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Selection by birds of shrub and tree species in the Sahel

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The Sahel is thinly covered by trees, but nevertheless forms an important habitat for millions of tree-dwelling birds. We describe tree availability and tree selection of 14 insectivorous Afro-Palearctic migrants and 18 Afro-tropical residents (10 insectivores, 3 frugivores and 5 nectarivores) inhabiting the Sahel from the Atlantic to the Red Sea. Of the 304 woody species identified across the region during systematic fieldwork in stratified plots, we noted height and canopy surface of 760,000 individual woody plants. Birds present in trees and shrubs were recorded separately per individual woody plant. 99.5% of the birds were concentrated in only 41 woody species. For 20 out of 32 bird species, Winter Thorn *Faidherbia albida* was the tree species most often used. Two other important tree species were Umbrella Thorn *Acacia tortilis* and Desert Date *Balanites aegyptiaca*. Representing only 11% of the total woody canopy cover, these three species attracted 89% of Western Bonelli's Warblers *Phylloscopus bonelli* and 77% of Subalpine Warblers *Curruca iberiae* + *subalpina* + *cantillans*. High selectivity for particular woody species was typical for migrants and residents, irrespective of their diet. Bird species feeding in shrubs used a larger variety of woody species than bird species feeding in tall trees. The highest bird densities (80–160 birds/ha canopy) were found in three shrubs with a limited distribution in the southern Sahara and northern Sahel: the berry-bearing Toothbrush Tree *Salvadora persica*, the small thorny shrub Sodad *Capparis decidua* and the small tree *Maerua crassifolia*. Other bird-rich woody species were without exception thorny (*Balanites aegyptiaca*, various species of acacia and ziziphus). In contrast, the five woody species most commonly distributed across the region (Cashew *Anacardium occidentale*, African Birch *Anogeissus leiocarpus*, *Combretum glutinosum*, *Guiera senegalensis* and Shea Tree *Vitellaria paradoxa*), representing 27% of the woody cover in the study sites, were rarely visited by foraging birds. In this sub-Saharan region, it is not total woody cover per se that matters to birds, but the presence of specific woody species. This finding has important implications: remote sensing studies showing global increase or decline of woody vegetation without identifying individual species have little value in explaining trends in arboreal bird populations. Local people have a large impact on the species composition of the woody vegetation in the Sahel, with positive and negative consequences for migrants wintering in this region. *Faidherbia albida*, the most important tree for birds in the sub-Saharan dry belt, is highly valued by local people and has the distinction of leafing in winter and being attractive to arthropods. On the other hand, migratory and African bird species have been negatively affected by the rapidly expanding cashew plantations since the early 1980s.

Key words: arboreal birds, Sahel, tree selection, Cashew, Shea Tree, *Faidherbia*

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Birds foraging in woody vegetation are highly selective in their choice of trees and shrubs. Frugivores are concentrated in the few trees where they can find their preferred fruit (e.g. Levey 1988, Herrera 1998, Jordano 2015) and nectarivores select nectar-producing flowering trees (e.g. Feinsinger 1976, Pettet 1977, Symes *et al.* 2008). The same principle applies to the many insectivorous tree-dwelling bird species (Zwarts *et al.* 2015). In West Africa, arboreal birds are concentrated in only 20 out of the 56 most common woody plant species. Woody species disregarded by foraging birds have coriaceous leaves, leaves with latex and/or leaves with a high crude fibre content (Zwarts *et al.* 2015). These traits have evolved as a defence mechanism against herbivorous insects, explaining the scarcity of insectivorous birds foraging in such woody species. Most insectivorous bird species are instead found in woody species with thorns or spines, such as acacias: these woody species have evolved mechanical defences against grazing by large herbivores, at the expense of chemical defences against arthropods. The consequence of this strategy is higher insect loads, precisely why many thorny trees are attractive to insectivorous tree-dwelling birds (Greenberg & Bichier 2005).

In African savannahs, the grazing pressure of large herbivores on woody plants has always been high but became even higher after domesticated herbivores, mostly cattle, sheep and goats, replaced the indigenous grazing fauna during the 20th century (at least in the Sahel; on the East African savannahs herbivore species-richness has remained very high (Prins & Olff 1998). In regions with an annual rainfall >800 mm, however, large herbivores are mostly absent due to the occurrence of the Tsetse Fly *Glossina morsitans*, which is the vector of tripanosomes responsible for causing sleeping sickness (Buxton 1955). This explains why acacias and other thorny shrubs and trees dominate the semi-arid and arid zone (100–600 mm rain/year) and are replaced in the more humid zone by non-thorny woody plants with better defences against arthropods. The humid zone looks greener and lusher than the adjacent more arid Sahel, superficially suggesting a richer food supply, but in fact it is the opposite: trees from savannahs are rich in arthropods and attract more insectivorous birds than trees from the adjacent humid zone (Zwarts *et al.* 2023b).

To unravel the intricate relationships between birds and their Sahelian habitat, Zwarts *et al.* (2015) counted birds per individual woody plant and measured for each woody plant its canopy surface, thus allowing calculation of bird density per ha of canopy and ranking of the attractiveness of woody species for birds. Densities ranged from 0 to 122 birds/ha canopy in the 56 most common tree and shrub species. The initial analysis was restricted to West Africa but covered a wide array of climate zones, where woody species as well as bird species experienced different levels of rainfall. Distributions of tree and bird species rarely overlap one-on-one, which complicates any assessment of tree preference by birds. Tree selection by bird species is therefore described only for woody species that are within the bird's distribution. The present analysis includes and expands upon the data used in Zwarts *et al.* (2015), and covers the entire transient zone south of the Sahara between Atlantic Ocean and Red Sea. Using this much larger data set, we quantify: (1) the distribution of the woody species across the region, (2) tree choice of bird species (species, height), (3) density of bird species foraging in woody species, (4) variation in bird density per woody species relative to traits of woody species presumed to be related to species-specific food supplies (tree size, presence of leaves, flowers, fruit and thorns, production of latex, whether tree is indigenous or exotic), (5) total woody cover of different shrubs and trees, and (6) total number of birds present in the different woody species.

METHODS

The methods used to count birds and woody plants are described in great detail by Zwarts & Bijlsma (2015) and briefly again in Zwarts *et al.* (2023a,b). In summary, birds and woody plants were counted between 2011 and 2019 at 1901 randomly selected study sites (each 4.5 ha) in Africa between 7° and 22°N and between 17°W and 42°E. We used data collected during the dry season (20 November – 10 March), a period during which tree-bird relationships are relatively stable (Zwarts *et al.* 2023d).

We counted and measured all trees and shrubs in the study sites and used the width of the canopy to calculate canopy surface per individual woody plant. Using a laser rangefinder, we measured the height of each larger tree at a distance of at least twice the tree height. The height of trees <4 m was estimated by eye. The width of the canopy was estimated by eye as fraction of the height which was checked in large trees by pacing steps beneath the crown and by taking pictures. A total of 765,960 woody plants with a combined canopy surface of 4,312 million m^2 were registered. Altogether we identified 304 woody species. We scored individual woody plants regarding their opacity on a five-point scale from 'leafless' to 'very dense crown'

(Zwarts & Bijlsma 2015); in this paper we only use the proportion of leafless woody plants. For each study site we calculated the total woody cover per woody species and for all woody species combined. The latter may overestimate the actual woody cover if shrubs occur underneath trees. Indeed, in one site, our method indicated a total woody cover of 105%, but this was an exception because the woody cover in most sites was so low that canopies of different woody plants did not overlap.

Birds present in trees and shrubs were recorded separately per individual woody plant. Each tree and shrub was examined for as long as necessary to detect all birds present (Zwarts & Bijlsma, 2015). This enabled the calculation of absolute bird density per tree species, expressed as birds per ha of canopy. The counts of birds and woody plants were converted into densities per study site, after which average densities were calculated for sites in 150 1° latitude × 1° longitude grid cells. In addition, for each bird species we also determined total woody cover within its distributional range, based on the grid cells where the species occurred. Most bird species were found in about a quarter of the grid cells and the most widely distributed species in half of the grid cells (Zwarts *et al.* 2023b). Distribution maps of the most common arboreal bird species are given as Supplementary Material in Zwarts *et al.* 2023b. The presence of a bird species in the 150 grid cells is used here to define the distribution area of the 32 most common bird species, of which 14 are Afro-Palearctic species (from now on called migrants) and 18 are Afro-tropical species (referred to as residents).

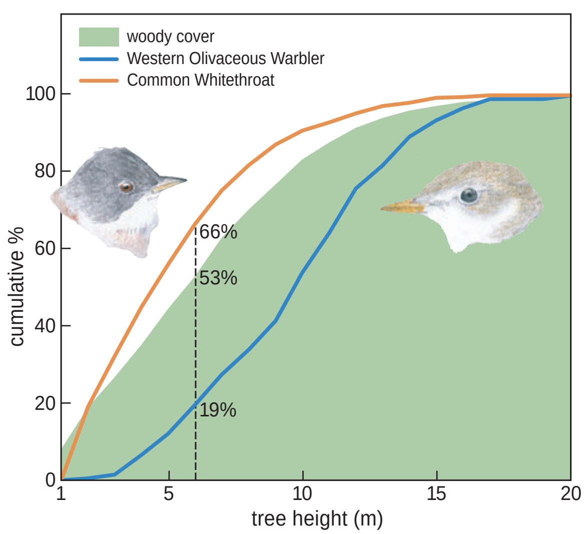

Figure 1. The cumulative frequency distribution of woody cover (%) as a function of height of woody plants ≥1 m used by two bird species compared to the height of all trees and shrubs in the sites where both species were recorded.

For each study site, we determined the average annual rainfall in the period 1950–2000 (Hijmans *et al.* 2005) and used this information to ascertain the average annual rainfall for each site and each grid cell. The grid cells span a range of climate zones from Sahara to Guinean forests, with an annual rainfall between 30 and 1800 mm (see Figure 4 in Zwarts *et al.* 2023a). Strictly, the Sahel is the climate zone where the annual rainfall varies between 100 and 600 mm (Figure 5 in Zwarts *et al.* 2023a) but we use the term Sahel here in a wider sense as the transition zone between Sahara in the north and the humid forests in the south.

In dry areas, the height of the woody vegetation tends to be far lower than in humid areas (Figure S9C). Even when excluding all shrubs ≤1 m, there is still a linear increase of the average height (H) of the woody vegetation from 3 m in the hyper-arid zone (<100 mm rainfall/year) to 6 m in the hyper-humid zone (>1200 mm rainfall/year):

$$H = 0.00166 \times \text{rain} + 2.9$$
$$(r^2 = 0.87, n = 16, P < 0.001), \quad (1)$$

where H = average height (m) of the woody vegetation and rain = annual rainfall (mm); regression line based on average values per rainfall classes of 100 mm over the range 0 to 2400 mm; rainfall classes 1300–2400 were combined in three categories in order to have >1000 woody plants in all categories.

The linear increase of tree height with rainfall explains why bird species confined to arid regions dwell in smaller trees than species typical of humid zones, as for example respectively Eastern Orphean Warbler *Sylvia crassirostris* (recorded in trees 4.7 m high, on average) and Northern Yellow White-eye *Zosterops senegalensis* (8.2 m; see Figure 5A in Zwarts *et al.* 2023b for the distribution of bird species along the rainfall gradient). Within the same rainfall zone, bird species may also differ in foraging height, as exemplified by Western Olivaceous Warbler *Iduna opaca* and Common Whitethroat *Curruca communis*. Western Olivaceous Warbler is typically a canopy-hugging passerine that was not recorded in woody plants <4 m tall, whereas 66% of all Common Whitethroats were detected in shrubs and trees <4 m tall. Had these species not been selective of their feeding niche, 53% of both species would have been expected to use trees up to and including 6 m high (Figure 1), where it was in fact respectively 19% and 66%. In this paper the 6-m threshold is used to discriminate bird species feeding in low and high woody vegetation.

Since the grid cells were unevenly distributed across the region, we calculated the average woody cover for 11 rainfall zones in six longitudinal bands for the region shown on Figure 2 (i.e. Africa between 7° and 22°N and between 17°W and 42°E, in total 10 million km^2) and used the surface area of the subregions (given in Figure S1 of Zwarts *et al.* 2023a) as weighting factors to estimate average woody cover and total woody cover in the region. We applied a split-half method (even and odd numbered sites) to assess the reliability of the estimated total woody cover (see Supplementary Material).

For the analyses of tree use by birds, shrub and tree species were selected in which >0.5% of arboreal birds were found. Tree preference by bird species was quantified with the proportion of birds observed in different woody species compared to the canopy cover of all woody species within the distribution area of each bird species (Table 1). The density of all bird species combined is calculated for 112 woody species, each with >2000 m^2 canopy cover in our sample, for the 29 most common woody species, each >0.9% of the canopy surface relative to the total cover of all woody plants, and separately per bird species (Table 2). Again, bird densities in the various woody species refer to the woody species present within the distribution areas of the bird species. These averages cannot be used to estimate the density of all birds together since most bird species occupy only a proportion of the woody species' distributions, and in differing proportions per bird species. Simply adding densities would, on average, result in an overestimate by a factor of two. Therefore, bird densities per woody species for all species together were calculated for all woody plants in the entire region.

RESULTS

Distribution of woody plants

The total woody cover increased from <1% in the desert to >15% in the humid zone (annual rainfall > 1000 mm) and averaged 9% for the entire region between 7° and 22°N (Figure S1). The five most common woody species each contributed 5–6% to the total woody cover. African Birch *Anogeissus leiocarpus* (Figure S6), *Combretum glutinosum* (Figure S7) and *Guiera senegalensis* (Figure S8) were widely distributed and found in about half of the grid cells though *Guiera* was largely restricted to the less humid zone. Cashew *Anacardium occidentale* (Figure S5) and Shea Tree *Vitellaria paradoxa* (Figure S9) were locally common, but large regional differences were apparent. Cashew was restricted to the more humid zone, being the dominant tree species in Guinea-Bissau and southern Mali but rare in the same humid zone of Central African Republic and southern Chad. Whereas Shea Tree was absent in the humid zone of Senegal and Guinea-Bissau, it was very common in the same climate zone in Mali and Burkina Faso. For *Anogeissus* it was the other way round: widely distributed in the Central African Republic and Chad but an erratic distribution in West Africa. The common denominator for these very common tree species was the scarcity of birds (see below).

Of all tree species available within the range of our study area, very few were preferred by foraging birds. Some of these were scarce or patchy in distribution and therefore, despite being highly attractive to birds, harboured a minor proportion of the overall bird population. Only Umbrella Thorn *Acacia tortilis*, Winter Thorn *Faidherbia* (=*Acacia*) *albida* and Desert Date *Balanites aegyptiaca* were rich in birds as well as widely distributed (Figures S2–S4). All three occurred throughout the region from Senegal to Ethiopia, with *A. tortilis*

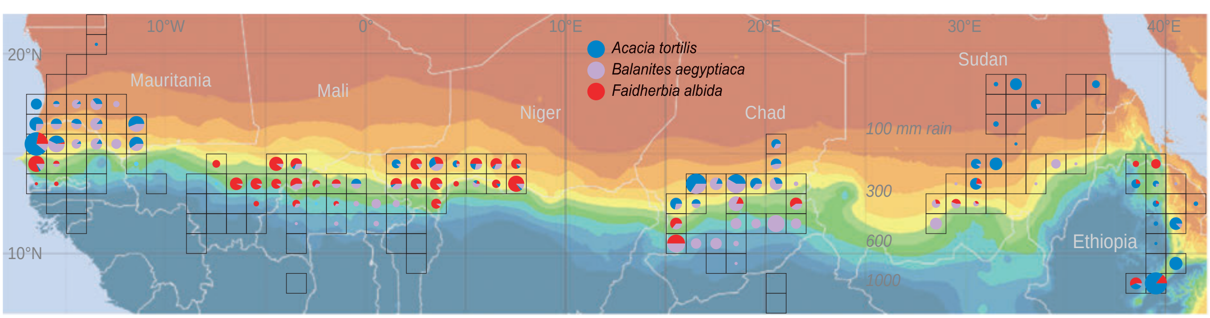

Figure 2. Relative woody cover of three bird-rich woody species combined (data from Figure S2–S4) in 150 grid cells. Woody cover of the three species, relative to woody cover of all species combined, amounts to 8.4%, on average, varying between 0 and 55% per grid cell. The three species were present in 83% of the grid cells.

Table 1. The percentage of the recorded birds found in 41 woody plants shown for the 32 most common bird species. Colours indicate which woody plants attract most birds (rank 1: orange, rank 2: yellow, rank 3: grey). Names of thorny shrubs and trees are shown in bold.

	Insectivorous migrants														Insectivorous residents										Frugivores			Nectarivores				
	Eurasian Wryneck	Iberian Chiffchaff	Common Chiffchaff	Eastern Olivaceous Warbler	Western Olivaceous Warbler	Western Bonelli's Warbler	Western Orphean Warbler	Eastern Orphean Warbler	Lesser Whitethroat	Subalpine Warbler	Rüppell's Warbler	Common Whitethroat	European Pied Flycatcher	Common Redstart	Green Wood Hoope	Grey Woodpecker	Sennar Penduline Tit	Northern Crombec	Yellow-bellied Eremomela	Senegal Eremomela	Green-backed Camaroptera	Tawny-flanked Prinia	Northern Yellow White-eye	Little Weaver	Blue-naped Mousebird	Vieillot's Barbet	Common Bulbul	Pygmy Sunbird	Nile Valley Sunbird	Scarlet-chested Sunbird	Beautiful Sunbird	Variable Sunbird
Acacia asak			7															1				1							2			13
Acacia ataxacantha														2				1		1	10	2						1			1	
Acacia ehrenbergiana		2	1	1		1	1	7	2	1	2							1											4	1		
Acacia etbaica								4	2		10							1											1			
Acacia mellifera			2	3					2									1	3										19	2		
Acacia nilotica			3	12		2		4	7	1	1	3	8	3	2		5	1		2	1	3		2	1	1					2	
Acacia senegal		7	1	2		3	10	11	2	1	4	1		1	2		8	1	1	2	1	1		4		1		3	9	2		
Acacia seyal		2	8	4	9	2	1	4	4		4	6		7	2		8	14	13	1	2	9		6		6		6	2	1	5	13
Acacia sieberiana													5							1	1	1		2		1	3			5	1	
Acacia tortilis	9	28	2	17	8	27	49	26	23	20	26	12		6	2	23	20	9	32	4	1	1		9	6	9	3	3	40	2	2	6
10 OTHER ACACIA's			13						3					2				1				3	2									4
Albizia amara	4													1		2		2			2	1				4		1	1			
Anogeissus leiocarpa													8	1				5		4	2	2		1		6	3	2		3	1	
Azadirachta indica		4		2	5									1							1				24	3	7			1	1	
Balanites aegyptiaca	30	12		6	3	6	13	4	12	26	5	12		5		8	48	13	20	14	11	22	2	13	26	11	2	9	1	2	6	
Bombax costatum																2				3						1		2		9	1	1
Boscia senegalensis							1			1		4		1					4		2											
Capparis decidua		1	2	1				15	7	4	11	6						1	1									2	8			
Commiphora africana			9																3													
Combretum glutinosum				1					1	1		3	5	2	13	2		7	8	10	5	6		1		3	1	19		11	24	1
Combretum micranthum	4											2		5				1		3	10	1						1			2	
Daniellia oliveri													3					1		2			16	1		1	6	3		8	3	3
Diospyros mespiliformis					1									1	2	2					1		7		5	4	2			1	3	
Euphorbia balsamifera		11			1							4		1					3	1										5		
Faidherbia albida	13	12	30	43	49	56	13	11	24	30	11	16		25	21	23		10		8	6	7	7	48	1	14	3	10	1	3	12	9
Ficus exasperata																											28					
Ficus sycomorus															2											4	2					
Ficus thonningii																										10	4					
Guiera senegalensis										1		3							3	1	3	3						1			1	3
Isoberlina doka													8		3												1			2		1
Maerua crassifolia								4	2	1	19	1		1											1			5	1			
Mangifera indica		2			7								8	2		2					1									2		
Mitragyna inermis														3	2	4					1						4			1		
Parkia biglobosa													8		2			1		7		1	18				4	1		2	1	
Piliostigma reticulatum	30		3	1	1		2		1	3		7		6	8	6		1	1	4	6	10	2	1				4	3	1	5	
Prosopis juliflora		4	1												11																	
Pterocarpus lucens														2				4		2	1	1				3	1					
Salvadora persica		4		1			4			2		3										1		1	16			1	2			
Sclerocarya birrea				1			1		1			1		2	7	6		5		4	1	2		1		4		3		2	3	
Tamarindus indica							1							2	8	6		2		3	3	3	5	1		4	4	2		5	3	
Vitellaria paradoxa													3	1		4		6		9	1	1	2	2				6		14	6	
Ziziphus mauritiana					6	1	1	4		1	4	2		7			5			1	5	5		3								2
SUM	91	89	82	94	90	97	96	93	92	94	96	87	57	88	86	92	93	86	93	85	77	85	61	92	80	93	78	82	95	84	79	57
A.tort.+Balanites+Faid.	52	52	32	66	60	89	76	41	59	77	42	40	0	36	23	54	68	32	52	26	19	30	9	70	33	34	8	21	42	7	20	14
all 21 Acacia species	22	51	67	82	66	90	75	67	68	54	57	38	14	47	28	46	40	38	49	19	22	28	9	70	8	33	9	22	78	16	22	45
all 26 thorny species	52	68	79	89	75	97	89	89	87	86	76	59	14	58	39	54	93	52	73	33	38	54	11	85	34	44	11	32	87	18	28	47

Table 2. Birds/ha canopy for the 32 common arboreal bird species, shown for the 29 most common trees and shrubs (each >0.9% of the total woody cover measured in the random study sites during winter) and 13 uncommon trees and shrubs in which birds reach a relatively high density. Five bird species and 5 woody species from the dry zone (<300 mm rainfall/year) are highlighted in dull yellow and 3 bird species and 5 woody species from the humid zone (>900 mm rainfall/year) marked blue. Names of thorny species are in bold. The bird densities are calculated for woody plants present in all sites within the grid cells where the bird species occur (Figures A2 – A34 in Zwarts *et al.* 2022b). Bird density is zero when the cell is empty. A cell is marked with • when a woody species did not occur, or scarcely so, within the distribution area of a bird species (i.e. surface area of the canopy <1000 m^2). Colours indicate common woody plant species in which birds reach their highest densities (rank 1: orange, rank 2: bright yellow).

	Insectivorous migrants														Insectivorous residents										Frugivores			Nectarivores				
29 common species	Eurasian Wryneck 518	Iberian Chiffchaff 227	Common Chiffchaff 707	Eastern Olivaceous Warbler 415	Western Olivaceous Warbler 560	Western Bonelli's Warbler 450	Western Orphean Warbler 287	Eastern Orphean Warbler 247	Lesser Whitethroat 318	Subalpine Warbler 368	Rüppell's Warbler 188	Common Whitethroat 466	European Pied Flycatcher 1124	Common Redstart 608	Green Wood Hoope 589	Grey Woodpecker 562	Sennar Penduline Tit 517	Northern Crombec 646	Yellow-bellied Eremomela 394	Senegal Eremomela 783	Green-backed Camaroptera 752	Tawny-flanked Prinia 725	Northern Yellow White-eye 1017	Little Weaver 579	Blue-naped Mousebird 503	Vieillot's Barbet 652	Common Bulbul 926	Pygmy Sunbird 699	Nile Valley Sunbird 216	Scarlet-chested Sunbird 930	Beautiful Sunbird 850	Variable Sunbird 896
Acacia nilotica			7.3	6.2	0.7	7.3		1.6	8.5	7.4	2.1	4.0	27	2.7	2.6		2.2	0.4		5.6	2.2	5.5		2.7	3.3	0.7		0.3			4.6	
Acacia senegal		4.0	3.4	0.5	0.5	5.6	8.6	2.0	1.0	4.0	1.5	1.1	•	0.3	1.4		2.1	0.2	0.3	0.5	0.7	2.3	•	3.3		0.5		2.4	5.7	2.5		
Acacia seyal			7.9	0.8	2.3	1.9	0.3	1.3	1.1	0.5	0.7	1.4	•	0.9	0.1		0.4	1.4	4.4	13	0.8	2.9	•	1.9		0.4		1.4	0.5	0.5	1.4	1.6
Acacia tortilis	1.0	2.6	0.7	2.4	1.7	23	7.4	2.7	8.3	13	4.9	3.6	•	0.9	0.4	2.2	1.4	1.4	1.9	2.0	0.6	0.6	•	3.8	1.9	1.1	0.5	1.1	14	0.7	4.1	2.7
Albizia amara	2.7	•				•			0.2		•	0.3	•	0.5		0.6		0.5		•	1.5	0.7	•	0.3		0.8		0.7	6.2			
Anacardium occidentale			•					•	•		•		0.9		5.9		•			0.5	0.7				•				•		0.9	
Anogeissus leiocarpus			•		0.2	1.0		•		0.7		0.2	0.5	0.2				0.5		1.5	0.5	0.9		0.2		0.4	0.2	0.4	•	0.4	0.1	
Azadirachta indica				2.6	3.6	0.4		•		1.6	•	0.3		0.8							1.0	0.9		0.5	22	3.2	5.7		•	0.7	0.7	
Balanites aegyptiaca	1.3	1.2		1.2	0.5	3.7	1.8	2.5	3.6	13	1.2	2.4		0.5		0.5	2.0	1.2	1.3	4.8	3.4	6.8	3.2	3.2	6.6	0.7	0.3	1.8	1.0	0.6	2.2	
Boscia senegalensis			•				0.3		0.7	1.5		3.9	•	0.2					0.9		2.7	0.7	•									
Calotropis procera		1.0	•				0.4			0.6		0.2	•						0.5			0.3	•					1.8	12	1.3		•
Combretum glutinosum				0.4	0.1	0.2		•	3.2	0.9		1.1	1.5	0.2	1.8	0.2		1.2	2.1	2.0	1.4	2.1		0.9		0.4	0.4	4.8	•	3.8	8.8	0.5
Combretum micranthum	0.4		•		0.1			•	•		•	1.0	•	0.9			•	0.5		0.9	5.8	0.9		0.3	•			0.9	•		1.4	
Detarium microcarpum		•	•			•	•	•	•		•	0.2					•		•		0.4	0.2		0.2	•			0.4	•			1.0
Eucalyptus spp.			1.8	0.6	0.8			•			•	1.0	•				•				0.2	0.3		0.6			0.3	0.8			0.5	
Faidherbia albida	0.2	0.6	23	5.7	5.3	24	1.8	13	22	14	61	3.2	•	2.0	1.7	1.2		1.5		1.7	1.8	2.6	4.4	15	1.2	1.3	0.4	2.4	4.0	1.6	2.6	1.1
Guiera senegalensis								•		0.4	•	0.6							0.4	0.1	0.8	0.8						0.2	•		0.2	1.3
Hyphaene thebaica		•	•																		0.8	1.3		1.1	•	1.2			•		0.4	•
Isoberlina doka	•	•	•			•		•	•	•	•		1.0		5.0		•		•	0.4	0.5				•		2.1	0.7	•	1.4		2.2
Lannea acida	2.4		•	1.0				•			•				6.2				•				•					1.4	•			
Leptadenia pyrotechnica			•				0.3			1.4	2.3	0.8	•					1.4									1.6		•		•	•
Parkia biglobosa						1.2		•	•	0.7	•	0.3	1.0				•	0.5	•	2.4	0.2	0.9	2.8	0.6	•			1.2	•	0.6	0.3	
Piliostigma reticulatum	2.2	2.1	1.3	0.4	0.6	0.5	1.5	•	1.9	7.3	•	4.3		1.6	2.4	1.0		0.2	0.6	1.8	4.3	7.8	1.0	0.4				2.3	•	0.4	1.9	
Pterocarpus lucens			•					•			•			0.7	•		•	1.5		1.4	1.2	1.0			•	1.9	1.3	0.3	•			
Sclerocarya birrea			•	0.7		0.7	0.4	•	0.7	0.5	•	0.6		0.4	6.1	1.0		1.0		2.2	0.7	1.5		0.4		0.7		1.4	•	1.4	2.0	
Sterculia setigera			•					•	•		•	0.4				1.7				0.5		0.5		0.9	•	0.6		0.6	•			
Tamarindus indica			•		0.5	2.5	1.6	•		2.2	•	0.2		0.7	4.8	1.5		0.6		2.3	2.4	3.1	1.1	0.6		0.8	0.9	1.3	•	1.8	1.0	
Vitellaria paradoxa					0.1			•	•		•		0.2	0.1		0.7	•	0.9		1.3	0.3	0.4	0.1	1.2	•			2.2	•	2.0	1.5	
Ziziphus mauritiana		2.5	2.6		5.0	2.4	1.4	•	0.9	6.2	25	3.4	•	4.4			3.4			1.7	9.7	12		5.2	20	0.7	•	4.2	•			
13 bird-rich species																																
Acacia ataxacantha			•					•		2.5	•			1.6				0.7		1.5	21	6.5						5.3			1.7	
Acacia ehrenbergiana	•	2.8	3.6	4.1	•	9.1	3.0	6.7	11	12	5.2	8.5	•	•	•	•	•	1.9	•				•	1.2				5.5	13	5.4		
Acacia etbaica	•	•	•	•	•	•	•	2.8	16	•	25	3.6	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		•	•	•
Bauhinia rufescens		•	•					•		15	•	7.1	•	2.1		9.4		3.5	9.4		5.7	6.7		5.6						•	•	•
Bombax costatum	•		•					•	•		•	1.6				3.3				5.8	0.7	2.3			•			6.2	•	22	3.9	2.6
Capparis decidua	•	•	•	2.4				28	26	51	34	39	•	•	•			3.6	4.6				•	1.7				10	70	•	•	•
Daniellia oliveri		•	•			•	•	•	•	•	•		0.8					0.7	•	3.2	0.8	1.1	6.6	2.1	•	0.9	4.4	5.7	•	5.8	3.7	3.2
Diospyros mespiliformis				2.3				•			•	1.0		2.1	2.1	2.1			•		4.2	2.2	8.4		•	7.1	2.6	0.7	•	1.4	5.4	
Ficus thonningii		•	•	•			•	•			•		•					1.5	•		2.8	6.8			•	13	8.8	3.9	•	1.9	2.1	
Maerua crassifolia	•	•	•				•		24	32	80	18	•	•	•	•	•	•	•	•	•	•	•	•	•		•	•	7.5	•	•	•
Salvadora persica	•	17	•	3.7			24	•		47		26	•	•	•	•				•		12	•	8.8	98		•	13	•	•	•	•
Ziziphus mucronate			•	•		3.7		•	•	7.6	•	2.8	•				•		•	3.7	10	10	•	3.6	•				•	•		
Ziziphus spina-christi		•		3.0	5.6	3.6	4.5		7.6	14.		1.6	•	1.5		•	•		2.1		6.2	8.5	•	6.5				2.0				

in drier habitats than *Faidherbia* and *Balanites* (Figure 2). The three species were present in 31–59% of the grid cells (Figures S2–S4). Their average woody cover in each grid cell varied mostly between 2 and 3% of the total woody cover in the zone with 100 to 600 mm rainfall per year.

Usage of woody plant species

As a first step to quantify the use of trees and shrubs by the 32 common arboreal bird species, we calculated their relative numbers counted in woody species that were most often frequented by birds (Table 1). Among the woody plants most important for birds were several of the 11 acacia species, including *Faidherbia albida*. There were 10 other acacia species with smaller distribution areas (e.g. only in Ethiopia: *Acacia abyssinica*, *Acacia lahai*, or only in Sudan and Ethiopia: *Acacia oerfota*) that were also attractive to arboreal birds, such as Common Chiffchaff *Phylloscopus collybita* in Ethiopia (lumped in Table 1). In terms of bird numbers, the 21 acacia species harboured 57% of the 14 migrant bird species and 35% of the resident bird species. Thorny tree species in general, not just acacia species, were very important to migrants (73% of the 14 migrants were found in 26 thorny species; in bold highlighted in Table 1), but less so to residents, at 46%.

Tree choice varied enormously between bird species, from highly specific to wide-ranging. For example, 99% of Western Bonelli's Warbler *Phylloscopus bonelli* were observed in just eight woody species and mostly in *Faidherbia albida* (56%). *Faidherbia* was the outstanding choice of tree for nine other bird species, for five species the second choice, and for six more species the third choice of tree. For 21 out of the 32 bird species, the choice for *Faidherbia* stands out from the tree species available, only matched in significance by *Acacia tortilis* and *Balanites aegyptiaca*. These three tree species are of prime importance for the insectivorous residents (except African Yellow-White-eye), and even more so for the insectivorous migrants (except for European Pied Flycatcher *Ficedula hypoleuca*, whose wintering grounds lie south of the distribution of *Faidherbia*, as they do for the resident African Yellow White-eye; see Figures S26 and S27 in Zwarts *et al.* 2023b). Of the insectivorous migrants (excluding Pied Flycatcher), 32–89% of the birds were concentrated in *Faidherbia*, *Acacia tortilis* and *Balanites* (56%, on average), as were 19–70% (41%, on average) of the insectivorous residents (excluding African Yellow White-eye). Three frugivorous species and five sunbirds were also frequently found in the same three woody species, but with lower relative numbers (25 and 21%, on average, respectively). Sunbirds were mainly recorded in woody species that flower during the dry season (e.g. *A. tortilis*, *Combretum glutinosum*) or species (e.g. Shea Tree) that host flowering parasites (*Tapinanthus* spp.). The frugivores were seen mainly in five fruit-bearing trees: Neem *Azadirachta indica*, *Balanites* and three *Ficus* species.

Bird density per woody plant species

In our study sites across the width of sub-Saharan Africa, we identified 304 woody species, of which more than half were relatively rare or had a patchy distribution. Only 144 woody species had a total canopy surface area of larger than 1000 m^2 (measured in a horizontal plane: 1000 m^2 = 0.023% per tree species of the total woody cover measured in the study sites). Most bird species also occurred in just a part of the study area. The number of woody species with a canopy surface >1000 m^2 within the range of the different bird species varied between 24 (Eastern Orphean Warbler *Curruca crassirostris*) and 128 (Green-backed Camaroptera).

A wide distribution and high relative density of trees did not necessarily equate to high numbers of birds in those trees. Indeed, the most widespread among trees and shrubs, *Guiera senegalensis*, a shrub usually 1–2 m tall, is the commonest species, comprising 7% of the total woody cover measured in all study sites combined (Figure S8). Even so, 20 out of 29 bird species were never recorded in *Guiera* (taking into account that *Guiera* does not occur within the range of three bird species mentioned in Table 2). Several other common tree species, notably *Combretum glutinosum*, Shea Tree and Cashew, characteristically held few birds, if any. In the same vein, tree species able to grow to majestic size, like *Albizia amara* and African locust bean tree *Parkia biglobosa*, were often remarkably poor in birds during the dry season.

Nearly all acacia species were rich in birds to the extent that all 32 bird species covered here were recorded in *A. tortilis* and all but two in *Faidherbia*. Clearly, these tree species are not just attractive to generalists but also to specialists. Ten bird species reached their highest density in *Faidherbia* (orange cells in Table 2) and nine in four other acacia species: *A. tortilis* (3 bird species), *A. nilotica* (2), *A. seyal* (2) and *A. senegal* (2). Seventeen of the 24 insectivorous species (71%) reached their maximal density in these five acacia species, but only two of the five sunbirds and, not surprisingly, none of the three frugivores.

The 29 most common woody species contribute, in total, 74.8% to the total woody cover. Among the other

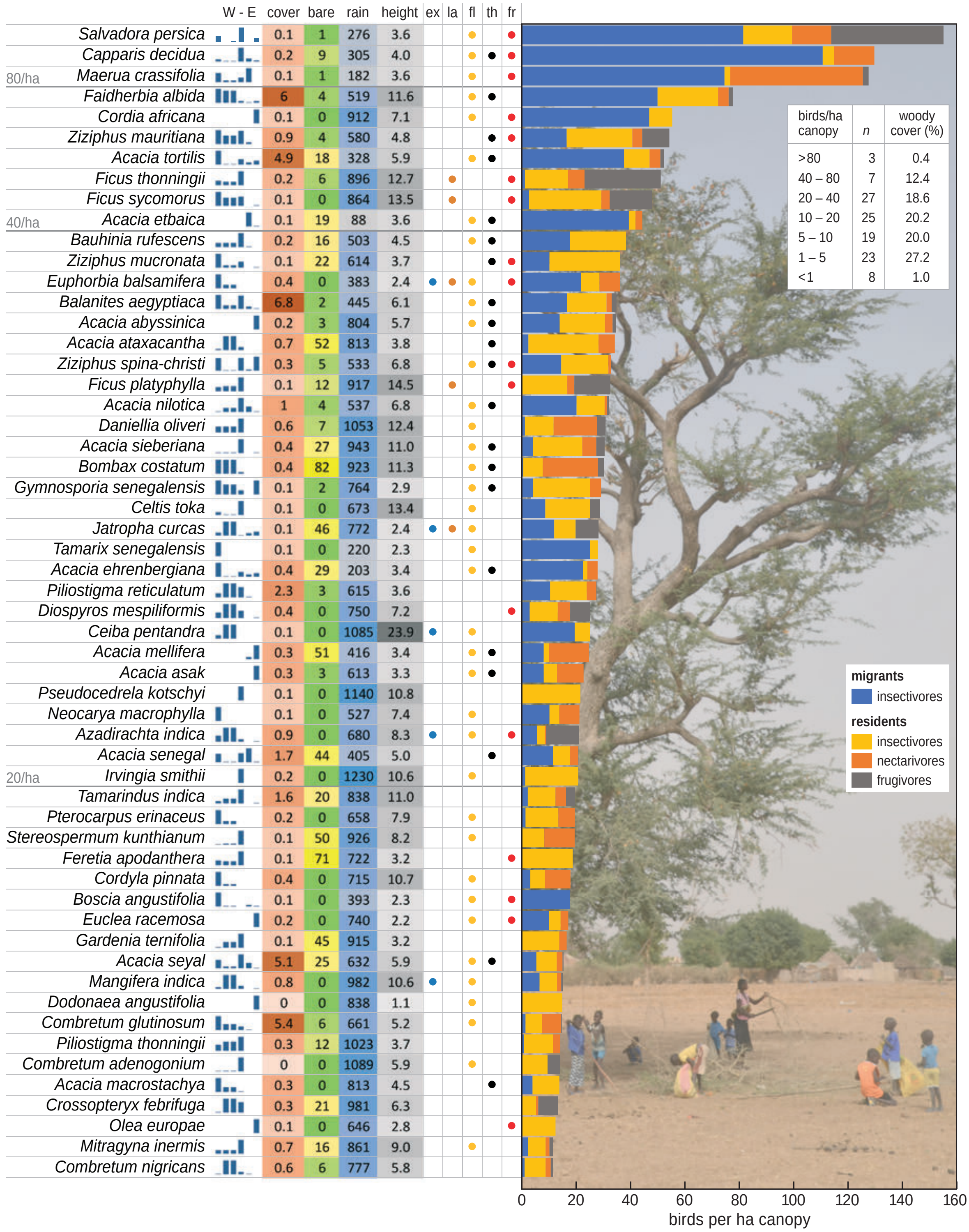

Figure 3. Birds per ha of canopy in 112 woody species ranked from bird-rich to bird-poor with the rightmost panel listing woody species with relatively low densities. Note that a different scale is used on the x-axis in both panels. Columns next to the names of woody species: W-E = relative occurrence along the west-east gradient for six longitudinal categories (17–9°W, 9–0°W, 0–8°E, 15–22°W, 28–37°E and 38–42°E), cover = % woody cover relative to the total woody cover in the study sites, bare = % of the woody plants without leaves, rain = average annual rainfall (mm), height = average height of the woody species (m),

	Species	W - E	cover	bare	rain	height	ex	la	fl	th	fr
	Combretum micranthum		2.3	0	627	2.7					
	Acacia lahai		0.1	18	739	4.8			●	●	
	Acacia dudgeoni		0.1	0	1007	4.4				●	
	Acacia oerfota		0.3	81	415	2.2			●	●	
	Cassia sieberiana		0.7	6	788	4.3			●		
10/ha	*Strychnos spinosa*		0.1	100	1022	4.5				●	
	Sclerocarya birrea		2.2	69	639	9.3					
	Dichrostachys cinerea		0.2	76	917	2.8				●	
	Prosopis juliflora		0.8	10	394	4.3	●		●	●	
	Khaya senegalensis		0.8	0	994	18.9					
	Vitellaria paradoxa		5.3	13	878	9.3		●	●		
	Boscia senegalensis		1.3	3	357	1.7			●		●
	Commiphora africana		0.1	100	529	5.1			●	●	●
	Oxytenanthera abyssinica		0.2	0	1235	10.2					
	Prosopis africana		0.2	0	1075	9.7					
	Acacia gourmaensis		0.1	0	817	5.1			●	●	
	Isoberlina doka		0.9	0	1113	9.3					
	Acacia pilispina		0.1	11	804	4.2			●	●	
	Pterocarpus lucens		1.2	20	707	7.3					
	Parkia biglobosa		2.2	2	1037	12.3					
	Gardenia erubescens		0.1	0	1005	1.9			●		
	Terminalia laxiflora		0.6	43	1004	7.5					
	Albizia amara		1.4	44	680	7.6					
	Combretum collinum		0.9	20	935	4.2					
5/ha	*Grewia flavescens*		0.1	32	814	3.2					●
	Opuntia ficus-indica		0	0	608	1.5	●				
	Tectona grandis		1.1	0	1066	8.9					
	Annona senegalensis		0.2	18	615	1.9					
	Lannea acida		0.9	55	780	7.9					●
	Gardenia sokotensis		0.1	0	678	1.6					●
	Anogeissus leiocarpus		5.1	68	825	10.9					
	Hyphaene thebaica		0.9	0	591	5.5					
	Laterna camara		0.1	6	907	2.1	●		●		●
	Entada africana		0.1	97	1086	5.2					
	Eucalyptus camaldulensis		1.5	1	753	10.5	●		●		
	Sterculia setigera		0.9	91	821	10.2					
	Leptadenia pyrotechnica		0.9	0	227	2.6		●			
	Terminalia macroptera		0.6	0	1011	7.3					
	Calotropis procera		1.2	1	353	2.2		●	●		
	Acacia polyacantha		0.2	86	908	8.2				●	
	Guiera senegalensis		7	15	606	2.0			●		
	Burkea africana		0.6	0	1027	11.6					
	Anacardium occidentale		1.5	0	1148	6.7	●		●		
	Hymenocardia acida		0.1	0	1427	4.2					
	Combretum molle		0.1	17	929	6.5			●		
	Eucalyptus globulus		0.8	2	911	9.5	●				
	Detarium microcarpum		1.3	77	1003	4.9					
1/ha	*Elaeis guineensis*		0.2	0	1151	11.8			●		
	Adansonia digitata		0.9	79	598	14.9					
	Borassus flabellifer		0.3	0	716	9.1					
	Acacia laeta		0.1	71	400	5.3				●	
	Afzelia africana		0.1	0	1061	10.9					
	Grewia tenax		0.2	62	594	1.6					●
	Pericopsis laxiflora		0.1	0	1495	9.1					
	Pteleopsis suberosa		0	0	916	3.0					
	Syzygium guineense		0.1	0	1051	7.8			●		●

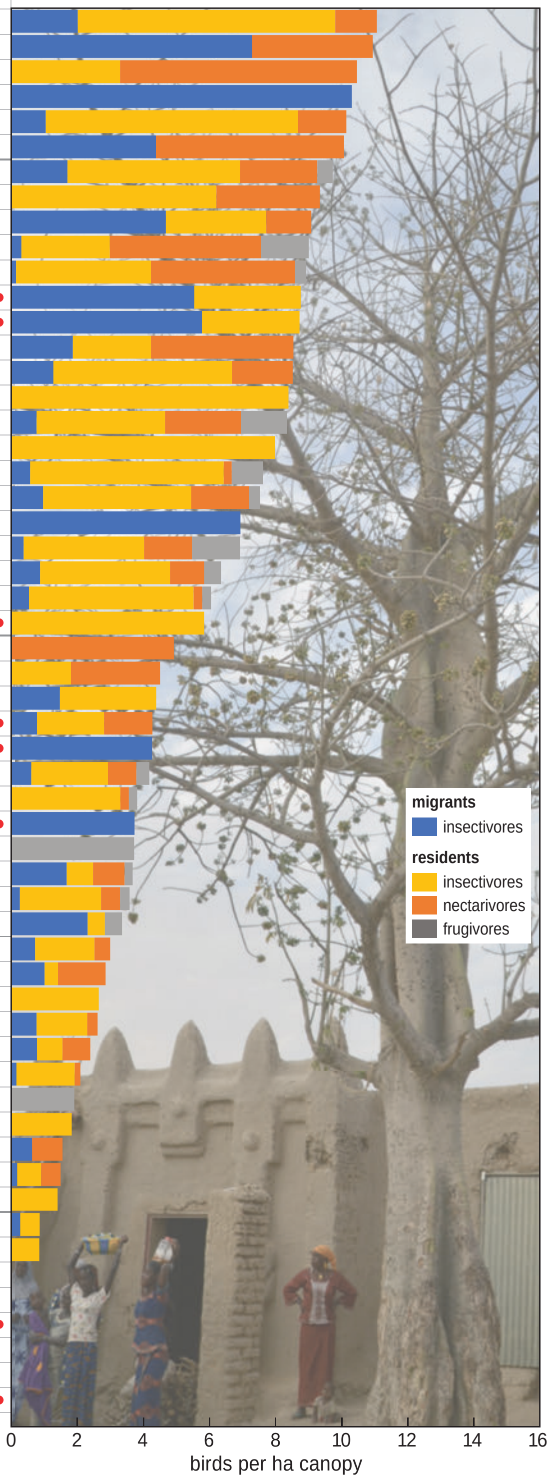

Figure 3 (continued). ex = exotic, la = latex-producing, fl = flowering in dry season, th = thorns or spines and fr = wet fruit in dry season. The inset table in the left panel gives the number of woody species (*n*) and the relative contribution to the total woody cover (set to 100%) for the seven density classes; see *y*-axis which woody species belong to these classes. Photo: Winter Thorn *Faidherbia albida* after pruning (left) and a Kapok Tree *Ceiba pentandra*, 26-year-old, planted by our deceased friend Sine Konta in the yard of his house in Akka (Inner Niger Delta) in 1984 (right).

275 less common woody species, only 13 stand out because of their high bird density (listed at the bottom of Table 2). Four of these 13 woody species occurred in the most arid part of our study area, which explains why many bird species, having a distribution area in the less arid zone, are lacking. However, the bird species in the arid zone reached exceptionally high densities in these small trees and shrubs. Toothbrush Tree *Salvadora persica* is particularly attractive because of its berries, not just for Blue-naped Mousebird *Urocolius macrourus*, a frugivore, but also for the insectivorous *Curruca* species.

The highest bird densities (80–160 birds/ha) were recorded in three shrubs that have a limited distribution in the semi-arid zone (400–600 mm rainfall/year), mainly in Chad and Sudan: the berry-bearing *Salvadora persica*, the small thorny shrub Sodad *Capparis decidua* and the low tree *Maerua crassifolia*. Most other bird-rich woody species were thorny (acacias and ziziphus; Figure 3). To investigate whether bird density is related to properties of woody species, Figure 3 gives several traits of the woody plants which are thought to have an impact on the food supply of the birds: the fraction of the woody plants being leafless, average height, average yearly rainfall (based on Hijmans *et al.* 2005) and whether the woody plant is exotic, produces latex, has flowers or fruit during the dry season, or has thorns. The percentage of bare woody plants and average plant heights are based on our own measurements. The other categories are based, apart from own observations, on Arbonnier (2019) and de Bie *et al.* (1998) for flowers and Schmidt *et al.* (2013) for fruit. Most frugivores take small fleshy fruit, therefore dry fruit and fruit >20 mm were excluded (except *Ficus sycomorus*, where birds were recorded eating from ripe figs of 2–6 cm).

Whether birds visit certain tree species was clearly associated with traits of the trees (Figure 4), which – insofar relevant to birds – are interrelated. For instance, woody species from the arid zone are more often thorny (correlation between rain and thorn is negative: $r = -0.33$) and small (correlation between rain and tree height is positive: $r = +0.42$). Whether trees occur solitarily or in continuous stands appears to have no impact on tree use by birds (Zwarts *et al.* 2018).

How strong is the preference for most intensively used tree species?

In terms of usage, the three most important species for insectivorous birds were *A. tortilis*, *Balanites* and *Faidherbia* (Table 1). The relative contribution of these species to the total woody cover in the distribution

status	diet	exotic	latex	flowers	thorns	fruit
resident	nectar	0.01	0.00	0.05*	0.01	0.02
resident	fruit	0.00	0.12***	0.00	0.01	0.13***
resident	insect	0.03	0.02	0.00	0.06**	0.03
migrant	insect	0.00	0.00	0.13***	0.06**	0.10***

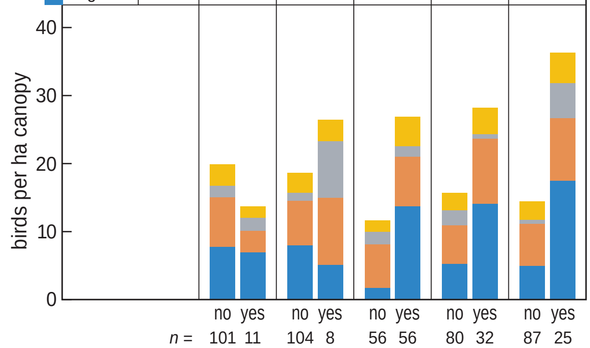

Figure 4. Average total bird density/ha canopy in woody plants that are exotic or indigenous, or have (yes) latex flowers, thorns or berries, or (no) lack them (number of woody species is given along *x*-axis). Data from Figure 3. The inset table gives the explained variance (r^2) in 20 one-way analyses of variance; significance level: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, $n = 112$.

areas of bird species varied between 0.0 and 22.6% (green bars in Figure 5). Had birds not been selective as to the choice of tree, we would have expected a random distribution among the tree species available. For many bird species the opposite was true (compare yellow with green bars in Figure 5). In fact, the fraction of birds recorded in the three favoured tree species was often much higher than expected (76%, or 71 out of the 93 comparisons made in Figure 5). The preferences differed per bird and tree species. On average, migrants were three times more common than expected in *Faidherbia*, 1.7 times more common in *A. tortilis* and showed no preference for *Balanites* (1.0 times). Insectivorous residents were 2.2 times more common than expected in *Faidherbia*, 2.0 times in *Balanites* and 1.7 times in *A. tortilis*. Sunbirds preferred *Faidherbia* (ratio 1.2) and *A. tortilis* (ratio 1.5), but not *Balanites* (ratio 0.7). Frugivores occurred less frequently than expected in the three woody species, with average ratios of 0.7 in *Faidherbia*, 0.9 in *Balanites* and 0.8 in *A. tortilis*.

Some bird species are more selective than others

Western Bonelli's Warblers were recorded in very few woody species, whereas Green-backed Camaropteras were seen in more than half of the available common woody species (Table 1). This does not necessarily imply that Bonelli's Warblers are more selective than Green-backed Camaropteras, because the diversity of woody species might differ within the distribution areas of both bird species (see green bars in Figure 5). For instance, most Western Bonelli's Warblers (56%) were recorded in *Faidherbia* (12% of the woody cover within the distribution area of this bird species). When *A. tortilis* was added, this proportion increased to 83% of the birds in 18% of the woody cover, and after *Balanites* was added: 92% of the birds in 29% of the woody cover (Figure 6). Several other insectivores also showed high selectivity, clearly deviating from random tree use (the $y=x$-line for 'no preference' in Figure 6), although none as extreme as Western Bonelli's Warbler.

The fraction of birds found in 50%, 80% and 90% of the woody cover for all 32 bird species showed that, on average, 50% of the individuals were found in only 19.9% of the woody cover and 3.9 woody species, 80% of the birds in 38.2% of the woody cover and in 9.5 tree species, and 90% of the birds in 48.5% of the woody cover and in 15.3 tree species.

The 32 bird species were observed in 30.6 woody species on average, varying between 7 and 77 woody species. As expected, common birds were seen in more tree species than rare ones ($r = 0.62$, $P < 0.001$; bird numbers given along vertical axis in Figure 7). Tree selectivity did not differ much between migrants and residents, nor between species with different diets: 80% of the migrants were found in 36.9 ± 9.5% (mean ± SD) of the woody cover, against insectivorous residents in 40.5 ± 14.6%. Corresponding figures for frugivores were 32.2 ± 14.3% and for sunbirds 40.7 ± 7.9%.

Selection for tree height

As described above, Common Whitethroats preferred low trees (66% in woody vegetation ≤ 6 m high) compared to the canopy-hugging Western Olivaceous Warbler which preferred taller trees (only 19% in trees ≤ 6 m high). Without selection 53% of both species would have used trees ≤ 6 m high (Figure 1). Similar calculations were made for 38 arboreal bird species (Figure 8). Four residents were even more selective for trees >6 m than Western Olivaceous Warbler, and 5 bird species, all residents, selected woody plants ≤ 6 m more often than Common Whitethroat. The tall-tree dwellers partly belonged to species that used treetops to advertise their presence (like Brubru *Nilaus afer*) but more often because their feeding was largely restricted to the canopy of trees. The latter included flower-visitors, like sunbirds, leaf-gleaners (passerines, both migrants and residents) and trunk and branch users. On the other hand, species preferring to forage in low trees and shrubs were mostly skulkers among twigs and

Photo 1. The woody cover was estimated by measuring the diameter of all individual shrubs and trees (South Mauritania, 16.476°N, 11.453°W, 25 January 2017; mainly Desert Date *Balanites* and Umbrella Thorn *Acacia tortilis*).

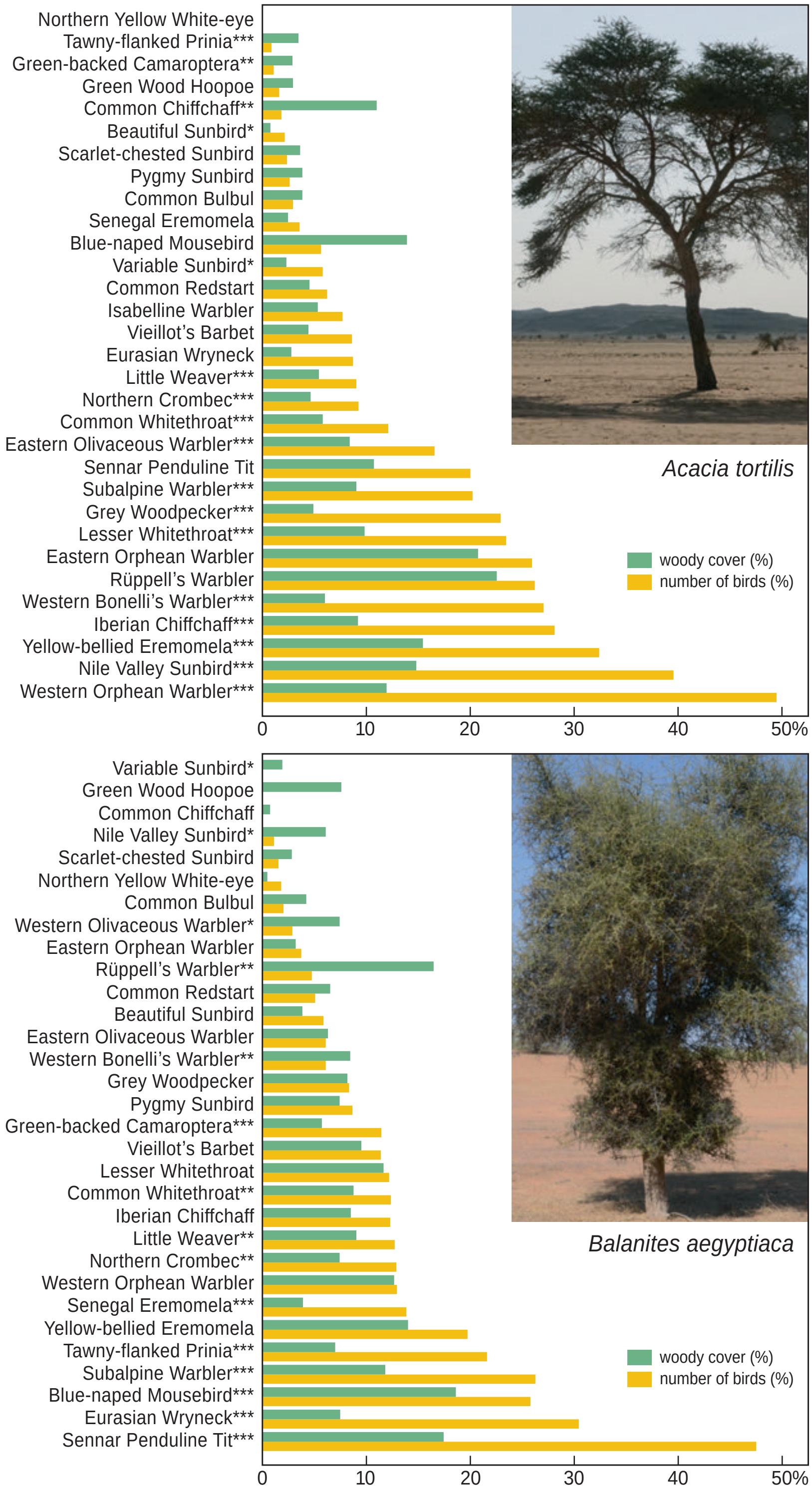

Figure 5. The contribution (%) of *Acacia tortilis*, *Balanites aegyptiaca* or *Faidherbia albida* to total woody cover (set at 100%) within the grid cells of occurrence of 36 bird species (see Supplementary Material of Zwarts *et al.* 2023b), compared to the percentage of the birds recorded in the three woody species. Green bars show the % contribution of each woody species and yellow bars the % of individual birds recorded in that woody species. Significance level in a χ^2_1 test: $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. The observed number of birds varied between 24 and 1009 and amounted to, on average, 256 birds per species.

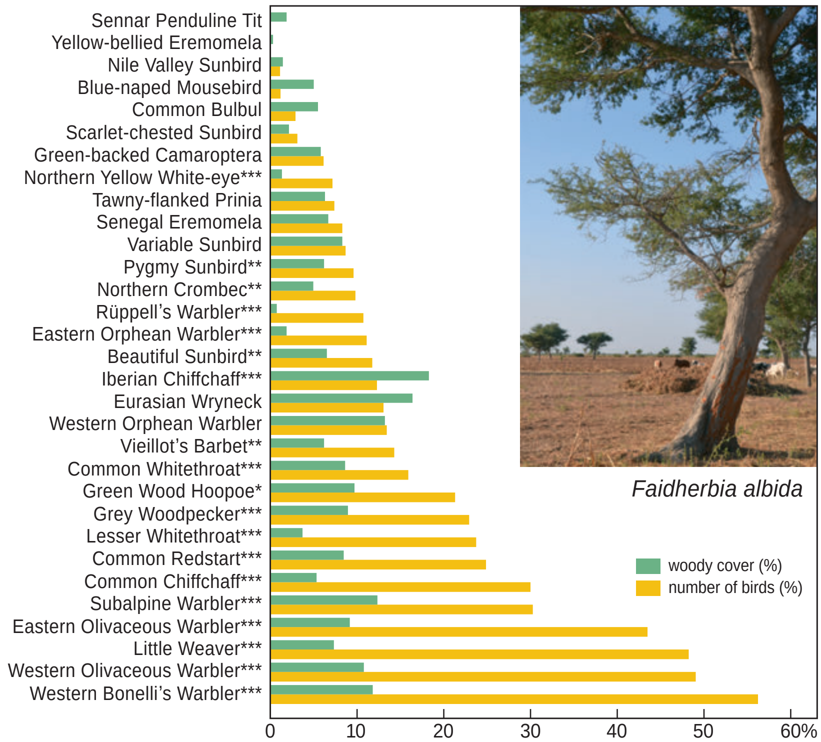

Figure 5. Continued.

leaves, often also actively foraging on, or near to, the ground (McLean 2018, Figure 1 in Zwarts *et al.* 2023b). Residents were especially well represented among this group. The species without a clear preference for foraging height showed an admixture of foraging strategies, using all parts of woody plants including the ground beneath trees, and were represented by African as well as migratory species. In the rest of this paper, we excluded six bird species: three feeding more than half of the time on the ground (marked G in Figure 8), two species using woody plants as a perch (marked P in Figure 8) and one for which the sample size was too small (Brubru). Some bird species always foraged in the tree canopy, others in low vegetation (Figure 4 in Zwarts *et al.* 2015). Their presence in low woody vegetation was, as expected, negatively correlated with the height above the ground where individual birds were detected, averaged per bird species:

$$H = 5.2 - 0.065 \times V, \quad (r^2 = 0.57, n = 29, P < 0.001), \qquad (2)$$

where H is the average height at which the bird species was observed (m above the ground; Figure 4 in Zwarts *et al.* 2015) and V = relative occurrence in low woody vegetation (% ≤ 6m; Figure 8).

For instance, Rufous-tailed and Black Scrub Robin, and among migrants Common Whitethroat, Woodchat Shrike, Eurasian Wryneck *Jynx torquilla* and Iberian Chiffchaff *Phylloscopus ibericus*, not only selected low woody vegetation, but were also often foraging in the lower part of tall trees. In contrast, migrants such as Western Olivaceous and Western Bonelli's Warbler selected tall trees and mainly foraged in the upper part of the canopy (Figure 4 in Zwarts *et al.* 2015; Figure 8).

Food supply and bird density

Watching the almost ceaseless foraging activity of birds in trees from sunrise to sunset, there can be no doubt that obtaining food is of paramount importance and – by default – that arthropod abundance must be the overriding factor explaining the selection of woody plants as described above for insectivorous birds. Unfortunately, we lack quantitative data on food supply per woody species to show variations in tree-specific food abundance. For insectivorous species, however, we have an indirect measure of feeding success: the fraction of recorded prey items being large, and for that reason presumed highly profitable. While searching for

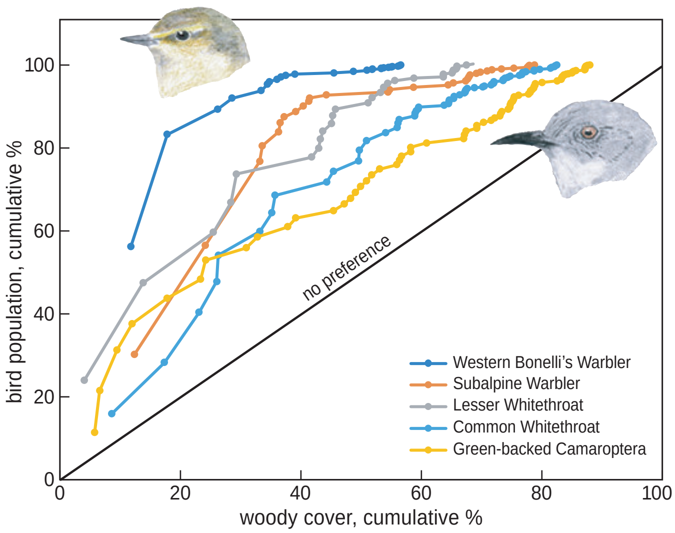

Figure 6. Cumulative percentage of five bird species occurring in different woody species as a function of the cumulative percentage of the woody cover of those woody species. The woody species are for each bird species ranked from most to least used. The total woody cover in the distribution area of each bird species is set to 100%. A random distribution would have resulted in the 'no preference' line.

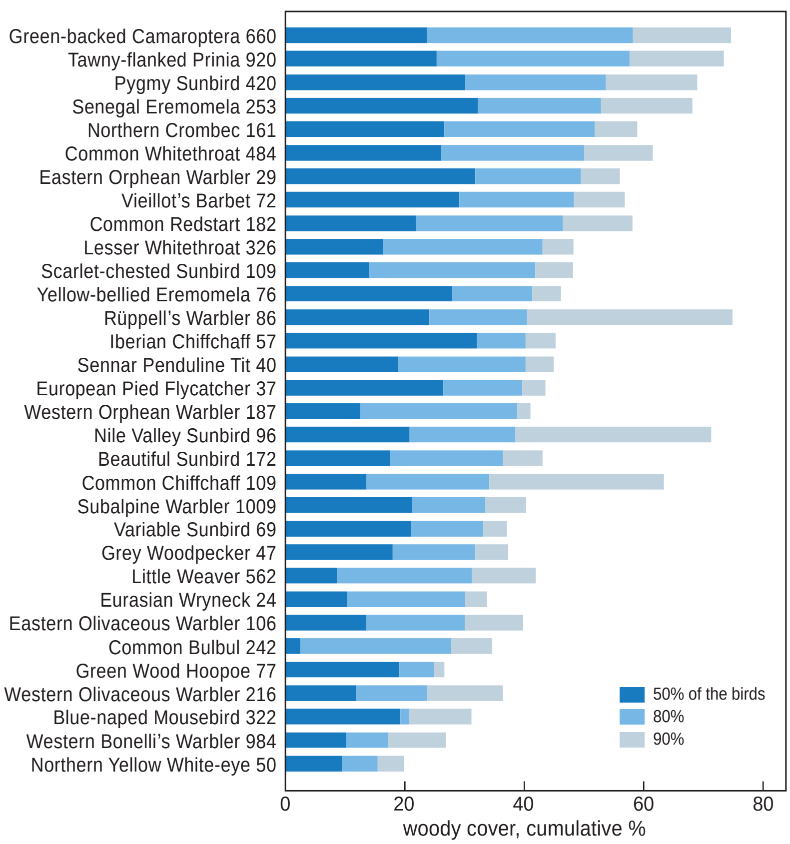

Figure 7. Thirty-two bird species ranked regarding their selectivity for woody species. Species with relatively low values of cumulative woody cover are more selective of woody species. The bars show woody cover (%) where 50%, 80% and 90% of the individuals of a bird species were found; total number of birds recorded given next to the bird's name. Same data are shown in more detail for five bird species in Figure 6.

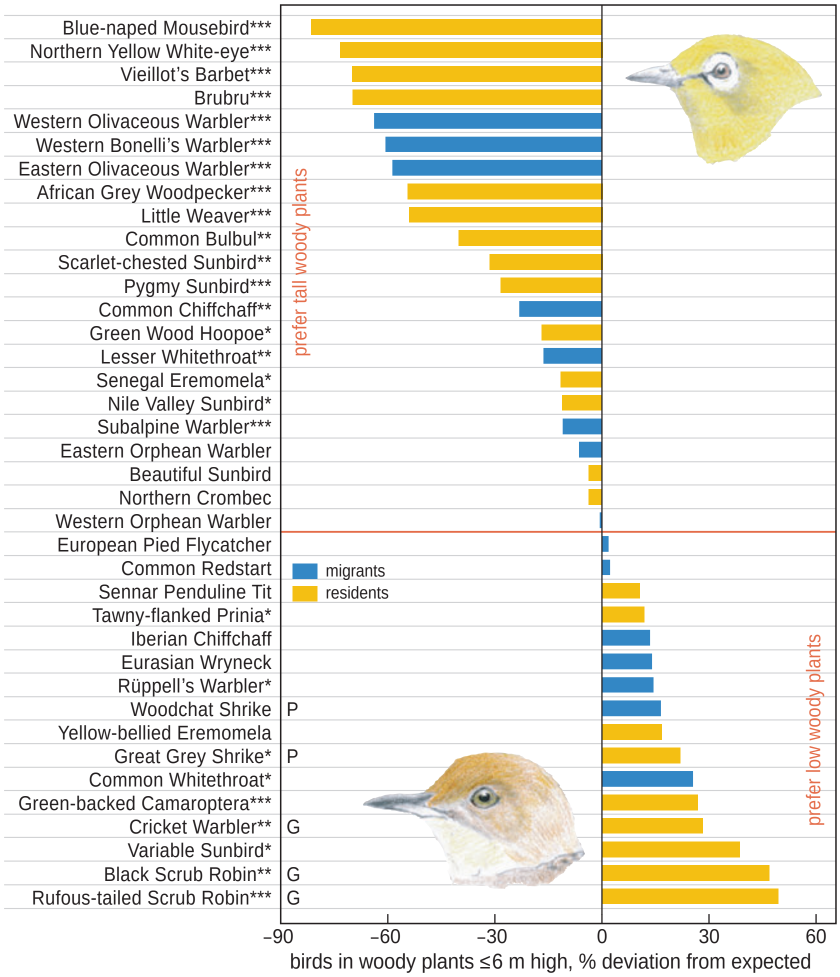

Figure 8. The occurrence of 38 bird species foraging in woody plants ≤6 m, given as percent deviation from expected, where the expectation is based on the fraction of the woody cover of all trees and shrubs being 1–6 m high within the distribution areas of the bird species. Two bird species use woody plants as perches (P) and in three species, more than 50% of the birds forage on the ground (G); see Figure 1 in Zwarts *et al.* 2023b. Significance level in a χ^2_1 test: $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. The observed number of birds varied for the different species between 23 and 1005, on average 215 birds.

birds in trees, we made notes about captured prey, which were usually too small to be identified (e.g. ant, or even smaller: aphid). Larger prey took more time to handle, providing opportunities to identify prey to species group (dragonfly, locust, caterpillar, etc.). This was systematically noted from October 2012 onwards. After October 2012 we registered 13,447 insectivorous birds, of which 232 birds (1.7%) were handling a large prey item, most often a moth (15%) or a caterpillar (70%). The fraction of birds seen with large prey varied per woody species, from highest in *Faidherbia* to lowest in tree species without thorns (Figure 9). The fraction of large prey in the five categories shown in Figure 9 is correlated with the average density/ha canopy of insectivorous birds ($r = +0.88$, $P = 0.02$).

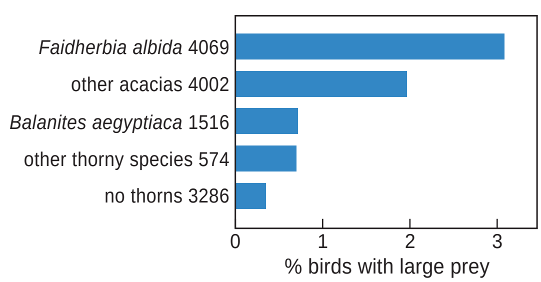

Figure 9. Percent of insectivorous birds handling a large insect during standard bird counts, given separately for *Faidherbia*, other acacias, *Balanites*, other thorny non-acacia species and all woody species without thorns. The number of birds observed is given next to the tree name. The difference is highly significant ($\chi^2_4 = 222$, $P < 0.0001$).

DISCUSSION

Selection for height in woody vegetation

The vertical stratification of foraging birds that we found (Figure 8) has already been described for birds in Africa (Cody 1985, Salewski *et al.* 2003, Wilson & Cresswell 2006, Mclean 2018) and is also known from other continents (Pearson 1971, Hinno *et al.* 2002, Walther 2002, Utschick 2006, Böhm & Kalko 2009, Hinsley *et al.* 2009). Leisler (1992) suggested that migrants and residents would be ecologically separated by feeding in different vertical layers of the woody vegetation. Our study shows, however, that within woody vegetation the vertical stratification is, on average, not different for migrants or residents (ANOVA: $r^2 = 0.02$, $n = 38$, $P = 0.44$), although the nine species showing the strongest preference for high or low woody vegetation were all residents (Figure 8).

The preference for vegetation height is not related to body mass of the 38 bird species, varying between 7 and 45 g (body mass taken from Urban *et al.* 1997, Fry& Keith 2000, 2004; see Figure 4 in Zwarts *et al.* 2015). Species with a higher body mass, i.e. African Grey Woodpecker *Dendropicos goertae* and Eurasian Wryneck, foraged on trunks and thick branches and might for that reason select larger trees than sunbirds and warblers feeding among leaves and flowers by hovering and making sallies or jump-flights. However, the expected negative relation between body mass and occurrence in low woody vegetation was not found (linear regression: $r^2 = 0.01$, $n = 38$, $P = 0.24$).

There are other reasons to expect that arboreal birds may prefer to feed in older woody plants. Young woody plants do not normally have flowers or fruit. Furthermore, at a young age tree architecture is still simple, lacking horizontal branches and a well-leafed canopy. The absence of shadow in small trees is probably an additional disadvantage at high ambient temperatures when birds actively seek protection from the sun (Walsberg 1993, Martin *et al.* 2015). Indeed, twice as many bird species were found in high than in low woody vegetation (omitting five bird species which preferred low woody vegetation because they use woody plants as perches or spend more than half of their time feeding on the ground; Figure 8).

Tree preference of birds across the Sahel

A first attempt to calculate tree preferences and densities of birds was restricted to data collected in West Africa (Zwarts *et al.* 2015, see their Figure 6 and Supplementary Material). The much larger dataset presented here covers the entire width of the Sahel, which enables a similar attempt that takes into account variations in the distribution and density of bird species in step with the distribution of trees and shrubs. In general, woody species rich or poor in birds in West Africa showed the same pattern across the entire Sahel. Some woody species that are rare in West Africa but much more common in the central and eastern Sahel proved to be highly attractive to birds, notably *Maerua crassifolia*, *Capparis decidua* and *Bauhinia rufescens*. Geographic differences were also found, especially regarding the average density of migrants (but not of residents) in most woody species: higher in the western than in central and eastern Sahel. This difference hinges intrinsically on a systematic longitudinal variation in bird density in migrants (Zwarts *et al.* 2023c).

Photo 2. Green-backed Eremomela *Eremomela canescens* feeding on insects in a Desert Date *Balanites aegyptiaca* (Ethiopia, 7.983°N and 38.623°E; 27 February 2019). This tree species has straight spines up to 10 cm long arranged in spirals which deter large grazers from browsing. Leafing in *Balanites* occurs from May through December, followed by partial defoliation in the latter part of the dry season. The investment of this tree species in mechanical defence against grazers instead of chemical defence against herbivorous arthropods explains why *Balanites* belongs to the tree species attracting insectivorous birds.

Closely related bird species often showed similar preferences for tree species, even when their distributions did not (appreciably) overlap. Eastern Bonelli's Warbler *Phylloscopus orientalis* replaced Western Bonelli's Warbler in Chad and Sudan, where all birds were found in acacia species (though based on only 9 birds), similar to the tree preferences of Western Bonelli's Warbler (90% in acacia species). In both subregions, Western and Eastern Olivaceous Warbler *Iduna pallida* were found in high numbers in *Faidherbia*

(43 and 49%, respectively), but rarely in *Balanites* (6 and 3%, respectively). For six *Curruca* species, *A. tortilis* was on average more important than *Faidherbia* (26% and 18%, respectively), but in three *Phylloscopus* species it was the other way round (18% in *A. tortilis* and 33% in *Faidherbia*). In *Balanites*, *Curruca* species were more common than *Phylloscopus* species (12 and 6%, respectively). Whether this is due to systematic differences in food supply in the different tree species (Morel 1968, Stoate 1998, Vickery *et al.* 1999), the diet of these bird species (Stoate 1997, 1998, Stoate & Moreby 1995, Wink 1981), their foraging modes or a combination of these factors is unknown.

The distinct preference for acacia trees by migrants, and less so by residents, may be illustrated by a bird count we did in the southern, humid part of Mali (11.600°N, 5.838°W; average annual rainfall 1073 mm), where nearly all trees in the site were *Acacia nilotica*, a tree usually found in the zone with an annual rainfall between 200 and 800 mm. The *A. nilotica* plantation (woody cover 8550 m^2) attracted, apart from 3 Green-backed Camaropteras, 5 migratory species (6 Common Chiffchaffs, 5 Western Olivaceous Warblers, 4 European Pied Flycatchers, 2 Common Whitethroats and 1 Melodious Warbler *Hippolais polyglotta*, amounting to 20 migrants per ha of canopy). Elsewhere in the humid zone densities rarely exceeded 1–2 birds per ha of canopy (Figure 3B in Zwarts *et al.* 2023b). Farther south in Ghana (Dowsett-Lemaire & Dowsett 2014) and in Togo + Benin (Dowsett-Lemaire & Dowsett 2019), the few Sahelian migrants were observed in – for that zone – equally rare Sahelian trees, e.g. Western Bonelli's Warbler in *Faidherbia* and *Balanites*; Subalpine Warbler in *A. nilotica* and Common Whitethroat in *A. seyal*.

Most arboreal birds in the Sahel feed on insects, but data are lacking about temporal and spatial variations in insect abundance per tree species. When trees attracted a lot of insects, as when flowering, standing in water or having a large well-leafed canopy, more birds were recorded (Figures 7, 15 and 18 in Zwarts & Bijlsma 2015). Birds taking large prey were recorded more often in thorny trees than in non-thorny trees. Figure 9 shows that the frequency at which birds take large prey is lowest in non-thorny woody species and high in acacia species, especially in *Faidherbia*. We hypothesize that the total food intake is high when more large prey can be taken, because large prey are more profitable. A bird must eat about 100 or 500 aphids (0.2 mg) to have a food intake equal to a single moth of 2 cm (dry weight: 20 mg) or a caterpillar of 3 cm (100 mg), respectively.

Variations on the overriding theme of rainfall and tree characteristics are abundant, each explicable by specific local conditions. Take for example sunbirds, a largely nectarivorous group of birds that usually avoids

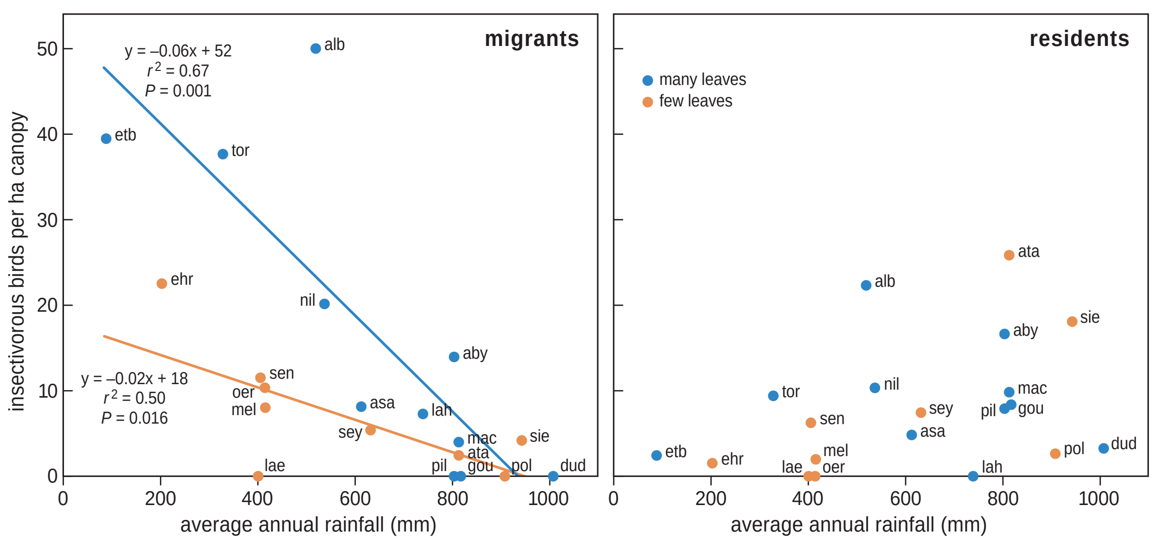

Figure 10. Average bird density of insectivorous migrants (left) and residents (right) during the dry season in twenty *Acacia* species as a function of average rainfall, separately for *Acacia* species with few leaves (range 0–47 %, on average 21%, of the woody plants being leafless) and many leaves (range 51–95%, on average 76%). All data from Figure 3, which also gives the full name of the *Acacia* species indicated here with three letters. In migrants, bird density in acacia trees declines significantly with rainfall and differs for trees with few or many leaves. In residents, the increase in bird density is not significant: it is also not significant for *acacias* with few or many leaves.

woody species without flowers (even when foraging for insects). However, they also avoid the majority of flowering species (not all tree species produce nectar when flowering, or only at night, or in different amounts; e.g. Adgaba *et al.* 2016). This explains the small difference between the average density of sunbirds in flowering and non-flowering species (Figure 4). Similar deviations from the general pattern can be found in the other categories, as for example in thorny trees. The average feeding density of migrants in thorny species was three times larger than in non-thorny species, but within the range of thorny species, four were found to contain no migrants at all. Two factors appear to have an impact on the density of migrants in acacia species: annual rainfall (acacias in humid zones were least attractive) and whether the species is leafless during the dry season (if so, devoid of migrants; Figure 10). Insectivorous resident bird species occurred at lower densities than insectivorous migrants and were indifferent to whether trees carried leaves or not. They were indifferent also to average rainfall (even to the point of showing a non-significant increase with rainfall; Figure 10).

There are several other possible explanations as to why some bird species were found in a wider variety of woody species than others (Figures 6 and 7). First, bird species with a larger range (i.e. found in more grid cells; see Supplementary Material in Zwarts *et al.* 2023b) are more likely to encounter a wider range of tree species. This effect was indeed found ($r = +0.46$, $P < 0.01$). The impact of the size of the distribution area is statistically independent of tree height since the two are not correlated ($r = 0.00$). Second, bird species in the humid zone encounter more tree species than those residing in the dry zone, because of the much higher tree diversity in the more humid region:

$$N_{tree} = 0.035 \times \text{rain}^{0.880} \text{ } (n = 140 \text{ grid cells, excluding Ethiopian highlands; } r = +0.78, P < 0.0001), \quad (3)$$

where N_{tree} = number of woody species in the random sites, averaged per grid cell and rain = average annual rainfall (mm).

However, the correlations between the 50%, 80% and 90% selection criteria shown in Figure 7 and annual rainfall in the distribution area of the bird species (shown in Figure 5A in Zwarts *et al.* 2023b) were close to zero and thus far from significant. In other words, despite the increase of tree diversity with rainfall, bird species from the humid zone were concentrated in the same number of woody species as the bird species bound to the dry zone.

Third, birds gleaning prey from leaves may be more selective in their choice of tree species than those hovering for their prey, as found in North American forests by Holmes & Robinson (1981). Nearly all species from Figure 7 are foliage gleaners, but Western Bonelli's Warblers, and to a lesser degree also Eastern Olivaceous Warblers, make sallies and jump-flights and hover (Table 5.11 in Lack 1980; Figure 9B in Zwarts & Bijlsma 2015; Rob Bijlsma unpubl.). However, both species were more, not less, selective in the choice of tree species than the gleaning bird species (Figure 7).

Fourth, bird species feeding in low trees and in shrubs were found in a larger variety of woody plants than species bound to the canopy of large trees (Figure 11). The explanation might be simple: the canopy surface of scrub and low trees is (much) smaller than of trees making it more likely that scrub-foraging birds will constantly move from one woody plant to another, and therefore visit more woody species than bird species feeding in the canopy of tall trees.

More Cashew and Shea trees, fewer birds

Cashew trees are avoided by arboreal birds: the density/ha canopy was a meagre 0.2 migrants and 2.0 residents (1.8 insectivores, 0.2 sunbirds and 0 frugivores; Figure 3). Cashew plantations cover a large part of the hyper-humid zone in West Africa, mainly in Côte d'Ivoire (not visited by us, beside Comoé National Park). In Guinea-Bissau, where we collected data from two grid cells, cashew plantations contributed 44.6% of the woody cover in the northern grid cell (the overall woody cover was 44.3% of which 19.8% cashew) and as much as 51.8% in the southern grid cell (overall cover 57.1% of which cashew 29.6%); see Figure S5 for the cover by cashew and Figure 6B in Zwarts *et al.* 2023a for the total woody cover.

In Guinea-Bissau cashew plantations were very rare in the early 1980s, but cashew planting has soared in later years. According to FAO data, cashew covered already 0.29 million ha of the country in 2020. At the same time, even larger areas were converted into cashew plantation in Côte d'Ivoire (2.03 million ha in 2020) and Benin (0.52 million ha in 2020) and for West Africa as a whole 3.37 million ha (www.fao.org/faostat/en/#data/QCL). Comparisons of high-resolution Google Earth satellite images available since 2004 clearly show that small Cashew trees, spaced at a distance of 5–8 m, had formed a closed canopy within 5 to 10 years after planting. Such plantations were usually without understorey of shrubs or small trees, instead were typified by bare ground with leaf litter (Photo 3).

We found no information if and how bird population changed after woody savannah or agroforestry parkland had been converted into Cashew plantation. But the newly created Cashew plantations in Guinea-Bissau must have had a negative impact on the average bird density: 2–5 birds/ha canopy in Guinea-Bissau compared to 17–43 birds/ ha canopy in the woody savanna in Chad and the Central African Republic in the same rainfall zone (Figure 3A and Figure 8 in Zwarts *et al.* 2023b). The impoverished bird fauna in monotonous Cashew plantations contrasts with the high bird diversity and density in natural woody vegetation of humid woody savanna, where a diversity of woody species attracts birds, especially when flowering (Tamarind *Tamarindus indica*, Kapok Tree *Ceiba pentandra*, Red Kapok Tree *Bombax costatum*, White Thorn *Acacia sieberiana*, Red Acacia *Acacia seyal*, West African Copal *Daniellia oliveri*) or bearing fruit (Candlewood *Zanthoxylum zanthoxyloides*, *Gymnosporia* (=*Maytenus*) *senegalensis*, *Ficus* spp.). Affected birds cover the complete range of residents, insectivores, frugivores and nectarivores, including four migrants: European Pied Flycatcher, Willow, Wood and Melodious Warbler (Figure 5 in Zwarts *et al.* 2023b).

Following conversion of agroforestry parkland into monoculture of Cashew overall woody cover did not decline, and sometimes may even have increased. Global forest maps (Hansen *et al.* 2013) fail to distinguish between tropical forests and plantations of Cashew, or, for that matter, of banana, oil palm or pineapple plantations. The net result is an underestimate of real forest loss (Tropek *et al.* 2014). Cashew plantations are economically profitable (Monteiro *et al.* 2017) and are considered as beneficial afforestation leading to less soil erosion, enhanced soil fertility, a cooler microclimate and rehabilitation of degraded lands (CILSS 2016). The flip side of the coin is: more Cashew equates to far fewer birds

The Shea Tree *Vitellaria paradoxa* (Photo 4) does not attract many birds, although it is not as poor in that respect as Cashew (Table 2 and Figure 3). However, its negative impact on overall bird density is large, since it is a dominant tree in the agricultural zone of Mali, Burkina Faso and Benin where the annual rainfall varies between 700 and 1000 mm (average cover of Shea alone was 2.1%, but for all woody species combined 9.6%; Figure S9 and Figure 5 in Zwarts *et al.* 2023a). The average bird density, calculated for 199 study sites within this region amounted to 5.0 birds/ha canopy, but it was 23.8 and 2.7 birds/ha canopy respectively when the data were split for sites where woody cover of Shea was less or more than half of the total woody cover. A similar large difference is found when the bird density in Mali, Burkina Faso and Benin (on average 17.1% Shea for all woody species combined) is compared to the one measured in Chad (0.4% Shea) within the same rainfall zones: 5 birds/ha canopy in Mali, Burkina Faso and Benin compared to 26.6 birds/ha canopy in Chad (92 sites; see also Figure 3 in Zwarts *et al.* 2023b). Obviously, the expansion of Shea agro-forestry parkland has had a large negative impact on tree-dwelling birds.

How many birds are present in different woody species?

The total woody cover in Africa between 7°N and 22°N amounts to 0.897 million km^2, equivalent to 9% of the total land surface (see Supplementary Material). The contribution of the woody species from the semi-arid zone, among which are several bird-rich trees, declines when correcting for the under-representation of the most arid and most humid region in our study sites.

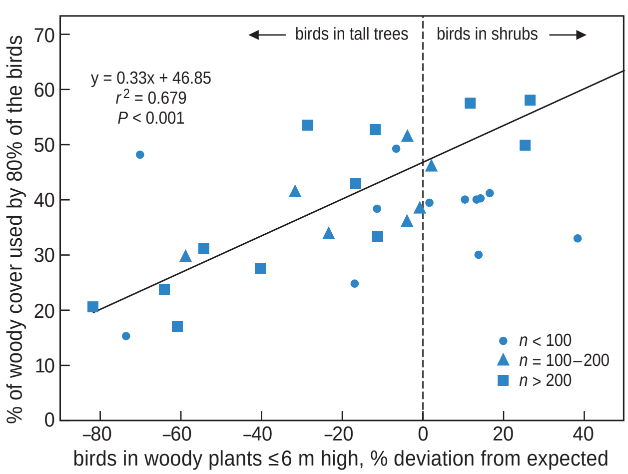

Figure 11. The relationship between degree of tree selection by bird species (% of woody cover utilized by 80% of the birds; same data as in Figure 7) and their habitat association with respect to vegetation height (occurrence of woody plants ≤6 m, given as percent deviation from expected; as in Figure 8). Symbols denote numerical classes for 32 bird species. The regression line refers to the 19 most common species (n > 100).

Photo 3. Monoculture of Cashew in Guinea-Bissau at 12.002°N and 14.834°W (500 × 700 m); all woody plants visible on this Google Earth image (28 February 2019) are cashew trees of different ages with the most recent plantation on the left and older ones on the right (see image taken on the spot on 3 February 2014).

The woody cover of *Faidherbia*, for instance, declines from 2.2% in the covered grid cells to 1.21% for the entire region (more details in Supplementary Material). Multiplying the woody cover per woody species with the corresponding bird density/ha canopy gives a total estimate of bird numbers and how they are distributed over the various woody species (Table 3). Most migrants are present in *A. tortilis* – 90 million (split-half: 85–92 million; based on an estimated 37.6 migrants/ha canopy and a total surface of 2.38 million ha canopy (split half: 2.26–2.46). The bird density in *Faidherbia* is higher (49.9 migrants/ha) but the associated surface area is much smaller (1.08 million ha canopy; split-half estimates the same) so that fewer migrants are found in *Faidherbia* – 54 million (Table 3). We estimate that 42 (split-half: 39–45) million migrants are present in *Balanites* because the lower density (16.6 migrant birds/ha) is more than compensated for by the large surface area of the woody cover (2.52 million ha; split half: 2.31–3.71). Two uncommon woody species *Maerua* (0.14 million ha canopy) and *Salvadora* (0.09 million ha) harbour 10.8 and 7.3 million migrants due to their high bird densities (74.6 and 81.4 migrants/ha canopy, respectively). For all woody species together, we arrive at 355 million arboreal migrants for the entire region (Table 3). In total, 186 million of these 355 million migrants (52%) are concentrated in three bird-rich and common trees, i.e. in only 6.7% of the total woody cover (Table 3).

The estimated total of 355 million arboreal migrants in Africa between 7 and 22°N is 0.7% above the estimate of 354 million birds for the same region given in Zwarts *et al.* (2023b). Thus, both estimates do not differ although they were calculated in different ways: directly (Zwarts *et al.* 2023b), based on bird counts in the sites assembled per subregion, or indirectly (this

Photo 4. Shea trees dominate the agro-forestry parkland in southern Mali, Burkina Faso and northern Benin. (Photo: Mali, 12.899°N, 6.813°W, 28 January 2012).

Table 3. The importance of various tree species ranked according to the estimated total number of arboreal migrants they support. Estimated total surface of the canopy (km^2), density (*n*/ha canopy) and number (millions) of arboreal migrants between 7 and 22°N; given separately for 22 woody species being most important for migrants. No more than 12% of the birds were present in 382 other woody species not mentioned, although their total woody cover amounts to 66%. The overall density of arboreal insectivorous birds declined to 4.0/ha canopy when all woody species were taken into account (on average 0.7 birds/ha canopy in trees not mentioned in the table).

Woody species	km^2	*n*/ha	million
Acacia tortilis	23,820	37.6	89.5
Faidherbia albida	10,831	49.9	54.1
Balanites aegyptiaca	25,248	16.6	42.0
Acacia nilotica	9194	20.1	18.5
Acacia seyal	26,546	5.4	14.3
Maerua crassifolia	1452	74.6	10.8
Mangifera indica	13,518	6.6	8.9
Acacia senegal	7227	11.5	8.3
Acacia ehrenbergiana	3441	22.5	7.7
Piliostigma reticulatum	7108	10.4	7.4
Salvadora persica	899	81.5	7.3
Acacia etbaica	1850	39.4	7.3
Acacia sieberiana	13,669	4.1	5.7
Ziziphus mauritiana	3164	16.6	5.2
Anogeissus leiocarpus	63,010	0.6	3.7
Mitragyna inermis	14,853	2.3	3.4
Parkia biglobosa	34,620	1.0	3.3
Tamarindus indica	15,140	2.2	3.3
Combretum glutinosum	21,560	1.4	3.0
Ceiba pentandra	1351	19.5	2.6
Azadirachta indica	4528	5.7	2.6
Ziziphus spina-christi	1450	14.5	2.1
All other species	592,091	0.7	44.0
TOTAL	**896,570**	**4.0**	**355.3**

paper), based on the estimated woody cover and average bird density/ha canopy per woody species.

The most important conclusion is that when 52% of the arboreal migrants are concentrated in 6.7% of the woody cover (Table 3), it is not total woody cover per se that matters for these birds, but the presence of their preferred woody species. For the same reason, global indications of increase or decline of the woody vegetation, although highly relevant in other respects; Brink & Eva 2009, Hansen *et al.* 2013) are not helpful in explaining trends in bird populations. Any explanation of these trends must take into account detailed knowledge about the presence and extent of bird-rich and bird-poor woody species within the wintering regions. Furthermore, Brink & Eva (2009) and Hansen *et al.* (2013) provided the extent of 'forest cover', not of 'woody cover'. In well-wooded regions this may equate the same, but definitely not in the Sahel where low densities of single trees in savannah or farmland cannot be detected with Landsat imagery having a resolution of 30 × 30 m (Figures 6 and 7 in Zwarts *et al.* 2023a), i.e. the data source used in their studies. This potential discrepancy has recently been solved with the advent of high-resolution satellite imagery with which woody cover can be estimated accurately (Brandt *et al.* 2020); even individual *Faidherbia* and other tree species can now be identified (Lelong *et al.* 2020).

Ecological and socio-economic values of woody species

How many arboreal birds may live in the Sahel depends on the woody cover of bird-rich trees and shrubs. If bird-rich trees were to decline or replaced by commercially interesting tree species, bird populations can be expected to suffer. Bird densities in, for example, Shea Tree and Cashew are extremely low, yet these commercially valuable tree species cover large tracts of land in West Africa, usually at the expense of indigenous tree species valuable to birds. Insect supply and richness are still major unknowns for the tree species in the Sahel, but it is obvious that some woody plants have more to offer to birds than others (Greenberg & Bichier 2005, Zwarts *et al.* 2015).

The total woody cover in the study area amounts to only 9%. A tiny fraction of the already scarce woody cover is exploited by arboreal birds. In some bird species more than half of the individuals make use of a single tree species during the dry season, a delicate dependency compared to birds with a wider use of tree species. Dependence on just a few woody species not only holds for several residents but also for many migratory bird species spending the non-breeding season in the Sahel and for migrants wintering farther south which use the Sahel to refuel during autumn migration (Zwarts *et al.* 2023d).

Farmers have some impact on woody cover when savannah is converted into agricultural land (Brandt *et al.* 2018). More important, however, is that people selectively remove specific woody species and guard and plant others and have determined in this way the species composition of the woody vegetation in large parts of the dry belt of the northern tropics (Zwarts *et al.* 2023e). Many woody species are highly valued by local people, not only for firewood, but also as a source

Photo 5. A still small Neem *Azadirachta indica* tree beside the trunk of a Winter Thorn *Faidherbia albida*. The evergreen Neem, native to India, has been planted in tropical Africa alongside roads and in settlements to provide shade. Its leaves are toxic and are used as a biopesticide. Exactly this quality results in a tree with very few insects, except ants (Stoate & Moreby 1995). Neem was largely avoided by birds, except small numbers of Eastern and Western Olivaceous Warblers which were observed preying on ants (own unpubl. data). The picture shows cropland in S Mali (13.049°N and 5.894°W, 2 February 2012), where the farmer has – uncharacteristically – replaced some of his White Thorns by Neem. Were this type of management to become more popular, the negative impact on birds, especially Bonelli's Warbler, would be very large.

for veterinary and human medicine (reviewed by Arbonnier 2019) and many other purposes (Lykke *et al.* 2004, Ouédraogo *et al.* 2017). The future of arboreal birds in the Sahel would be bleak should trees ranking high on socio-economic values be bird-poor. Fortunately, a bird-rich tree as *Faidherbia* ranks high concerning its socio-economic values but, alas, an extremely bird-poor indigenous tree, Shea Tree *Vitellaria paradoxa*, has a large economic value, and this also holds for plantations of exotic tree species virtually devoid of birds (Cashew, Teak *Tectona grandis* and *Eucalyptus* spp.; Figure 3). The impact on arboreal bird species of the conversion of the dry sub-Saharan zone into a semi-natural open farmland with scattered trees in fields and pastures is dealt with separately (Zwarts *et al.* 2023e).

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SAMENVATTING

In de Sahel, hier opgevat als de brede overgangszone tussen Sahara en natte tropische bossen verder naar het zuiden, komen nauwelijks bossen voor. Maar het gebied is bepaald niet arm aan bomen, integendeel. En wat nog opmerkelijker is: het struikgewas en de losstaande bomen zijn opvallend vogelrijk. Voor een groot deel bestaat de lokale vogelbevolking in de winter uit Afro-Palearctische trekvogels, waaronder soorten die in het broedgebied juist in aaneengesloten bossen voorkomen. Dit artikel beschrijft welke bomen en struiken worden geselecteerd door 14 insectivore trekvogels en 18 Afro-tropische vogelsoorten (10 insectivoren, 3 frugivoren en 5 nectarivoren) op basis van een gestratificeerde inventarisatie van de gehele Sahel. In totaal werden 760.000 bomen en struiken op naam gebracht (304 soorten). Van elk boom en struik apart werden hoogte en breedte gemeten. Met die gegevens werd vervolgens het oppervlak van elke boom uitgerekend, de zogenaamde kroonbedekking. Vogels werden afzonderlijk geregistreerd per boom/struik. Van de vogels was 99,5% geconcentreerd in slechts 41 soorten bomen/struiken. Voor 20 van de 32 vogelsoorten was *Faidherbia albida*, een acacia, de meest benutte boomsoort. Twee andere belangrijke bomen waren *Acacia tortilis* en de Woestijndadel *Balanites aegyptiaca*, die het vaakst werden gebruikt door respectievelijk zeven en zes vogelsoorten.

In deze drie boomsoorten, tezamen goed voor slechts 11% van de totale kroonbedekking, werden 89% van de Bergfluiters *Phylloscopus bonelli* waargenomen en 77% van de Baardgrasmussen *Curruca iberiae + subalpina + cantillans*. Vogelsoorten die zich vooral in struiken ophielden werden in grotere diversiteit van bomen en struiken gezien dan soorten die bij voorkeur in (hoge) boomkronen foerageerden. De hoogste vogeldichtheden (80–160 vogels/ha kroon) werden aangetroffen in drie houtige soorten met een beperkte verspreiding in de zuidelijke Sahara en de noordelijke Sahel: de bessendragende Tandenborstelboom *Salvadora persica*, de doornige struik *Capparis decidua* en de kleine boom *Maerua crassifolia*. Andere vogelrijke boomsoorten waren zonder uitzondering doornig (*Balanites aegyptiaca*, diverse soorten acacia's en *Ziziphus*). 27% van de totale kroonbedekking kwam voor rekening van slechts vijf algemene soorten: Cashew *Anacardium occidentale*, *Anogeissus leiocarpus*, *Combretum glutinosum*, *Guiera senegalensis* en Karitéboom *Vitellaria paradoxa*, maar deze boomsoorten werden zelden door foeragerende vogels bezocht. Sterker nog, negen insectenetende soorten werden er nooit in aangetroffen. Honingzuigers waren geconcentreerd in een beperkt aantal bloeiende bomen, fruiteters in een klein aantal vruchtdragende soorten. Insectenetende vogels beperkten zich grotendeels tot doornige boomsoorten, vermoedelijk vanwege de aanwezigheid van rupsen en motten. In de Sahel is niet de totale bosbedekking sec van belang voor vogels, maar de aanwezigheid van specifieke boomsoorten. Deze bevinding heeft belangrijke implicaties voor uitspraken over de geschiktheid van het gebied voor vogels in de winter. Satellietbeelden die een algemene toename of afname van bosvegetatie laten zien, zeggen in dat opzicht niet zo veel. Het gaat namelijk om wélke bomen toe- of afnemen. Het voorkomen van bomen en struiken in de Sahel hangt in sterke mate af van de jaarlijkse regenval, maar wordt mede bepaald door de plaatselijke bevolking die selectief soorten kapt én aanplant. De gevolgen voor vogels zijn enorm. *Faidherbia albida*, de belangrijkste boom voor een aantal trekvogelsoorten in de Sahel, wordt door de plaatselijke bevolking zeer gewaardeerd (en dus aangeplant of gespaard) en staat vrijwel uitsluitend op boerenland. Anderzijds zijn cashewplantages buitengewoon vogelarm en betekent de snelle uitbreiding daarvan sinds 1980 een groot habitatverlies voor trek-, maar vooral voor lokale vogels. Ook de wijdverbreide en door de lokale bevolking gekoesterde Karitéboom heeft een negatieve invloed op het voorkomen van insectenetende trekvogels.

RÉSUMÉ

Le Sahel, vaste zone de transition entre le Sahara et les forêts tropicales humides plus au Sud, n'abrite quasiment pas de forêts. Mais la région n'est pas pauvre en arbres, bien au contraire, et la savane y est remarquablement riche en oiseaux. En hiver, de nombreux migrateurs afro-paléarctiques la fréquentent, y compris des espèces qui se reproduisent dans des habitats purement forestiers. Cet article identifie les espèces ligneuses préférentiellement sélectionnées par 14 espèces d'oiseaux migrateurs insectivores et 18 espèces d'oiseaux afro-tropicaux (10 insectivores, 3 frugivores et 5 nectarivores) sur la base d'un inventaire par échantillonnage stratifié de l'ensemble du Sahel. Au total, 760 000 arbres et arbustes appartenant à 304 espèces ont été inventoriés. Pour chacun, la hauteur et la largeur ont été mesurées, afin de calculer la superficie de houppier, et tous les oiseaux présents y ont été recensés. 99,5% étaient concentrés dans seulement 41 espèces ligneuses. *Faidherbia albida*, un acacia, était l'essence préférentielle de 20 des 32 espèces d'oiseaux étudiées, tandis que l'Acacia faux-gommier *Acacia tortilis* l'était pour sept espèces et le Dattier du désert *Balanites aegyptiaca* pour six. À elles trois, ces essences qui ne représentent que 11 % de la couverture totale de la canopée, accueillaient 89 % des Pouillots de Bonelli *Phylloscopus bonelli* et 77 % des fauvettes du complexe « passerinette » *Curruca iberiae + C. subalpina + C. cantillans*. Les espèces d'oiseaux qui s'alimentent principalement dans les arbustes ont été observées dans une plus grande diversité d'essences que les espèces qui se nourrissent dans la canopée. Les plus fortes densités (80–160 oiseaux/ha de houppier) ont été trouvées dans trois essences à la distribution restreinte au Sud du Sahara et au Nord du Sahel : le Siwak ou « Arbre brosse à dents » *Salvadora persica*, le Karira, un arbuste épineux *Capparis decidua* et l'Agar *Maerua crassifolia*. Les autres espèces d'arbres fréquentées étaient sans exception épineuses (*Balanites aegyptiaca*, diverses espèces d'acacia et de jujubier). Cinq essences communes composent à elles seules 27% de la couverture totale de la canopée – l'Anacardier *Anacardium occidentale*, le Bouleau d'Afrique *Anogeissus leiocarpus*, *Combretum glutinosum*, le Guier du Sénégal *Guiera senegalensis* et le Karité *Vitellaria paradoxa* – mais ces essences d'arbres sont rarement visitées par les oiseaux en quête de nourriture. Neuf espèces insectivores n'y ont même jamais été trouvées. Les souimangas ne fréquentaient quant à eux qu'un nombre limité d'arbres à fleurs et les frugivores uniquement quelques essences fruitières. Les insectivores étaient essentiellement présents dans les essences épineuses, probablement en raison de la présence de chenilles et de papillons de nuit. Au Sahel, ce n'est donc pas la couverture forestière totale mais la composition spécifique des peuplements arborés qui est importante pour les oiseaux. Ces résultats ont des implications importantes pour la conservation des oiseaux hivernants. Les évolutions du couvert forestier visibles par images satellites n'ont qu'un intérêt limité : ce qui compte, c'est de connaître l'évolution de l'abondance des différentes essences. La présence d'arbres et d'arbustes dans le Sahel dépend en grande partie des précipitations annuelles, mais elle est également influencée par l'importance des coupes et des plantations sélectives réalisées par la population locale et donc les conséquences pour les oiseaux sont énormes. *Faidherbia albida*, essence privilégiée par un certain nombre d'espèces migratrices au Sahel, est très appréciée par la population locale (et donc plantée ou préservée) et se rencontre presque exclusivement dans les zones cultivées. A l'opposé, les plantations de cajou sont extrêmement pauvres en oiseaux et leur expansion rapide depuis les années 1980 a entraîné une importante perte d'habitat pour les migrateurs, mais encore plus pour les espèces locales. De même, le Karité, très répandu et apprécié par la population locale, a un impact négatif sur la présence d'oiseaux migrateurs insectivores.

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SUPPLEMENTARY MATERIAL

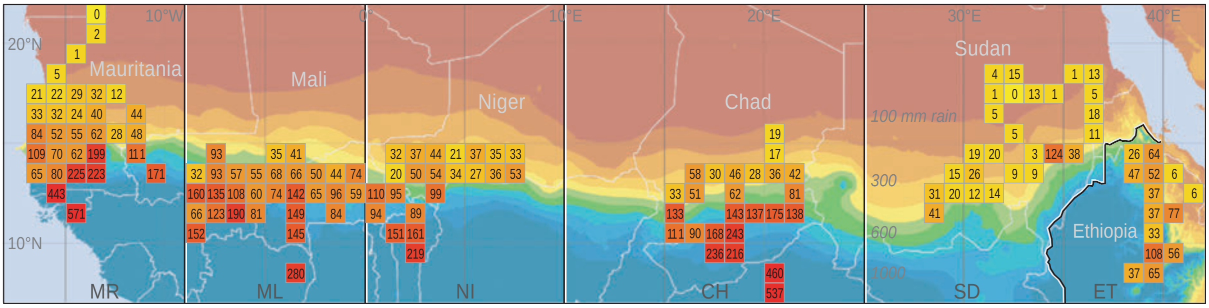
Table 2 gives bird density/ha canopy separately for different woody species as well as for woody cover. The total number of birds present in the different trees may be calculated by multiplying, for each woody species, bird density and woody cover. The numbers generated in this way cannot be used, however, to estimate the total number of birds present in the region between 7 and 22°N because the sites are not entirely representative for this region (too many sites in the western and too few in the eastern Sahel, too few in the most arid and most humid zones). This problem is solved by combining sites into 150 1° × 1° grid cells and using mean densities in grid cells to calculate an overall mean. This procedure has no impact on average woody cover, i.e. 75‰ as grand mean (based on 1901 sites) compared to 75‰ as mean of the means (based on 150 grid cells). Species composition, however, differs, depending on the way it is calculated. The average woody cover of *Faidherbia* in the 1901 sites amounts to 6.0‰ but is reduced to 2.2‰ when calculated over the 150 grid cells (Figure S4). A smaller difference was found in *Balanites* (mean of the sites 6.8‰ and mean of the grid cells 3.5‰; Figure S2) and in *A. tortilis* (2.7‰ for sites and 2.3‰ grid cells; Figure S3). However, even the grid cells are not fully representative of the entire region (see Zwarts *et al.* 2023a), which is why the entire region was divided into eleven rainfall zones and six longitudinal bands. The average woody cover of all species is calculated for 65 subcategories using the surface area of these zones as weighting factor (Figure S1 in Zwarts *et al.* 2023a). The same procedure was used to calculate average woody cover in the entire region; further explanation given in Zwarts *et al.* 2023a.

The next five pages give distribution maps of the total woody cover for eight woody species, three most important for birds (Figures S2–S4) and five of the most common species (Figures S5–S10). The table in the legend to Figures S1–S4 gives the average woody cover (‰) for eleven rainfall zones and six longitudinal bands; interpolated values are marked grey. Figure S1 in Zwarts *et al.* 2023a gives the land surface area of the 65 subregions. These data are available for 53 of the 65 subregions. To estimate the woody cover in the 12 missing subregions, we averaged the densities in two adjacent cells with a similar rainfall. Since the grid cells of South Sudan differ drastically from those in the nearby Ethiopian Highlands, we substituted the adjacent values of Chad and the Central African Republic for missing South Sudan cells. The woody cover between 7 and 22°N is calculated by using the measured or interpolated average woody cover in 65 subareas multiplied with the surface area (Figure S1 in Zwarts *et al.* 2023a). For all woody species combined we arrived at a total woody cover of 0.897 million km^2 or 8.99% of the total land surface (9.974 million km^2). To estimate the reliability of these estimates, we split the sites in two halves (even and odd) and repeated all calculations. The two estimates obtained with the split-half method are given in the legends.

Number of trees

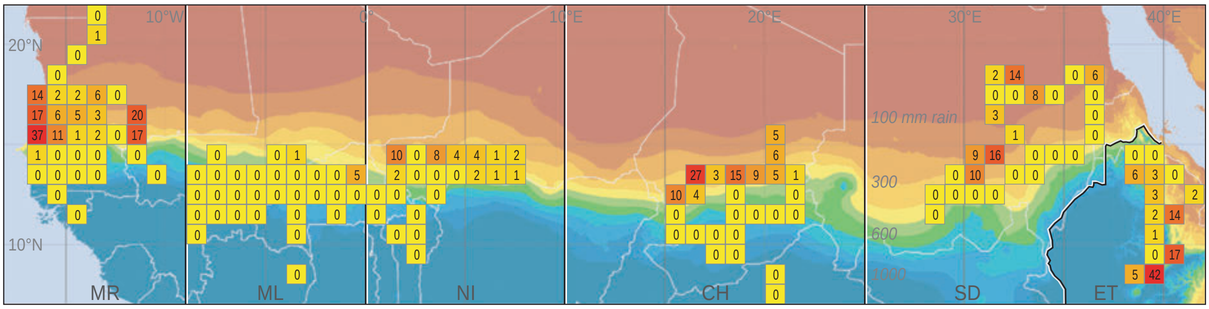
The increase of woody cover with rainfall (Figure S10A) is due mainly to an increase of tree density, from 6 woody plants/ha in the hyper-arid zone (<100 mm) to more than 200 in the hyper-humid zone (Figure S10B). Trees are also taller in the humid zone. The average height increases from 3 m in the hyper-arid to 9 m in the hyper-humid zone (Figure S10C) and the average canopy surface per tree increases from 7 to 20 m^2 (Figure S10D).

The average number of woody plants in the 150 grid cells amounted to 101/ha, but after accounting for sites in the desert that are under-represented, we arrived at an overall average of 86 trees and shrubs per ha, which implies that in the entire region between 7–22°N and 17°W–42°E, 87 billion trees and shrubs may be found (80–94 billion; split half). This estimate may be compared to data collected by Brandt *et al.* (2020) who used satellite imagery with a resolution of 0.5 m to count and measure the crown surface of individual trees in the western Sahel (west of 6°W) in the rainfall zone of 0 to 1000 mm rainfall per year (i.e. between 13 and 22°N), an area of 1.3 million km^2. Within this area, they detected 13.4 trees per ha, in total 1.8 billion trees, with an average crown surface of 12 m^2. When we select the same area, our data suggest a much higher total of 9.4 billion trees. This difference was to be expected, since we counted during our field work all trees of ≥1 m high, being equivalent to woody plants with a crown surface of about ≥0.8 m^2, whereas Brandt *et al.* (2020) took >3 m^2 as their lower limit. In total, 51.4% of our counted trees had a diameter of 1 m (0.8 m^2) and 25.9% a diameter of 2 m (3.1 m^2). Discarding these small woody plants, we arrive for the region surveyed by Brandt *et al.* (2020) at 3.7 billion trees >0.8 m^2 and 2.1 billion trees >3.1 m^2. Our field data underline the conclusion of Brandt *et al.* (2020) that there are many more trees in drylands than assumed so far.



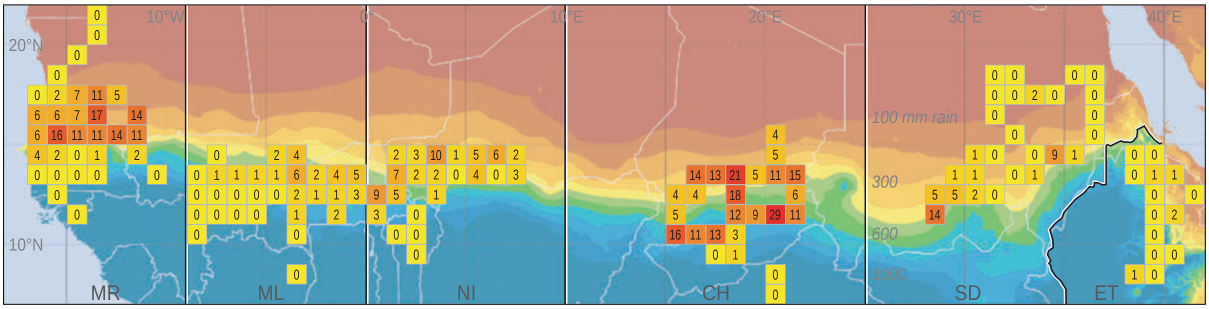
rain (mm)	MR	ML	NI	CH	SD	ET
<100	2	3	4	5	6	
100–200	24	21	19	17	15	3
200–300	29	26	23	23	21	15
300–400	61	45	30	44	14	18
400–500	49	36	30	33	42	18
500–600	112	52	58	97	84	63
600–700	67	66	88	93	93	90
700–800	128	74	97	138	138	18
800–900	251	104	96	165	165	28
900–1000	290	147	109	217	217	58
>1000	497	154	168	387	387	80

Figure S1. Woody cover (‰) of all woody plants together; present in 98% of the 150 cells. Average woody cover (mean ±SD) in grid cells: 75‰ ± 92.
Estimated overall woody cover in Africa in the region shown on the map (10 million km^2; 7–22°N, 17°W–42°E): 90‰, based on averages given in the table for 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey. Estimated total woody cover: 896,550 km^2, of which 118,110, km^2 interpolated; range 883,180–909,930 km^2 (split-half).



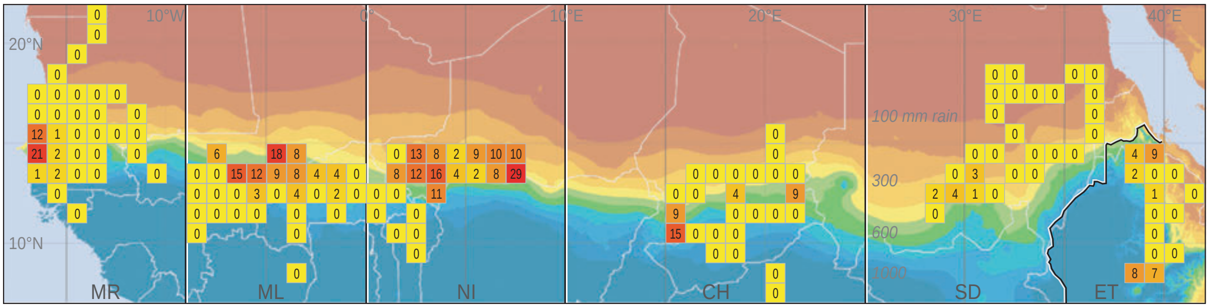
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.29	1.09	1.89	2.69	63.49	
100–200	6.15	5.92	5.68	5.45	4.54	1.41
200–300	7.51	5.46	0.64	6.87	9.35	4.32
300–400	20.26	11.22	2.18	13.68	0.17	1.78
400–500	4.85	3.62	1.37	7.24	0.01	0.55
500–600	0.48	0.17	0.00	0.32	0.11	20.81
600–700	0.01	0.00	0.00	0.00	0.00	8.02
700–800	0.04	0.00	0.00	0.00	0.00	0.63
800–900	0.00	0.00	0.00	0.00	0.00	5.37
900–1000	0.00	0.00	0.00	0.00	0.00	0.25
>1000	0.00	0.00	0.00	0.00	0.00	1.99

Figure S2. Woody cover (‰) of Umbrella Acacia *Acacia tortilis*; present in 49% of the 150 cells. Average woody cover (mean ±SD) in grid cells: 2.7‰ ± 6.1. Estimated overall woody cover: 2.3‰ based on averages given in the table for 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey. Estimated total woody cover: 23,330 km^2, of which 7520 km^2 interpolated; range: 22,580–24,050 km^2 (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.07	0.16	0.16	0.16	0.25	
100–200	4.74	4.17	4.17	3.61	0.09	0.26
200–300	6.47	4.40	2.32	5.19	0.53	0.12
300–400	10.79	7.09	3.39	10.85	0.73	0.05
400–500	6.50	2.55	1.89	9.73	6.14	1.01
500–600	3.90	2.87	1.07	10.17	10.34	1.01
600–700	1.28	1.76	0.25	11.01	11.01	1.10
700–800	0.14	1.36	7.05	15.84	15.84	0.00
800–900	0.00	0.77	4.08	13.98	13.98	0.22
900–1000	0.00	0.45	0.04	2.64	2.64	0.19
>1000	0.00	0.00	0.04	0.52	0.52	0.23

Figure S3. Woody cover (‰) of *Balanites aegyptiaca*; present in 72% of the 150 cells. Average woody cover (mean ±SD) in grid cells: 3.5‰ ± 5.4.
Estimated overall woody cover: 2.5‰ based on averages given in the table for 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey. Estimated total woody cover: 25,200 km^2, of which 8250 km^2 interpolated; range: 23,110–27230 km^2 (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.00	0.00	0.00	0.00	0.00	
100–200	0.04	0.03	0.02	0.00	0.00	0.00
200–300	0.05	0.60	1.15	0.11	2.58	0.00
300–400	2.59	6.48	10.37	0.02	0.19	0.00
400–500	11.89	14.11	5.76	0.00	1.93	0.00
500–600	17.48	6.84	8.54	10.68	0.00	0.69
600–700	0.96	8.68	9.52	6.32	6.32	3.11
700–800	0.01	2.12	0.00	0.13	0.13	5.67
800–900	0.00	1.26	0.00	0.00	0.00	4.09
900–1000	0.03	0.22	0.00	0.01	0.01	2.64
>1000	0.00	0.01	0.00	0.02	0.02	1.72

Figure S4. Woody cover (‰) of *Faidherbia albida*; present in 41% of the 150 cells. Average woody cover (mean ±SD) in grid cells: 2.2‰ ± 4.3.
Estimated overall woody cover: 1.2‰ based on averages given in the table for 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey. Estimated total woody cover: 11,130 km², of which 1220 km² interpolated, range: 11,110–11,400 km² (split-half).

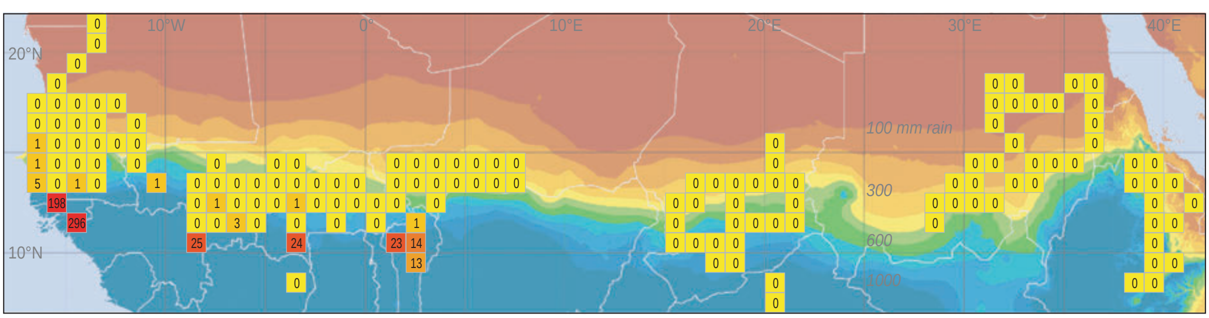


Figure S5. Woody cover (‰) of Cashew *Anacardium occidentale*, mean ± SD: 4.1 ± 29.1; present in 13% of the 150 cells.

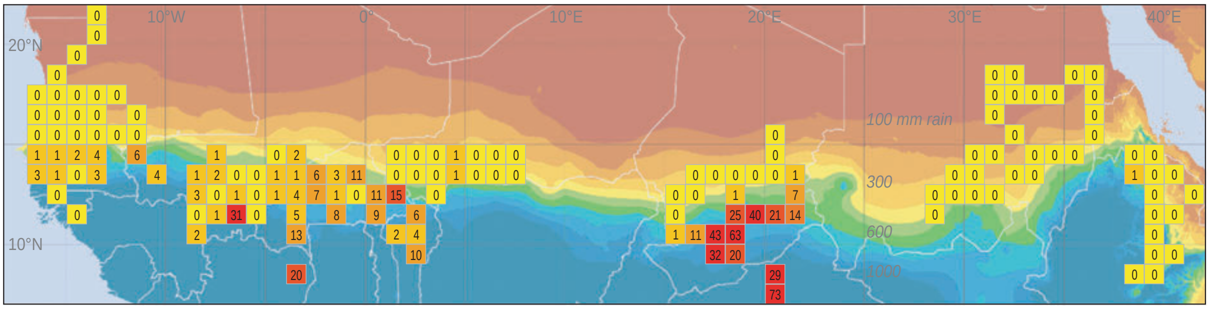


Figure S6. Woody cover (‰) of African Birch *Anogeissus leiocarpus*, mean ± SD: 3.9 ± 10.6; present in 45% of the 150 cells.

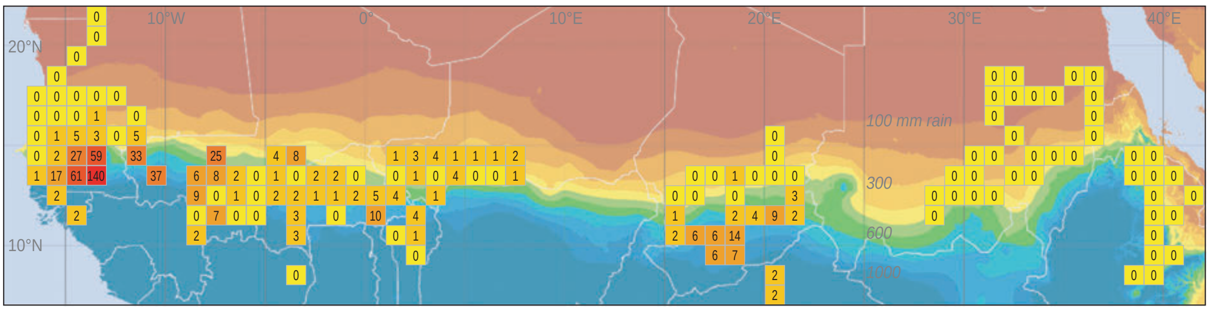


Figure S7. Woody cover (‰) of *Combretum glutinosum*, mean ± SD: 4.0 ± 14.1; present in 59% of the 150 cells.

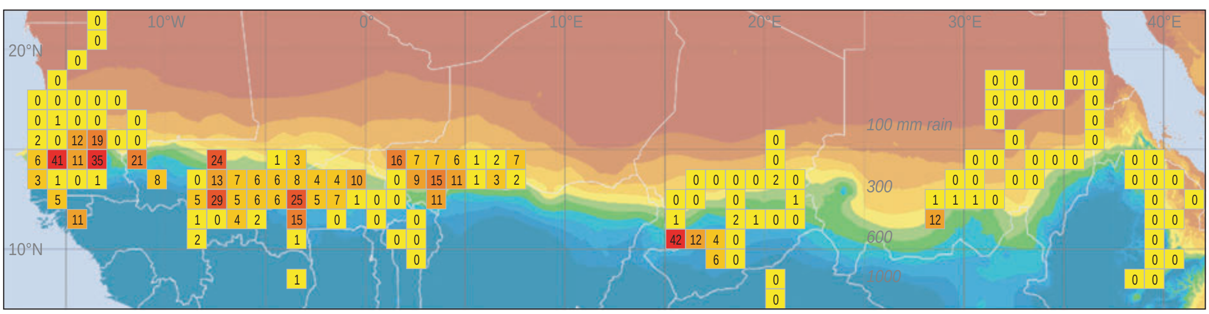


Figure S8. Woody cover (‰) of *Guiera senegalensis*, mean ± SD: 3.8 ± 7.4; present in 53% of the 150 cells.

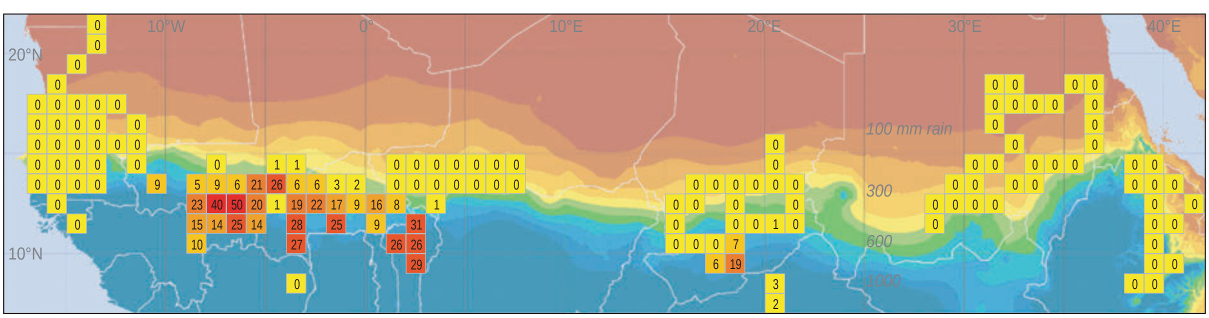


Figure S9. Woody cover (‰) of Shea Tree *Vitellaria paradoxa*, mean ± SD: 4.3 ± 9.2; present in 30% of the 150 cells.

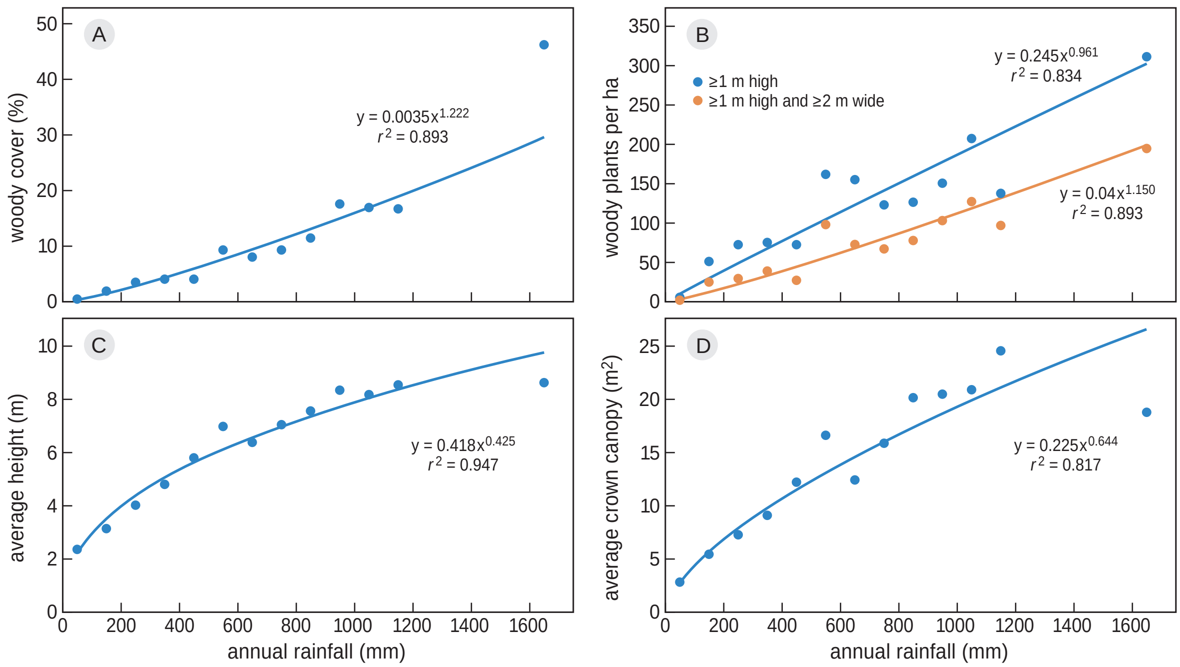
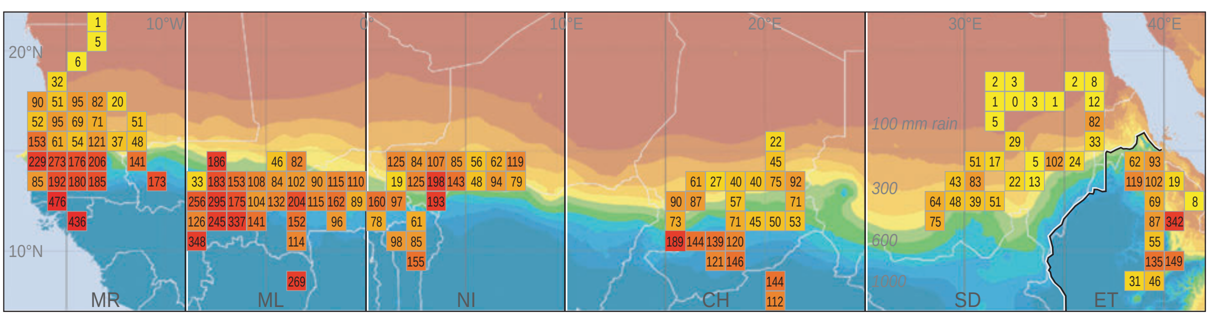


Figure S10. (A) Woody cover (%), (B) number of woody plants (≥1 m high or ≥1 m high and diameter ≥2 m), (C) height (m) and (D) crown canopy (m^2), all averaged per 100 mm rainfall zones, as a function of annual rainfall. All relations are highly significant. Trees from the rainfall zones 1300–2300 mm are taken together, due to the smaller sample size.



rain (mm)	MR	ML	NI	CH	SD	ET
<100	10	8	7	5	3	
100–200	68	53	37	22	45	7
200–300	77	106	135	48	49	13
300–400	112	97	81	62	37	43
400–500	75	55	95	61	58	44
500–600	247	89	192	75	57	109
600–700	168	130	191	59	59	324
700–800	158	135	97	90	90	30
800–900	158	167	97	109	109	71
900–1000	221	182	79	134	134	71
>1000	458	228	101	58	58	133

Figure S11. Density per ha of woody plants ≥1 m high. Average number of woody plants (n/ha ±SD) in grid cells: 108 ± 82.
Estimated overall density in Africa in the region shown on the map (10 million km^2; 7–22°N, 17°W–42°E): 87 per ha, based on averages given in the table for 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number of woody plants in the same region: 87 billion, of which 10 billion is interpolated; range 80–94 billion (split-half).