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THE DISTRIBUTION OF MIOMBO WOODLAND IN SOUTHERN AFRICA

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SUMMARY

Miombo woodland occurs over a vast area of Africa and is an important habitat, making knowledge of its distribution important to African biogeography. In Southern Africa, the distribution of the Miombo Region – where miombo naturally dominates landscapes – is relatively well-known, but maps in the standard texts are equivocal in the Mozambique Lowlands. The distribution of small miombo patches outside the Miombo Region is also not well known, yet outliers can be important in driving faunal distributions, even at a regional scale. Here, given limited vegetation mapping, the distribution of the Miombo Region in the southern Mozambique Lowlands is modelled using the distributions of miombo bird specialists. Outlying miombo patches are also mapped across Southern Africa, using primary distribution data sourced from relevant vegetation surveys and herbaria specimens.

The Miombo Region mapped here differs conceptually and spatially from the standard texts, and provides a more comprehensive distribution for southern Mozambique. But major gaps in knowledge – which have important implications for conservation management – remain, and are identified. Tracks of patches of miombo associated with the complex topography at the eastern edge of the Great African Plateau are identified. While miombo ecosystems generally naturally dominate landscapes spatially, these tracks show that large parts of the distribution of miombo woodland consist of small patches confined to unusual, highly localised ecotopes. These offer potential connections between major parts of the Miombo Region and likely routes for its expansion and contraction over geological time. They also likely support metapopulations of miombo specialist fauna, which are at greater risk from habitat loss because the patches cover such small areas and are naturally fragmented. The track that includes Gonarezhou National Park requires special conservation management given the broad-scale loss of miombo woodland which has already occurred from the area due to a combination of drought, fire and elephants.

KEY WORDS: Miombo Region − woodland − biogeography − biotope − transition woodland

INTRODUCTION

'Miombo' is the name given to the distinctive woodland type in which trees of the genera *Brachystegia*, *Julbernardia* and/ or *Isoberlinia* dominate the canopy (Wild & Barbosa 1967, White 1983, Campbell 1996). It is the major vegetation type of White's Zambezian Region (White 1983), naturally dominating landscapes from Angola to southern Tanzania southwards to Zimbabwe and Mozambique (Campbell 1996). It is most typical of poor, sandy soils formed from Basement Complex rocks on the moist plateaus of south-central Africa (Frost 1996), but also occurs at lower altitudes across eastern Africa (Fig. 1). The miombo avifauna is large and distinctive (Benson & Irwin 1966), and miombo probably also supports specialist small mammal, dung beetle, lepidoptera and spider faunas (Frost 1996, Penney 2013). Therefore, knowledge of the distribution of miombo is important to African biogeography and is required to the level of the patch or stand.

Vegetation mapping of south-central Africa is generally limited to reconnaissance mapping of regional mosaics. White (1983) remains the most detailed mapping for the region as a whole and Figure 1 outlines where he showed miombo woodland to naturally dominate landscapes. That is, although miombo woodland is spatially dominant, other vegetation types occur naturally within these mosaics. The mosaics show *potential* vegetation, and have been made even more complex with broad-scale anthropogenic transformation. The standard texts (Campbell 1996, Chidumayo 1997, Desanker *et al.* 1997, Frost, Timberlake & Chidumayo 2002, Dewees *et al.* 2010, Timberlake, Chidumayo & Sawadogo 2010, Timberlake & Chidumayo 2011) use White's (1983) polygons to map miombo, although there remains a lack of clarity regarding which are included. For example, Dewees *et al.* (2010) included *Brachystegia bakeriana* thicket (White's type 47) in Angola, but excluded Mozambican *Brachystegia spiciformis* "transition woodland" (type 16a) – a term used by White (1983) to describe woodland approaching forest. There is therefore some uncertainty regarding the distribution of miombo due to the wide variation of physiognomic types in which the miombo genera dominate canopies and how different authors treat forest and thicket formations, as well as the broad resolution of White's (1983) continental mapping.

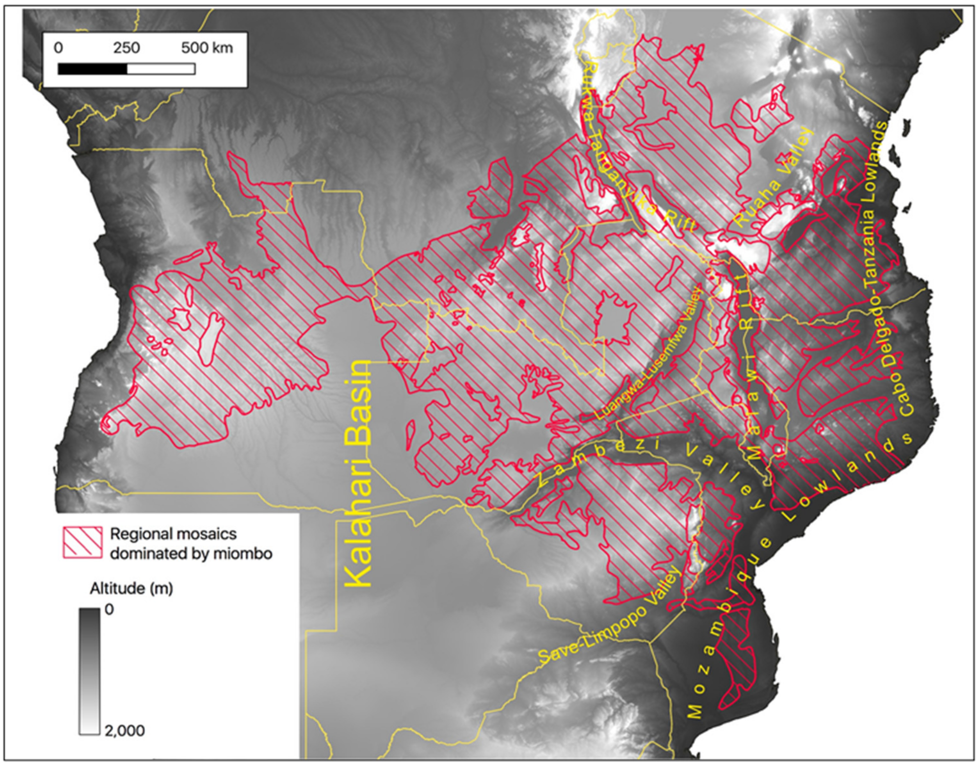

Figure 1. The distribution of regional mosaics spatially dominated by miombo woodland (after White 1983).

There is more detailed mapping, notably that of Wild and Barbosa (1967) for the Flora Zambesiaca region (Fig. 2), which forms the core of the distribution. They showed miombo woodland to be widespread across the Mozambican lowlands, where it is naturally co-dominant spatially with other vegetation, especially types of forest. These were mapped by White (1983) as forest mosaics. Together, these miombo regional mosaics – where miombo is naturally spatially dominant or co-dominant with other vegetation types – form the Miombo Region.

Wild and Barbosa (1967) also showed the distribution of miombo to be much more fragmented than might be appreciated from the standard texts and White's polygons. For example, distinctive temperate grasslands and non-miombo tree savannas (Wild & Barbosa's types 39, 65, 67) fragment the distribution of miombo on the Zimbabwe Plateau but were lumped into White's miombo regional mosaics. The naturally fragmented nature of the Miombo Region has significant implications for miombo faunas. For example, there are specific and subspecific differences in the avifauna either side of the major river valleys, which have acted as biogeographic barriers (Benson, Irwin & White 1962). There are patches of miombo lying outside the Miombo Region in regional mosaics spatially dominated by other vegetation types that were too small for Wild and Barbosa to delineate in their sub-continental mapping. Examples include patches in temperate grasslands in the drier rainshadow portions of the Nyanga Highlands and Serra Choa. Other outliers have since been discovered, notably at Gundani, northern South Africa (Hurter & van Wyk 2001). Outlying patches are potentially important because they could provide 'stepping stone' connections between sub-populations of miombo faunas, or even support metapopulations (*sensu* Hanski 1998). Alternatively, the lack of outliers connecting populations suggests there could be a lack of gene flow, and genetic and morphological differentiation should be investigated. Climates are projected to change significantly across the distribution of miombo over this century (Shongwe *et al.* 2009) and outlying patches are important because many lie at the leading edges of distribution. Therefore, better knowledge of the distribution of outliers is important to modelling potential future distributions of miombo vegetation–habitats–ecosystems. Evidence of patches lying outside the Miombo Region is collated here and their distributions mapped. The distribution of miombo ecosystems across the lowlands of southern Mozambique is also assessed more generally given that the maps in the standard texts are equivocal and outliers can only be identified once the Miombo Region is defined spatially.

STUDY SITE

The area south of the Zambezi River was assessed, as were areas just to the north that could potentially support outliers that are parts of tracks between major parts of the Miombo Region, for example the Middle Zambezi Valley north of the Zambezi.

METHODS

A search was made for all relevant vegetation surveys and visits made to the large collections of the herbaria of the National Botanical Gardens, Harare and Royal Botanical Gardens, Kew, London to search for specimen records. *Isoberlinia* species do not occur in the study region, so specimen searches focused on the genera *Brachystegia* and *Julbernardia*. The issues in identifying and mapping patches of miombo using these sources of information are discussed below.

1. *Variability in the physiognomy of stands with canopies dominated by miombo genera*

Miombo typically has a woodland structure (Frost 1996) and the typical miombo faunas are woodland specialists. But there is great variability in the degree of canopy cover where miombo genera are dominant, so specimen records in particular need to be treated with caution as there is often no information on the label regarding the structure, composition, etc. from where the specimen was taken. Most problematic are forest and tall thicket formations with canopies dominated by *Brachystegia spiciformis* on deep sands in coastal areas from southern Mozambique to Kenya. White (1983) noted that, in woodland, the crowns of adjacent trees are "often in contact but are not densely interlocking", but stands on these coastal sands often have dense canopies with interlocking crowns more accurately identified as 'forest' (e.g. at Pomene, southern Mozambique, Fig. 3). White considered these formations to be generally secondary and transitional to forest proper ("transition woodland"), but also noted that the sands can be so nutrient-poor as to limit the succession. Therefore, *B. spiciformis* forest-thicket can be a climax formation, and Burgess and Clarke (2000) included them in the 'coastal forests' of eastern Africa. There is a complex mosaic of more open-canopied miombo woodland proper occurring with dense *B. spiciformis* forest-thicket (and other forest and thicket types) along the eastern African coast, so care needs to be taken in determining whether stands dominated by *B. spiciformis* on the Mozambique Lowlands are considered as proper miombo woodland.

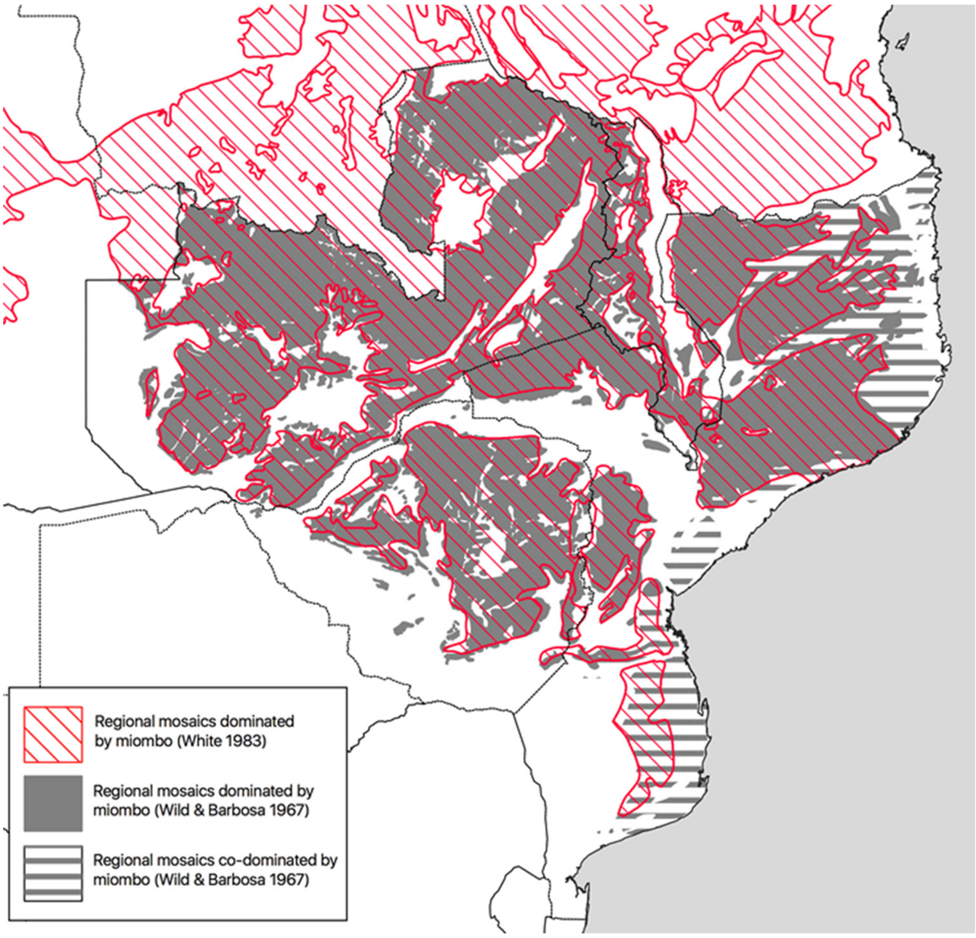

Figure 2. The Miombo Region within the Flora Zambesiaca region (after Wild & Barbosa 1967).

There is also variability in how the terms 'woodland' and 'savanna' are used. Wild and Barbosa (1967) mapped miombo woodland and savanna woodland, but also recognised miombo tree savanna types in the drier parts of the Miombo Region around the 600−700 mm annual rainfall limit identified by Frost (1996). Although White (1983) based his classification on that of Greenway (Pratt, Greenway & Gwynne 1966, Greenway 1973), who classified woodland as a vegetation formation with tree cover >20%, he defined woodland as "An open stand of trees with crowns which form a canopy from 8 m in height and cover at least 40% of the surface of the land". Chidumayo & Gumbo (2010) used the term 'woodland' even more broadly − for >10% tree canopy cover − which they recognised included what others would call 'savanna'. Notwithstanding the differences in

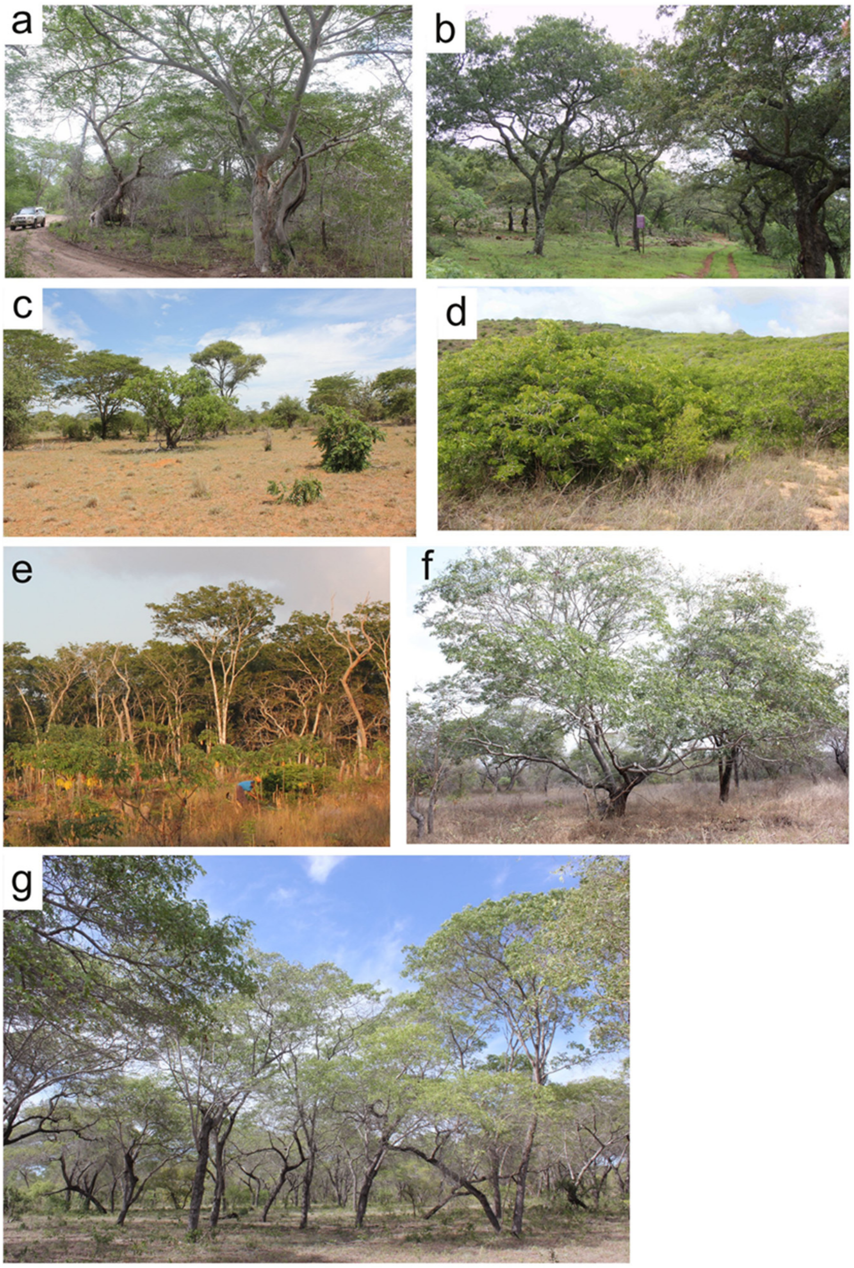

Figure 3. Examples of stands outside the Miombo Region (a–b, g), and some of the issues with identifying outliers (c–f): (a) small patch of *Brachystegia tamarindoides* subsp. *torrei* woodland, Coutada 4, Mozambique; (b) *Brachystegia spiciformis* woodland, Gundani, northern South Africa; (c) *B. t. torrei* individuals, some heavily impacted and coppicing (front right), in mixed tree savanna, Gonarezhou National Park, Zimbabwe; (d) dense short thicket of *B. spiciformis* on littoral sands, Pomene Nature Reserve, Mozambique; (e) tall, dense *B. spiciformis* "transitional woodland" (sensu White 1983) with a forest structure, Pomene; (f) small colony of *Julbernardia globiflora* trees in mixed tree savanna on the Sul do Save sands to the east of Machaila, Mozambique; (g) stand of well-developed *J. globiflora* woodland, Guluene–Chefu–Mwenezi watershed, Gonarezhou National Park.

nomenclature, the lower limits of tree canopy cover forming the typical physiognomy of climax miombo remain to be defined empirically. For example, there are no data on this in Frost (1996) or Chidumayo (1997). This is important because the miombo specialist faunas have lower limits of tree canopy cover (as well as upper limits), with Cumming *et al.* (1997), for example, showing that specialist bird species were lost from miombo canopies heavily impacted by elephants. It remains to be determined if undisturbed stands typical of Wild and Barbosa's miombo tree savanna types (36, 42) are suitable, especially as appreciable parts of these regional mosaics have a diverse, mixed canopy where *Julbernardia globiflora* is patchy (Fig. 3f). Here, while *B. spiciformis* 'transitional woodlands'/ forest-thickets were excluded *a priori* from a search for miombo, until more canopy cover and composition data are available tree savannas are included.

Miombo dominant species, especially *B. spiciformis*, also show exceptional intraspecific phenotypic plasticity, with shrub or small tree ecotypes that are so short as to form climax (short) thicket or dwarf woodland on the Mozambique coastal plain and Manica Highlands, respectively (see Fig. 3). Here, littoral thickets are excluded but dwarf woodlands are included.

2. *Defining the Miombo Region in the Mozambique Lowlands*

The complex spatial patterns of vegetation in the Mozambique Lowlands were highlighted by Wild and Barbosa (1967) in mapping miombo as *co-dominant*, and by White (1983) in defining his Zanzibar-Inhambane Region as a Regional Mosaic. Finer-resolution mapping is required to identify precisely where miombo woodland occurs within these mosaics, but in Mozambique there is little of this so the distributions of bird species generally confined to the miombo canopy are used here as a surrogate to indicate the general distribution of miombo woodland proper. Of the miombo canopy specialists identified by Benson and Irwin (1966), the Southern Hyliota *Hyliota australis*, Yellow-bellied Hyliota *Hyliota flavigaster*, Green-backed Honeybird *Prodotiscus zambesiae*, Western Violet-backed Sunbird *Anthreptes longuemarei* and Cabanis's Bunting *Emberiza cabanasi* occur in the lowlands of southern Mozambique, and are mapped using data from Parker (1999, 2005). Canopy insectivores were chosen specifically as they form the core of the miombo specialist guild and are probably the most indicative of tree canopy cover and function, i.e. while typical of briefly deciduous miombo woodland they will generally be absent from the dense canopies typifying semi-evergreen *Brachystegia spiciformis* tall forest-thicket. Records of the Olive-headed Weaver *Ploceus olivaceiceps* are not included as this species may be more willing to inhabit these 'transition woodlands'/forest-thickets. Other species that occur in southern Mozambique that are typical of miombo but prone to wander into other woodland types, such as the White-breasted Cuckooshrike *Coracina pectoralis* and Black-eared Seedeater *Crithagra mennelli,* are also not included.

3. *Mapping miombo biotopes*

Figure 3a shows a small patch of *Brachystegia tamarindoides* subsp. *torrei* woodland occupying a rocky outcrop in an otherwise very thinly wooded (≤10%) *Julbernardia globiflora* tree savanna in Coutada 4 just north of the Save River. This patch of miombo woodland proper is well-defined from the surrounding landscape because it occupies a distinctive ecotope − the smallest spatial entity or element of a geographical landscape that is ecologically homogeneous (Troll 1950). Rocky outcrops can provide more moisture (e.g. stored in crevices) and/or refuge from fire, thus support greater canopy development than the surrounding landscape. Sourcing vegetation mapping and specimens from rocky outcrops was important in the search for patches outlying the Miombo Region.

Different approaches are required to map miombo biotopes (occupying ecotopes) and miombo regional mosaics since they cover such vastly different extents. Here, Wild and Barbosa's miombo regional mosaics (where miombo is naturally dominant across landscapes) are mapped as polygons, while outlying patches in non-miombo regional mosaics are too small to be delineated at this scale and are mapped by quarter-degree-square (QDS). (One-degree square cells are divided into 16 quarter degree square cells.) There is a lack of precision; for example, the c.20 ha patch of miombo at Gundani, northern South Africa, covers only 1/3,000 of the relevant QDS. However, this approach allows for the locations of outlying patches to be mapped at a regional scale.

4. *How big does a colony of trees have to be in order to be considered a patch of miombo?*

Some of the miombo dominants occur in colonies of only a few individuals, for example Chris Hines (pers. comm. 2009) reports localised colonies of five or fewer *B. spiciformis* trees in Namibia just west of Katima Mulilo. It remains to be determined how large a colony needs to be before it is defined as 'miombo'. Miombo is defined here at the level of the ecosystem (*sensu* Noss 1996), a physical habitat with an associated assemblage of interacting organisms including faunal elements. Miombo is more than simply a colony of a few (likely related) trees. But, notwithstanding the number and patterns of patches across a landscape, the size of the individual patch required by, say, specialist butterflies will likely be one or two orders of magnitude smaller than required by specialist birds. Distinction is made in the mapping here between small colonies (and those of unknown size) and larger patches that can be considered miombo with confidence. Specimen records needed to be treated with care and a patch was assigned as of unknown size unless supported by information on the specimen label.

5. *Assessing dominance by the miombo genera in the tree canopy*

The Miombo Ecoregion (Byers 2001) was defined by a dominance of deciduous woodland composed of broad-leaved trees of the legume subfamily Caesalpinioideae (Timberlake & Chidumayo 2011), a wider use of the term 'miombo' which is confusing because it also includes woodlands dominated by, for example, *Baikiaea plurijuga* and *Colophospermum mopane*. The Caesalpinioideae has since been split into a number of sub-families and the genera *Brachystegia*, *Julbernardia* and *Isoberlinia* occur with *Afzelia*, *Baikiaea*, *Colophospermum*, *Guibourtia* and *Schotia* in the sub-family Detarioideae (LPWG 2017). The miombo avifauna is well-differentiated from the assemblages typical of these other types (Benson & Irwin 1966), and the term miombo is used here in its stricter sense (as defined by Wild & Barbosa 1967, White 1983 and Campbell 1996) specifically for woodland with canopies dominated by trees of the genera *Brachystegia*, *Julbernardia* and *Isoberlinia*. Therefore, all woodlands dominated by other genera in the sub-family Detarioideae are excluded. Also excluded are other woodland types associated with miombo *sensu stricto* in landscape mosaic complexes, such as stands of *Terminalia* species at the ecotone between interfluve miombo woodland and a grassy drainage line.

The miombo dominant genera generally do not occur in mixed woodland or tree savanna; usually they are dominant in a canopy or not present at all. However, *B. spiciformis*, in particular, can be invasive into other types of woodland (Mike Bingham, pers. comm. 2017), hence care needs to be taken in defining miombo simply by the presence of *B. spiciformis*, especially on Kalahari sands where it might simply be a constituent of a mixed canopy rather than a dominant in a miombo canopy proper. Similar care needs to be taken with *B. tamarindoides* subsp. *torrei* and *J. globiflora* records on the Sul do Save (the area south of the Save River) sands (see Fig. 3).

RESULTS

Distribution of the Miombo Region in the Mozambique Lowlands

Records of bird canopy specialists (Fig. 4) show that miombo woodland is distributed more widely across the Mozambique Lowlands south of the Zambezi River than is suggested by the mapping of the Miombo Region in the standard texts such as Campbell

(1996) and Timberlake & Chidumayo (2011). Notably, miombo bird specialists occur across the Inhaminga–Cheringoma Platform (topographical features are described in Fig. 5). However, the known occurrence of miombo specialist birds to the south is more circumscribed than the extent of Wild and Barbosa's regional mosaics co-dominated by miombo. South of the Save River the miombo canopy specialists are known only from the Panda–Homoine Raised Plains, with scattered records from the Northern Inhambane Raised Plains (Fig. 5). The Panda–Homoine Raised Plains support populations of all the miombo specialists occurring in the region south of the Save River (Sul do Save), and many others like the White-breasted Cuckooshrike *Coracina pectoralis* and Black-eared Seedeater *Crithagra menelli*, both typical of miombo but also prone to wandering into other woodland types. In contrast, there are published records from only four scattered QDS in the north (a total of only four records across all species) including two wanderers in mixed woodland (Parker 1999). There are no records of the Black-eared Seedeater from the northern Sul do Save and only two isolated records of the White-breasted Cuckooshrike (see Parker 1999), which further suggests the generally limited occurrence of miombo woodland proper in this area. However, miombo woodland *does* occur here as Stalmans and Peel (2010) mapped their mosaic type 6 which includes *J. globiflora*-dominated short, closed woodlands and *B. spiciformis*-dominated tall, closed woodlands in the south-eastern parts of Zinave National Park. There are no records of these birds from the flats between the raised plains in the north and south of Inhambane Province, and there are no records at all from the block of miombo tree savanna (Wild & Barbosa's type 42, Deciduous miombo tree savanna (sublittoral)) mapped across the low-lying, low-relief plains between the Save and Buzi rivers.

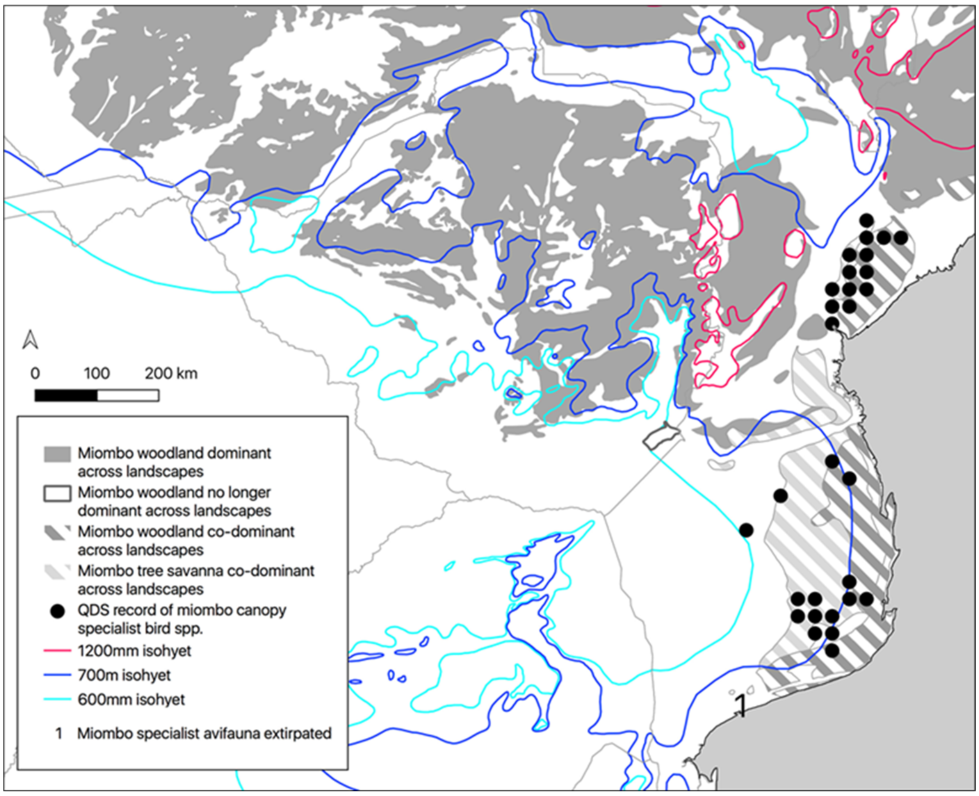

Figure 4. Distribution of miombo canopy specialist bird species in the southern Mozambique Lowlands where Wild & Barbosa (1967) mapped miombo woodland or miombo tree savanna to co-dominate landscapes with other vegetation types.

Patches of miombo lying outside the Miombo Region

Colonies of *Brachystegia* species and/or *Julbernardia globiflora*, larger (i.e. forming stands) or smaller, occur widely outside the Miombo Region in southern Africa (Table 1, Fig. 5). Wild and Barbosa (1967) mapped a number of outlying blocks of miombo on elevated landforms in the Middle and Lower Zambezi valleys, including the Chewore Inliers, Songo−Chipera Platform, Muamba−Lupata Volcanic Complex, Manje Hills and Mutarara−Chiwawa−Nsanje Hills. There are also outliers on smaller patches of higher ground in the Zambezi Valley, including Magoe Ridge, Mt Changaudze, the Luia outcrops and the sandy Comboio Plateau ('The Train'; Cunliffe 2002). In the Save-Limpopo Valley, stands of *B. tamarindoides* subsp. *torrei* occur on hills in the Save Valley Conservancy (Fay Robertson, pers. comm. 2008, pers. obs.), in the Malilangwe Hills (Clegg & O'Connor 2012), and formerly occurred across the Chivonja Platform in northern Gonarezhou National Park where Wild and Barbosa (1967) mapped a part of the Miombo Region. But Cunliffe, Müller & Mapaura (2012) have now found this area to be utterly transformed by elephants. (There were small areas of "havoc" where one could see "at least 10 standing dead trees and 10 fallen ones" surrounded by "large open spaces where the destruction had been completed".) Therefore, this former part of the Region is mapped as an open polygon in Figure 4 to show its recent loss. Although no longer spatially dominant, patches do remain with Cunliffe *et al.* (2012) mapping *B. spiciformis−J. globiflora* tree savanna to open woodland on and to the east of the Chilojo Cliffs, and stands of *J. globiflora* (some with a well-developed woodland structure, Figure 3) as far south as the Guluene−Chefu−Mwenezi watershed plains (Farrell 1968, Cunliffe *et al.* 2012). However, stands of *B. tamarindoides* subsp. *torrei* are also generally heavily disturbed in this central part of the national park (Cunliffe *et al*. 2012, Fig. 3).

Further south, at the southern edge of the Save−Limpopo Valley / northern edge of the South African Plateau, is a patch at the eastern edge of the Soutpansberg Mountains. Hills in the west of the Zimbabwe Save−Limpopo Valley also extend the known distribution of miombo well to the south of the Zimbabwe Plateau, for example on Mt Towla and possibly also the Jopempi Ranges (Raoul du Toit, pers. comm. 2008).

On the Zimbabwe Plateau there are outlying patches, for example in the northern parts of Insiza District (Lang 1952) and the Matobo Hills, where *B. tamarindoides* subsp. *glaucescens* has been recorded as far west as 2028C2 (Hyde *et al.* 2020). The Longwe and Ghoko hill ranges south-west of Gweru support well-developed miombo (*B. spiciformis*, *B. tamarindoides* subsp. *glaucescens*, *B. boehmii* and *J. globiflora*), patchy within the thornveld plains (Kevin Barry, pers. comm. 2008). Mundy *et al.* (1992) reported *B. tamarindoides* subsp. *glaucescens* woodland on Wabai Hill. Elevated landforms within the grassy landscapes on top of the Zimbabwean watershed also support miombo, for example to the south and east of Chivhu (pers. obs.).

On the northwest of the Zimbabwe Plateau, *Baikiaea plurijuga* (co-)dominates woodlands on the Kalahari sands as rainfall declines (Timberlake, Nobanda & Mapaure 1993) and the Miombo Region is also fragmented by the Hwange Trough (generally vegetated by *Colophospermum mopane* woodland types, see Timberlake *et al.* 1993). Wild and Barbosa (1967) mapped a small block of miombo lying outside the general Zambian Plateau distribution (isolated by the Zambezi River above the Victoria Falls) on the eastern edge of the Chobe−Matetsi−Hwange Watershed Plains, in an area of slightly higher rainfall (>700 mm/year). This is associated with the Matetsi River drainage where *B. boehmii* occurs at the bases of the ridges of Kalahari sands along a contact zone with the underlying basalts and where the sand was washed away by the palaeo-Zambezi River (Sue Childes, pers. comm. 2008). Otherwise on these plains and Hwange Trough the presence of the miombo dominants is mostly limited to *B. boehmii* trees along drainage lines (type F1 of Timberlake *et al.* 1993) and small colonies of *B. boehmii* on gravelly soils at the bases of basalt hills (Sue Childes, pers. comm. 2008). *J. globiflora* was also recorded in Rogers' (1994) type 5 *Colophospermum−Julbernardia−Combretum* wooded bushland on Basement Complex soils in the north of Hwange National Park, while Hyde *et al.* (2020) report *J. globiflora* as far west as 1825B2. To the northwest there are colonies of *B. spiciformis* and *J. globiflora* just inside the Botswana border in the vicinity of Pandamatenga (Blair Rains & McKay 1968, Chikuni 2007). In general, it seems unlikely that the colonies of *B. boehmii* or *J. globiflora* that occur across the Chobe−Matetsi−Hwange watershed plains and Hwange Trough form stands large enough to be considered patches of miombo proper, except perhaps in the region of higher rainfall.

Table 1. Sources of information for patches lying outside the Miombo Region.

Region	Source	Herbarium specimens
South-western Zambia	Jeanes & Baars (1991)	
Zambezi Region (Caprivi), Namibia	Chris Hines (pers. comm. 2009)	
North-eastern Botswana	Blair Rains and McKay (1968)	Brummitt *et al.* (2007)
Western Zimbabwe	Timberlake *et al.* (1993), Rogers (1994), Sue Childes (pers. comm. 2008), Hyde *et al.* (2020)	
Northern and north-eastern Zimbabwe	du Toit (1993), Timberlake *et al.* (1993), Timberlake *et al.* (1998)	
Tete Province, Mozambique	Cunliffe (2002), Wild (1953)	Macédo 4796 & 4763 (SRGH); Bond 40 (SRGH); Wild 2643 & 2664 (K); Torre & Correia 14003 cited in FZ
Central Plateau, Zimbabwe, Gweru to Matobo Hills	Lang (1952), Mundy et al. (1992), Kevin Barry (pers. comm. 2008), Hyde *et al.* (2020), pers. obs. (E. Matobo, Mbalabala)	Orpen 44239 & 44240 (SRGH); Simon (SRGH)
Save-Limpopo Inselberg Middleveld, Zimbabwe: West Nicholson to Mashoko	Timberlake & Mapaure (2007), Raoul du Toit (pers. comm. 2008)	
South-east Lowveld, Zimbabwe	Farrell (1968), Fay Robertson (pers. comm. 2008), Clegg & O'Connor (2012), Cunliffe *et al.* (2012)	Drummond 7726 (K)
Manica Provinces, Mozambique & Zimbabwe	Hyde et al. (2020)	Swynnerton 1026 (K)
Sul do Save, Mozambique	Stalmans & Peel (2010)	Mogg 29152 (SRGH), Smuts 35 (K), Barbosa 5081 (K), pers. obs. *B. t. torrei* at 22°12.191'S, 33°12.936'E; pers. obs. *J. globiflora* at 22°09.328'S, 33°21.717'E, Sept 2017 (see Fig. 3)
Northern South Africa	Mucina & Rutherford (2006)	

Wild and Barbosa (1967) showed miombo to be distributed generally again north of the Ngamiland−Machile Trough on raised plains east of the Upper Zambezi floodplains. To the west, between the Zambezi and Cuando rivers, Jeanes and Baars (1991) mapped stands of their type BK5 *Digitaria* spp.−*Schizachyrium jeffreysii* / *Brachystegia* *spiciformis*–*Dialium englerianum*–*Julbernardia paniculata* woodland, mapped as patches of miombo in Figure 5. Some of these patches occur on the Zambia–Namibia border and, although Curtis and Mannheimer (2005) do not list any of the miombo dominant trees from Namibia, Chris Hines (pers. comm. 2009) reports localised colonies of five or fewer *B. spiciformis* trees in Namibia just west of Katima Mulilo.

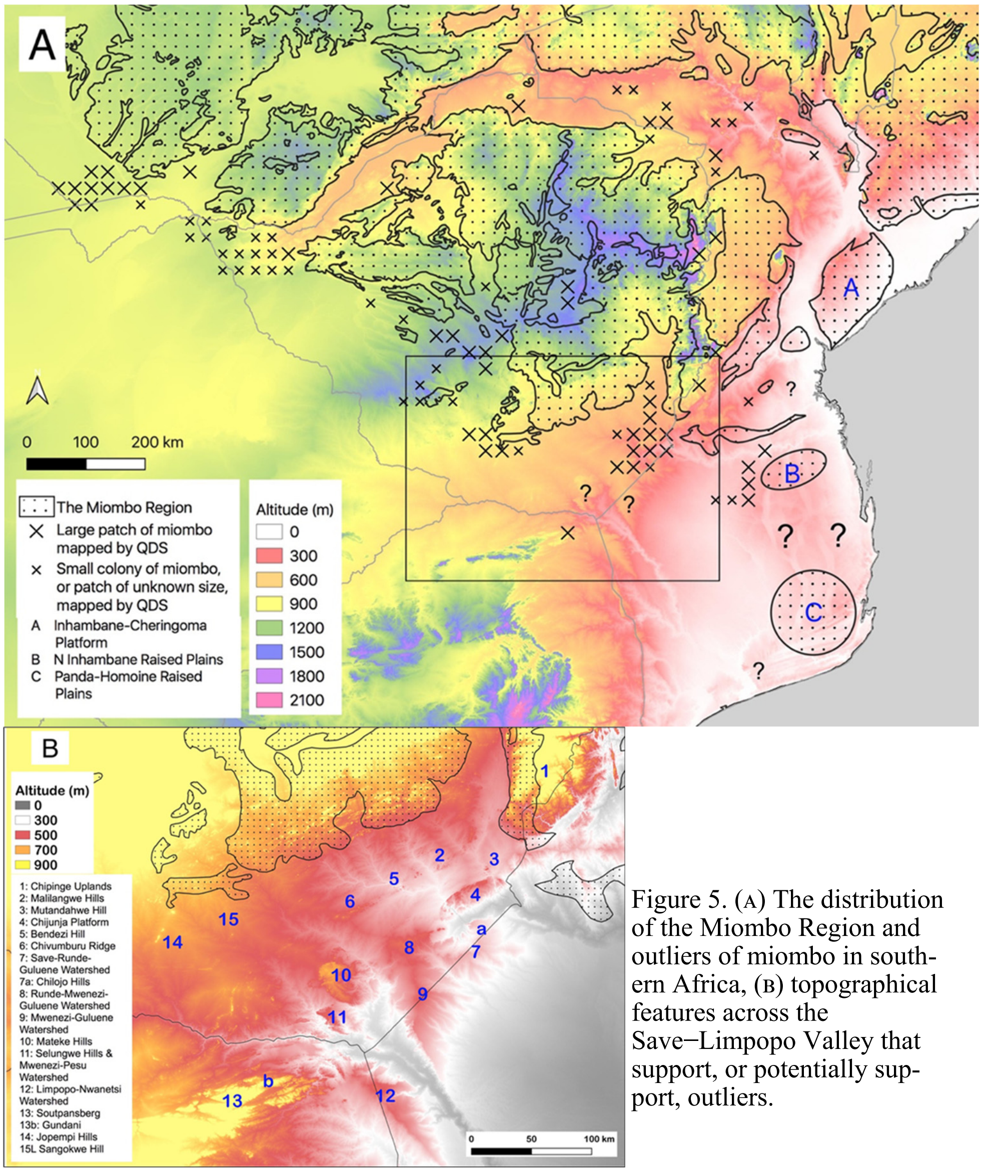

Figure 5. (A) The distribution of the Miombo Region and outliers of miombo in southern Africa, (B) topographical features across the Save–Limpopo Valley that support, or potentially support, outliers.

Miombo grades into seasonally dry forest at c. >1200 mm mean annual precipitation (Frost 1996), generally limiting its distribution in the region of high rainfall associated with the windward parts of the Manica Highlands and the south-eastern edge of the Manica Plateau. However, precipitation patterns are complex in the Manica Highlands with sharp gradients and moist miombo occurs, for example, on the lower coast-facing slopes of the Serra Choa (west of Catandica; Cizek 2009), in the Honde Valley in Zimbabwe and in the vicinity of the Haroni–Rusitu confluence lowland forest (pers.

obs.). Stunted *B. spiciformis* 'dwarf woodland' is patchy within the grassy highlands too. Miombo has a naturally limited distribution on the Chipinge Uplands in the south, where Wild and Barbosa mapped their type 39 (Semi-evergreen high rainfall *Parinari curatellifolia* tree savanna), but miombo patches occur (at least historically) in the vicinity of Chirinda Forest (pers. obs.).

DISCUSSION

The distribution of miombo in southern Africa presented here (Figs. 4, 5) differs from maps in the standard texts in its inclusion of miombo woodlands in coastal parts of the Mozambique Lowlands into the Miombo Region, and in the mapping of outliers away from this. Improved knowledge of miombo distribution has important implications for ecological and biogeographical understanding which, in turn, influence conservation management. However, many questions remain and are discussed below.

The Miombo Region in the Mozambique Lowlands

The Miombo Region as defined here is distinct from WWF's 'Miombo Ecoregion' (Byers 2001, Timberlake & Chidumayo 2011, WWF 2012), both conceptually and spatially, because it includes regional mosaic complexes in the Mozambique Lowlands where miombo woodlands and tree savanna are co-dominant with non-miombo vegetation. This inclusion is important because all miombo ecosystems should be included in assessments of miombo conservation management priorities. The southern Mozambique Lowlands support important populations of miombo specialist birds, including a small and potentially isolated population of the Yellow-bellied Hyliota on the Inhaminga−Cheringoma Platform and the apparently isolated populations of a number of miombo specialist bird species (the Southern Hyliota, Green-backed Honeybird, Western Violet-backed Sunbird and Cabanis' Bunting) centred on the Panda−Homoine Raised Plains.

Much fieldwork remains to be done to accurately map limits to the Miombo Region in the southern Mozambique Lowlands. This is a very large area with complex vegetation patterns and little vegetation mapping. Mapping of the major parts of the conservation estate (Stalmans, Gertenbach & Carvalho-Serfontein 2004, Stalmans & Wishart 2005, Stalmans & Peel 2010) has pushed forward collective understanding of the region's vegetation and shows that only Zinave National Park supports miombo woodland, but moister coastal areas – where miombo woodland is expected to interdigitate with forests and thickets − remain to be mapped in detail. Records of miombo bird specialists are patchy and localised south of the Save River, in part probably due to broad-scale clearance of natural vegetation for agriculture as the coastal parts of this area are amongst the most densely populated and heavily transformed areas of southern Africa. Interpreting natural vegetation patterns is thus more challenging, but the remnant patches of relatively undisturbed vegetation confirm that stands dominated by *B. spiciformis* can develop into forest which is completely unsuitable for bird specialists of miombo woodland (see Fig. 3). Rather, typical specialists of the coastal forests of eastern Africa, such as the Chestnut-fronted Helmetshrike *Prionops scopifrons* (Parker 2001, Cizek 2017), support their inclusion in the eastern African Coastal Forests Region (*sensu* Burgess & Clarke 2000). A *B. spiciformis* canopy with a woodland physiognomy (i.e. miombo proper) is probably much more limited spatially in the higher rainfall parts closer to the coast than *B. spiciformis* forest-thicket so, notwithstanding losses to agriculture, it is not unexpected that there are few records of the miombo canopy specialist birds.

Where exactly, and under what ecological conditions, does a miombo woodland canopy proper develop closer to the coast? Better understanding of the spatial patterns and ecological drivers of vegetation along the southern Mozambique coast away from the littoral, and specifically within Wild and Barbosa's regional mosaic type 20, is an urgent conservation priority since it is these habitats that support important populations of threatened species, notably the Olive-headed Weaver (Nuttall & Parker 2001). The habitat requirements of this species require fine-resolution investigation − is it a species of miombo woodland canopy proper, or of *B. spiciformis* forest-thicket, or both, dependent more on the presence on pendent lichens (*Usnea* spp.)? Formerly known from the Inhaminga−Cheringoma Platform (Clancey 1996), there are no recent records between the Zambezi and Save rivers, and it is a highly localised habitat specialist experiencing decline due to habitat loss. Although not miombo proper (and outside the scope of this study), *B. spiciformis* transition woodland/ forest-thicket must be amongst the most critically endangered vegetation-habitat-ecosystems in southern Africa and needs to be surveyed urgently in Mozambique.

Rainfall declines steeply from the coast to the interior and much of the distribution of miombo south of the Save River receives less than 700 mm/year (Fig. 4). Thus the situation on the Sul do Save sands is quite different from the sharp transition from miombo to dominance by *Baikiaea plurijuga* as annual rainfall declines below 700 mm on the Kalahari sands in western Zimbabwe (Timberlake *et al.* 1993). *B. plurijuga* does not occur in Mozambique and it is possible that *B. spiciformis* and *J. globiflora* are able to expand into a niche on the Sul do Save sands otherwise occupied by *Baikiaea* on Kalahari sands. The only part of the area south of the Save River where there are large populations and assemblages of the miombo specialists is in the Panda−Homoine Raised Plains. Although occurring in the south of Wild and Barbosa's regional mosaic type 36 (*J. globiflora* miombo tree savanna with patches of *Androstachys johnsonii* woodland), these raised plains support tall *B. spiciformis* woodland laden with lichens including pendent *Usnea* species (Nuttall & Parker 2001). Therefore, the limits to Wild and Barbosa's polygons need to be amended.

The general lack of records of miombo bird specialists across the low-lying mixed *J. globflora* tree savannas (Wild & Barbosa's types 36 and 42) suggests they are generally too dry and it is no coincidence that the few records are associated with elevated ground of the Northern Inhambane raised plains where some parts will intercept moist airflow and thus support patches of moister types of miombo. There are indications that these dry, mixed tree savannas with *J. globiflora* are an important characteristic of the Sul do Save region because they support specialist near-endemic birds such as Neergaard's Sunbird *Cinnyris neergaardi*, which avoids 'pure *Brachystegia* woodlands' (i.e. miombo *sensu stricto*, Parker 1999). The floristic, physiognomic and functional characteristics of these tree savannas need to be defined and compared with more typical miombo woodlands. In the same way that *B. spiciformis* forest-thicket canopies in coastal areas are not miombo, these Sul do Save tree savannas could also fall outside the definition of 'miombo', for example, if *J. globiflora* only occurs as a constituent of a mixed canopy.

Ecological drivers in the distribution of outliers

Outliers occur on small elevated landforms in the eastern parts of the Zambezi and Save−Limpopo valleys that intercept moist south-easterly airflows, hence are able to support patches of miombo requiring moister conditions than provided in surrounding landscapes. Outlying patches in the drier southwest of the Zimbabwe Plateau are also found in areas of locally higher rainfall such as the Matobo Hills, although geology probably also plays a role as the granite kopjes promote run-off. The isohyets shown in Figure 4 show only broad patterns across landscapes. Outlying patches with higher rainfall are difficult to delineate at such broad scales, not only cartographically but because rain gauge records for these small landforms do not exist. Furthermore, *guti* − a thin drizzle typical of moist, south-easterly airflow − does not register on rain gauges. Even simply greater cloud cover around these landforms is likely enough to lower the temperature and reduce evapotranspiration (Jonathan Timberlake, pers. comm.). Therefore, topography and aspect better show where outliers of miombo might occur in these major river valleys than rainfall models do.

The nature of the outliers is different on the deep sands (both Kalahari and the Sul do Save area) where the miombo dominants are more likely to be invasive into mixed woodland types. Also, groundwater is an important determinant, for example in maintaining the best-developed patches of *J. globiflora* on the Guluene−Chefu−Mwenezi watershed (Farrell 1968). But moist south-easterly airflow is also important since the miombo dominants need to compete with the ironwood *Androstachys johnsonii*, which has the unusual ability to access moisture through its leaves (Alvin 1987). Therefore, distinctive ironwood forests and woodlands occur widely on the south-eastern edges of elevated landforms across Gaza Province and adjacent areas of Zimbabwe and South Africa receiving <600 mm annual rainfall, and it is likely that *B. tamarindoides* subsp. *torrei* can only outcompete it on the rockiest outcrops where water is stored in fissures.

Tracks of patches lying outside the Miombo Region

The prevalence of small patches of miombo on elevated landforms associated with the complex topography at the eastern edge of the Great African Plateau has emerged from this study. Of considerable interest are the patches of miombo across the track of elevated landforms along the south-eastern Zimbabwe−Mozambique border from the Chipinge Uplands to the Soutpansberg in South Africa. Patches of different kinds of miombo, including with *B. spiciformis,* are known from across the Chivonja Platform and in the Ghonarezhou National Park parts of the Guluene−Chefu−Mwenezi Watershed Plains, extending the distribution of miombo 125 km south of the Miombo Region proper on the Chipinge Uplands (Fig. 5b). Patches could also occur within 50−100 km of the patch at Gundani in the Soutpansberg in the Mateke and Selungwe hills, which appear to have been never been surveyed fully. For example, Timberlake, Mapaure & Chapano (1999) could not access the Selungwe Hills during their pioneering survey. Although Stalmans *et al.* (2004) did not map any miombo on the Limpopo−Nwanetsi Watershed Plain, they surveyed at a broad resolution and small patches probably occur as Wild and Barbosa (1967) reported *J. globiflora* in Mozambique south of the Limpopo River. This track challenges the assumption that miombo ecosystems naturally dominate landscapes spatially since a significant part of the distribution of miombo in southern Africa consists of small patches limited to unusual, highly localised ecotopes.

Tracks occur across the Zambezi Valley too, the shortest being via the outliers mapped by Wild and Barbosa (1967) in the Chewore Hills. Potential sites have been located using specimen data but the sizes of the patches need to be confirmed. A more continuous series of outlying records of miombo dominants occurs across the edge of the Hwange Trough, but most probably refer to colonies of a few individuals of *B. boehmii*, so cannot be considered a track of canopy miombo woodland *sensu stricto*.

Landscape ecology of miombo and miombo specialist birds

Understanding of the landscape ecology of miombo is relatively poorly developed, although Bingham (1994) noted that the explosively-dehiscent pods of miombo canopy dominants have many limitations for seed dispersal compared with other dispersal methods. Scattering does not much exceed crown extent, suggesting only a 2 km advance per millennium through this method alone (Bingham 1994). Although the miombo dominants also reproduce vegetatively, this still limits their ability to jump natural barriers and colonise outlying patches of potential habitat. It is therefore likely that outlying patches on elevated landforms are relicts of a once wider distribution over geological time. The situation is different on the extensive deep sand sheets, where miombo dominants can be invasive, but the range of colonisation would still be limited unless benefitting from an unusual dispersal event, such as (accidental) ingestion by Black Rhino (Bingham 1994). Dispersal by water most likely accounts for the widest dispersal events, which could be relevant on the Kalahari sands where miombo dominants can favour rocks exposed by water flow. However, these sites occur as thin patches limiting the development of miombo proper, and dispersal by rivers would not account for colonisation of elevated landforms.

The landscape ecology of the miombo avifauna is also poorly known but these tracks of miombo have the potential to influence bird distributions at regional scales by providing connections between major parts of a species' distribution. Many miombo bird specialists are sedentary and there are distinct populations on the Zambian and Zimbabwean plateaux generally isolated by the Middle Zambezi Valley, as evident in subspecific differentiation. For example, there are different subspecies of the Southern Hyliota (*H. a. australis* and *H. a. pallidipectus*) on the Zimbabwean and Zambian plateaux, even though this species is more vagile than many of the miombo specialists, willing to move into riparian woodland in the dry season (Cizek 2011). The Southern Hyliota also occurs in the Chewore Hills, which occupies a key position in the species' distribution between the two plateaux. This track across the Middle Zambezi Valley is a bottleneck in its distribution. If it were lost it could cause the full isolation of the two populations and potentially lead to specific differentiation. The situation is also interesting in the south of its range where there is likely to be a meta-population occupying small outlying stands of miombo across the Save−Limpopo Valley track (Cizek 2012b), a population that is very small and prone to differentiate from *H. a. australis* on the Zimbabwe Plateau if not already genetically distinct. The patches of miombo on this track are so small that this population is unlikely to survive without the maintenance of the track as a whole (and so is a true meta-population *sensu* Hanski 1998).

Conservation management of tracks of outliers

Miombo occurred across the northern part of the South African Plateau south to Mookgophong only 19,000 years BP (Scott 1982), 350 km south of the current limit to the Miombo Region, and the Save−Limpopo Valley track seems the most likely historical connection between the Zimbabwe−Manica and South African plateaux. This rapid contraction of miombo distribution illustrates that even small changes in climate may have significant impacts (Campbell 1996). The changes in climate projected for south-central Africa (Shongwe *et al.* 2009) would have major impacts on miombo distribution, with Pienaar *et al.* (2015) showing both a general contraction in the potential distribution of *B. spiciformis* on the Zimbabwe and Manica plateaux in the 21st century but also an expansion in its 'climatic envelope' on the South African Plateau. However, they note that the limited dispersal ability of *B. spiciformis* would hinder its ability to spread from the Soutpansberg outlier to this expanded potential distribution in South Africa. It remains to be seen how the change in climate projected for the 21st century might influence the outlying patches of *B. spiciformis* in northern Gonarezhou National Park as these were not included in the modelling of Pienaar *et al.* (2015). This highlights the importance of fine-resolution plant species distribution data, such as assembled here.

Other disturbance factors, notably elephants and fire, can act with climate change to exacerbate the impacts, as evident in the recent almost complete loss of woodland from northern Gonarezhou National Park (Tafangenyasha 1997, 2001). Cunliffe *et al.* (2012) found that, in tandem with fire, increased elephant density to the highest ever recorded (2 animals/km^2) was leading to a serious decline in woody cover right across the national park. They considered the dense elephant population to be a critical threat to plant diversity and called for the immediate introduction of elephant exclusion zones in sensitive areas. Elephants should be excluded from the remaining patches of miombo woodland − of all types − in Gonarezhou so as to ensure the persistence of the Save−Limpopo Valley track and metapopulations of miombo faunal specialists.

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2018 marked the 50th anniversary of the publication of Hiram Wild and Luís Grandvaux Barbosa's *Flora Zambesiaca* vegetation map, which still provides the most detailed mapping for the region as a whole. During the course of this study, I was repeatedly struck by the map's general accuracy and the detail of the nomenclature used, which emphasised the spatial structural and functional complexity of the mosaics they delineated.

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