and 2002, after which there was only a small recovery of - mainly non-preferred - woody species. These major habitat losses and shifts also negatively affected migratory bird species, especially those breeding in southern Europe. Although based on data collected in NW Senegal and SW Mauritania, these conclusions are presumably valid (but need substantiation) for the Sahel at large.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2018.01.013.

References

Adriansen, H.K., 2008. Understanding pastoral mobility: the case of Senegalese Fulani. Geogr. J. 174, 207–222.
Ancey, V., Wane, A., Müller, A., André, D., Leclerc, G., 2008. Payer l'eau au Ferlo. Stratégies pastorales de gestion communautaire de l'eau. Autrepart 46, 51–66.
Andersen, G.L., 2006. How to detect desert trees using CORONA images: discovering historical ecological data. J. Arid Environ. 65, 491–511.
Arbonnier, M., 2004. Trees, Shrubs and Lianas of West African Dry Zones. Markgraf, Weikersheim.
Barral, H., 1982. Le Ferlo des Forages, gestion ancienne et actuelle de l'espace pastoral. OSTOM, Dakar.
Barral, H., Bénéfice, E., Boudet, G., Denis, J.-P., De Wispelaere, G., Diaite, I., Diaw, O.T., Dieye, K., Doutre, M.P., Meyer, J.F., Noel, J., Parent, G., Piot, J., Planchenault, D., Santoir, C., Valentin, C., Valenza, J., Vassiliades, G., 1983. Systèmes de production d'élevage au Sénégal dans la région du Ferlo : synthèse de fin d'études d'une équipe de

recherches pluridisciplinaire. ORSTOM, Paris.
Bille, J.-C., 1974. Recherches écologiques sur une savane sahélienne du Ferlo septentrional, Sénégal : 1972, année sèche au Sahel. La Terre et la Vie 28, 5–20.
Bille, J.-C., 1992. Tendances évolutives comparées des parcours d'Afrique de l'Ouest et d'Afrique de l'Est. In: Le Floc'h, E., Grouzis, M., Cornet, A., Bille, J.-C. (Eds.), L'Aridité : Une Contrainte Au Développement. ORSTOM, Paris, pp. 181–195.
Bille, J.-C., Poupon, H., 1972a. Recherches écologiques sur une savane sahélienne du Ferlo septentrional, Sénégal : description de la végétation. La Terre et la Vie 26, 351–365.
Bille, J.-C., Poupon, H., 1972b. Recherches écologiques sur une savane sahélienne du Ferlo septentrional, Sénégal : biomasse végétale et production primaire nette. La Terre et la Vie 26, 366–382.
Bonnet-Dupeyron, F., 1945. L'élevage en Afrique Occidentale et Centrale. Bull. Assoc. Geogr. Fr. 22, 40–50.
Bonnet-Dupeyron, F., 1950. Densité des bovins au km2 - Densité des ovins - caprins au km2. Cartes de l'élevage pour le Sénégal et la Mauritanie. No. 3164 in. http://sphaera.cartographie.ird.fr/.
Bourlière, F., 1972. Recherches écologiques sur une savane sahélienne du Ferlo septentrional, Sénégal : introduction. La Terre et la Vie 26, 325–331.
Brochet, A.-L., et al., 2016. Preliminary assessment of the scope and scale of illegal killing and taking of birds in the Mediterranean. Bird. Conserv. Int. 26, 1–28.
Browne, S., Aebischer, N., 2005. Studies of west palearctic birds: Turtle dove. Br. Birds 98, 58–72.
Carrière, M., 1989. Les communautés végétales sahéliennes en Mauritanie (région de Kaedi); analyse de la reconstitution annuelle du couvert herbacé. Université Paris-sud, Paris.
CILSS, 2016. Landscapes of West Africa – a Window on a Changing World. U.S. Geological Survey EROS, Garretson, USA.
del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A., de Juana, E. (Eds.), 2017. Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona retrieved from: http://www.hbw.com/ on 23 July 2017.
Diouf, M., Akpo, L., Rocheteau, A., Do, F., Goudiaby, V., Diagne, A., 2002. Dynamique du peuplement ligneux d'une végétation sahélienne au Nord-Sénégal (Afrique de l'Ouest). J. Des. Sci. 2, 1–9.
Gillon, Y., Gillon, D., 1973. Recherches écologiques sur une savane sahélienne du Ferlo septentrional, Sénégal: données quantitatives sur les arthropodes. La Terre et la Vie 27, 297–323.
Gillon, D., Adam, F., Hubert, B., Kahlem, G., 1983. Production et consommation de graines en milieu sahel-soudanien au Sénégal : bilan général. La Terre et la Vie 38, 3–35.
Gonzalez, P., 2001. Desertification and a shift of forest species in the west african sahel. Clim. Res. 17, 217–228.
Grouzis, M., 1992. Germination et établissement des plantes annuelles sahéliennes. In: Le Floc'h, E., Grouzis, M., Cornet, A., Bille, J.-C. (Eds.), L'Aridité : Une Contrainte Au Développement. ORSTOM, Paris, pp. 267–282.
Grouzis, M., Le Floc'h, E. (Eds.), 2003. Un arbre au désert : Acacia raddiana. IRD, Paris.
Hiernaux, P., Diarra, L., Trichon, V., Mougin, E., Soumaguel, N., Baup, F., 2009. Woody plant population dynamics in response to climate changes from 1984 to 2006 in Sahel (Gourma, Mali). J. Hydrol. 375, 103–113.
Juul, K., 1996. Post drought migration and technological innovations among Fulani herders in Senegal: the triumph of the tube. IEED Paper 64, 1–25.
Le Houérou, H.N., 1989. The Grazing Land Ecosystems of the African Sahel. Springer, Berlin Heidelberg New York.
Lind, M., Rasmussen, K., Adriansen, H., Ka, A., 2003. Estimating vegetative productivity gradients around watering points in the rangelands of northern Senegal based on NOAA AVHRR data. Dan. J. Geogr. 103, 1–15.
Maranz, S., 2009. Tree mortality in the African Sahel indicates an anthropogenic ecosystem displaced by climate change. J. Biogeogr. 36, 1181–1193.
Miehe, S., Kluge, J., Von Wehrden, H., Retzer, V., 2010. Long-term degradation of Sahelian rangeland detected by 27 years of field study in Senegal. J. Appl. Ecol. 47, 692–700.
Morel, G., 1968. Contribution à la synécologie des oiseaux du Sahel sénégalais. Mémoires ORSTOM no 29, Paris.
Morel, G., Morel, M.Y., 1972a. Recherches écologiques sur une savane sahélienne du Ferlo septentrional, Sénégal : l'avifaune et son cycle annuel. La Terre et la Vie 26, 410–439.
Morel, G., Morel, M.Y., 1972b. Étude comparative du régime alimentaire de cinq espèces de Tourterelles dans une savane semi-aride du Sénégal : premiers résultats. In: Kendeigh, S.C., Pinowski, J. (Eds.), Productivity, Population Dynamics and Systematics of Granivorous Birds. Polish Scientific Publishers, Warszawa, pp. 351–355.
Morel, G., Morel, M.-Y., 1974. Recherches écologiques sur une savane sahélienne du Ferlo septentrional, Sénégal: influence de la sécheresse de l'année 1972-1973 sur l'avifaune. La Terre et la Vie 28, 95–123.
Morel, G.J., Morel, M.-Y., 1978. Recherches écologiques sur une savane sahélienne du Ferlo septentrional, Sénégal. Etude d'une communauté avienne. Cahiers ORSTOM. série Biologie 13, 3–34.
Morel, M.-Y., Morel, G., 1992. Instabilité climatique et communautés aviennes dans une région semi-aride de l'Ouest africain : la steppe arbustive dans le Nord-Sénégal. In: Le Floc'h, E., Grouzis, M., Cornet, A., Bille, J.-C. (Eds.), L'Aridité : Une Contrainte Au Développement. ORSTOM, Paris, pp. 335–352.
Newton, I., 2017. Farming and Birds. Collins, London.
Niang, A.J., Ozer, A., Ozer, P., 2008. Fifty years of landscape evolution in Southwestern Mauritania by means of aerial photos. J. Arid Environ. 72, 97–107.
ould Taleb, N., 1999. Ressources Forestières en Mauritanie. Report for European Commission and FAO.
Pierre, C., Bergametti, G., Marticorena, B., Mougin, E., Lebel, T., Ali, A., 2011. Pluriannual comparisons of satellite-based rainfall products over the Sahelian belt for seasonal vegetation modeling. J. Geophys. Res. 116, 1–25.
Poulet, A.R., 1974. Recherches écologiques sur une savane sahélienne du Ferlo septentrional, Sénégal : quelques effets de la sécheresse sur le peuplement mammalien. La Terre et la Vie 28, 124–130.
Poupon, H., 1980. Structure et dynamique de la strate ligneuse d'une steppe sahélienne au nord du Sénégal. Travaux Documents ORSTOM 115, 1–351.
Poupon, H., Bille, J.C., 1974. Recherches écologiques sur une savane sahélienne du Ferlo septentrional, Sénégal: influence de la sécheresse de l'année 1973-1973 sur la strate ligneuse. La Terre et la Vie 28, 49–75.
Sanderson, F.J., Donald, P.F., Pain, D.J., Burfield, I.J., van Bommel, F.P.J., 2006. Long-term population declines in Afro-Palearctic migrant birds. Biol. Conserv. 131, 93–105.
Sankaran, M., et al., 2005. Determinants of woody cover in african savannas. Nature 438, 846–849.
Sanon, H., Nianogo, J., Nanglem, N., Sanou, S., 2007. Amount of fallen fodder components from *Acacia raddiana, Balanites aegyptiaca* and *Ziziphus mauritiana* available to ruminants in selected Sahelian pastures. Livest. Res. Rural Dev. 17, 1–8.
Santoir, C., 1983. Raison pastorale et développement. Les Peuls sénégalais face aux aménagements. Travaux et Documents de l'ORSTOM 166, Paris.
Stancioff, A.M., Staljanssens, M., Tappan, G., 1986. Mapping and Remote Sensing of the Resources of the Republic of Senegal: a Study of the Geology, Hydrology, Soils, Vegetation, and Land Use Potential. South Dakota State University/Remote Sensing Institute, Brookings.
Sternberg, M., Gutman, M., Perevolotski, A., Kigel, J., 2003. Effects of grazing on soil seed bank dynamics: an approach with functional groups. J. Veg. Sci. 14, 375–386.
Tappan, G.G., Sall, M., Wood, E.C., Cushing, M., 2004. Ecoregions and land cover trends in Senegal. J. Arid Environ. 59, 427–462.
Théboud, B., 1990. Politiques d'hydraulique pastorale et gestion de l'espace au Sahel. Cah. Des. Sci. Hum. 26, 13–31.
Thiollay, J.-M., 2006. Severe decline of large birds in the Northern Sahel of West Africa: a long-term assessment. Bird. Conserv. Int. 16, 353–365.
Touré, I., Diop, A., Wane, A., Casaro, J., Niang, I., 2010. Le Ferlo des forages. In: Touré, I., Ickowicz, A., Wane, A., Garba, I., Gerber, P. (Eds.), Système d'information sur le pastoralisme au Sahel : Atlas des évolutions des systèmes pastoraux au Sahel 1970-2012. FAO CIRAD, Rome Paris, pp. 24–25.
Tréca, B., Tamba, S., 1997. Rôle des oiseaux sur la régénération du ligneux *Boscia senegalensis* (Pers.) Lam., en savane sahélienne au nord Sénégal. La Terre et la Vie 52, 239–260.
Tréca, B., Tamba, S., Akpo, L.E., Grouzis, M., 1996. Importance de l'avifaune sur les apports en azote et en phosphore dans une savane sahélienne du nord Sénégal. La Terre et la Vie 51, 359–373.
Vincke, C., Diédhiou, I., Grouzis, M., 2010. Long term dynamics and structure of woody vegetation in the Ferlo (Senegal). J. Arid Environ. 74, 268–276.
Zwarts, L., Bijlsma, R.G., 2015. Detection probabilities and absolute densities of birds in trees. Ardea 103, 99–122.
Zwarts, L., Bijlsma, R.G., van der Kamp, J., Wymenga, E., 2009. Living on the Edge: Wetlands and Birds in a Changing Sahel. KNNV Publishing, Zeist. http://www.altwym.nl/uploads/file/540_1433753005.pdf.
Zwarts, L., Bijlsma, R.G., van der Kamp, J., Sikkema, M., Wymenga, E., 2015. Moreau's Paradox reversed, or why insectivorous birds reach high densities in savanna trees. Ardea 103, 123–144.

Supplementary data

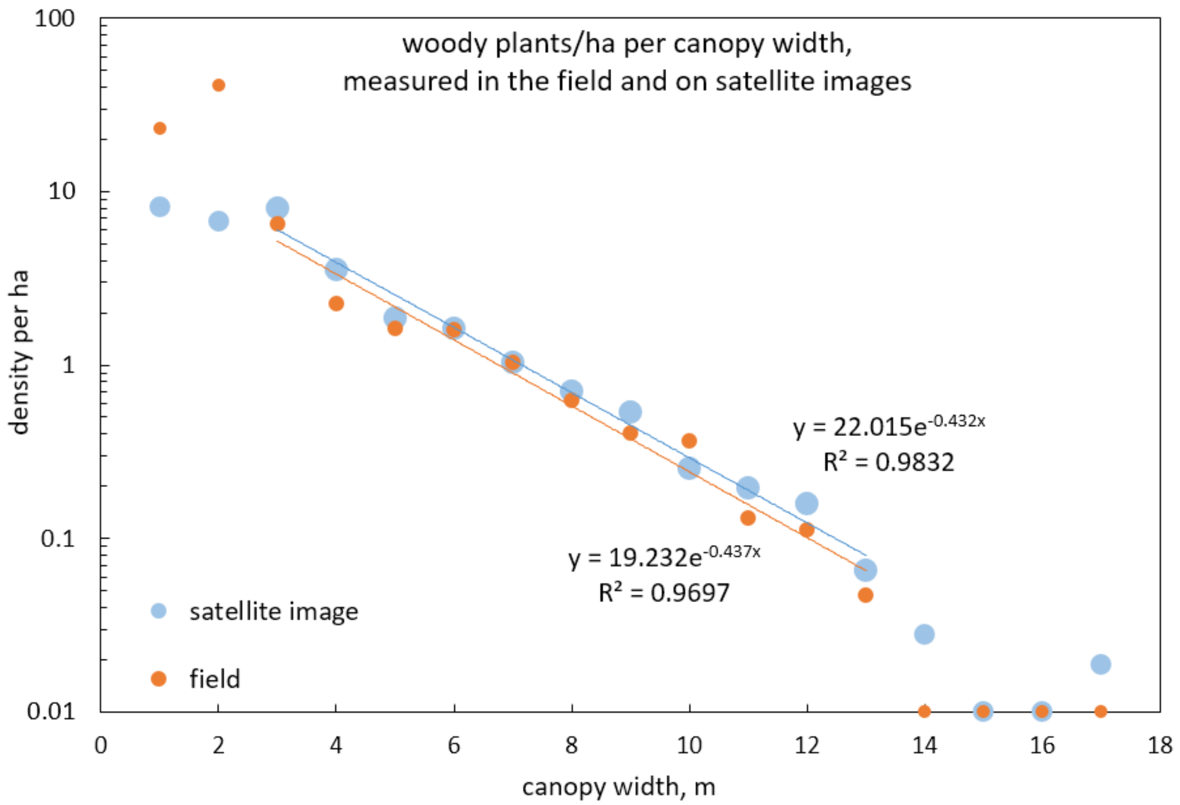

Fig. S1. The density of woody plants per ha per canopy width (m) given separately for woody plants measured in the field and on Google Earth satellite images in the same 28 sites (106.5 ha), - a random selection from the 123 sites shown in Fig. 1A. The frequency is similar for woody plants with a diameter of 3 m or more (R=0.993, N=11, P<0.00001), but woody plants of 1 and 2 m were overlooked on the satellite images. Note log scale is used on Y-axis. Regression lines are calculated for trees with diameters of 3-13 m; smaller trees were overlooked on the images and trees wider than 13 m were too rare to provide reliable data. These data emerged from a preliminary analysis of images which showed that only a fraction of the shrubs *Leptadenia pyrotechnica* and *Calotropis procera* were detected on satellite images. All other data used in this paper (Figs. 7 - 9, Suppl. data: Table S3 – S7) took account of this finding.

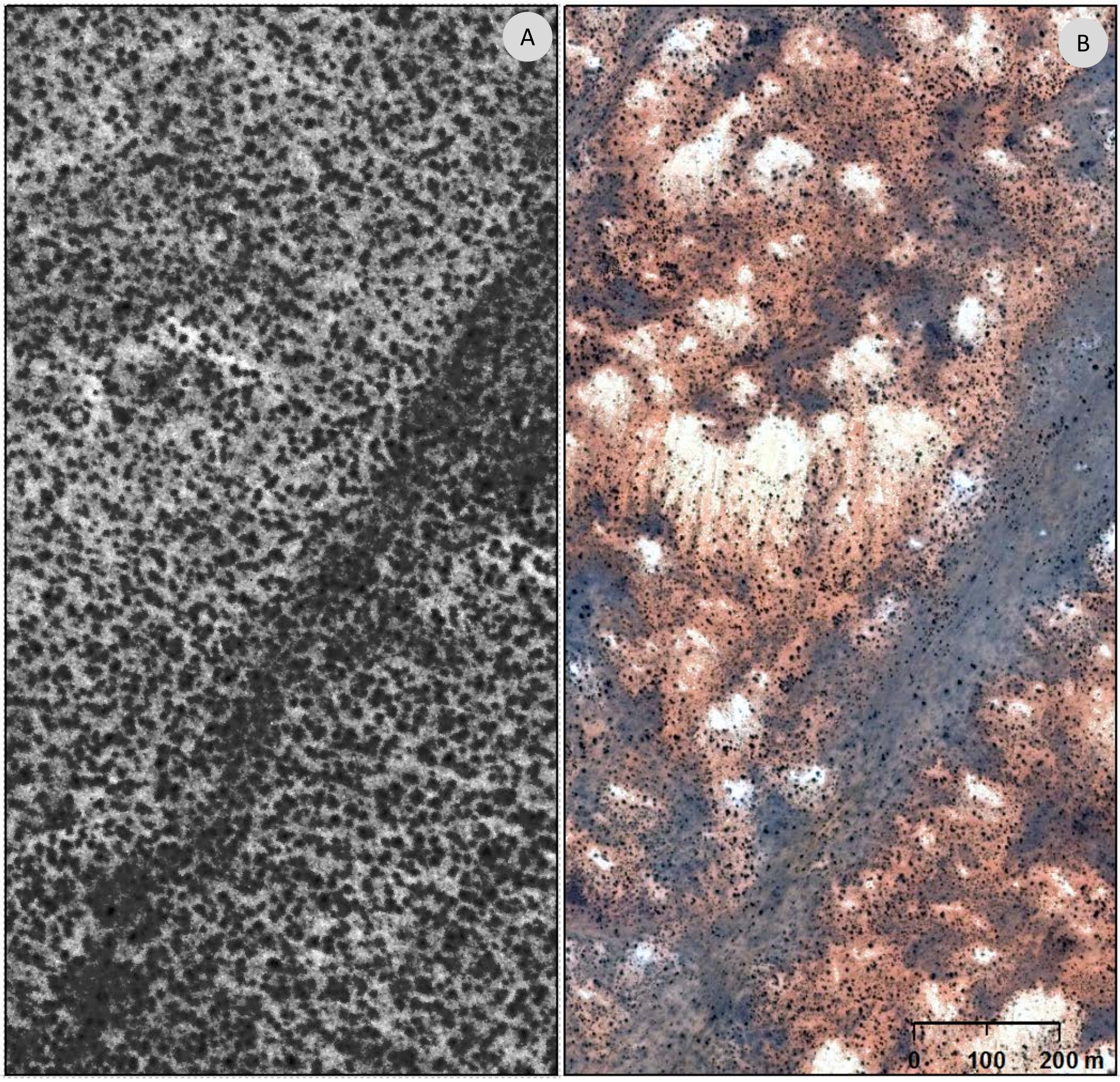

Fig. S2. Loss of woody vegetation between 31 January 1968 (A; Corona satellite photo) and 11 May 2010 (B; © Bing Map Microsoft|Here) in SW Mauritania at 15.776°W and 16.973°N. In 1968, woody cover was relatively sparse on the dunes and dense in the valleys, but the difference was not large. In 2010, the dunes (white) were bare and the valleys had only a few scattered trees (grey); most trees were still found on the slopes and especially in the depressions along the slopes. The woody cover in this region (15.5-16.0°W and 16.5-17.5°N) amounted to 13% (range 2-42%) in 1968 and 5% (0-13%) in 2013-2016 (averages and ranges based on 93 circular plots; see Fig. 8A for position).

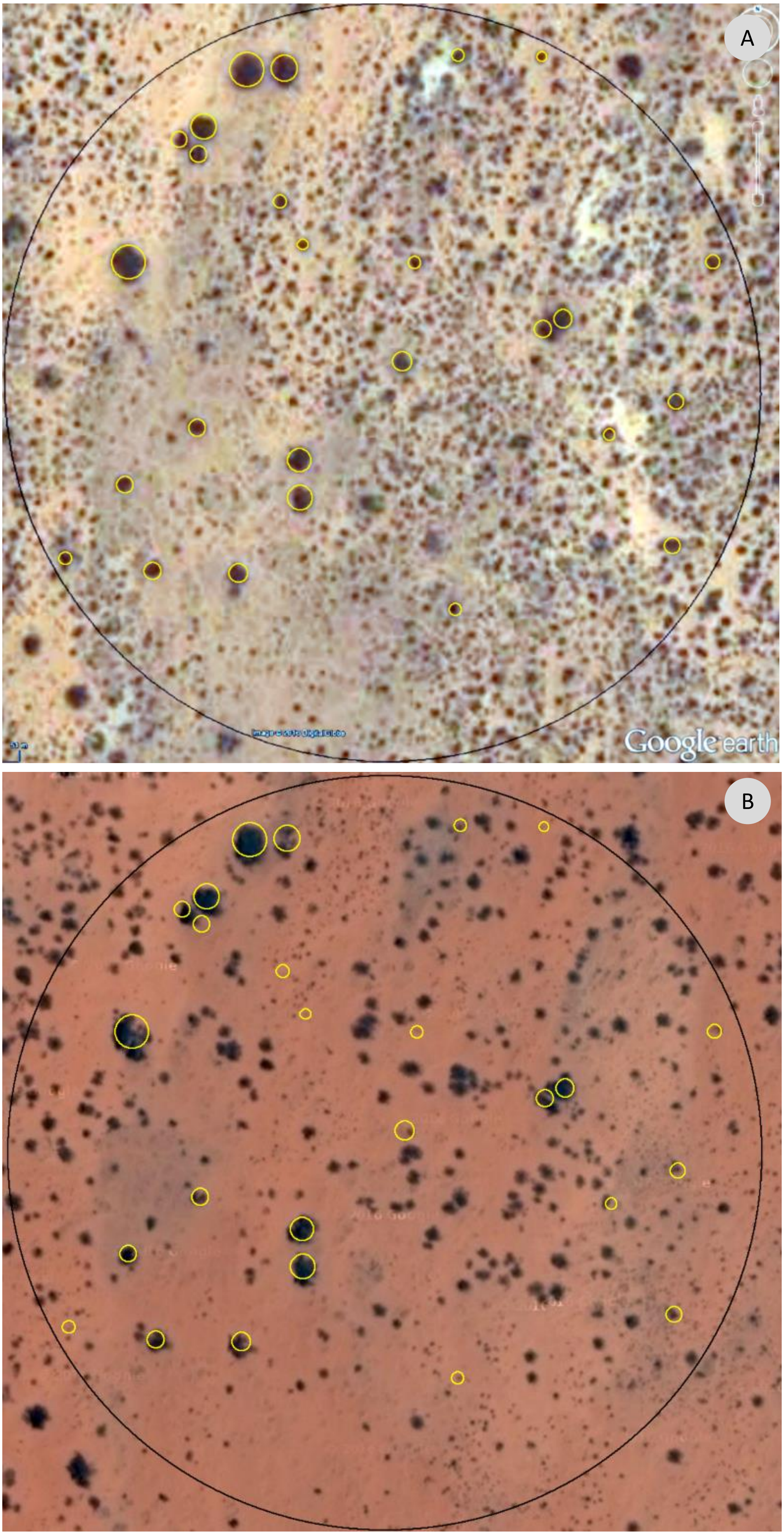

Fig. S3. Google Earth images from plot #263, a circle (radius 100 m) at 17.256°N and 15.956°W from (A) 19 May 2003 and (B) 11 May 2016.

The few larger trees in 2003 are marked with a yellow circle. The same circles are also indicated in the 2016-image to show that most are still present but have not grown in width.

Small *Leptadenia* shrubs (canopy width ≤ 2m), still present with 382/ha in 2003, have declined to 159/ha in 2016, but at the same time woody plants with a canopy surface of 4-8 m^2 have come into existence. As a consequence, the total density of woody plants has declined from 390/ha to 208/ha, but the woody cover has increased from 5.6 to 6.3% in the course of 13 years.

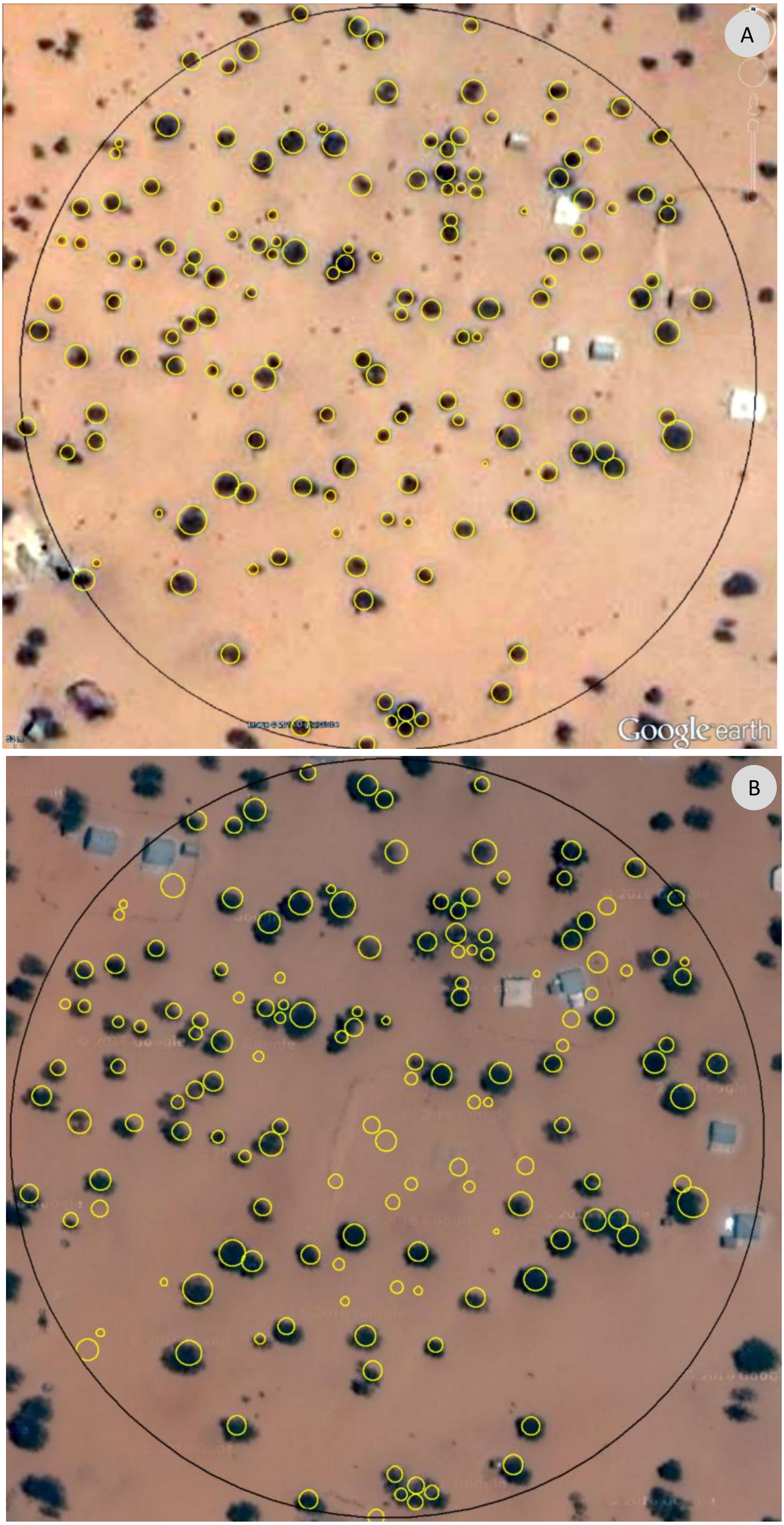

Fig. S4. Google Earth images from plot #268, a circle (radius 100 m) at 17.125°N and 15.929°W from (A) 24 June 2003 and (B) 11 May 2016. The square structures are small houses.

All large woody plants in 2003 are marked with a yellow circle. The same circles are also indicated in the 2016-image to show that 38 of the 147 woody plants have disappeared (a total loss of 417 m^2 or 1.3% of the woody cover).

However, the remaining trees have grown, from, on average, 17.2 m^2 to 29.2 m^2 canopy surface per tree. As a result, the total woody cover has increased from 8.1 to 10.1% in the course of 13 years.

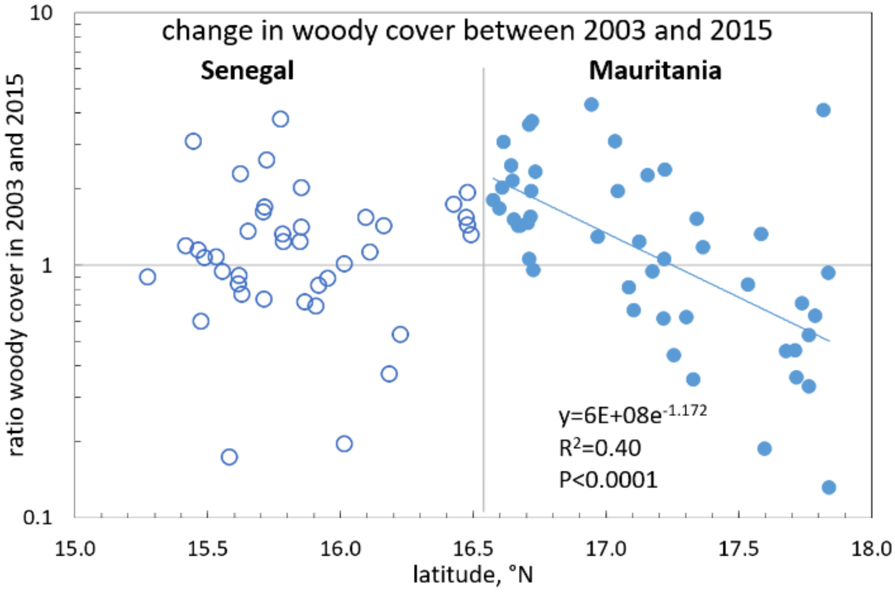

Fig. S5. Change in the woody cover between 2002-2004 and 2014-2016 (both determined for circular plots (see Fig. 8A) using Google Earth or Bing satellite images) given as a ratio; note that a log-scale is used on the Y-axis; <1 is decline, >1 is increase of woody cover during the intervening period. There is no relation between change in woody vegetation and latitude in Senegal (R=+0.02, n=40), but the trend is significantly negative for the 49 plots in Mauritania due to a decline of woody cover in the southern Sahara Desert but a considerable recovery in southern Mauritania near the Senegal River.

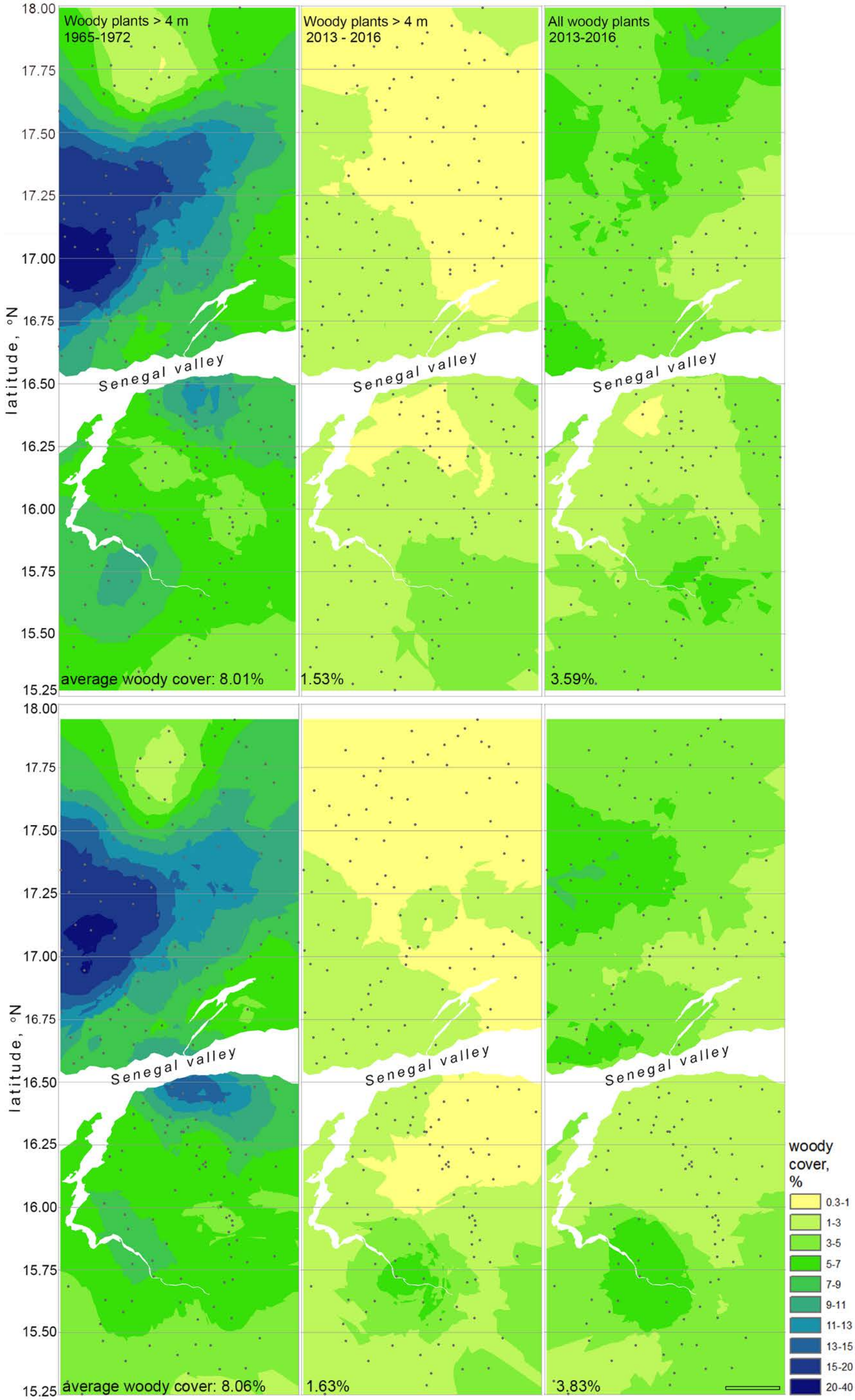

Fig. S6. Split-half method applied on the 390 circular plots used to construct the three maps in Fig. 8 (15 - 16°W and 15.25 - 18°N). The upper and lower row of the three maps are based on 195 odd and 195 even plots after ranking according to latitude. Grey dots indicate the position of the plots. The split-half maps differ in detail from the maps based on all plots (Fig. 8), but their average woody cover is the same.

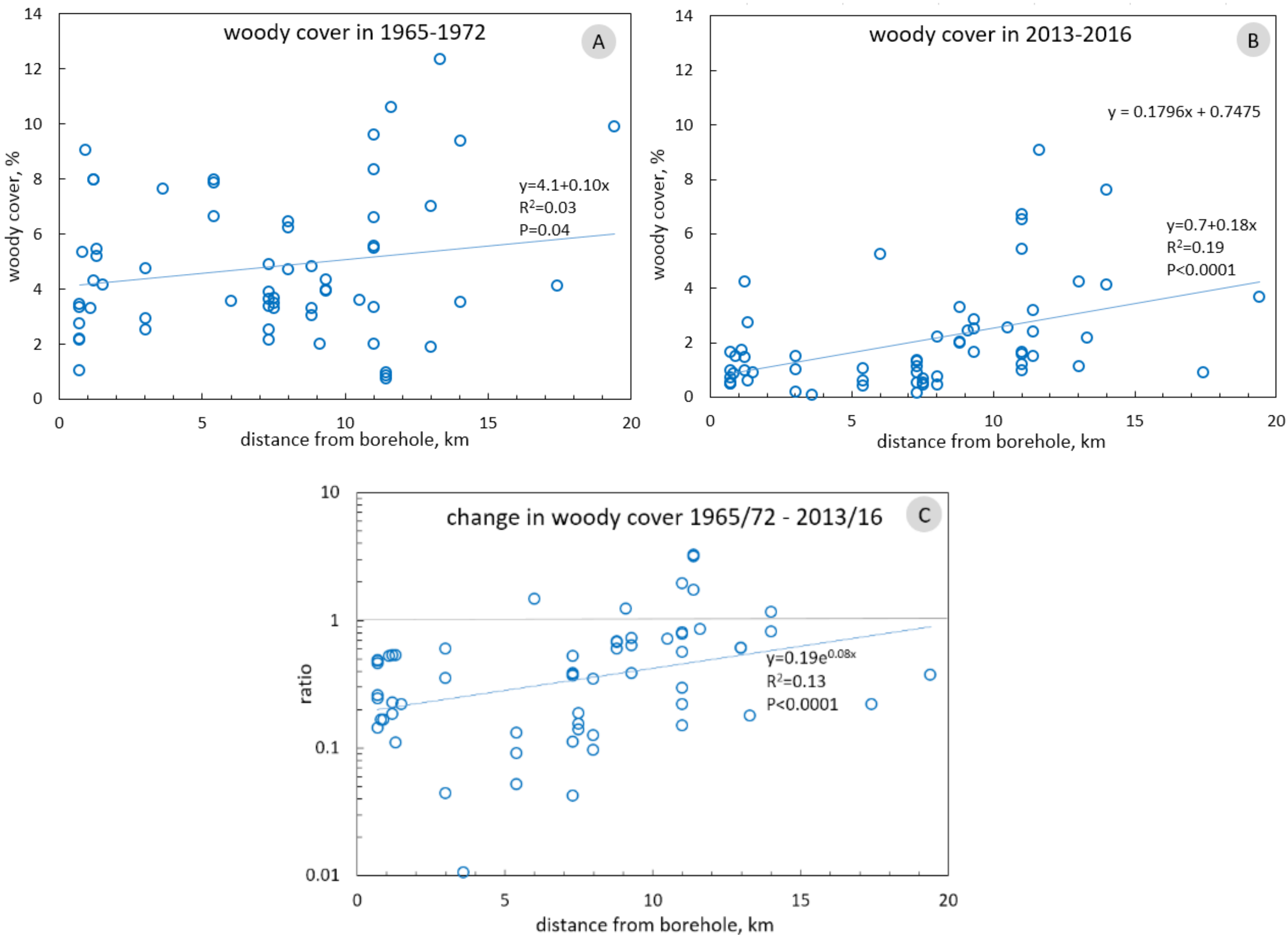

Fig. S7. Woody cover (%) in (A) 1965-1972 (based on Corona photos) and (B) 2013-2016 (Google Earth and Bing images) as a function of the nearest borehole, based on measurements in 97 circular plots (for location see Fig. 8A) around 11 boreholes in the Ferlo (Amali, Belil Bogal, Bouteyni, Diaglé, Gamine, Mbidi, Niassante, Tatki, Tessekré, Widou Thiengoly and one between Niassante, Tatki and Widou Thiengoly of which we do not know the name). (C) Change in the woody cover between 1965-1972 and 2013-2016 given as a ratio; note log-scale is used on Y-axis; <1 is decline, >1 is increase of woody cover during the intervening period.

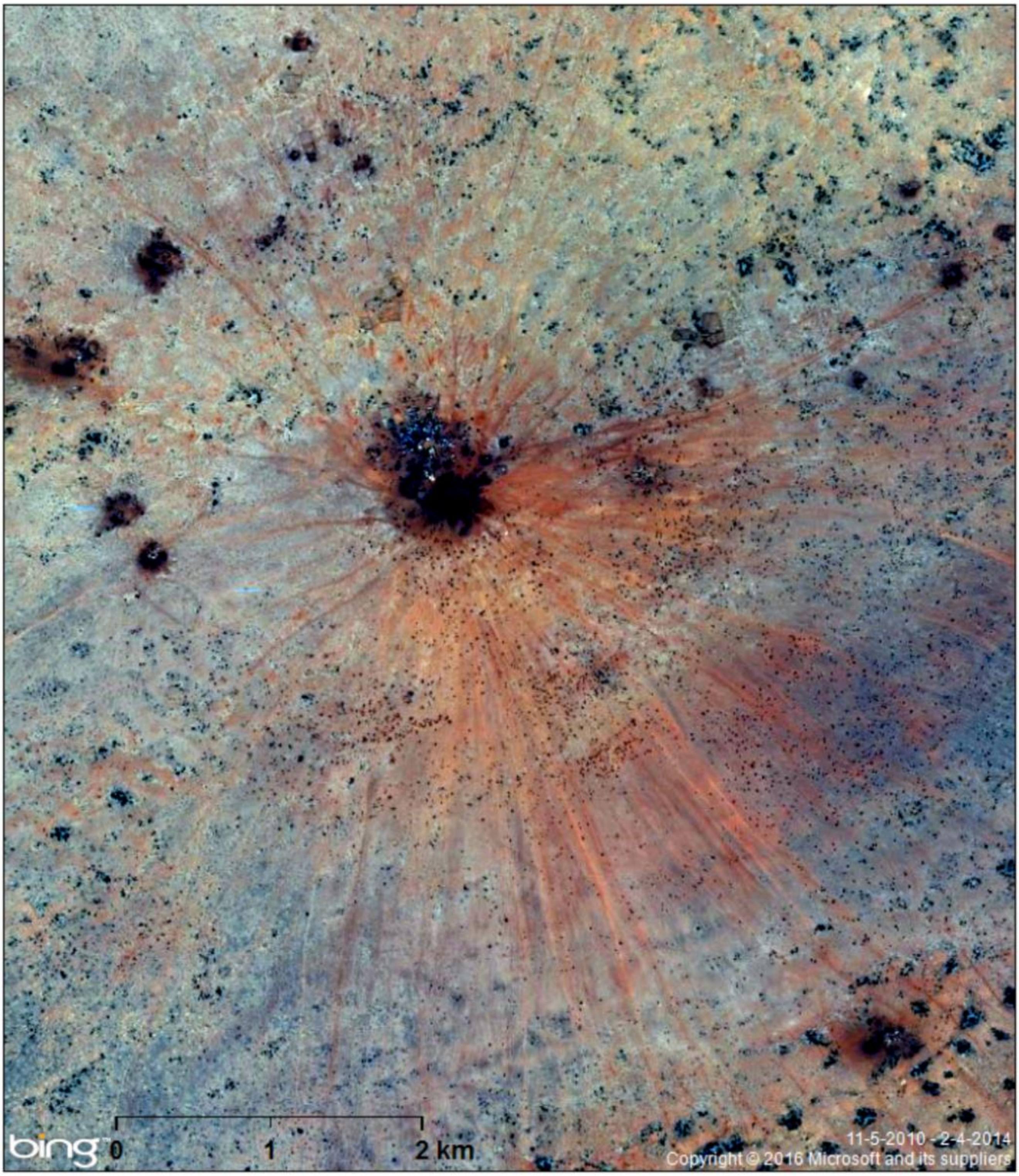

Fig. S8. The partly treeless surroundings of Tatki (16.220°N and 15.279°W). Note the numerous paths radiating from the borehole due to the intense traffic of donkey carts with water containers and the movements of livestock herds to and from the watering point.

Table S1. Sites visited in the field, with date, coordinates, number of transects and total surface where bird and woody plants were counted, bird density (n/ha) and woody cover (%).

site	date	north	west	transects	ha	birds/ha	woody cover, %	remarks
w05	11-1-2014	15.9226	-15.2841	3	5	1.80	6.90	
w05e	11-1-2014	15.9279	-15.2876	1	2.1	7.14	7.29	exclosure Widou
w06	12-1-2014	15.9267	-15.2758	3	5.25	9.90	10.24	
w06e	12-1-2014	15.9306	-15.2799	1	3.38	50.30	7.14	exclosure Widou
w07	12-1-2014	15.9461	-15.2778	3	4.25	10.12	7.48	
w07e	12-1-2014	15.9447	-15.2855	1	5	13.60	5.93	exclosure Widou
w08	12-1-2014	15.9654	-15.2876	3	4.85	7.78	4.67	
w08e	12-1-2014	15.9622	-15.2904	1	5	11.80	6.42	exclosure Widou
r60	11-1-2014	16.2969	-15.3596	10	15	1.47	1.75	
r67	13-1-2014	16.2387	-15.4535	10	16.25	2.03	3.47	
m30	20-12-2014	18.0503	-15.8119	3	4.5	0.00	1.69	
m31	20-12-2014	18.0004	-15.6526	3	4.5	12.00	2.66	
m32	20-12-2014	17.9505	-15.5021	3	3.75	0.00	4.59	
m33	20-12-2014	17.9000	-15.3146	3	4.5	0.00	0.25	
m34	20-12-2014	17.8503	-15.2052	3	4.5	0.00	0.16	
m35	19-12-2014	17.8003	-15.1061	3	9.5	1.16	4.40	
m36	19-12-2014	17.7492	-15.0163	3	4.5	0.00	1.61	
m37	19-12-2014	17.6998	-14.9140	3	4.5	0.00	5.20	
m38	19-12-2014	17.6501	-14.8220	3	4.5	2.00	2.12	
m39	19-12-2014	17.6013	-14.7636	3	4.25	0.71	3.60	
m40	19-12-2014	17.4999	-14.7369	3	4.5	3.78	2.27	
m41	19-12-2014	17.4499	-14.7809	3	4.5	0.00	1.19	
m42	19-12-2014	17.3999	-14.8374	3	4.5	0.22	1.02	
m43	19-12-2014	17.3502	-14.8842	3	4.5	45.33	8.46	
m44	19-12-2014	17.3001	-14.9369	3	4.5	0.22	0.49	
m45	19-12-2014	17.2499	-14.9876	4	5.75	1.57	0.90	
m46	19-12-2014	17.2002	-15.0362	3	4.5	2.44	2.48	
m47	19-12-2014	17.1515	-15.0669	3	4.5	20.89	2.12	
m48	18-12-2014	17.0992	-15.1224	3	4.75	0.00	1.65	
m49	18-12-2014	17.0478	-15.1568	3	4.5	13.33	5.70	
m50	18-12-2014	16.9998	-15.1993	3	4.5	0.22	0.15	
m51	18-12-2014	16.9501	-15.2802	3	4.5	2.44	0.13	
m52	18-12-2014	16.9529	-15.3799	3	3.5	1.71	8.28	
m53	18-12-2014	16.9998	-15.4457	3	4.5	1.56	3.30	
m54	18-12-2014	17.0385	-15.5126	3	4.5	0.44	4.47	
m55	18-12-2014	17.0001	-15.5632	3	4.5	3.78	4.36	
m56	18-12-2014	16.9508	-15.6400	3	4.5	6.67	10.54	
m57	17-12-2014	16.8991	-15.6671	3	4.5	2.00	3.58	
m58	17-12-2014	16.8506	-15.7195	3	4.5	10.44	7.72	
m59	17-12-2014	16.7888	-15.7508	3	4.5	5.33	5.09	
m60	17-12-2014	16.7499	-15.7826	3	4.5	4.67	6.15	
m61	17-12-2014	16.7010	-15.8124	3	4.5	2.00	4.48	
m62	17-12-2014	16.6507	-15.8439	2	3	5.67	13.54	
m63	17-12-2014	16.6005	-15.8694	2	3	2.33	11.46	
r68	16-12-2014	16.4496	-15.6370	3	4.5	1.11	0.55	
r69	15-12-2014	16.4008	-15.5364	3	4.5	2.89	2.50	
r70	15-12-2014	16.3496	-15.5171	3	4.5	2.44	4.71	

site	date	north	west	transects	ha	birds/ha	woody cover, %	remarks
r71	15-12-2014	16.3001	-15.4801	3	4.5	1.56	2.86	
r72	15-12-2014	16.2503	-15.4604	3	4.5	8.67	3.54	
r73	15-12-2014	16.2048	-15.4248	3	4.5	15.11	3.55	
r74	14-12-2014	16.1525	-15.4117	4	5.55	4.32	1.79	
r75	14-12-2014	16.1008	-15.3931	3	4.5	1.56	2.89	
r76	14-12-2014	16.0504	-15.3642	3	4.5	2.00	2.63	
r77	14-12-2014	15.9999	-15.3231	3	4.5	2.22	8.04	
r79	13-12-2014	15.9000	-15.2914	3	4.5	15.11	10.72	
r80	12-12-2014	15.8505	-15.2897	1	1.5	14.00	21.98	
r81	12-12-2014	15.8001	-15.2815	3	4.5	0.00	2.13	
r82	12-12-2014	15.7500	-15.2835	3	4.5	1.78	4.13	
r83	12-12-2014	15.6998	-15.3085	3	4.5	1.33	1.71	
r84	12-12-2014	15.6499	-15.3414	1	1.5	5.33	4.28	
r85	12-12-2014	15.6002	-15.3540	4	6	6.17	0.92	
r86	12-12-2014	15.5506	-15.4194	1	1.5	15.33	12.61	
r87	12-12-2014	15.5005	-15.4221	1	0.65	20.00	7.59	
r88	11-12-2014	15.4504	-15.4276	2	3	2.33	13.42	
r89	11-12-2014	15.4007	-15.4542	1	1.5	14.00	4.62	
w05	13-12-2014	15.9226	-15.2841	3	4.5	2.89	8.52	
w05e	13-12-2014	15.9279	-15.2876	1	2.1	54.29	7.27	exclosure Widou
w06	13-12-2014	15.9267	-15.2758	3	4.5	2.44	5.30	
w06e	13-12-2014	15.9306	-15.2799	1	3.38	16.57	4.85	exclosure Widou
w07	13-12-2014	15.9461	-15.2778	3	4.5	2.44	2.60	
w07e	13-12-2014	15.9447	-15.2855	1	9	10.78	3.24	exclosure Widou
w08	14-12-2014	15.9654	-15.2876	3	4.85	2.47	2.32	
w08e	14-12-2014	15.9622	-15.2904	1	9	21.44	4.81	exclosure Widou
t01	25-2-2015	16.4997	-15.4033	3	4.5	0.67	1.54	
t02	25-2-2015	16.4502	-15.4035	3	4.5	1.11	2.92	
t03	26-2-2015	16.4053	-15.3226	3	4.5	1.56	2.68	
t04	26-2-2015	16.3623	-15.3137	3	4.5	0.67	1.53	
t05	26-2-2015	16.3150	-15.3098	3	4.5	0.00	6.16	
t06	26-2-2015	16.2650	-15.3147	3	4.5	0.67	3.47	
t07	26-2-2015	16.2456	-15.2902	3	4.5	0.67	1.68	
t08	26-2-2015	16.2375	-15.2899	3	4.5	0.22	1.00	
t09	26-2-2015	16.2313	-15.2733	3	4.5	1.56	2.47	
t10	26-2-2015	16.2286	-15.2664	3	4.5	0.00	0.72	
t11	26-2-2015	16.2310	-15.2342	3	4.5	0.44	1.62	
t12	26-2-2015	16.2299	-15.1730	3	4.5	0.44	2.18	
t13	27-2-2015	16.2313	-15.1227	3	4.5	0.67	1.88	
t1423	27-2-2015	16.2189	-15.0909	10	25	0.36	3.73	Fété-Olé
t24	27-2-2015	16.1995	-15.0637	3	4.5	0.00	1.47	
t25	27-2-2015	16.1798	-15.0173	3	4.5	0.22	1.52	
t26	27-2-2015	16.1606	-14.9794	3	4.5	0.22	1.91	
t27	27-2-2015	16.1490	-14.9480	3	4.5	0.22	2.40	
t28	28-2-2015	16.1459	-14.9438	3	4.5	0.67	1.66	
t29	28-2-2015	16.1496	-14.9311	3	4.5	1.33	2.17	
t30	28-2-2015	16.1552	-14.9318	3	4.5	0.44	2.52	
t31	28-2-2015	16.1842	-14.9209	3	4.5	0.22	3.04	
t32	28-2-2015	16.2271	-14.9094	3	4.5	0.67	3.51	
t33	28-2-2015	16.2500	-14.8952	3	4.5	0.44	4.10	
t34	28-2-2015	16.2999	-14.8605	3	4.5	0.44	2.12	
t35	28-2-2015	16.3502	-14.8189	3	4.5	0.44	2.08	
t36	28-2-2015	16.4010	-14.8054	3	4.5	0.00	1.91	

site	date	north	west	transects	ha	birds/ha	woody cover, %	remarks
t37	28-2-2015	16.4501	-14.8058	3	4.5	0.89	3.44	
t38	1-3-2015	16.5001	-14.8298	3	4.5	3.56	7.56	
t39	2-3-2015	16.5000	-15.1302	3	4.5	0.22	3.58	
t40	3-3-2015	16.3530	-15.8834	3	4.5	0.00	1.16	
t41	3-3-2015	16.2508	-15.8782	3	4.5	1.78	9.65	
t42	3-3-2015	16.1497	-15.9502	3	4.5	0.22	1.91	
t43	3-3-2015	16.0498	-16.0086	3	4.5	0.67	0.87	
t44	3-3-2015	15.9502	-15.9754	3	4.5	2.22	3.63	
r68	29-10-2015	16.4491	-15.6385	3	4.5	16.89	1.33	
r69	29-10-2015	16.4001	-15.5665	3	4.5	2.67	0.19	
r70	29-10-2015	16.3498	-15.5170	3	4.5	0.89	0.80	
r71	29-10-2015	16.2999	-15.4799	3	4.5	3.78	2.75	
r72	29-10-2015	16.2504	-15.4604	3	4.5	7.33	3.20	
r73	29-10-2015	16.2053	-15.4243	3	4.5	11.56	2.00	
r74	29-10-2015	16.1528	-15.4127	3	4.5	3.33	0.97	
r75	29-10-2015	16.1007	-15.3931	3	4.5	1.33	1.77	
r76	30-10-2015	16.0503	-15.3644	3	4.5	11.11	4.81	
r77	30-10-2015	15.9999	-15.3231	3	4.5	5.11	3.04	
r79	30-10-2015	15.9004	-15.2894	3	4.5	12.67	9.59	
r80	30-10-2015	15.8612	-15.2903	3	4.5	1.33	4.71	
r81	30-10-2015	15.8001	-15.2815	3	4.5	4.89	3.36	
r82	30-10-2015	15.7500	-15.2837	3	4.5	2.67	1.47	
r83	30-10-2015	15.7008	-15.3089	1	1.5	0.00	0.53	
r84	31-10-2015	15.6499	-15.3414	1	6	18.83	0.43	
r85	31-10-2015	15.6001	-15.3549	3	4.5	15.56	3.43	
r86	31-10-2015	15.5499	-15.4198	3	4.5	5.56	2.07	
r87	31-10-2015	15.5005	-15.4221	1	0.3	0.00	54.35	
r88	31-10-2015	15.4502	-15.4274	3	4.5	2.22	1.82	
r89	31-10-2015	15.4341	-15.4361	3	4.5	4.89	8.55	

Table S1. Woody cover (%) per latitude between 15 and 16°W, given separately for 11 latitudinal zones and for woody plants with a canopy diameter larger than 10, 7 and 4 m, as determined by measuring individual trees in 390 random circles (radius 100 m; n = number of circles) on Corona satellite images (1965-1968) or Google Earth or Bing satellite images (2013-2016). Results of one-way analyses of variance: R^2 (explained variance), P < 0.001 ***, P < 0.01 **, P < 0.05 *. Averages also shown in Fig. 9.

		diameter > 10 m				diameter > 7 m				diameter > 4 m			
latitude, °N	n	'65/68	'13/16	R^2	P	'65/68	'13/16	R^2	P	'65/68	'13/16	R^2	P
15.25 - 15.50	52	0.53	0.44	0.00		1.89	1.07	0.07		3.77	2.17	0.15	**
15.50 - 15.75	54	1.43	1.33	0.00		3.84	2.71	0.02		6.29	4.12	0.05	
15.75 – 16.00	78	0.55	0.53	0.01		2.85	1.31	0.14	***	5.75	2.36	0.30	***
16.00 - 16.25	92	0.50	0.27	0.02		2.14	0.47	0.39	***	4.87	0.90	0.50	***
16.25 - 16.50	92	2.17	0.40	0.18	***	6.04	0.71	0.28	***	9.07	1.16	0.51	***
16.50 - 16.75	54	0.68	0.24	0.08	*	3.59	0.86	0.36	***	7.31	2.47	0.45	***
16.75 - 17.00	78	3.28	0.13	0.09	**	7.24	0.52	0.20	***	10.50	1.16	0.31	***
17.00 - 17.25	100	2.52	0.02	0.21	***	7.14	0.34	0.23	***	11.44	1.20	0.44	***
17.25 - 17.50	64	2.00	0.01	0.26	***	8.48	0.08	0.52	***	13.53	0.49	0.70	***
17.50 - 17.75	64	0.80	0.01	0.14	**	3.45	0.18	0.22	***	6.55	0.64	0.28	**
17.75 - 18.00	46	0.56	0.03	0.15	**	2.14	0.15	0.28	***	4.40	0.63	0.37	***

Table S3. Woody cover (% in sites) per latitude (15.5=15.25-15.75°N, etc. but the 16.5-band has been subdivided for Senegal (16.4=16.25-16.5°N) and Mauritania (16.7=16.50-16.75°N). Woody species with a high bird density are indicated (●). Data were collected during field work done between January 2014 and October 2015. Results of one-way analyses of variance to test the latitudinal variation: P<0.001 ***, P<0.01 **, P<0.05 *. Averages also shown in Fig. 10A. Woody species with a high bird density are indicated (●).

latitude	15.5	16.0	16.4	16.7	17.0	17.5	18.0	P
sites (N)	15	47	25	4	15	9	6	
Acacia nilotica ●	0.000	0.006	0.000	0.000	0.000	0.000	0.000	
Acacia senegal ●	4.337	0.062	0.020	3.843	0.251	0.134	0.000	
Acacia seyal ●	0.000	0.010	0.001	0.099	0.000	0.000	0.000	***
Acacia tortilis ●	1.122	0.426	0.718	3.016	1.115	0.112	0.610	*
Adansonia digitata	0.000	0.004	0.009	0.000	0.000	0.000	0.000	
Balanites aegyptiaca ●	2.238	1.564	0.288	0.916	0.533	0.871	0.013	*
Bauhinia rufescens	0.000	0.000	0.004	0.000	0.000	0.000	0.000	
Boscia senegalensis	0.000	0.694	0.901	0.000	0.005	0.000	0.000	***
Calotropis procera	0.000	0.348	0.312	0.004	0.000	0.100	0.155	
Combretum glutinosum	0.011	0.094	0.000	0.000	0.000	0.000	0.000	
Euphorbia balsamifera	0.062	0.008	0.003	0.000	0.000	0.000	0.000	
Faidherbia albida ●	0.005	0.018	0.000	0.000	0.000	0.000	0.000	
Guiera senegalensis	0.000	0.018	0.000	0.000	0.000	0.000	0.000	
Leptadenia hastata	0.008	0.001	0.001	0.000	0.000	0.000	0.000	
Leptadenia pyrotechnica	0.000	0.019	0.228	1.011	2.126	1.668	1.477	***
Prosopis juliflora	0.000	0.000	0.168	0.000	0.000	0.000	0.033	
Salvadora persica ●	0.000	0.006	0.012	0.000	0.000	0.000	0.000	
Sclerocarya birrea	0.248	0.584	0.000	0.000	0.000	0.000	0.000	*
Tamarix senegalensis	0.000	0.000	0.252	0.000	0.000	0.000	0.000	
Ziziphus mauritiana	0.000	0.003	0.010	0.000	0.000	0.000	0.000	
all woody species	8.031	3.893	2.959	8.907	4.031	2.885	2.290	
preferred species ●	7.702	2.090	1.035	7.874	1.900	1.113	0.610	**

Table S4. Bird density (n/ha) per latitude (15.5=15.25-15.75°N, etc. but the 16.5-band has been subdivided in 16.4 = 16.25-16.5°N and 16.7 = 16.50-16.75°N) in December 2014. Results of one-way analyses of variance: P<0.001 ***, P<0.01 **, P<0.05 *. Averages also shown for birds feeding in trees in Fig. 10B and for birds feeding on the ground in Fig. 10C. Common and Iberian Chiffchaffs *Phylloscopus collybita* and *P. ibericus* were lumped.

food/habitat/status; latitude, °N					15.5	16.2	16.4	16.7	17.0	17.5	18.0	P
sites (N)					8	17	5	4	15	9	6	
area surveyed (ha)					23.2	88.0	22.5	15.0	68.2	40.3	31.3	
number of bird species					29	28	18	19	24	11	8	
insectivorous, arboreal migrants (n/ha)		ins	arb	mig	0.83	0.78	0.58	1.25	0.73	0.05	0.14	
insectivorous, arboreal residents (n/ha)		ins	arb	res	2.08	0.27	0.31	0.72	0.34	0.15	0.04	
insectivorous, ground-feeding migrants (n/ha)		ins	grd	mig	0.30	0.36	0.71	0.25	0.28	0.15	0.04	
insectivorous, ground-feeding residents (n/ha)		ins	grd	res	2.46	1.24	0.13	0.33	0.42	0.30	0.05	
granivorous, ground-feeding residents (n/ha)		gran	grds	res	2.61	2.68	0.27	1.33	3.29	5.39	1.93	
all bird species (n/ha)					8.37	5.38	3.33	4.06	5.06	6.03	2.19	
Mourning Collared-dove	*Streptopelia decipiens*	gran	grd	res	0.00	0.00	0.00	0.17	0.00	0.00	0.00	
Vinaceous Dove	*Streptopelia vinacea*	gran	grd	res	0.17	0.06	0.00	0.00	0.00	0.00	0.00	
Laughing Dove	*Spilopelia senegalensis*	gran	grd	res	0.04	0.22	0.00	0.00	0.06	0.00	0.00	
Namaqua Dove	*Oena capensis*	gran	grd	res	0.25	1.06	0.00	0.00	0.00	0.05	0.00	
Black-headed Lapwing	*Vanellus tectus*	ins	grd	res	0.00	0.31	0.09	0.00	0.00	0.00	0.00	
Cream-coloured Courser	*Cursorius cursor*	ins	grd	mig	0.00	0.00	0.00	0.00	0.07	0.00	0.00	
Blue-naped Mousebird	*Urocolius macrourus*	fruit	arb	res	0.08	0.06	1.33	0.17	0.00	0.00	0.00	
Red-billed Hornbill	*Tockus erythrorhynchus*	ins	grd	res	0.00	0.23	0.00	0.00	0.00	0.00	0.00	***
Common Hoopoe	*Upupa epops*	ins	grd	mig	0.00	0.02	0.18	0.00	0.01	0.02	0.00	
Green Woodhoopoe	*Phoeniculus purpureus*	ins	arb	res	0.00	0.00	0.00	0.17	0.00	0.00	0.00	***
Vieillot's Barbet	*Lybius vieilloti*	ins	arb	res	0.00	0.02	0.00	0.17	0.01	0.00	0.00	
Black-crowned Tchagra	*Tchagra senegalus*	ins	grd	res	0.00	0.04	0.00	0.06	0.00	0.00	0.00	
Great Grey Shrike	*Lanius excubator*	ins	grd	res	0.50	0.02	0.04	0.00	0.11	0.07	0.05	*
Woodchat Shrike	*Lanius senator*	ins	grd	mig	0.24	0.09	0.09	0.06	0.03	0.00	0.00	
Sennar Penduline-tit	*Anthoscopus punctifrons*	ins	arb	res	0.67	0.00	0.00	0.08	0.00	0.00	0.00	*
Yellow Penduline-tit	*Anthoscopus parvulus*	ins	arb	res	0.08	0.00	0.00	0.00	0.00	0.00	0.00	
Greater Hoopoe-lark	*Alaemon alaudipes*	ins	grd	res	0.00	0.00	0.00	0.00	0.03	0.00	0.00	
Chestnut-backed Sparrow-lark	*Eremopterix leucotis*	gran	grd	res	0.00	0.00	0.00	0.14	0.00	0.00	0.00	***
Black-crowned Sparrow-lark	*Eremopterix nigriceps*	gran	grd	res	0.00	0.00	0.00	0.00	0.69	0.35	0.00	
Northern Crombec	*Sylvietta brachyura*	ins	arb	res	0.08	0.00	0.00	0.00	0.03	0.00	0.00	
Yellow-bellied Eremomela	*Eremomela icteropygialis*	ins	arb	res	0.58	0.00	0.00	0.00	0.03	0.00	0.00	
Cricket Warbler	*Spiloptila clamans*	ins	arb	res	0.35	0.13	0.00	0.00	0.22	0.15	0.04	
Tawny-flanked Prinia	*Prinia subflava*	ins	arb	res	0.00	0.00	0.00	0.08	0.00	0.00	0.00	
Eurasian Reed-warbler	*Acrocephalus scirpaceus*	ins	arb	mig	0.00	0.00	0.00	0.00	0.03	0.00	0.00	
Western Bonelli's Warbler	*Phylloscopus bonelli*	ins	arb	mig	0.17	0.33	0.09	0.33	0.24	0.00	0.05	
Common/Iberian Chiffchaff	*Phylloscopus collybita/ibericus*	ins	arb	mig	0.00	0.00	0.00	0.31	0.00	0.00	0.00	***
Western Orphean Warbler	*Sylvia hortensis*	ins	arb	mig	0.08	0.04	0.22	0.53	0.28	0.00	0.02	
Subalpine Warbler	*Sylvia cantillans*	ins	arb	mig	0.47	0.37	0.13	0.00	0.18	0.05	0.07	
Common Whitethroat	*Sylvia communis*	ins	arb	mig	0.10	0.05	0.13	0.08	0.00	0.00	0.00	
Fulvous Babbler	*Argya fulva*	ins	grd	res	0.00	0.00	0.00	0.28	0.24	0.00	0.02	
Chestnut-bellied Starling	*Lamprotornis pulcher*	ins	grd	res	1.96	0.62	0.00	0.00	0.00	0.00	0.07	
Greater Blue-eared Starling	*Lamprotornis chalybaeus*	gran	grd	res	0.08	0.02	0.00	0.00	0.00	0.22	0.00	
Rufous-tailed Scrub-robin	*Cercotrichas galactotes*	ins	arb	res	0.00	0.00	0.00	0.08	0.00	0.00	0.00	
Black Scrub-robin	*Cercotrichas podobe*	ins	arb	res	0.23	0.12	0.31	0.14	0.04	0.00	0.00	
Northern Anteater-chat	*Myrmecochicla aethiops*	ins	grd	res	0.00	0.00	0.00	0.00	0.06	0.00	0.00	
Northern Wheatear	*Oenanthe oenanthe*	ins	grd	mig	0.00	0.14	0.09	0.19	0.13	0.00	0.00	
Desert Wheatear	*Oenanthe deserti*	ins	grd	res	0.00	0.00	0.00	0.00	0.01	0.00	0.00	
Black-eared Wheatear	*Oenanthe hispanica*	ins	grd	mig	0.00	0.00	0.04	0.00	0.00	0.05	0.04	
White-billed Buffalo-weaver	*Bubalornis albirostris*	gran	grd	res	0.38	0.02	0.09	0.00	0.00	0.00	0.00	
Speckle-fronted Weaver	*Sporopipes frontalis*	gran	grd	res	1.04	0.66	0.13	0.00	0.00	0.00	0.00	
Little Weaver	*Ploceus luteolus*	ins	arb	res	0.08	0.28	0.04	0.00	0.04	0.00	0.00	
Village Weaver	*Ploceus cucullatus*	gran	grd	res	0.02	0.00	0.00	0.00	0.00	0.00	0.00	
Red-cheeked Cordonbleu	*Uraeginthus bengalus*	gran	grd	res	0.00	0.06	0.04	0.00	0.00	0.00	0.00	
Bronze Mannikin	*Spermestes cucullata*	gran	grd	res	0.04	0.00	0.00	0.00	0.00	0.00	0.00	
African Silverbill	*Euodice cantans*	gran	grd	res	0.06	0.00	0.00	0.06	0.25	0.10	0.07	
Northern Grey-headed Sparrow	*Passer griseus*	gran	grd	res	0.44	0.00	0.00	0.33	0.00	0.00	0.00	
Sudan Golden Sparrow	*Passer luteus*	gran	grd	res	0.00	0.57	0.00	0.50	2.06	4.67	1.85	
Sahel Bush-sparrow	*Gymnoris dentata*	gran	grd	res	0.00	0.02	0.00	0.00	0.00	0.00	0.00	
Tawny Pipit	*Anthus campestris*	ins	grd	mig	0.04	0.11	0.04	0.00	0.03	0.00	0.00	
Western Yellow Wagtail	*Motacilla flava*	ins	grd	mig	0.02	0.00	0.27	0.00	0.00	0.00	0.00	***
Tawny Pipit	*Anthus campestris*	ins	grd	mig	0.04	0.11	0.04	0.00	0.03	0.00	0.00	

Table S5. Woody cover (%) of 19 woody species as a function of the distance to the nearest borehole (N=48), as determined in a simple regression and a multiple regression analysis with latitude as additional variable. The table gives the unstandardized coefficients (a=constant, b_{km}=distance to borehole in km; b_{lat}=latidude), the standardised coefficient of the distance to the borehole (β_{km}) and its significance level (P_{km}<0.01 **, P<0.05 *). All relationships are positive (higher cover at larger distance), except those printed in italic. Woody species with a high bird density are indicated (●).

regression analyses	simple				multiple				
	a	b_{km}	β_{km}	P_{km}	A	b_{km}	b_{lat}	β_{km}	P_{km}
Acacia senegal ●	0.027	0.001	0.078		1.62	0.002	-0.099	0.137	
Acacia tortilis ●	0.141	0.050	0.242		17.40	0.060	-1.096	0.294	*
Adenium obesum	0.000	0.000	0.064		0.02	0.000	0.001	0.049	
Balanites aegyptiaca ●	1.126	0.042	0.087		115.61	0.111	-7.133	0.230	
Bauhinia rufescens	0.000	0.000	0.372	**	0.2	0.000	0.001	0.359	*
Boscia senegalensis	0.713	0.005	0.034		*-24.83*	*-0.100*	*1.592*	*-0.068*	
Calotropis procera	0.386	0.004	0.023		*-16.26*	*-0.006*	*1.037*	*-0.037*	
Combretum glutinosum	0.039	0.001	0.023		5.17	0.004	-0.320	0.106	
Combretum micranthum	-0.001	0.000	0.298	*	0.00	0.000	-0.000	0.299	*
Dalbergia melanoxylon	-0.000	.0000	0.125		-0.01	0.000	0.000	0.112	
Euphorbia balsamifera	-0.001	0.000	0.298	*	0.00	0.000	-0.000	0.299	*
Feretia apodanthera	0.000	0.000	0.030		0.05	0.000	-0.003	0.076	
Guiera senegalensis	-0.036	0.007	0.299		0.01	0.007	-0.003	0.300	*
Leptadenia pyrotechnica	-0.026	0.008	0.399	**	-2.39	0.006	0.147	0.323	*
Maerua crassifolia	0.000	0.000	0.088		-0.09	0.000	0.006	0.046	
Salvadora persica ●	0.002	0.001	0.098		-0.69	0.000	0.043	0.029	
Sclerocarya birrea	0.515	0.001	0.007		58.63	0.037	0.710	0.169	
Tamarindus indica	-0.001	0.000	0.262		-0.07	0.000	0.004	0.223	
Ziziphus mauritiana	0.007	0.000	0.028		-0.01	0.000	0.001	0.027	
all woody species	0.123	2.919	0.177		155.39	0.215	-9.499	0.310	*
preferred species ●	0.992	0.085	0.149		104.06	0.147	-6.422	0.259	

Table S6. Bird density as a function of the distance to the nearest borehole (N=24, combining bird counts from January and December 2014), as determined in a simple regression and a multiple regression analysis with latitude as additional variable. The table gives the unstandardized coefficients (a=constant, b_{km}=distance to borehole in km; b_{lat}=latidude), the standardised coefficient of the distance to the borehole (β_{km}) and its significance level (P_{km}<0.01 **, P<0.05 *). All relationships are positive (higher cover at larger distance), except those printed in italic.

regression analyses		simple				multiple				
		a	b_{km}	β_{km}	P_{km}	a	b_{km}	b_{lat}	β_{km}	P_{km}
Subalpine Warbler	*Sylvia cantillans*	0.095	0.034	0.237		11.634	0.044	-0.724	0.306	
Bonelli's Warbler	*Phylloscopus bonelli*	-0.133	0.054	0.383		11.87	0.064	-0.753	0.456	*
insectivorous, arboreal migrants		-0.049	0.108	0.423	*	15.849	0.122	-0.998	0.476	*
Insectivorous, arboreal residents		*0.696*	*-0.025*	*-0.108*		*16.657*	*-0.012*	*-0.996*	*-0.050*	
Common Hoopoe	*Upupa epops*	*0.155*	*-0.016*	*-0.269*		*-6.639*	*-0.021*	*0.427*	*-0.368*	**
Woodchat Shrike	*Lanius senator*	*0.416*	*-0.039*	*-0.545*	**	*3.155*	*-0.036*	*-0.172*	*-0.512*	**
insectivorous, ground-feeding migrants		*0.670*	*-0.036*	*-0.310*		*-15.340*	*-0.049*	*1.005*	*-0.429*	*
insectivorous, ground-feeding residents		0.474	0.052	0.131		15.050	0.065	-0.915	0.162	
granivorous, ground-feeding residents		-0.125	0.309	0.250		44.366	0.348	-2.793	0.281	
all bird species		1.358	0.494	0.056		56.600	0.541	-3.468	0.158	

Table S7. Woody cover (%) in a 1-ha site near Souilène (1989) compared to 10 4.5-ha sites in the surrounding (2014-2015). Woody species with a high bird density are indicated (●). Results of one-way analyses of variance: P < 0.001 ***, P < 0.01 **, P < 0.05 *. Averages also shown in Fig. 11A.

year	1989	2014/5	P
sites (N)	1	10	
Acacia senegal ●	0.500	0.019	***
Acacia tortilis ●	23.500	0.626	***
Balanites aegyptiaca ●	12.500	0.557	***
Boscia senegalensis	1.600	1.117	
Calotropis procera	0.000	0.111	
Combretum glutinosum	0.500	0.000	***
Leptadenia pyrotechnica	0.000	0.059	
Salvadora persica ●	0.000	0.031	
Ziziphus mauritiana	0.500	0.024	***
all woody species	39.100	2.577	***
preferred species ●	36.500	1.233	***

Table S8. Bird density (n/ha) in a 1-ha site near Souilène during the dry season in 1993/94 (October-January; 4 counts per month; data from Tréca et al. (1996) and in the surrounding of this site in October-January 2014/15. Results of one-way analyses of variance: P < 0.001 ***, P < 0.01 **, P < 0.05 *. Averages are shown for arboreal birds in Fig. 11B and for birds feeding on the ground in Fig. 11C. Olivaceous and Isabelline Warblers *Iduna pallida* and *I. opaca* were lumped, as were Common and Iberian Chiffchaffs *Phylloscopus collybita* and *P. ibericus*.

food/habitat/status; year		food	hab	status	1993/4	2014/5	P
sites (N)					1	10	
Area surveyed (ha)					20.0	67.3	
Number of bird species					34	36	
insectivorous, arboreal migrants (n/ha)		ins	arb	mig	4.38	0.38	***
Insectivorous, arboreal residents (n/ha)		ins	arb	res	2.32	.40	**
insectivorous, ground-feeding migrants (n/ha)		ins	grd	mig	1.50	.54	*
insectivorous, ground-feeding residents (n/ha)		ins	grd	res	2.19	.91	
granivorous, ground-feeding residents (n/ha)		gran	grd	res	20.89	.64	***
all bird species (n/ha)					31.38	3.37	***
Double-spurred Francolin	*Pternistis bicalcaratus*	gran	grd	res	0.00	0.02	
African Collared-dove	*Streptopelia roseogrisea*	gran	grd	res	3.75	0.00	**
Mourning Collared-dove	*Streptopelia decipiens*	gran	grd	res	0.63	0.00	**
Vinaceous Dove	*Streptopelia vinacea*	gran	grd	res	0.25	0.05	
Laughing Dove	*Spilopelia senegalensis*	gran	grd	res	10.88	0.00	**
Namaqua Dove	*Oena capensis*	gran	grd	res	0.69	0.10	*
Spotted Thick-knee	*Burhinus capensis*	ins	grd	res	0.00	0.01	
Black-headed Lapwing	*Vanellus tectus*	ins	grd	res	0.00	0.20	
Common Buttonquail	*Turnix sylvaticus*	gran	grd	res	0.55	0.00	
Blue-naped Mousebird	*Urocolius macrourus*	fruit	arb	res	0.38	0.74	
African Grey Hornbill	*Lophoceros nasutus*	ins	grd	res	0.00	0.02	
Red-billed Hornbill	*Tockus erythrorhynchus*	ins	grd	res	0.81	0.00	**
Common Hoopoe	*Upupa epops*	ins	grd	mig	0.19	0.00	**
Abyssinian Roller	*Coracias abyssinicus*	ins	grd	res	0.00	0.05	
Vieillot's Barbet	*Lybius vieilloti*	ins	arb	res	0.13	0.00	**
Sahelian Woodpecker	Dendropicos elachus	ins	arb	res	0.19	0.00	
Rose-ringed Parakeet	*Psittacula krameri*	fruit	arb	res	0.06	0.00	
Black-crowned Tchagra	*Tchagra senegalus*	ins	grd	res	0.00	0.01	
Great Grey Shrike	*Lanius excubitor*	ins	grd	res	0.00	0.02	
Woodchat Shrike	*Lanius senator*	ins	grd	mig	0.06	0.16	
Black-crowned Sparrow-lark	*Eremopterix nigriceps*	gran	grd	res	0.00	0.05	
Horsfield's Bushlark	*Mirafra javanica*	ins	grd	res	0.40	0.12	
Senegal Eremomela	*Eremomela pusilla*	Ins	arb	res	0.00	0.02	
Bleating Camaroptera	*Camaroptera brachyura*	Ins	arb	res	0.75	0.03	***
Tawny-flanked Prinia	*Prinia subflava*	Ins	arb	res	0.19	0.02	*
Olivaceous/Isabelline Warbler	*Iduna pallida/opaca*	Ins	arb	mig	0.44	0.02	*
Common Bulbul	*Pycnonotus barbatus*	Ins	arb	res	0.00	0.04	
Western Bonelli's Warbler	*Phylloscopus bonelli*	ins	arb	mig	2.13	0.04	***
Western Orphean Warbler	*Sylvia hortensis*	ins	arb	mig	0.63	0.15	
Sardinian Warbler	*Sylvia melanocephala*	ins	arb	mig	0.00	0.01	
Subalpine Warbler	*Sylvia cantillans*	ins	arb	mig	0.81	0.06	***
Common Whitethroat	*Sylvia communis*	ins	arb	mig	0.00	0.09	
Chestnut-bellied Starling	*Lamprotornis pulcher*	ins	grd	res	0.94	0.47	
Greater Blue-eared Starling	*Lamprotornis chalybaeus*	gran	grd	res	0.06	0.00	**
Rufous-tailed Scrub-robin	*Cercotrichas galactotes*	ins	arb	res	0.00	0.02	
Black Scrub-robin	*Cercotrichas podobe*	ins	arb	res	1.06	0.26	
Spotted Flycatcher	*Muscicapa striata*	ins	arb	mig	0.06	0.00	
European Pied Flycatcher	*Ficedula hypoleuca*	ins	arb	mig	0.31	0.00	
Common Redstart	*Phoenicurus phoenicurus*	ins	grd	mig	0.88	0.00	**
Northern Wheatear	*Oenanthe oenanthe*	ins	grd	mig	0.06	0.13	
Black-eared Wheatear	*Oenanthe hispanica*	ins	grd	mig	0.15	0.02	
Pygmy Sunbird	*Hedydipna platurus*	nectar	arb	res	0.06	0.00	
Beautiful Sunbird	*Cinnyris pulchella*	nectar	arb	res	0.06	0.00	
White-billed Buffalo-weaver	*Bubalornis albirostris*	gran	grd	res	0.00	0.07	
Chestnut-crowned Sparrow-weaver	*Plocepasser superciliosus*	gran	grd	res	0.00	0.05	
Speckle-fronted Weaver	*Sporopipes frontalis*	gran	grd	res	2.88	0.07	***
Little Weaver	*Ploceus luteolus*	ins	arb	res	0.00	0.02	
Red-cheeked Cordon-bleu	*Uraeginthus bengalus*	gran	grd	res	0.69	0.05	***
House Sparrow	*Passer domesticus*	gran	grd	res	0.06	0.00	
Northern Grey-headed Sparrow	*Passer griseus*	gran	grd	res	0.44	0.00	**
Sudan Golden Sparrow	*Passer luteus*	gran	grd	res	0.00	0.17	
Tree Pipit	*Anthus trivialis*	ins	grd	mig	0.25	0.00	
Tawny Pipit	*Anthus campestris*	ins	grd	mig	0.00	0.09	
Western Yellow Wagtail	*Motacilla flava*	ins	grd	mig	0.00	0.15	

Table S9. Bird density (n/ha) in a 25-ha site in the NW Ferlo, between Richard-Toll and Souilène during the dry season in 1960-1962; 10 counts; data from Morel *et al*. (1968) and in the surrounding on 25 sites in January and December 2014 and February and October 2015. Results of one-way analyses of variance: P < 0.001 ***, P < 0.01 **. Averages are shown for arboreal birds in Fig. 12B and for birds feeding on the ground in Fig. 12C. Common and Iberian Chiffchaffs *Phylloscopus collybita* and *P. ibericus* were lumped.

food/habitat/status; year		food	hab.	status	1960/2	2014/5	P
sites (N); 10 times counted					1	25	
area surveyed (ha)					250	123	
number of bird species (N)					54	24	
insectivorous, arboreal migrants (n/ha)		ins	arb	mig	0.59	0.40	
Insectivorous, arboreal residents (n/ha)		ins	arb	res	0.85	0.21	
insectivorous, ground-feeding migrants (n/ha)		ins	grd	mig	0.69	0.04	
insectivorous, ground-feeding residents (n/ha)		ins	grd	res	0.22	0.02	***
granivorous, ground-feeding residents (n/ha)		gran	grd	res	1.45	0.88	***
all bird species (n/ha)					3.82	1.64	
Helmeted Guineafowl	*Numida meleagris*	gran	grd	res	0.03	0.00	
Double-spurred Francolin	*Pternistis bicalcaratus*	gran	grd	res	0.01	0.00	
African Collared-dove	*Streptopelia roseogrisea*	gran	grd	res	0.15	0.00	
Vinaceous Dove	*Streptopelia vinacea*	gran	grd	res	0.01	0.00	
Laughing Dove	*Spilopelia senegalensis*	gran	grd	res	0.06	0.01	
Namaqua Dove	*Oena capensis*	gran	grd	res	0.21	0.75	
Chestnut-bellied Sandgrouse	*Pterocles exustus*	gran	grd	res	0.11	0.00	
Spotted Thick-knee	*Burhinus capensis*	ins	grd	res	0.03	0.00	
Black-headed Lapwing	*Vanellus tectus*	ins	grd	res	0.05	0.00	
Cream-coloured Courser	*Cursorius cursor*	ins	grd	mig	0.02	0.00	
Blue-naped Mousebird	*Urocolius macrourus*	fruit	arb	res	0.06	0.06	
Red-billed Hornbill	*Tockus erythrorhynchus*	ins	grd	res	0.06	0.00	
Common Hoopoe	*Upupa epops*	ins	grd	mig	0.10	0.00	
Green Woodhoopoe	*Phoeniculus purpureus*	ins	grd	res	0.01	0.00	
Abyssinian Roller	*Coracias abyssinicus*	ins	grd	res	0.03	0.00	
Vieillot's Barbet	*Lybius vieilloti*	ins	arb	res	0.02	0.02	
Senegal Parrot	*Poicephalus senegalus*	fruit	arb	res	0.01	0.00	
Rose-ringed Parakeet	*Psittacula krameri*	fruit	arb	res	0.01	0.00	
Black-crowned Tchagra	*Tchagra senegalus*	ins	grd	res	0.00	0.01	
Great Grey Shrike	*Lanius excubator*	ins	grd	res	0.00	0.01	
Woodchat Shrike	*Lanius senator*	ins	grd	mig	0.04	0.02	
Yellow Penduline-tit	*Anthoscopus parvulus*	ins	arb	res	0.04	0.00	
Chestnut-backed Sparrow-lark	*Eremopterix leucotis*	gran	grd	res	0.17	0.00	
Horsfield's Bushlark	*Mirafra javanica*	ins	grd	res	0.02	0.00	
Northern Crombec	*Sylvietta brachyura*	ins	arb	res	0.30	0.02	**
Yellow-bellied Eremomela	*Eremomela icteropygialis*	ins	arb	res	0.12	0.02	
Senegal Eremomela	*Eremomela pusilla*	ins	arb	res	0.00	0.01	
Cricket Warbler	*Spiloptila clamans*	ins	arb	res	0.00	0.03	
Bleating Camaroptera	*Camaroptera brachyura*	ins	arb	res	0.12	0.00	
Desert Cisticola	*Cisticola aridulus*	ins	grd	res	0.02	0.00	
Tawny-flanked Prinia	*Prinia subflava*	ins	arb	res	0.00	0.05	
Melodious Warbler	*Hippolais polyglotta*	ins	arb	mig	0.01	0.00	
Common Bulbul	*Pycnonotus barbatus*	ins	arb	res	0.06	0.00	
Western Bonelli's Warbler	*Phylloscopus bonelli*	ins	arb	mig	0.15	0.16	
Common/Iberian Chiffchaff	*Phylloscopus collybita/ibericus*	ins	arb	mig	0.00	0.02	
Western Orphean Warbler	*Sylvia hortensis*	ins	arb	mig	0.13	0.04	
Subalpine Warbler	*Sylvia cantillans*	ins	arb	mig	0.08	0.12	
Common Whitethroat	*Sylvia communis*	ins	arb	mig	0.21	0.06	
Chestnut-bellied Starling	*Lamprotornis pulcher*	ins	grd	res	0.01	0.00	
Greater Blue-eared Starling	*Lamprotornis chalybaeus*	gran	grd	res	0.27	0.00	
Rufous-tailed Scrub-robin	*Cercotrichas galactotes*	ins	arb	res	0.04	0.00	
Black Scrub-robin	*Cercotrichas podobe*	ins	arb	res	0.02	0.06	
Spotted Flycatcher	*Muscicapa striata*	ins	arb	mig	0.01	0.00	
Common Redstart	*Phoenicurus phoenicurus*	ins	grd	mig	0.10	0.00	
Northern Wheatear	*Oenanthe oenanthe*	ins	grd	mig	0.25	0.01	***
Black-eared Wheatear	*Oenanthe hispanica*	ins	grd	mig	0.02	0.00	
Pygmy Sunbird	*Hedydipna platurus*	nectar	arb	res	0.04	0.02	
Scarlet-chested Sunbird	*Chalcomitra senegalensis*	nectar	arb	res	0.00	0.01	
Beautiful Sunbird	*Cinnyris pulchella*	nectar	arb	res	0.15	0.00	
White-billed Buffalo-weaver	*Bubalornis albirostris*	gran	grd	res	0.22	0.01	***
Speckle-fronted Weaver	*Sporopipes frontalis*	gran	grd	res	0.02	0.01	
Red-headed Quelea	*Quelea erythrops*	gran	grd	res	0.08	0.00	
Little Weaver	*Ploceus luteolus*	ins	arb	res	0.00	0.00	
Village Weaver	*Ploceus cucullatus*	gran	grd	res	0.00	0.08	

Green-winged Pytilia	*Pytilia melba*	gran	grd	res	0.04	0.00
Red-cheeked Cordon-bleu	*Uraeginthus bengalus*	gran	grd	res	0.00	0.02
Cut-throat Finch	*Amadina fasciata*	gran	grd	res	0.02	0.00
African Silverbill	*Euodice cantans*	gran	grd	res	0.03	0.00
Northern Grey-headed Sparrow	*Passer griseus*	gran	grd	res	0.01	0.00
Sudan Golden Sparrow	*Passer luteus*	gran	grd	res	0.01	0.00
Yellow-spotted Bush-sparrow	*Gymnoris pyrgyta*	ins	arb	res	0.03	0.00
Tree Pipit	*Anthus trivialis*	ins	grd	mig	0.05	0.00
Tawny Pipit	*Anthus campestris*	ins	grd	mig	0.11	0.00
Western Yellow Wagtail	*Motacilla flava*	ins	grd	mig	0.00	0.01

Table S10. Woody cover (%) in grazed and ungrazed area in Widou Thiengoly in January and December 2014. Woody species with a high bird density are indicated (●). Results of one-way analyses of variance: P<0.001 ***, P<0.01 **, P<0.05 *. Averages also shown in Fig. 14A. To increase sample size for the grazed area, 9 sites within some km of Widou were added to 8 sites at 100 and 400 m from the exclosures.

grazed vs. ungrazed sites (N)	grazed 17	ungrazed 8	P
Acacia nilotica ●	0.007	0.000	
Acacia senegal ●	0.051	0.765	**
Acacia seyal ●	0.018	0.006	
Acacia tortilis ●	0.825	0.154	
Adansonia digitata	0.012	0.008	
Balanites aegyptiaca ●	2.944	2.543	
Boscia senegalensis	0.745	1.259	
Calotropis procera	0.171	0.000	
Combretum aculeatum	0.000	0.005	
Commiphora africana	0.002	0.026	*
Combretum glutinosum	0.118	0.028	
Feretia apodanthera	0.001	0.050	*
Grewia tenax	0.000	0.031	*
Sclerocarya birrea	1.265	0.978	
Ziziphus mauritiana	0.010	0.000	
all woody species	6.191	5.869	
preferred species ●	3.846	3.469	

Table S11. Bird density (n/ha) in the Widou Thiengoly exclosures (“ungrazed”) and surroundings (“grazed”) during the dry season, given separately for January 2014 and December 2014, and for both periods combined. Results of one-way analyses of variance: P < 0.001 ***, P < 0.01 **, P < 0.05 *. The density in the grazed and the ungrazed area did not differ between January and December 2014 for most species, so the data were pooled for both periods. Averages for the two months combined are also shown for birds feeding in trees in Fig. 14B and for birds feeding on the ground in 14C.

food/habitat/status; grazed vs. ungrazed		food	hab.	status	grazed			ungrazed			grazed-ungrazed		
					Jan14	Dec14	P	Jan14	Dec14	P	grazed	ungrazed	P
sites (N)					5	12		4	4		17	8	
area surveyed (ha)					45.6	42.4		23.5	23.5		44.0	23.5	
number of bird species					26	28		26	30		39	38	
insectivorous, arboreal migrants (n/ha)		ins	arb	mig	0.77	0.78		0.35	0.29		0.78	0.32	
Insectivorous, arboreal residents (n/ha)		ins	arb	res	0.82	0.27	**	0.74	0.35		0.43	0.55	
insectivorous, ground-feeding migrants (n/ha)		ins	grd	mig	0.22	0.36		0.71	0.79		0.31	0.75	**
insectivorous, ground-feeding residents (n/ha)		ins	grd	res	0.99	1.24		1.87	4.80		1.16	3.34	*
granivorous, ground-feeding residents (n/ha)		gran	grd	res	3.53	2.68		17.03	19.55		2.93	18.29	**
all bird species (n/ha)					6.33	5.38		20.71	25.77		5.66	23.24	***
Double-spurred Francolin	*Pternistis bicalcaratus*	gran	grd	res	0.00	0.00		0.05	0.06		0.00	0.05	*
African collared-dove	*Streptopelia roseogrisea*	gran	grd	res	0.19	0.00		0.45	0.00		0.06	0.23	
Mourning Collared-dove	*Streptopelia decipiens*	gran	grd	res	0.00	0.00		0.44	0.00		0.00	0.22	
Vinaceous Dove	*Streptopelia vinacea*	gran	grd	res	0.00	0.06		0.00	0.00		0.04	0.00	
Laughing Dove	*Spilopelia senegalensis*	gran	grd	res	0.05	0.22		2.55	3.05		0.17	2.80	***
Namaqua Dove	*Oena capensis*	gran	grd	res	0.45	1.06		1.70	6.84		0.88	4.27	
Savile's Bustard	*Lophotis savilei*	ins	grd	res	0.00	0.00		0.20	0.17		0.00	0.18	***
Eurasian Thick-knee	*Burhinus oedicnemus*	ins	grd	mig	0.00	0.00		0.05	0.00		0.00	0.03	
Spotted Thick-knee	*Burhinus capensis*	ins	grd	res	0.02	0.00		0.00	0.27		0.01	0.13	
Black-headed Lapwing	*Vanellus tectus*	ins	grd	res	0.00	0.31		0.40	1.17		0.22	0.78	
Blue-naped Mousebird	*Urocolius macrourus*	fruit	arb	res	0.00	0.06		0.00	0.00		0.04	0.00	
Red-billed Hornbill	*Tockus erythrorhynchus*	ins	grd	res	0.04	0.23		0.85	0.29		0.18	0.57	
Common Hoopoe	*Upupa epops*	ins	grd	mig	0.00	0.02		0.00	0.11		0.01	0.06	
Vieillot's Barbet	*Lybius vieilloti*	ins	arb	res	0.00	0.02		0.00	0.06		0.01	0.03	
Black-crowned Tchagra	*Tchagra senegalus*	ins	grd	res	0.09	0.04		0.17	0.06		0.05	0.11	
Great Grey Shrike	*Lanius excubator*	ins	grd	res	0.04	0.02		0.00	0.17		0.02	0.08	
Woodchat Shrike	*Lanius senator*	ins	grd	mig	0.09	0.09		0.54	0.11		0.09	0.32	*
Sennar Penduline-tit	*Anthoscopus punctifrons*	ins	arb	res	0.19	0.00		0.00	0.00		0.06	0.00	
Black-crowned Sparrow-lark	*Eremopterix nigriceps*	gran	grd	res	0.00	0.00		0.00	0.33		0.00	0.17	*
Horsfield’s Bushlark	*Mirafra javanica*	ins	grd	res	0.00	0.02		0.15	0.00		0.01	0.08	
Yellow-bellied Eremomela	*Eremomela icteropygialis*	ins	arb	mig	0.12	0.00	*	0.00	0.00		0.03	0.00	
Cricket Warbler	*Spiloptila clamans*	ins	arb	res	0.00	0.13		0.10	0.00		0.09	0.05	
Bleating Camaroptera	*Camaroptera brachyura*	ins	arb	res	0.06	0.00		0.00	0.11		0.02	0.06	
Tawny-flanked Prinia	*Prinia subflava*	ins	arb	res	0.01	0.00		0.00	0.00		0.00	0.00	
Common Bulbul	*Pycnonotus barbatus*	ins	arb	res	0.00	0.00		0.15	0.00		0.00	0.08	
Western Bonelli's Warbler	*Phylloscopus bonelli*	ins	arb	mig	0.22	0.33		0.07	0.03		0.30	0.05	
Western Orphean Warbler	*Sylvia hortensis*	ins	arb	mig	0.10	0.04		0.07	0.06		0.05	0.06	
Sardinian Warbler	*Sylvia melanocephala*	ins	arb	mig	0.01	0.00		0.00	0.00		0.00	0.00	
Subalpine Warbler	*Sylvia cantillans*	ins	arb	mig	0.44	0.37		0.00	0.17		0.39	0.09	
Common Whitethroat	*Sylvia communis*	ins	arb	mig	0.00	0.05		0.20	0.03		0.03	0.11	
Long-tailed Glossy-starling	*Lamprotornis caudatus*	gran	grd	res	0.00	0.00		0.00	0.22		0.00	0.11	
Chestnut-bellied Starling	*Lamprotornis pulcher*	ins	grd	res	0.78	0.62		0.10	2.68	**	0.67	1.39	
Greater Blue-eared Starling	*Lamprotornis chalybaeus*	gran	grd	res	0.00	0.02		0.00	0.06		0.01	0.03	
Rufous-tailed Scrub-robin	*Cercotrichas galactotes*	ins	arb	res	0.09	0.00		0.10	0.00		0.03	0.05	
Black Scrub-robin	*Cercotrichas podobe*	ins	arb	res	0.35	0.12		0.39	0.19		0.19	0.29	
Northern Wheatear	*Oenanthe oenanthe*	ins	grd	mig	0.09	0.14		0.12	0.37		0.12	0.25	
Black-eared Wheatear	*Oenanthe hispanica*	ins	grd	mig	0.00	0.00		0.00	0.12		0.00	0.06	
White-billed Buffalo-weaver	*Bubalornis albirostris*	gran	grd	res	0.00	0.02		0.00	0.06		0.01	0.06	
Speckle-fronted Weaver	*Sporopipes frontalis*	gran	grd	res	0.97	0.66		0.00	1.88		0.75	0.94	
Little Weaver	*Ploceus luteolus*	gran	grd	res	0.00	0.28		0.00	0.00		0.20	0.00	
Green-winged Pytilia	*Pytilia melba*	gran	grd	res	0.00	0.00		0.10	0.00		0.00	0.05	
Red-cheeked Cordon-bleu	*Uraeginthus bengalus*	gran	grd	res	0.05	0.06		0.00	0.00		0.05	0.00	
African Silverbill	*Euodice cantans*	gran	grd	res	0.49	0.00		0.45	0.22		0.14	0.34	
Northern Grey-headed Sparrow	*Passer griseus*	gran	grd	res	0.12	0.00	*	3.75	1.20		0.04	2.47	*
Sudan Golden Sparrow	*Passer luteus*	gran	grd	res	1.22	0.57		7.55	5.63		0.76	6.59	*
Sahel Bush-sparrow	*Gymnoris dentata*	gran	grd	res	0.00	0.02		0.00	0.00		0.01	0.00	
Tawny Pipit	*Anthus campestris*	ins	grd	mig	0.04	0.11		0.00	0.07		0.09	0.04	