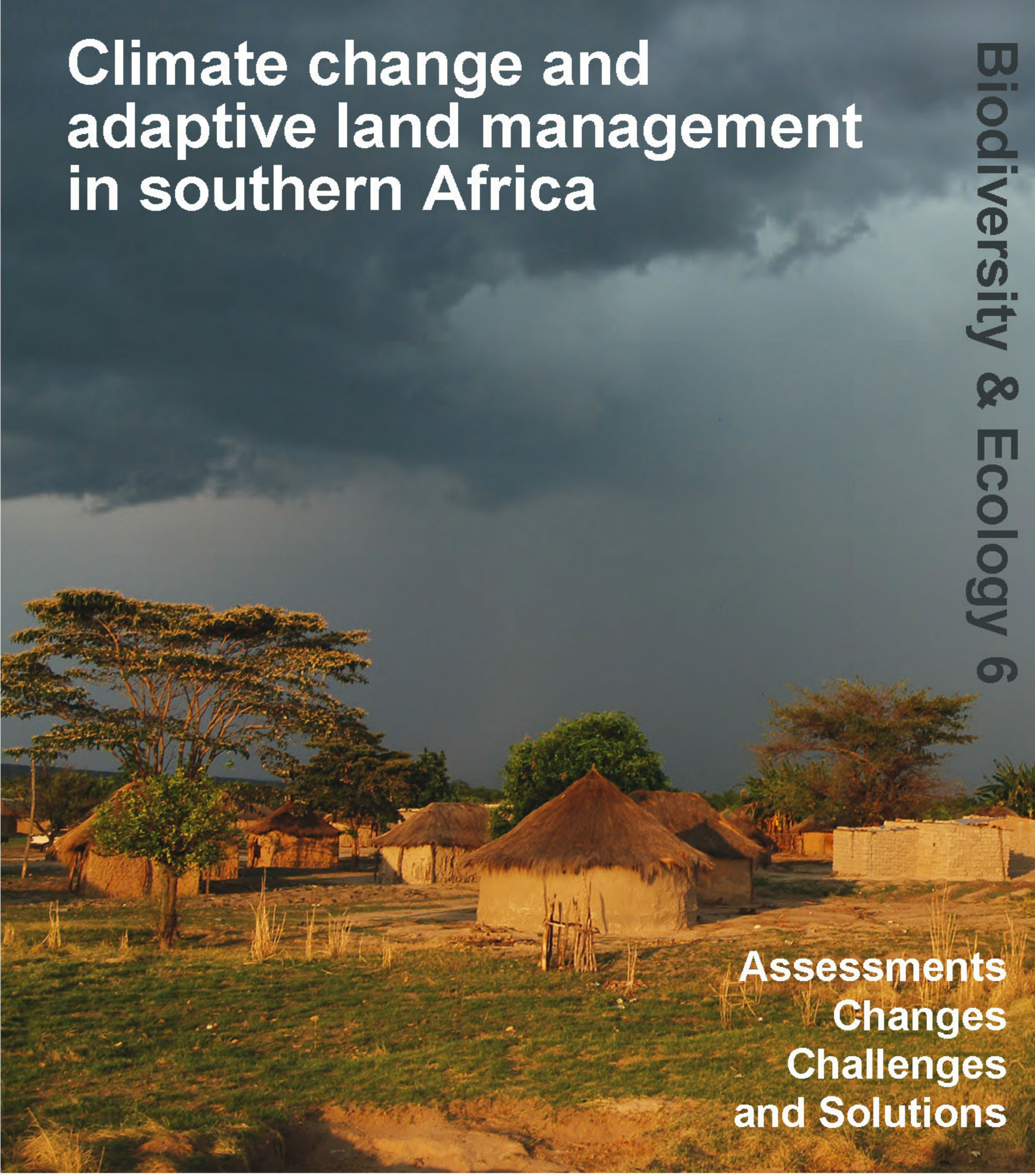
Climate change and adaptive land management in southern Africa

Biodiversity & Ecology 6



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Changes
Challenges
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Climate change and adaptive land management in southern Africa

Assessments, changes, challenges, and solutions

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Seasonal changes of biodiversity patterns and habitat conditions in a flooded savanna – The Cameia National Park Biodiversity Observatory in the Upper Zambezi catchment, Angola

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Abstract: Eastern Angola and western Zambia are dominated by the Zambezi catchment, where high precipitation and a dense river network cause annual flooding of extensive areas from January to ¬May. Cameia National Park in Angola is such a seasonally flooded savanna. A SASSCAL Biodiversity Observatory was established in May 2016, as little is known about the area's particular flora and fauna. Based on three visits to the observatory, we present a first description of the ecology of this dynamic ecosystem, its vegetation units and plant species, occurrence and turnover of bird assemblages, and human land-use practices. We observed that the turnover in species composition, temporal niches of functional groups and guilds, and land uses are controlled by seasonally changing flood, fire, and precipitation patterns. Our results highlight the conservation value of the area; sustainable management plans and conservation strategies are urgently needed to restore the formerly dominant herbivore guilds and to prevent destructive agro-industrial development schemes.

Resumo: Angola Oriental e Zâmbia Ocidental são dominadas pela bacia hidrográfica do Zambezi, onde a alta precipitação e a densa rede fluvial causam inundações anuais de extensas áreas entre os meses de Janeiro e Maio. O Parque Nacional da Cameia em Angola tem as suas savanas inundadas sazonalmente. Foi estabelecido em Maio de 2016 um Observatório de Biodiversidade do SASSCAL, já que pouco se sabe sobre a sua flora e fauna particulares. Com base em três visitas ao observatório, apresentamos uma primeira descrição da ecologia deste ecosistema dinâmico, das suas unidades de vegetação e espécies de plantas, da ocorrência e rotatividade de conjuntos de aves, e das prácticas humanas de uso das terras. Observámos que a rotatividade da composição de espécies, os nichos temporários de grupos funcionais e guildas, e o uso das terras são controlados pelos regimes sazonais de inundações, fogos e precipitação. Os nossos resultados realçam o valor de conservação da área; são urgentemente necessários planos de gestão sustentáveis e estratégias de conservação, de modo a recuperar as guildas de herbívoros outrora dominantes e prevenir esquemas destrutivos de desenvolvimento agro-industrial.

Introduction

Seasonally flooded savannas are dynamic landscapes that occur particularly in the South American and African tropics. Iconic examples are the Pantanal in Brazil, Paraguay, and Bolivia; the Llanos of Venezuela and Colombia; the Lake Chad region in West Africa; and the catchment area of the Upper Zambezi in Angola and Zambia. In such regions, plane landscapes with slowly draining rivers, impermeable soil layers, and high annual precipitation provide conditions that contribute to annual flooding (Junk & Furch, 1993; Welcomme, 1979). These ecosystems are home to specialized plants and animals, thus representing a particular biodiversity (Ward, 1998). Concurrently, humans make use of the flooding cycle by fishing in the flood season and grazing their cattle in the dry period (Abbott et al., 2007).

While other flooded savannas have already been the target of extensive studies, little is known about the species richness and ecology of seasonally flooded grasslands in south-central Africa. In particular, the still largely natural Zambezi catchment in Angola and Zambia lacks data as a result of difficult accessibility and the long-lasting civil war in Angola. The intactness and functionality of the ecosystems are, however, essential on a local as well as a continental scale, as the middle and lower reaches of the Zambezi River provide livelihoods for millions of people (Chenje et al., 2000; Emerton, 2003; Turpie et al., 1999). Therefore, to study and monitor biodiversity in the area and gain knowledge on land use and ecosystem function, we implemented a biodiversity observatory according to the BIOTA Africa standard (Jürgens et al., 2012) in Cameia National Park, Moxíco Province, in eastern Angola, in May

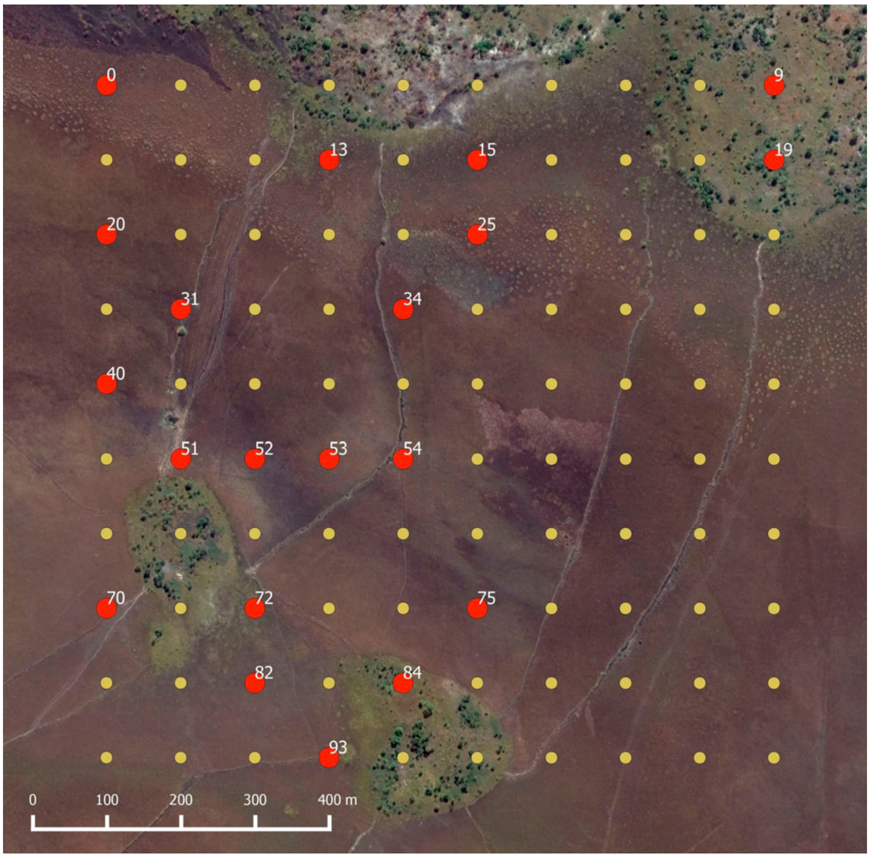

Figure 1: Observatory S76 in Cameia National Park. Fish dams between the woodland islands are clearly visible. Suffrutex grasslands surrounding the woodland patches are visible by the point pattern of termite mounds, which are not present in the flooded grasslands. Red dots mark the center points of the permanent plots. (Image source: Google Earth, 2014)

2016 (Hillmann et al., 2018; SASSCAL ObservationNet, 2017). This article summarizes initial insights into the ecology, plant and bird diversity, and human land use of Cameia National Park.

Our specific aims for this first assessment were to (a) gather preliminary information on habitat types, plant species richness, and diversity for the Cameia National Park Observatory S76 and (b) get a basic understanding of spatio-temporal niches for plants, animals, and human land use in this particular ecosystem, with its dramatic changes between dry and aquatic phases.

Methods

Study site

The eastern Moxico Province forms the major part of the Angolan headwaters of the Zambezi catchment. Its center is dominated by the extended sandy plains that characterize the landscapes of Cameia National Park. The western tributaries of the Zambezi flow in a southeasterly direction towards the Zambezi, cutting through the deposits of Kalahari sands with which the basin is filled (Wellington, 1955). Slightly elevated interfluves form wide plains intersected by small rivers. The fluvial beds in the Zambezi catchment tend to be meandering and swampy because of a low gradient that increases only after the river passes over Chavuma Falls at the Angolan-Zambian border (Nugent, 1990).

Observatory S76 is situated at the northern border of the national park (Fig. 1), between the villages Lumeje and Cassai Gare along the Benguela Railway, very close to the Great Equatorial Divide between the Zambezi and Congo catchments. It is subject to seasonal flooding, approximately from January to May, causing dynamic transitions between terrestrial and aquatic phases. As a consequence we observe, among other phenomena, temporal occurrence of fish, changing dominances in plant and birds communities, and changing land-use practices of local people. Grassland fires set by local communities after the flooded areas have dried out are a further seasonal disturbance.

Temperature recording

We used temperature loggers (Tinytag Plus 2, Gemini, UK) to assess microclimatic differences in various habitat types. Additionally, the data allowed us to infer the flooding period from buffered diurnal temperature fluctuations registered by inundated temperature sensors. We installed in total four loggers: (a) in low-lying grasslands that get inundated during the flood season, (b) 5 m from the first logger on a termitarium covered by grasses and geoxylic suffrutices (White, 1977; this vegetation type is hereafter referred to as suffrutex grassland), (c) in extended homogenous suffrutex grasslands and d) in open woodland. The loggers were buried with only the sensors protruding from earth, thus recording surface air temperatures close to the ground (0 cm–15 cm) at 15 min intervals from mid-November 2016 to the end of June 2017 (so far).

Vegetation survey

The installation of the observatory followed the standardized biodiversity observatory design of Jürgens et al. (2012). A 1 km² area was divided into a rectangular grid of 100 1 ha cells. The predominant vegetation unit and thus habitat type of each 1 ha cell was classified based upon visible vegetation structure in satellite images (Google Earth, 2014). Twenty 1 ha cells were selected according to a stratified sampling corresponding to the spatial cover of the four main vegetation units: woodland (three cells), suffrutex grassland (five cells), wet grassland (seven cells), and grassland (five cells) (see Fig. 1). In each of the selected cells, a 50 m x 20 m plot with a central 10 m x 10 m subplot was established. The surveys were conducted by recording species presence/absence in the whole plot plus their cover in the subplot. Since installation, the site has been visited three times: the first vegetation survey in May 2016 (dry season, flooded) was followed by another assessment in November 2016 (rainy season, dry) and a complementary collection of plant species in June 2017.

Bird observations

To complement the quantitative vegetation and flood phase surveys, we conducted opportunistic bird observations during each campaign and recorded bird species within the observatory. This encompassed mainly diurnal and conspicuous species identified by sight. However, our species lists were compared to and extended by the collection of specimens from Cameia National Park housed at the ornithological museum at ISCED Lubango. Furthermore, using the IBA species checklist (Leonard, 2010) of the comparable habitats from nearby Liuwa Plain National Park, Zambia, we compared species composition and overlap between the parks. This checklist, together with avifaunal information about Cameia National Park from BirdLife International (2017), was used to identify threatened and significant bird species. Finally, we categorized the observed bird species according to feeding guilds.

Land use

Information on the use of the landscape throughout the year by local communities was gathered by observations of human activity during the three field visits and informal conversations with members of local communities concerning their livelihoods and ways of life.

Results

Flood duration

The temperature curves recorded by our loggers indicate that the main flood season 2017 was from January to May, which is evident from buffered temperature oscillations at low-lying ground compared to more elevated sites (Fig. 2). The loggers on the slightly elevated termitarium in the flooded grassland, in the homogenous suffrutex grassland, and in the open woodlands did not show any phase of inundation. The water depths in the grasslands reached approximately 0.5 m but can be deeper locally in permanent pools or where earthen dams made for fishing purposes (see below) retain water. Temperatures in all vegetation units reach their maximum at noon and are lowest shortly before sunrise (6:00 a.m.). While the amplitudes were comparable between woodlands, suffrutex grasslands, and low-lying grasslands (grassland and wet grassland) in the early dry season (June), ranging diurnally between 10 °C and 37 °C, microclimatic differences were evident in the rainy and flooded season (March). In woodlands, temperatures range between 18 °C and 38 °C, in suffrutex grasslands from 22 °C to 42 °C, and in flooded grasslands from 26 °C to 36 °C during the day.

Vegetation survey

According to the initial vegetation unit classification based on satellite imagery of 100 ha cells in the observatory, the units are distributed and characterized as follows: slight sandy elevations above the flood level are covered by woodlands (ca. 13%; Fig. 3), their ecotones are subject to high rising ground water tables and host suffrutex grasslands (24%; Fig. 4), and the remaining 63% of the observatory corresponds to seasonally flooded savanna (grassland and wet grassland) (Fig. 5 and 6).

In the first vegetation assessment in May 2016, we recorded 215 different

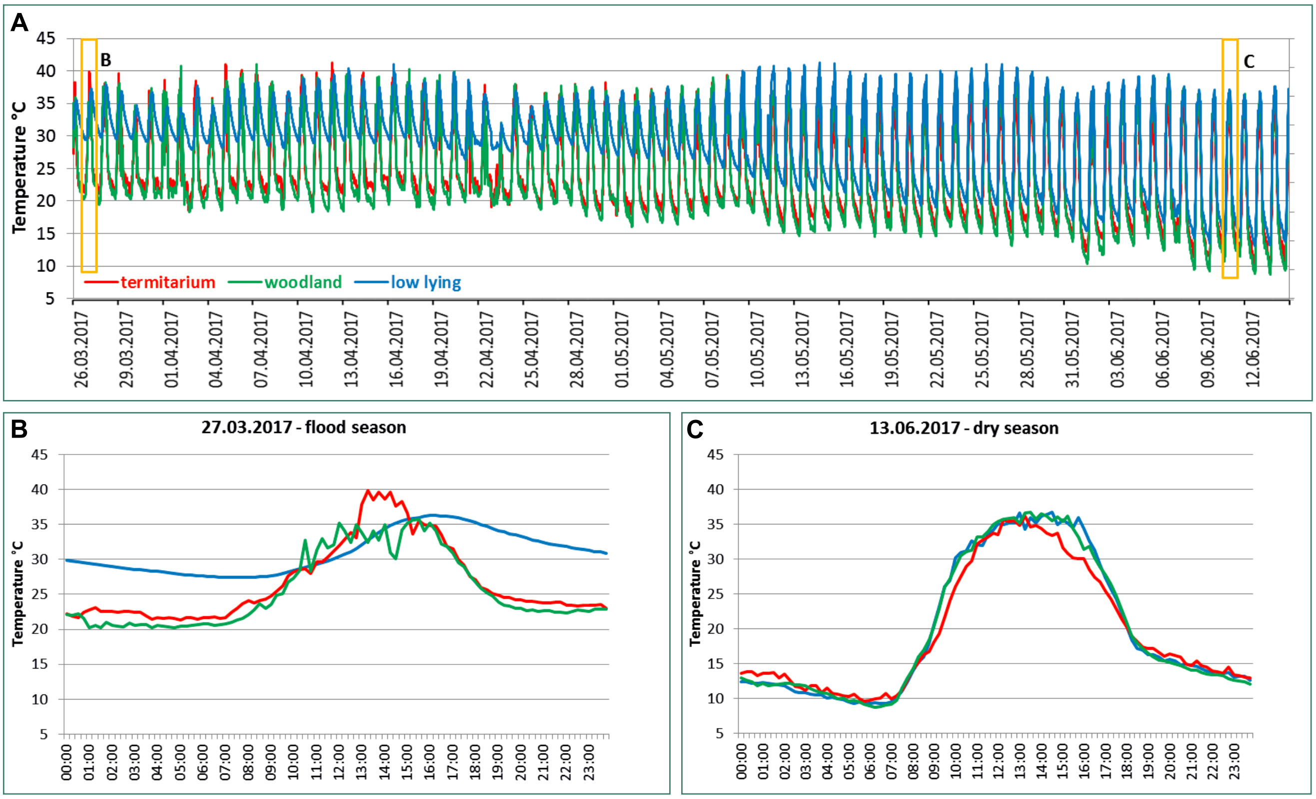

Figure 2: Ground temperature comparison of seasonally flooded savanna (blue line, logger a), an elevated termitaria within (red line, logger b), and surrounding open woodland (green line, logger d) from 26 March to 14 June 2017 in Cameia National Park (A). During the flood season (27 March 2017), the temperatures of inundated sites differ strongly from those of elevated or woodland sites. The water body buffers daily temperature fluctuations (lower and smoother amplitude of the blue line) (B). On the other hand, all temperature curves are comparable in the dry season (13 June 2017) and show similarly high amplitudes between cold morning and hot afternoon (C).

plant species in the whole observatory and in the second survey in November 2016, 167 different species were found. By the end of the third sampling in June 2017, we had counted more than 270 individual plant species within our 1 km² observatory, of which many are still waiting for identification. Figure 7 shows the mean seasonal species counts in the 100 m² subplots for each vegetation unit.

In the seasonally flooded plots, the plant communities differed most strongly between the early dry season (flooded phase) and the early rainy season (terrestrial phase), whereas the dominant communities in the woodland and suffrutex grassland plots (namely, woody species) did not show such strong seasonal floristic changes.

In the woodlands at elevated sites and islets, we observed the following dominant tree species: *Monotes glaber, Cryptosepalum exfoliatum* subsp. *pseudotaxus, Syzygium guineense* subsp. *guineense*, *Pterocarpus angolensis, Burkea africana, Bobgunnia madagascariensis, Uapaca gossweileri, U. robynsii, Erythrophleum africanum, Baphia massaiensis, Parinari curatellifolia, Pericopsis angolensis Brachystegia longifolia*, and *B. bakeriana*. In our observatory, trees start resprouting and flowering in mid-August/early September and keep their foliage until June. Leaves are then shed as the dry season begins. Once enough dry fuel is present, the fire season starts. Grass species in the open woodlands start flowering (and closing the ground layer) from January onwards and dominate the ground layer until the fire season starts. Commonly occuring grass species include *Andropogon eucomus* subsp. *huillense, Trachypogon spicatus, Monocymbium ceresiiforme*, and *Loudetia simplex*, and woodland-specific grass species are *Ctenium concinnum* and *Hyparrhenia rufa*.

Figure 3: Open woodland with patchy grass cover after a passage of fire. Photo: P. Zigelski, 2017.

Figure 4: Suffrutex grassland in the ecotones and on elevated termitaria within flooded plains. Photo: M. Finckh, 2016.

The suffrutex grasslands at the fringes and ecotones between woodland and grassland show higher grass proportions than the woodlands with *Hyparrhenia* spp., *Digitaria* spp., and *Pogonarthria squarrosa* as well as several Cyperaceae and the abovementioned ubiquitous C4 grasses. Codominant with grasses are geoxylic suffrutices that start to resprout and flower at the peak of the dry season (mid-August/early September) after being burned. Occurring species include *Parinari capensis, Cryptosepalum exfoliatum* subsp. *suffruticans*, *Ochna*

Figure 5: Grassland at the beginning of the rainy season in November, not yet inundated. Photo: P. Zigelski, 2016.

Figure 6: Approximately the same location in May, now fully flooded. Photo: P. Zigelski, 2016.

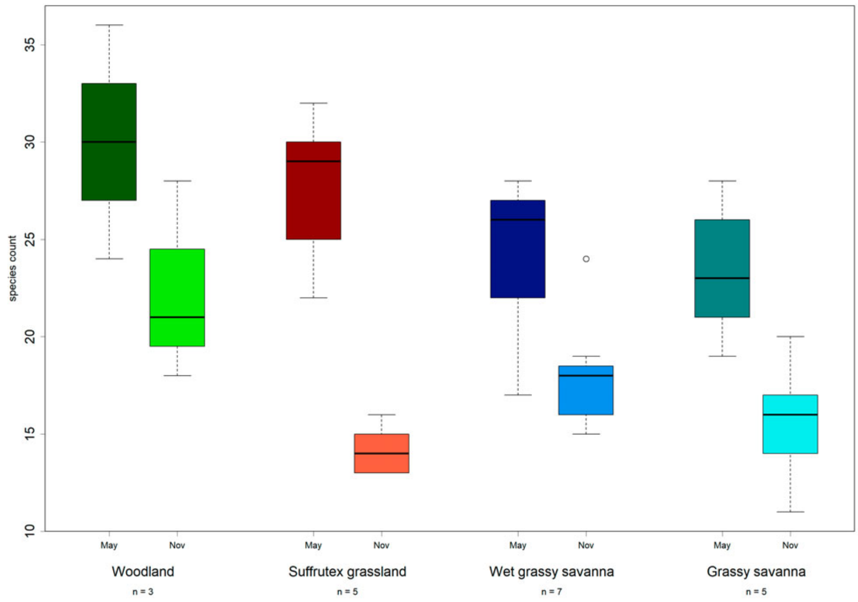

Figure 7: Mean species counts per vegetation unit and season in the 100 m² plots. Each unit is shown with its respective counts from May 2016 (darker box) and November 2016 (lighter box); whiskers indicate 1.5 times the interquartile range.

arenaria, Syzygium guineense subsp. *huillense, Magnistipula sapinii, Annona stenophylla* subsp. *nana, Eugenia malangensis, Anisophyllea quangensis,* and *Combretum platypetalum*. These geoxyles dominate the aspect of the suffrutex grassland until mid-rainy season (from mid-December onwards), when the C4 grasses start to develop their inflorescences and take over.

The grassland on lower ground is subject to seasonal flooding from January to May (see above) and lacks any woody species. These sites are dominated by hydrogeophytes and therophytes (e.g., *Nymphaea nouchali* var. *caerulea* and *Utricularia* spp.) during flooding, by small terrestrial therophytes (e.g., *Eriocaulon* spp., *Sebeae minuta, Burmannia madagascariensis, Drosera burkeana*, and *Utricularia pentadactyla*) when floods are receding (May–July), and by terrestrial geophytes such as *Ledebouria revoluta, Gladiolus* sp., *Heterotis canescens*, and *Polygala* sp. which survive the flooding but whose aboveground biomass development is reset by burning. Other perennial species include Cyperaceae such as *Eleocharis* sp., *Fuirena* sp., and *Rhynchospora* sp., several Xyridaceae, and a diversity of grass species, particularly *Microchloa kunthii, Andropogon eucomus* ssp. *huillense*, *Trachypogon spicatus, Monocymbium ceresiiforme*, and *Loudetia simplex*, which all seem to be well adapted to flooding.

Grasslands of similar species composition occur at midground, though these sites have shorter inundation periods. Their species numbers are slightly higher, but the dominant species and their phenology are similar to those of the lower ground.

Bird observations

So far, after three visits to the observatory, we have recorded 79 different bird species. Species composition and dominance differs strongly with seasonal change. Generalist and resident woodland or grassland species such as doves and pigeons (Cape turtle dove *Streptopelia capicola*, African green pigeon *Treron calvus*), crows (pied crow *Corvus albus*, Cape crow *C. capensis*) and fork-tailed drongos (*Dicrurus adsimilis*) occur throughout the year in their respective habitats. Birds of prey (e.g., brown snake eagle *Circaetus cinereus*, black-chested snake eagle *C. pectoralis*, dark chanting goshawk *Melierax metabates*, martial eagle *Polemaetus bellicosus*, bateleur *Terathopius ecaudatus*, white-headed vulture *Trigonoceps occipitalis*) have also been observed year-round but are most abundant and diverse in the early rainy season. At this time of year, as well as during receding flood, waders such as Temminck's stint *Calidris temminckii*, ruff *Philomachus pugnax*, and common greenshank *Tringa nebularia* occurred in the open grasslands and at pools.

With the onset of the flood season, aquatic species become dominant, particularly water fowl (e.g., spur-winged goose *Plectropterus gambensis*, hamerkop *Scopus umbretta*), egrets, cranes and storks (e.g., rufous-bellied heron *Ardeola rufiventris*, grey crowned crane *Balearica regulorum*, saddle-billed stork *Ephippiorhynchus senegalensis*), kingfishers (e.g., malachite kingfisher *Alcedo cristata*, African pygmy kingfisher *Ispidina picta*, giant kingfisher *Megaceryle maxima*) and other fish-feeding species (e.g., African fish eagle *Haliaeetus vocifer*).

Ground-dwelling species appear with receding flood and drying grasslands, particularly larks and pipits (e.g., Angolan lark *Mirafra angolensis*, Grimwood's longclaw *Macronyx grimwoodi*, dusky lark *Pinarocorys nigricans*), quails (e.g., harlequin quail *Coturnix delegorguei*), and bustards (e.g., black-bellied bustard *Lissotis melanogaster*, Denham's bustard *Neotis denhami*).

Seedeaters and insectivores were mainly observed in the flood phase, when grasses are fruiting and midges and mosquitos thrive over the water body. Among others, widowbirds (e.g., long-tailed widowbird *Euplectes progne*, fan-tailed widowbird *E. axillaris*), and waxbills and canaries (e.g., yellow-fronted canary *Serinus mozambicus*, common waxbill *Estrilda astrild*) are most conspicuous as well as chats (e.g., sooty chat *Myrmecocichla nigra*, capped wheatear *Oenanthe pileata*, common stonechat *Saxicola torquatus*), swallows (e.g. lesser striped swallow *Cecropis abyssinica*, Black-and-rufous swallow *Hirundo nigrorufa*, red-throated swallow *Petrochelidon rufigula*, grey-rumped swallow *Pseudhirundo griseopyga*), and cisticolas (e.g., zitting cisticola *Cisticola juncidis*).

In combination with the collection of bird specimens deposited at ISCED Lubango, Angola, we have counted so far a total of 209 different bird species recorded for Cameia National Park. In the structurally similar Liuwa Plain National Park in Zambia, 349 different bird species were recorded (Leonard, 2010), of which Cameia National Park shares 151 species (72.2%), though 58 species (27.8%) of the species occurring in Cameia National Park do not occur in Liuwa Plain National Park. According to the Zambian conservation categories, 14 species show a restricted range (Forbe's plover *Charadrius forbesi*, Dambo cisticola *Cisticola dambo*, Cape crow *Corvus capensis*, common quail *Coturnix coturnix*, lark-like bunting *Emberiza impetuani*, long-tailed widowbird *Euplectes progne*, greater kestrel *Falco rupicoloides*, red-throated wryneck *Jynx ruficollis*, Grimwood's longclaw *Macronyx grimwoodi*, Angola lark *Mirafra angolensis*, white-throated francolin *Peliperdix albogularis*, red-throated swallow *Petrochelidon rufigula*, black-chested prinia *Prinia flavicans*, whinchat *Saxicola rubetra*) and six species are threatened (grey crowned crane *Balearica regulorum*, African marsh harrier *Circus ranivorus,* slaty egret *Egretta vinaceigula*, saddle-billed stork *Ephippiorhynchus senegalensis*, Denham's bustard *Neotis denhami*, bateleur *Terathopius ecaudatus*). According to BirdLife International, five species that are poorly known or locally restricted occur in Cameia National Park: rufous-bellied heron *Ardeola rufiventris*, Forbe's plover *Charadrius forbesi*, brown firefinch *Lagonosticta nitidula*, white-throated francolin *Peliperdix albogularis*, and southern masked-weaver *Ploceus velatus*.

People and land use

Fish constitutes the main "cash crop" of the adjacent communities. The broad but very shallow flood channels in the plains are crisscrossed by small earthen dams (Fig. 1, Fig. 8) of about 1 m height, with multiple water outlets fitted with traditional fish traps made of grass stalks (Fig. 9). Fish migrate into the grasslands with rising water levels – and are harvested on their way back to the permanent water bodies. The catch is sun-dried on small wooden tables on the woodland islands (Fig. 10), where families build temporary huts for the fishing season. Dried fish is then transported in sacks and mostly on cargo bikes towards the larger marketplaces where middlemen buy the catches and sell the fish toward the urban centers of Angola.

Figure 8: Small earthen dams of about 1 m height crisscross the plains and serve for fish harvesting along the outlets. Photo: M. Finckh, 2016.

Figure 9: Fish traps made of grass stalks are inserted into the water outlets of earthen dams. Photo: M. Finckh, 2016.

Figure 10: Catch is sun-dried on small wooden tables on the woodland islands. Photo: M. Finckh, 2016.

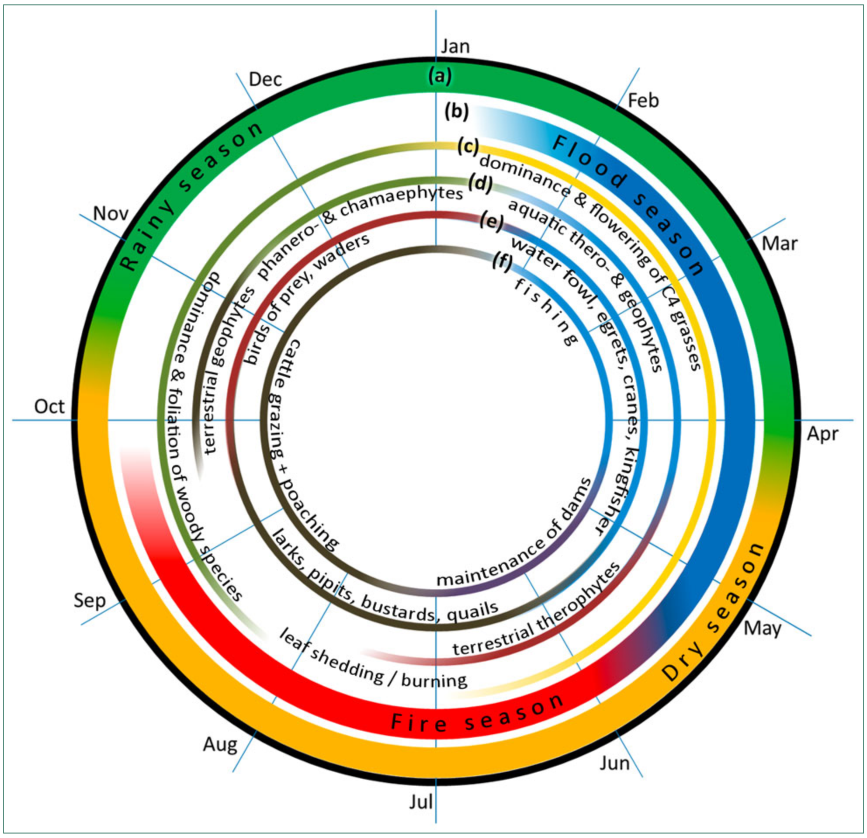

Figure 11: “Seasonal clock” of ecological events in Cameia National Park. The outer rings show the rainy and dry seasons (a) and the flood and fire seasons (b). The next ring (c) indicates the phenology of dominating perennial plant groups, and ring (d) describes the occurrence and dominance of seasonally limited plant groups. The inner rings show dominating or conspicuous bird groups (e) and the main practices of land use of local communities (f).

Fish dams are maintained and repaired at the beginning of the dry season, when soils are still humid and easy to dig. Fishing has an impact not only on the flooded areas but also on the habitats of the drier high ground. As dams are maintained and used by families, during the fishing season people settle temporarily in the small woodland islands and build small huts and the tables to dry the fish. This means that most of the small woodland patches are disturbed to a certain degree by woodcutting (for huts, tables, and firewood), debarking (for ropes), and the permanent presence of humans in areas which otherwise would be refugia for terrestrial fauna during the flooding season.

Cattle grazing is the main economic activity in the dry season. Shortly after the grasslands fall dry, around mid-June, people start to burn the grasslands, thus initiating the sprouting of the perennial C4 grasses. Once fresh grasses appear, adjacent communities start grazing their cattle on the grasslands close to the national park border or poach small game that is also attracted (Hall, 1984). Grazing goes on until flooding starts at the beginning of January, when cattle herding retreats to the reachable remaining high ground.

Currently there are no active fields within the observatory, but old fallows of former cassava plantations are recognizable in the woodlands. Google Earth images from 2002 indicate that cassava was produced there during the final phase of the civil war (e.g., on Plot 19, see Fig. 1).

Discussion

The vegetation surveys and bird observations both show seasonally changing species assemblages produced by changing environmental conditions. In addition, we observe different modes of land use by local communities throughout the year. The turnovers coincide with the seasonal change between flood, fire, dry, and rainy phases. These abiotic drivers hence control the prevalent assemblages and land-use activities (Fig. 11).

Flooding regime and origin

Based on buffered diurnal temperature fluctuations observed in the study (see Fig. 7), we see that the flood is delayed by about three months from the beginning of the rainy season (October to April; SASSCAL WeatherNet Station Mwinilunga in Zambia, 2017) (see Fig. 11 (a)/(b)). Flooding of the grasslands is thought to be a consequence of high precipitation in the catchment area (SASSCAL WeatherNet Station Mwinilunga: 1,400 mm/a), causing rising ground water tables on partly impermeable soil horizons within or below the leached sandy deposits (Welcomme, 1979; White, 1983). This leads to the apparently nutrient-poor waters, as indicated by numerous specialized carnivorous plant taxa such as Drosera spp. and Utricularia spp. Alternatively, in other parts of the national park, laterally overflowing rivers and streams probably also contribute to the inundation of the surrounding grasslands (Junk & Furch, 1993; Welcomme, 1979). While the latter, alluvial flooding type (Tockner & Stanford, 2002) is fairly well known and occurs for instance 400 km downstream the Zambezi at the Barotse Plains in Zambia (Moore et al., 2007) and at the Okavango Delta in Botswana (Wolski & Savenije, 2006), the rainfed sheet flooding is best described for savannas in South America such as the Llanos Baixos of the Orinoco basin in Venezuela (Godoy et al., 1999; Junk & Furch, 1993) or the Pantanal in Brazil (Alho, 2008). Thus, based on our observations on flooding pattern and species occurrences/preferences, we can show that similar systems also occur in Africa. During several flooded months, the water evaporates and slowly drains towards the tributaries of the Zambezi (review of the South American systems by Junk & Furch, 1993); only after the end of the rainy season do the surface waters drain off first and finally the ground water table drops, so that the ecosystem then switches into an extended terrestrial phase (June to December) (Fig. 11 (b)).

Responses in vegetation to the seasonal drivers

This flooding regime shapes the vegetation units and their species composition in the observatory. Most woody species avoid the waterlogged sites and are adapted to disturbance by fire (tree and suffrutex species in the ecotones and woodlands, such as *Burkea africana*) (Rutherford, 1981). Nonwoody perennials are adapted to flooding and fire (herb, grass, and sedge communities in the plains and under tree cover (Keeley & Rundel, 2005) (see Fig. 11 (c)).

Interestingly, with the beginning of the flood, aquatic therophytes and hydrogeophytes appear within the standing water body. After the water recedes it leaves behind wet, clayey-sandy patches between the grass tussocks, which are then occupied by semiterrestrial annuals (see Fig. 11 (d)) and geophytes. Thus, alternating life forms of annuals and (hydro-) geophytes subsequently use sophisticated spatial niches in this system dominated by bulky C4 grasses. In the case of the therophytes, first we find *Utricularia* spp. floating among the grass inflorescences, while later on semiterrestrial *Eriocaulon* spp. and other small sedges colonize the humid sands between the grass tufts. In a similar way, the space is first used by hydrogeophytes with their leaves floating among the grasses on the water surface (flooded phase: e.g., *Nymphaea* spp.), whereas after the flood terrestrial geophytes (e.g., *Gladiolus* sp., *Heterotis canescens*) start to flower between the grass tufts (see Fig. 12).

The number of recorded plant species was considerably higher in May than in November (see Fig. 7). This trend was evident in all four vegetation units, though the species counts in suffrutex grasslands differ more markedly. Since the low-lying areas (grassland and wet grassland) are still inundated in May, the aquatic species add to the species number in May and are not visible in November. The suffrutex grasslands benefit from the moist soil conditions in the second half of the rainy season, when the herbs and suffrutices are still visible and numerous small annual species and herbs are present (see Fig. 12). Similarly, species numbers in woodland units (particularly annuals) appear to be higher thanks to better water availability towards the end rather than in the first half of the rainy season. There is probably still a detection bias in our species data, however, as most of the perennial grasses only start to flower in January, so some grass species may have been overlooked in November. We furthermore expect the final plant species number to be higher since similar well-studied wetland ecosystems such as the Okavango Delta in Botswana present a much higher count (Ellery et al., 2000).

Seasonal change in bird species composition

Several bird groups, not only water-associated species, make use of the seasonal flooding (Fig. 11 (e)) as the inflowing water provides rich fishing grounds, attracts insect swarms, and promotes ripening and distribution of seeds and fruits (comparable to the wetlands in the Sahel; Zwarts et al., 2009). The small-scale heterogeneity of Cameia National Park allows for multiple aquatic guilds to coexist. Piscivorous birds, for instance, use the fishing dams and trees/shrubs at the trenches along the Benguela Railway and in the ecotones as lookout perches (African fish eagle *Haliaeetus vocifer*, giant kingfisher *Megaceryle maxima*), hover over the water surface (pied kingfisher *Ceryle rudis*), or stride through the water in the open plains (great egret *Ardea alba*). These aquatic guilds are at least local migrants, as their stay at Cameia National Park is temporally limited; little is known about their routes and where they stay after the flood, though it is likely that they withdraw to the vicinity of major perennial river runs (e.g., Zambezi). Soon after the flood recedes, terrestrial bird groups become dominant in the open plains. While larks and pipits require low vegetation strata, which they find in recently burned areas (Sinclair et al., 2010c,d), quails and bustards are attracted by standing grasses and use them for cover (Sinclair et al., 2010a,b). Thus, small-scale heterogeneity once more contributes to species richness, in this case as a consequence of anthropogenic, patchy burning of grasslands.

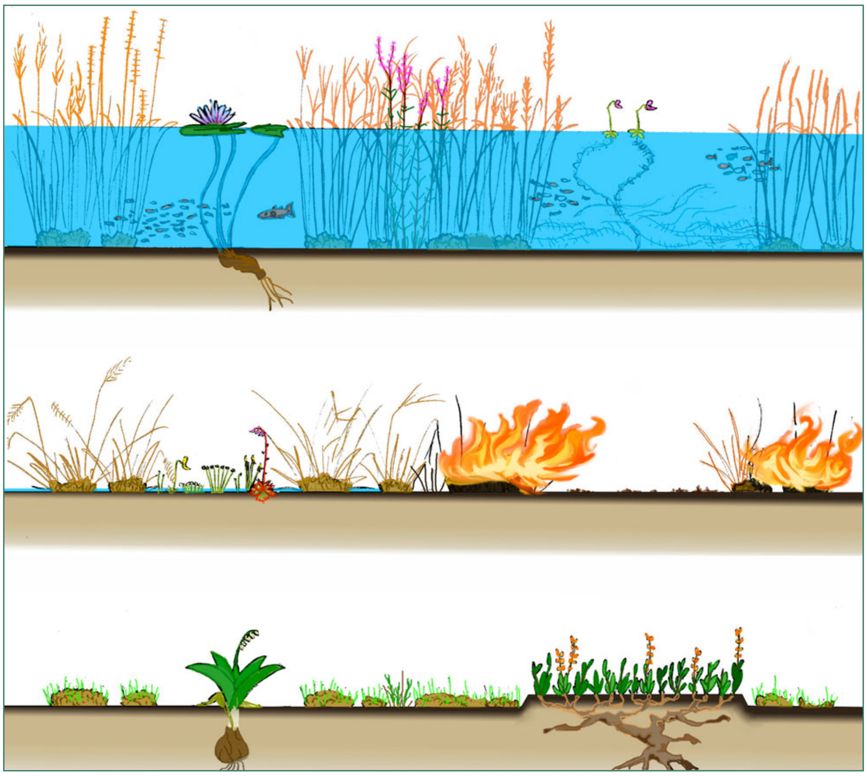

Figure 12: Schematic overview of the seasonal shifts from the aquatic to the terrestrial phases and the resulting dynamics of niches: (A) During the floods the space between perennial grasses (e.g., Andropogon eucomus subsp. huillense) and herbs (e.g., Heterotis canescens) is used by hydrogeophytes with floating leaves (e.g., Nymphaea nouchali var. caerulea) and therophytes (e.g., Utricularia benjaminiana). Fish and other small aquatic animals roam among the stalks. (B) Shortly after the flood, the still-moist soil between the tussocks offers niches for semiaquatic therophytes (Drosera sp., Eriocaulon spp.), which later burn away in the fire season. (C) Subsequently and with the beginning of the rainy season, terrestrial geophytes (particularly orchids and bulbous plants) start flowering between the resprouting C4 grasses. On higher ground (e.g., elevated termitaria) that is not inundated, geoxylic suffrutices (e.g., Parinari capensis) start to flower and develop their leaves. They dominate until the C4 grasses take over again from mid-December onwards.

Comparing the bird species composition and numbers to the famous Okavango Delta in Botswana or the Liuwa Plain in Zambia, we observe the same dominant families and guilds in these ecosystems. Though the recorded number of 209 species for Cameia National Park is much lower (Okavango Delta: 444 species; Liuwa Plain National Park: 349 species), nevertheless Accipitridae, Sylviidae, Ploceidae, and Ardeidae are particularly prevalent (African Parks, 2017; Leonard, 2010; Ramberg et al., 2006). This leads to the conclusion that either the Cameia National Park is severely impoverished with regard to bird species or, more likely, that data deficiency is great and more investigation is needed (see below).

Seasonal change in human land-use practices

The modes of human land use in Cameia National Park are another example of the use of spatially diverse and seasonally changing "resource niches" (see Fig. 11 (f)). In general, human land use has a major impact on landscape integrity and thereby on species diversity and composition in Africa (Anderson, 2014). However, and fortunately, in contrast to other protected areas in Angola (e.g., Mupa National Park and Quissama National Park), the seasonal flooding so far has prevented the encroachment of permanent settlements into the area. Nevertheless, the communities adjacent to Cameia National Park, mostly Chokwe, use the floodplains in multiple ways according to the season and certainly have influence on the flooding pattern (water-retaining fishing dams) and overall species composition (favoring species resilient to fire and cattle grazing) (Belsky, 1992). Next to the abiotic drivers shaping this particular ecosystem, human land use could hence be regarded as a biotic driver, affecting its species diversity and composition (see also below regarding mammals).

Outlook: Challenges for management and conservation

The Cameia National Park has formerly been home to high numbers of large vertebrates such as blue wildebeest Connochaetes taurinus, plains zebra Equus quagga, oribi Ourebia ourebi, lechwe Kobus leche, lion Panthera leo, cheetah Acinonyx jubatus, wild dog Lycaon pictus, and crocodile Crocodylus niloticus (Da Silva, 1952; Huntley, 1974). Indeed, not far away across the Zambian border, the seasonally flooded savannas of the Liuwa Plain National Park still teem with huge numbers of wildebeest, zebra, smaller antelopes, and the predators that hunt them (African Parks, 2017). The park is furthermore famous for its bird diversity (Leonard, 2010). Angola's national parks, however, suffered during the civil war from the mid-1960s to 2002, in which uncontrolled and heavily armed hunting brought most populations of large mammals to the point of collapse. Cameia National Park was no exception in this sense; the once-famous big migrations of tens of thousands of blue wildebeest and other larger herbivores have been wiped out.

No exact information is available about the current status of larger fauna in Cameia National Park; however, the park seems to be largely devoid of larger mammals. It is safe to assume that the elimination of the former herbivore guild has changed the food webs and nutrient dynamics in the grasslands considerably, but again, scientific studies are missing. The landscapes and the avifauna (and probably most of the smaller fauna) are, however, still pristine. There are probably few areas in Africa where so large unspoiled natural grasslands are still to be found, and the avifauna is still remarkable in species composition and seasonal shifts.

To conclude, our first results indicate the particularity of the ecosystems and their conservation value as well as the current conservation challenges for Cameia National Park, which arise from conflicting interests between sustainable ecosystem maintenance and growing human demands. Scientific data are almost nonexistent. Thus, there is an urgent need for studies of ecosystems and biodiversity in this area. This is particularly of interest since seasonally flooded grasslands in Africa are in general poorly studied (Turpie et al., 1999; Turpie, 2008) and new challenges for conservation are looming large. The provincial and the national governments favor economic development above conservation, and large-scale land conversion to industrial rice cropping and aquiculture is under discussion for Moxico (ANGOP, 2017), including parts of Cameia National Park. To assess possible effects for the park's unique ecosystems (e.g., in terms of direct conversion, changes in nutrient status of the waters, invasive fish species, etc.) a better understanding of the ecology, diversity, and resilience of this macro-ecosystem is urgently needed.

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