

DISTRIBUTION MAPPING AND NICHE CHARACTERIZATION OF THE
ENDEMIC AFRICAN STORKS

by

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DEDICATION

For Barry Woods, my teacher, colleague, and friend.

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ABSTRACT

The endemic African storks—African Openbill *Anastomus lamelligerus*, Abdim's Stork *Ciconia abdimii*, African Woollyneck *Ciconia microscelis*, Saddlebill Stork *Ephippiorhynchus senegalensis*, Marabou Stork *Leptoptilos crumeniferus*, and Yellow-billed Stork *Mycteria ibis*—generally are poorly studied and their conservation status assessments have been created using mixed methods that are neither transparent nor replicable. Besides standardized population surveys, empirical distributions and environmental requirements are two of the most fundamental knowledge gaps that can contribute to the development of a data-driven status assessment for each species. Distribution mapping is a valuable proxy for determining population trends and range changes over time, albeit with caveats, that can provide some baseline information for assessing status. Environmental niche modeling (ENM) further contributes by estimating species-environment relationships that can be used to infer ecological needs (e.g. preferred habitats) and susceptibility to threats (e.g. climate change, land use change). Therefore, I employed both mapping and ENM to evaluate current distribution and environmental associations of African storks at two spatial scales, range-wide and regionally.

The six stork species were widespread from East to Southern Africa and varied in their degree of change in distribution in these regions between the historic (pre-1990) and recent (1990–2020) time periods. The African Openbill, African Woollyneck, Saddlebill Stork, Marabou Stork, and Yellow-billed Stork each exhibited a highly fragmented range

in West Africa and all species but the African Woollyneck declined regionally from the historic to the recent period. Environmental niche models had high predictive capacity and stork species had scale-dependent responses to environmental variation. Annual and seasonal precipitation variables as well as land cover were the most important inputs across most models. All species had an optimum range of annual precipitation between *c.* 500–1000 mm regardless of scale. The African Openbill stood apart from the other species in its contrasting responses to several seasonal precipitation variables at several model scales, indicating important differences in ecology. All species had strong positive associations with flooded land cover types at all scales, and all but the African Openbill had the weakest association with croplands in West Africa. Niche similarity among species was high in all models, regardless of scale, suggesting similar environmental requirements and susceptibility to environmental changes.

The findings of this study represent a significant improvement to the understanding of the ecological needs and primary threats to African storks. Particularly, results highlight regional declines of potential metapopulations in West Africa, which, among other anthropogenic impacts such as overfishing and dam construction, can be attributed to multi-year drought beginning in the 1970s. Recovery of depleted West African populations is threatened by near-future climate change and habitat degradation. While populations in other regions certainly face similar threats, storks in West Africa appear most at risk of extinction and require immediate conservation attention.

1. RANGE-WIDE DISTRIBUTION ASSESSMENTS OF THE ENDEMIC AFRICAN STORKS

Introduction

Knowledge of where a species occurs and how it is distributed within its geographic range is among the most rudimentary information required for a conservation status assessment, and is an important component in the fields of macroecology and biogeography (Gaston 2003). The International Union for the Conservation of Nature (IUCN) uses two measures of distribution, extent of occurrence (EO) and area of occupancy (AO), as criteria for which to categorize the status of a species on the Red List (IUCN 2019). Whereas AO is a measure of actual range size, EO is a crude estimate of the entire geographic extent in which a species occurs. Despite the widespread availability of high-resolution occurrence data for measuring AO of birds with the advent of open-source databases such as eBird, iNaturalist, and the Global Biodiversity Information Facility, the IUCN and BirdLife International still largely use EO for determining status. This is also in spite of the widespread evidence that measures of EO frequently overestimate range size and thus impact status assessment outcomes. For example, Jetz *et al.* (2008) found that most of the 1,158 bird species they investigated only occurred in 40–70% of the EO range put forth by the IUCN. However, they also showed proportional range overestimation decreased with increasing actual range size. Using environmental niche models in India's Western Ghats, Ramesh *et al.* (2017) demonstrated the EO for 17 of 18 endemic birds was overestimated, and 10 of the 18 species were inaccurately assessed on the Red List and required uplisting based on

geographic range criteria. In a similar study on 586 species in global biodiversity hotspots, just 51% were appropriately assessed on the Red List based on EO; of the remaining species, 6% met criteria to be downlisted from their current Red List category and 43% met criteria for uplisting based on EO alone (Ocampo-Peñuela *et al.* 2016). One-hundred and eighty-nine species that required uplisting were listed in a non-threatened category. Besides casting significant doubt about the reliability of one component of the IUCN assessment process, these case studies highlight the reality that not all of the EO is suitable or of equal suitability. The studies do, however, underscore the importance of properly assessing even simple metrics such as EO and the value of using empirically-defensible and repeatable methods to help ascertain species' distributions and conservation status.

The need for accurate measures of distribution patterns is especially relevant given evidence that changes in distribution can be used to assess threat level or range-wide status and trends (Wilson *et al.* 2004; Senyatso *et al.* 2013; Gula *et al.* 2019). However, the spatial and temporal scale at which distribution is mapped may influence conclusions about population-level changes (Thomas and Abery 1995; Gaston 2003; Hartley and Kunin 2003). The coarser the scale, the less likely declines in the form of range contractions will be detected. This is another major shortcoming of EO as a measure of distribution as it cannot account for inherent spatial variation within a species' range.

The stork family, Ciconiidae, has a widespread distribution globally and exhibits significant sympatry in tropical Africa (Kahl 1971; Luthin 1987). Of the 20 species

currently recognized on the IUCN Red List, eight are sympatric in parts of sub-Saharan Africa at some point during the year, depending on the occurrence of the three long-distance migrants, the Abdim's Stork *Ciconia abdimii*, White Stork *Ciconia ciconia* and Black Stork *Ciconia nigra*. Six of these species—African Openbill *Anastomus lamelligerus*, Abdim's Stork, African Woollyneck *Ciconia microscelis*, Saddlebill Stork *Ephippiorhynchus senegalensis*, Marabou Stork *Leptoptilos crumeniferus*, and Yellow-billed Stork *Mycteria ibis*—are endemic to Africa. All six are assessed as Least Concern on the IUCN Red List based on primarily EO threshold criteria since demographic metrics are largely unavailable for all mentioned species. Despite recognition of the paucity of information on storks worldwide over thirty years ago (Luthin 1987), all species remain notoriously under-studied. In particular, AO distributions have never been mapped using repeatable methods and thus the validity and accuracy of current species status assessments remains unknown.

The distributions of the African Woollyneck and Saddlebill Stork have been mapped recently using records spanning more than a century (Gula *et al.* 2019; 2020). The temporal scale at which “historic” (pre-1970) and “recent” (post-1970) distributions were mapped in both studies, however, demonstrates the potential for scale-dependent oversight of range loss. The map developed for the Saddlebill Stork did not communicate the more recent range contractions (especially in peripheral areas) discussed in detail by Gula *et al.* (2019) nor did the map for the African Woollyneck (Gula *et al.* 2020). The aim of this study is to develop empirical range maps of the remaining four African storks—African Openbill, Abdim's Stork, Marabou Stork, and Yellow-billed Stork—and

detail changes in distribution over time to assess regional trends in distribution. We also build upon the existing work for the African Woollyneck and Saddlebill Stork with updated range maps incorporating new data and a more meaningful time scale that reflects recent distribution trends. This work represents the first steps to assess the conservation status of the African storks using an empirical approach and provides important insights into the limitations of using EO to inform the status of a species.

Methods

Range-wide locality data for the African Openbill, Abdim's Stork, African Woollyneck, Saddlebill Stork, Marabou Stork, and Yellow-billed Stork were collated from a variety of sources spanning the years 1859–2020. First, records were downloaded and vetted from the following online databases: eBird (eBird 2020), the Global Biodiversity Information Facility (<https://www.gbif.org>), Observation.org (<https://observation.org>), and the West African Bird Database (<https://www.wabdab.org>). Distribution data also were extracted from a number of country-specific bird atlases across Africa: Benin and Togo (Dowsett-Lemaire and Dowsett 2019), Botswana (Penry 1994), eSwatini (previously Swaziland; Parker 1994), Ethiopia and Eritrea (Ash and Atkins 2009), Ghana (Dowsett-Lemaire and Dowsett 2014), Kenya (Lewis and Pomeroy 1989), Malawi (Dowsett-Lemaire and Dowsett 2006), Mauritania (Nature Mauritanie 2016), Mozambique (Parker 1999; 2005), Nigeria (<http://nigeriabirdatlas.adu.org.za>), Senegal/The Gambia (Morel and Morel 1990), Somalia (Ash and Miskell 1983; 1998), Sudan (Nikolaus 1987), Tanzania (N. Baker, unpub. data), Uganda (Carswell et al. 2005), and Zambia (Dowsett et al. 2008). Additional sources included Snow (1978; manually digitized), the Southern African Bird

Atlas Project (SABAP) 1 (Harrison et al. 1997) and SABAP2 (<http://sabap2.birdmap.africa>), the National Geographic Okavango Wilderness Project (M. Mills, unpub. data), and the West African Ornithological Society's journal *Malimbus*, from which records in the text were manually mapped. Finally, records were located by tracing citations from known literature (see supplementary material in Gula *et al.* 2019) and were provided by in-country experts in some cases. In cases where records were manually traced in known literature, locations were georeferenced as precisely as possible based on the authors' descriptions. This exercise was already completed for the African Woollyneck (Gula et al. 2020) and Saddlebill Stork (Gula et al. 2019) but herein we update both distributions using new or overlooked records—particularly Morel and Morel 1990, which was not incorporated into either study—and create maps at a different temporal scale (see below). Finally, it should be noted that African Waterbird Census data were only made available by Wetlands International for the Saddlebill Stork (i.e. from Gula *et al.* 2019) and data were not provided for the remaining species.

Distribution maps were developed in QGIS 3.12 (QGIS 2020) at a resolution of 30 arcseconds (0.5°), as this was the highest resolution of many atlases. The Sudan atlas was the only one to use a lower resolution of 60 arcminutes (1°). Previous maps developed for the African Woollyneck and Saddlebill Stork followed many atlases in using 1970 as a cutoff year for dividing between “historic” and “recent” records. Herein, however, pre-1990 was considered the “historic” period and 1990–2020 as the “recent” period to better reflect recent population declines and regional environmental changes. In the case of some atlases, years of occurrence could not be determined, so those occupied cells were

assigned to the recent period to not overestimate range loss. Therefore, the assessment of range loss in some countries should be considered conservative, especially in a country like Zambia where atlassing began in 1975. Along with maps for each species, we report the number of cells occupied during each period and the proportion of cells limited to the historic period as a coarse metric of potential range loss. Finally, we visually compared existing IUCN range maps with the updated distribution maps we developed.

Results

African Openbill

Excluding the 60-arcsecond cells of the Sudan atlas, the African Openbill was recorded in a total of 1,462 30-arcsecond cells during the historic and recent periods combined (Figure 1.1). It was recorded in 1,109 cells from 1990–2020 and in 677 cells prior to 1990, 353 of which were solely during the historic period (24% potential range loss). The new distribution mostly agrees with the IUCN range map aside from South Africa, Madagascar, Cameroon, and coastal Benin and Togo, yet the IUCN misrepresents occurrence more widely in West Africa. This stork species is locally abundant throughout the core of its range from East to Southern Africa, where seasonal congregations (in and out of the breeding season) often number in the thousands. Elsewhere its distribution is very patchy. The records used in this study show counts do not exceed 590 in West Africa and support previous observations that it is much less abundant in that part of its range (Bannerman 1953).

The African Openbill is only one of the five wetland-dependent species (i.e. excluding

the Abdim's Stork) that does not occur in The Gambia, Guinea-Bissau, or Senegal aside from three historic records (Morel and Morel 1990). Bannerman (1953) reported historic breeding in Sierra Leone without specific locale, and the only known breeding site in the country currently is Lake Sonfon, where locals collect chicks from the colony for food (P. Bai-Sesay, pers. comm.). The breeding population in the Inner Niger Delta was extirpated after the 1980s (Zwarts et al. 2009), but local people have found it at several locales east of the delta more recently (S. Canney, pers. comm.). Breeding also formerly occurred in Somalia (Ash and Miskell 1983) but the species has not been reported from the country since 1993. It is reported in low numbers on Madagascar, where the population is considered a separate subspecies, *A. l. madagascariensis*, but status and trend are not well understood. The population declined in the 1990s (Rabarisoa 2001), which likely was caused by multiple cyclones that killed a large number of birds (R. Rabarisoa, pers. comm.). In the early 1970s its range and population were apparently expanding in coastal southwest Nigeria (Gee and Heigham 1977), and the same has happened in more recent decades in South Africa (Loftie-Eaton 2014).

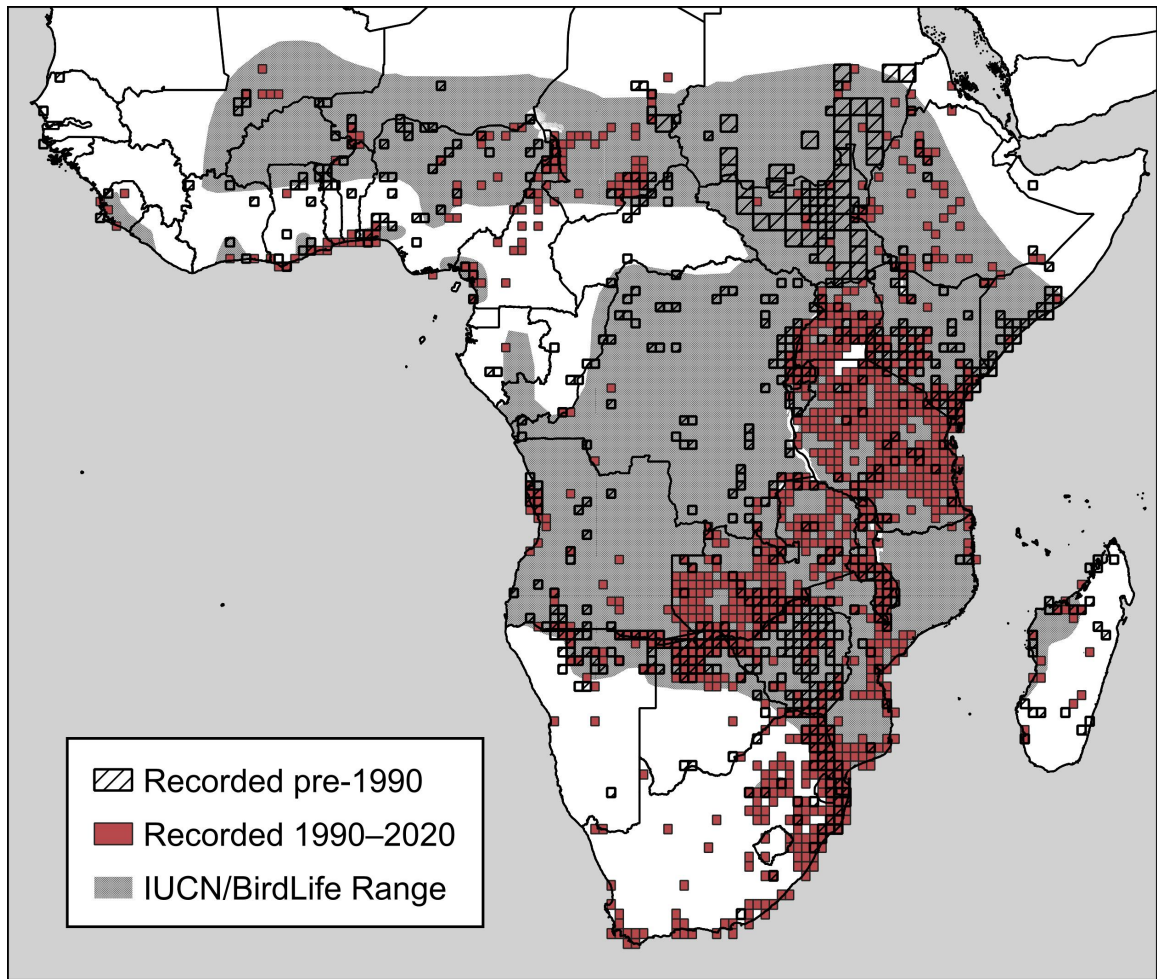


Figure 1.1. Historic (pre-1990) and recent (1990–2020) distribution of the African Openbill, with the IUCN distribution map (developed by BirdLife International) for comparison. Note: country borders (sourced from www.hub.arcgis.com) are purely for display purposes and do not reflect the authors' particular support for or against existing national claims on international borders.

Abdim's Stork

Excluding the 60-arcsecond cells of the Sudan atlas, the Abdim's Stork was recorded in a total of 1,773 cells in the historic and recent periods combined (Figure 1.2). It was recorded in 1,290 cells from 1990–2020 and in 965 cells prior to 1990, 483 of which were solely during the historic period (27% potential range loss). The distribution developed with these data largely agrees with the IUCN range map aside from records in Oman. Although many countries have experienced fewer records in the past thirty years, there is evidence of increased occurrence and numbers in Oman since the 1980s when

Gallagher (1986) identified a handful of observations. At that point, 61 was the maximum count for the country; since 2012, however, groups as large as 900 (\bar{x} =150, n =165) have been reported every year, with some observers noting these congregations are common each winter, especially at refuse dumps.

Across sub-Saharan Africa the Abdim's Stork occurs almost anywhere because of its biannual long-distance migration (Hancock *et al.* 1992; Anderson 1997). During migration it can occur in groups ranging from hundreds to thousands, including a record 148,000 observed at Tanzania's Lake Engaruka in January 1995 (Baker 1996). Collated records during the non-breeding season were not limited to southern African countries, as is commonly generalized (Brown *et al.* 1982; Hancock *et al.* 1992; Anderson 1997), but included a high number of records in southern Kenya and northern Tanzania, supporting more recent findings that these areas are important for wintering (Jensen *et al.* 2006). The last nest recorded in the Inner Niger Delta was in *c.* 2005–2006 (M. Diallo, pers. comm.), and it is becoming increasingly rare in Mali (S. Canney, pers. comm.). Apparently, it no longer breeds in Nigeria either (P. Hall, pers. comm.). It was considered a very common breeder in the Sudans (South Sudan and Sudan) in the 1980s (Nikolaus 1987; 1989), but very few recent records exist. It is only a passage migrant in the Democratic Republic of Congo (DRC) and we found very few recent records from there.

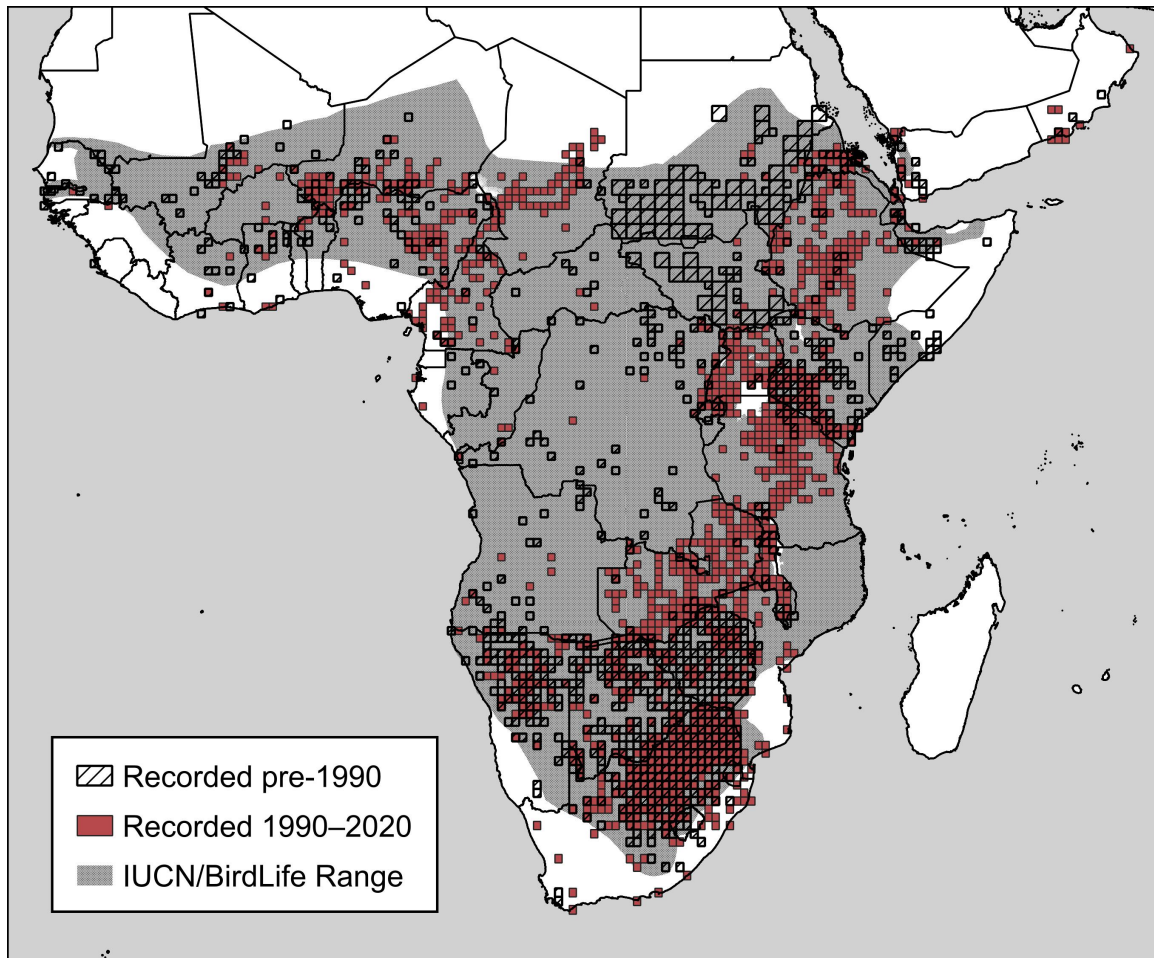


Figure 1.2. Historic (pre-1990) and recent (1990–2020) distribution of the Abdim's Stork, with the IUCN distribution map (developed by BirdLife International) for comparison. Note: country borders (sourced from www.hub.arcgis.com) are purely for display purposes and do not reflect the authors' particular support for or against existing national claims on international borders.

African Woollyneck

Excluding the 60-arcsecond cells of the Sudan atlas, the African Woollyneck was recorded in a total of 1,332 cells in the historic and recent periods combined (Figure 1.3). It was recorded in 1,010 cells from 1990–2020 and in 596 cells prior to 1990, 322 of which were solely during the historic period (24% potential range loss). Gula *et al.* (2020) did not report numbers of occupied cells, but the proportional range loss from their data using 1970 as a cutoff between periods was 12.2%—half of that estimated with a 1990 cutoff. As noted by Gula *et al.* (2020), the IUCN range map closely matches the

extent of known records, yet distribution within that extent is relatively sparse outside several countries in East and Southern Africa. It is the only species to not have historically occurred in the Inner Niger Delta of Mali. Besides Central Africa, Somalia, and the Sudans, noticeably large areas of the range do not appear to have been lost; rather, cells restricted to the historic period are sparsely and widely distributed across the range, suggesting that the existing range map overestimates the species' area of occurrence. It may have declined in Togo (Dowsett-Lemaire and Dowsett 2019), but this needs confirmation as agricultural areas are poorly surveyed (Gula *et al.* 2020). The Nigerian Bird Atlas has relatively widespread coverage—probably more than some other West African countries—and still there are a fair number of cells only occupied in the historic period, which is indicative of a decline. The population in South Africa has expanded into urban areas in recent years (Thabethe and Downs 2018).

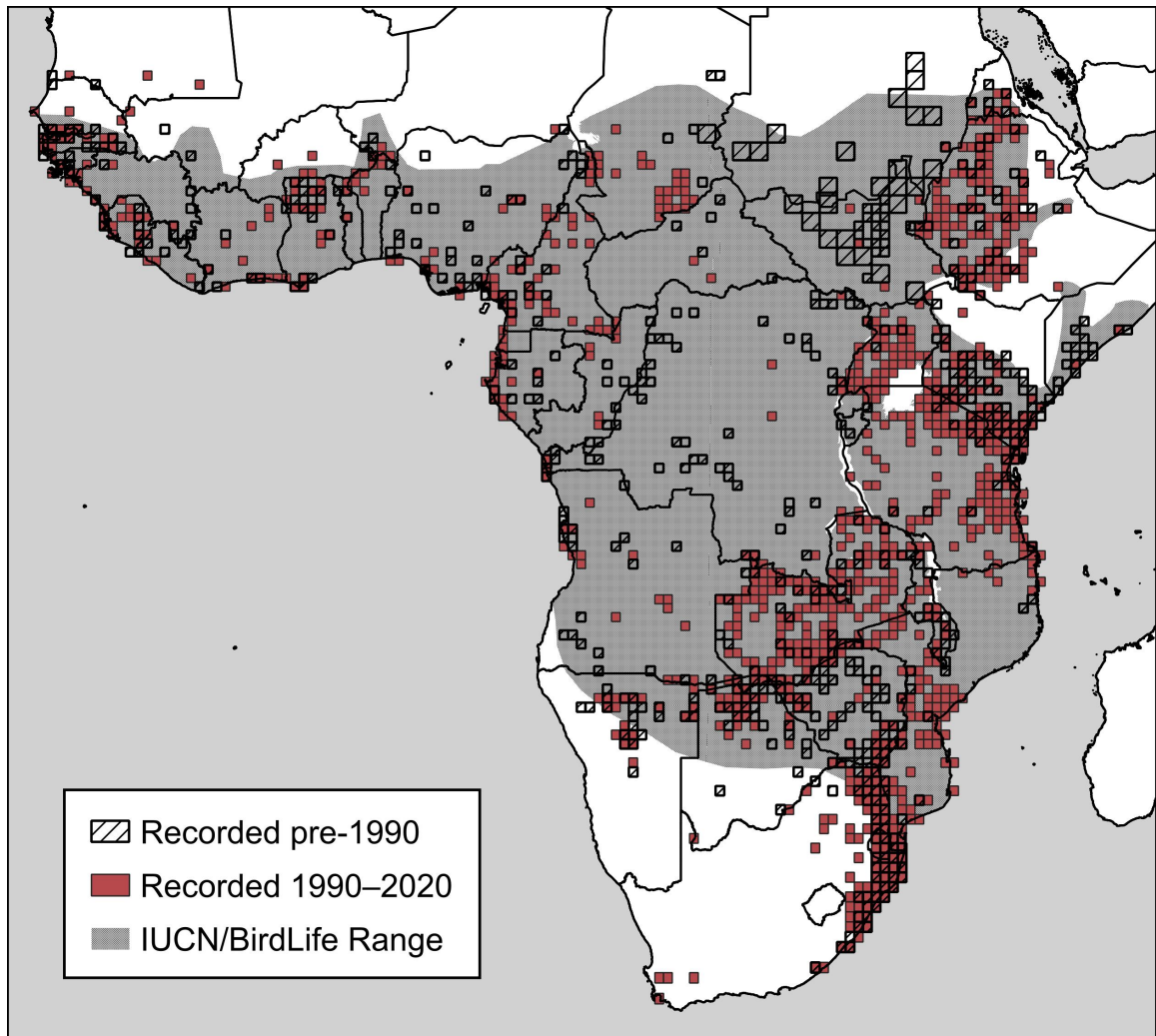


Figure 1.3. Historic (pre-1990) and recent (1990–2020) distribution of the African Woollyneck, with the IUCN distribution map (developed by BirdLife International) for comparison. Note: country borders (sourced from www.hub.arcgis.com) are purely for display purposes and do not reflect the authors' particular support for or against existing national claims on international borders.

Saddlebill Stork

Excluding the 60-arcsecond cells of the Sudan atlas, the Saddlebill Stork was recorded in a total of 1,137 cells in the historic and recent periods combined (Figure 1.4), the smallest range of the six species in this study. It was recorded in 821 cells from 1990–2020 and in 584 cells prior to 1990, 316 of which were solely during the historic period (28% potential range loss). Although not explicitly reported, Gula *et al.* (2019) found a proportional range loss of 9.7% when 1970 was used as a cutoff between the historic and

recent periods—nearly a third of the estimate when 1990 is used as a cutoff. This study also updated some errors of georeferencing from the 2019 range map (mostly from Snow 1978), which is reflected in the shift of some cells, especially those that predate 1970. The IUCN range map for this species is a very coarse representation of actual distribution and will benefit from being updated.

Overall, the Saddlebill Stork has a sparse distribution outside East and Southern Africa, including the most limited historic distribution in West Africa. Gula *et al.* (2019) already discussed range-wide distribution in detail, but the timescale used in this study shows very few recent records exist from Somalia and the Sudans after 1990, much like other African stork species. Namibia and Zimbabwe also seem to have a fair number of cells occupied only during the historic period, but whether this is representative of a change in distribution is unknown. Chapin (1932) reported it was common in Katanga Province and numerous along the Kasai River in the DRC historically, yet there exists only a single recent record of a pair in Katanga (S. Doppagne, pers. comm.). One overlooked detail of note in the previous study was historic breeding in Senegal’s Niokolo-Koba National Park, which has not been recorded since 1981 (Morel and Morel 1990). Besides one record of apparent breeding in the Potiskum area of Nigeria in 1972 (Elgood *et al.* 1994), the only other area it seems to have been a breeding resident in the country was in Yankari Game Reserve, where no more than three birds were ever recorded (P. Hall and U. Ottosson, unpub. data). It has not been observed in Yankari since 2015, so it likely has disappeared from Nigeria completely. The lack of records from the Nigerian Bird Atlas, which has fairly good coverage, and multiple decades of travel across the country by

several ornithologists (P. Hall and U. Ottosson, pers. comm.) suggests there is no connectivity between the Cameroon-Chad population and that in the W-Arli-Pendjari National Parks complex. New evidence from local people in Mali—which we consider valid given the ease of identification of the species—indicates the Saddlebill Stork persists at Lake Korarou, east of the Inner Niger Delta (S. Canney, per. comm.). Although its status in Mali is unclear, there also seems to be no connectivity between the W-Arli-Pendjari National Parks population and that in The Gambia, Guinea-Bissau, and Senegal. Finally, investigation into occurrence in Sierra Leone—although not part of the historic range—found no evidence of the species there (P. Robinson and M. Sesay, pers. comm.).

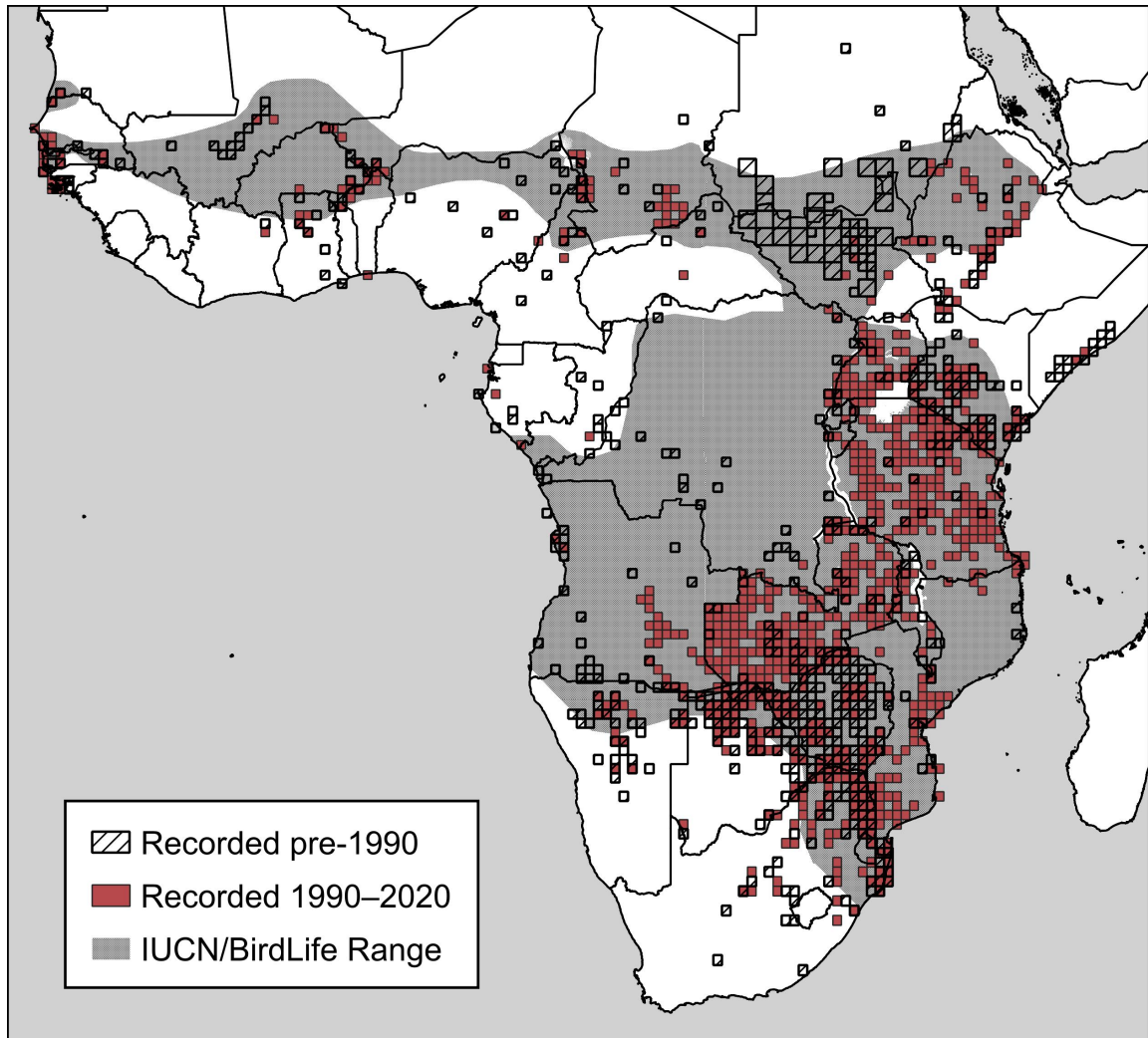


Figure 1.4. Historic (pre-1990) and recent (1990–2020) distribution of the Saddlebill Stork, with the IUCN distribution map (developed by BirdLife International) for comparison. Note: country borders (sourced from www.hub.arcgis.com) are purely for display purposes and do not reflect the authors' particular support for or against existing national claims on international borders.

Marabou Stork

Excluding the 60-arcsecond cells of the Sudan atlas and vagrants north of the Sahel, the Marabou Stork was recorded in a total of 1,658 cells in the historic and recent periods combined (Figure 1.5). It was recorded in 1,217 cells from 1990–2020 and in 922 cells prior to 1990, 441 of which were solely during the historic period (27% potential range loss). The IUCN range map appears to arbitrarily represent distribution in many peripheral areas of the species' distribution range developed in this study. There are at

least 27 records from Portugal and Spain, but due to uncertainty about the origin of these storks (i.e. potential captive escapees; de Juana 2003; de Juana and Garcia 2015), these occurrences were not mapped. However, it is possible some of the records are indeed of wild vagrants because individuals are known to cover vast distances in Southern Africa (Monadjem *et al.* 2008) and several vagrant records have been accepted for Morocco (Bergier 2004; de Juana 2005). Similarly, three vagrants were recorded in Israel during the 1950s (Shirihai 1996).

The Marabou Stork is widespread from Ethiopia to Namibia and South Africa, although there has been range loss in northern Kenya, Somalia, and Zimbabwe. The DRC and the Sudans have more historically occupied cells than recent. In West Africa it appears to remain in three populations segments: (1) Chad and northern Cameroon, (2) the W-Arli-Pendjari Nationals Parks complex of Benin, Burkina Faso, and Niger, and (3) The Gambia. As many as 500 have been observed congregating in Chad's Zakouma National Park during the dry season (WABDaB 2020), and ground surveys in the Waza-Logone floodplain in Cameroon, where breeding colonies have been recorded (Scholte 2006), found 1,860 as recently as 2001 (Zwarts *et al.* 2009). The breeding population in the Inner Niger Delta of Mali was extirpated in the 1960s (Zwarts *et al.* 2009), breeding has not been recorded in the small population of Ghana's Mole National Park since 2005 (Dowsett-Lemaire and Dowsett 2014), and its range has decreased in Nigeria. The only known modern breeding colonies west of Cameroon are in Pendjari National Park in Benin, where only seven nests were counted in 2017 (Dowsett-Lemaire and Dowsett 2019), and in The Gambia, where only several small colonies persist (C. Barlow, pers.

comm.). Breeding near the Senegal River delta in 1981 was a one-time event (Morel and Morel 1990), as no other nests have been observed in Senegal since (B. Piot, pers. comm.).

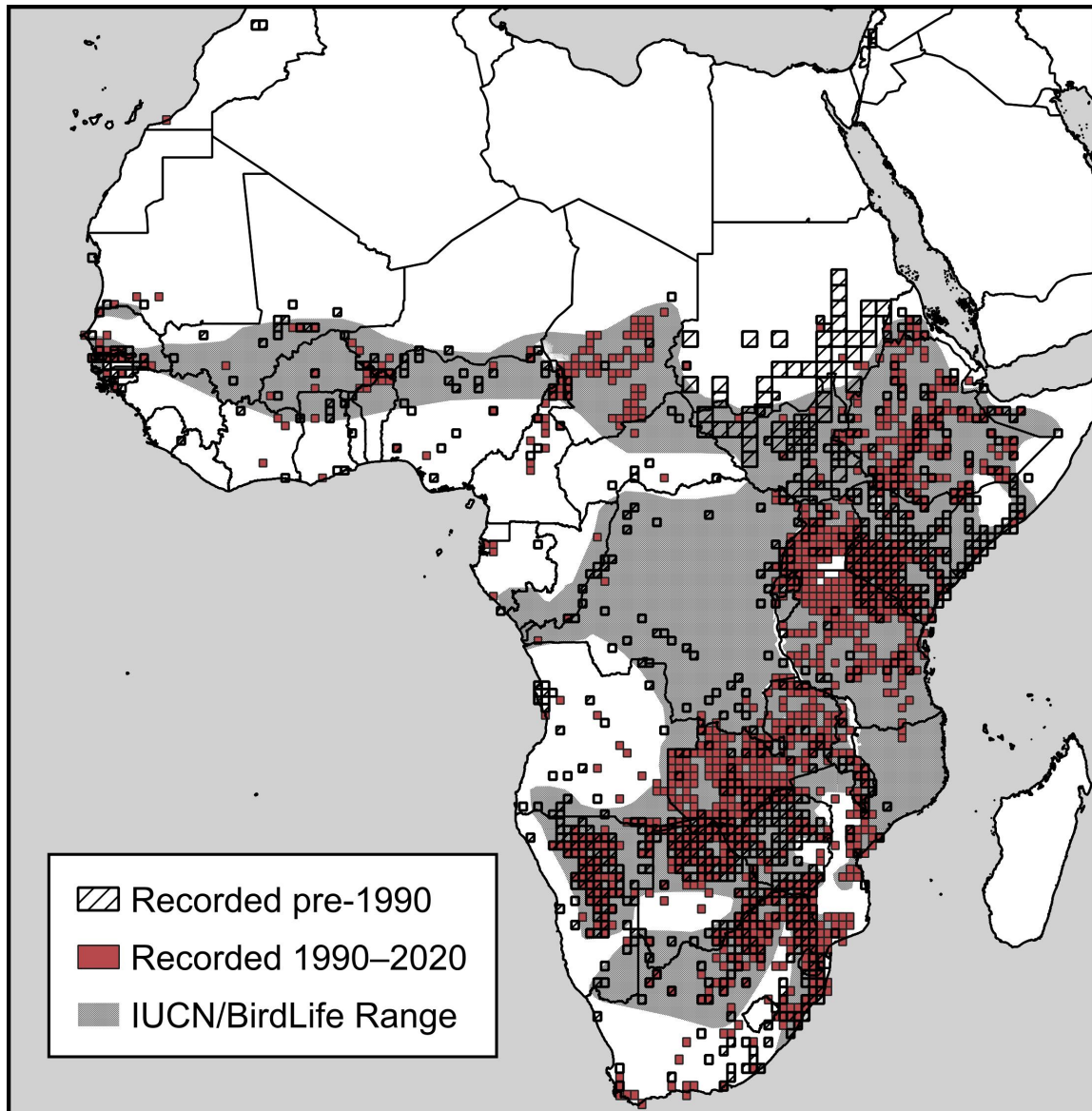


Figure 1.5. Historic (pre-1990) and recent (1990–2020) distribution of the Marabou Stork, with the IUCN distribution map (developed by BirdLife International) for comparison. Note: country borders (sourced from www.hub.arcgis.com) are purely for display purposes and do not reflect the authors' particular support for or against existing national claims on international borders.

Yellow-billed Stork

Excluding the 60-arcsecond cells of the Sudan atlas and vagrants north of the Sahel, the Yellow-billed Stork occupied a total of 1,596 cells in the historic and recent periods combined (Figure 1.6). From 1990–2020, 1,129 cells were occupied, and 986 cells were occupied prior to 1990, 467 of which were solely during the historic period (29% potential range loss). Overall, the IUCN range map agrees with the distribution developed in this study. However, it remains unclear why hollow parts of the IUCN range were retained as part of the distribution for this species and not others where comparable regional absences exist.

This species is more prone to widespread vagrancy than others (Figure 1.7). It has become a fairly regular summer vagrant in Israel, so much so that the Israeli Rarities and Distribution Committee will no longer review records as rarities (Israel Birding 2019). Apparently, it was a common seasonal vagrant along the Nile in Egypt prior to 1913 (Goodman and Meininger 1989), but details for only two records during the historic period could be found. Groups of vagrants were common throughout the recent period, however, including as many as 150 in May 2014. Vagrants determined to be of wild origin have also been reported from Bulgaria (Ragyov *et al.* 2003), Jordan (Andrews *et al.* 1999), Morocco (Castan and Olier 1959), Qatar (Hellyer 2000), São Tomé (Jones and Tye 2006), and Tunisia (Castan and Olier 1959; Ouni 2007). Although it has been reported in Spain many times, the Spanish Rarities Committee has only accepted three records as being of wild origin, so only these are mapped. Other records from the Mediterranean region are considered to be escaped captive storks (Brichetti *et al.* 1996;

Alessandria *et al.* 1997; de Juana 1998).

Migratory patterns in some regions, such as West Africa (Isenmann *et al.* 2010; Dowsett-Lemaire and Dowsett 2014), the Sudans (Nikolaus 1987), and possibly parts of Southern Africa, appear to indicate movement of storks tracking suitable hydrological conditions. Beyond recognition of this pattern, nothing is known about this aspect of its ecology. Nevertheless, it is widespread and common throughout East and Southern Africa with range loss in the DRC, Somalia, the Sudans, and Zimbabwe. It also occurs in western Madagascar where the largest group reported was 81 at Lake Kinkony. While breeding has yet to be confirmed on the island, it likely occurs based on observations of very young juveniles (Hancock *et al.* 1992). In Chad and Cameroon, occurrence is primarily concentrated in the Bahr Aouk and Bahr Salamat River floodplains and the Lake Chad Basin, respectively. The highest count in Chad's Zakouma National Park was 1,500 during peak dry season, but most records are of small groups. Breeding colonies have been recorded in the Waza-Logone floodplain of Cameroon but have yet to be recorded in southeastern Chad despite high counts.

In Benin, Ghana, and Togo the Yellow-billed Stork has been virtually extirpated: there are several records of one to four individuals, most from the mid-1990s. Storks were last seen at a traditional breeding colony in northern Togo in early 1990 (Cheke and Walsh 1996; Dowsett-Lemaire and Dowsett 2019), so those records were relegated to the historic period (Figure 1.6) given that they have been absent for all but the first three months of the recent period. There has only been one record in Ghana since 1975, and all

known historic breeding colonies were abandoned by the 1960s (Dowsett-Lemaire and Dowsett 2014). Similar to the other aquatic storks, it has disappeared as a breeder in Mali's Inner Niger Delta in recent decades. However, the species is still abundant as a seasonal migrant to the east of the delta, and in December 2020 it was observed in the thousands (S. Canney, pers. comm.). It has remained a common breeder in Senegal and possibly The Gambia.

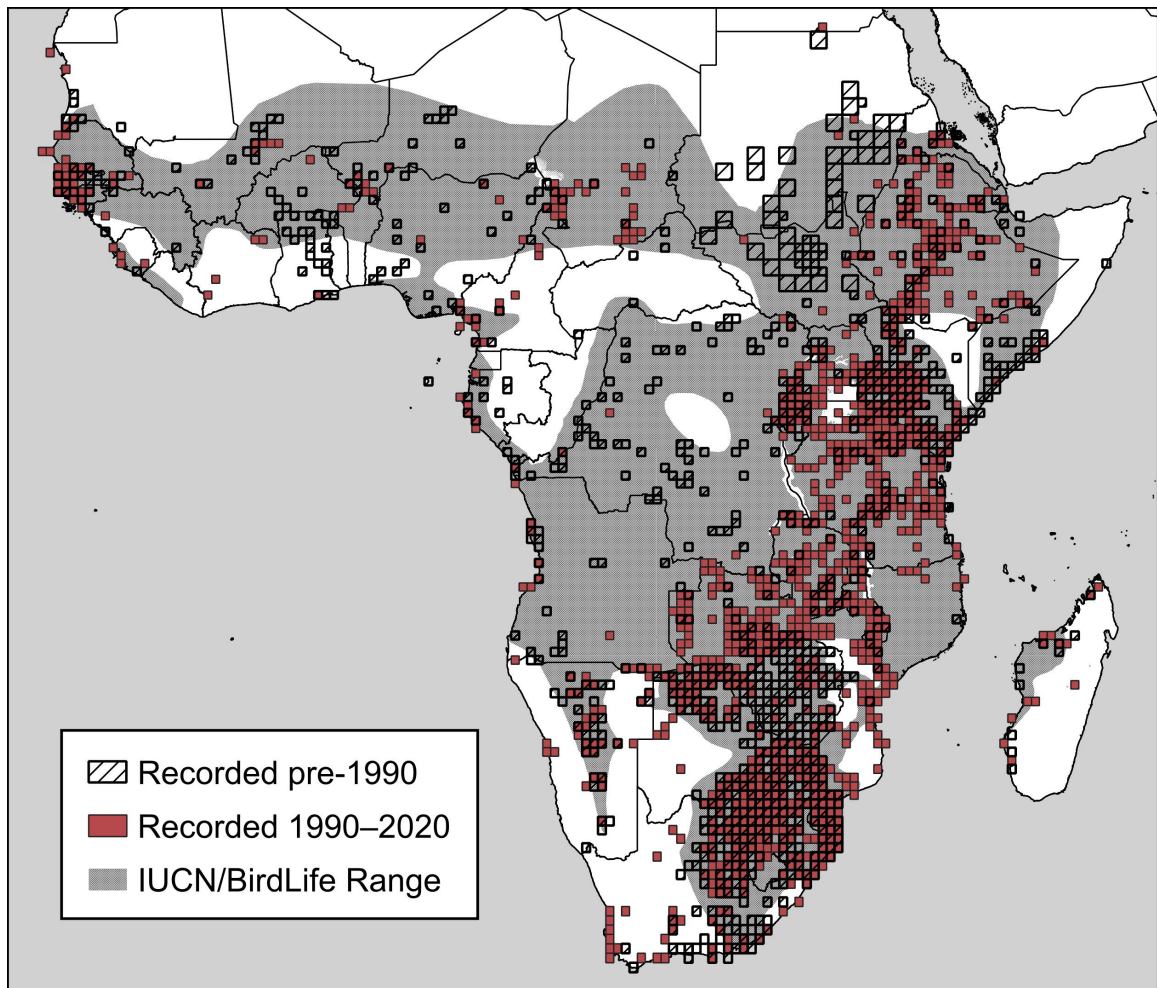


Figure 1.6. Historic (pre-1990) and recent (1990–2020) distribution of the Yellow-billed Stork, with the IUCN distribution map (developed by BirdLife International) for comparison. Note: country borders (sourced from www.hub.arcgis.com) are purely for display purposes and do not reflect the authors' particular support for or against existing national claims on international borders.

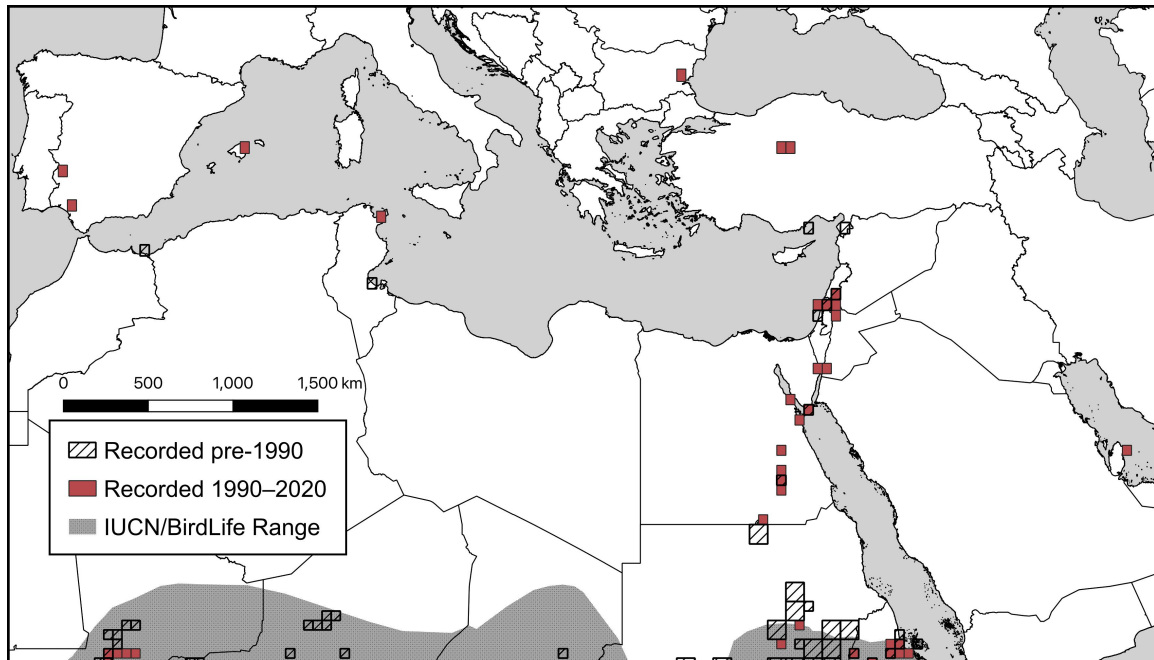


Figure 1.7. Historic (pre-1990) and recent (1990–2020) distribution of extralimital Yellow-billed Stork occurrence in the Mediterranean region. Note: country borders (sourced from www.hub.arcgis.com) are purely for display purposes and do not reflect the authors’ particular support for or against existing national claims on international borders.

Discussion

Our estimates of range contraction of the endemic African storks, especially in West Africa, and the finding that their IUCN distribution maps do not accurately represent distribution in some parts of the ranges demonstrate a need for reassessing the status of each species and ensuring the process is data-driven. Along with the recent studies on the African Woollyneck (Gula *et al.* 2020) and Saddlebill Stork (Gula *et al.* 2019), the present study is among the first attempts to robustly map range-wide distribution of the African storks using repeatable methods. While the results of this research are indeed a first step in addressing the need for updated assessments and demonstrate how changes in distribution may be used to deduce population trends (Wilson *et al.* 2004), they also show there is a great need for standardized surveys across each species’ range because inferences regarding distribution changes are limited in some countries. Published

country-specific atlases have addressed national status and distribution of storks yet many are outdated or have neglected records from volunteer databases, thus leaving out valuable information. Although we remedied this using a multitude of sources, the estimates and discussion of range loss in this study should only be considered preliminary due to a number of caveats discussed below.

Generally, the greatest range loss for all species from the historic to recent period occurred in West Africa, the DRC, Somalia, the Sudans, and Zimbabwe. Estimated range loss in Zimbabwe is probably biased using the new maps because SABAP2 coverage has been concentrated around major cities and protected areas to the neglect of other parts of the country (see SABAP2 2020). Recent absences in Angola, the DRC, Somalia, and the Sudans can most likely be explained by a lack of ornithological coverage due to political instability in recent decades. In the DRC, the lack of recent records of the Abdim's Stork, many of which migrate across the region twice annually, is particularly indicative of poor coverage in comparison to the historic period. The same is probably true for a complete lack of records for any species—historic or recent—from inland northern Mozambique. However, there is evidence that habitat loss has occurred in the DRC, Somalia, and South Sudan (Fishpool and Evans 2001; Gula *et al.* 2019). The DRC and Somalia represent range peripheries and the limits of each species' environmental tolerances (see Chapter 2), yet the Sudd of South Sudan may represent one of the single most important wetlands on the continent. Aerial surveys of the Sudd from 1979–1981 found some of the highest counts ever recorded for five of the six stork species and demonstrated striking seasonal variation in abundance (Howell *et al.* 1988; Table 1.1). Given an estimated 19% net

decrease in surface water in the Sudd (Gula *et al.* 2019), the lack of recent data represents a critical knowledge gap for assessing range-wide status as new surveys following similar protocols and seasons could provide a measure of population change. Future surveys in South Sudan are not likely to occur soon due to ongoing conflict, however.

Table 1.1. Cumulative counts from systematic aerial surveys carried out over multiple days in the Sudd of South Sudan from 1979–1981 (Howell *et al.* 1988).

Species	Mid wet season (September)	Early dry season (November–December)	Late dry season (March)
<i>African Openbill</i>	13,469	288,536	344,487
<i>Abdim's Stork</i>	0	0	858
<i>African Woollyneck</i>	1,350	2,475	1,485
<i>Saddlebill Stork</i>	3,640	4,017	4,158
<i>Marabou Stork</i>	196	359,719	194,007
<i>Yellow-billed Stork</i>	0	3,775	11,154

A similar spatial bias to Zimbabwe likely exists in many parts of West Africa where the greatest declines have been observed: biologists and birdwatchers mostly spend time in national parks and avoid agricultural areas where the Abdim's Stork and African Woollyneck may do well (W.J.R.D, pers. observ.). However, the observed range loss in the region is probably much more accurate than in Zimbabwe based on the observed collapse of breeding colonies/populations of African Openbill, Saddlebill Stork, Marabou Stork, and Yellow-billed Stork in several countries following detrimental hydrological changes caused by dams in aquatic systems such as Mali's Inner Niger Delta (Zwarts *et al.* 2009) and the White Volta of Ghana and Oti River of Togo (Dowsett-Lemaire and Dowsett 2014; 2019). Many areas of Madagascar are likely to experience poor coverage as well, and the uncertainty surrounding the African Openbill and Yellow-billed Stork

populations there should be addressed. One particular avenue of research that has conservation implications is the issue of genetic connectivity with the mainland as this could influence the sustainability of those populations, as is the case with fragmented West African populations (Frankham 2005).

Along with environmental change, human persecution and poaching has been a prominent issue in some parts of Africa. Local people harvest African Openbill chicks for food from the species' only known breeding colony in Sierra Leone's isolated population (P. Bai-Sesay, pers. comm.). Similar poaching occurs in some years at a significantly large (>1,000 nests) African Openbill colony in Botswana and may cause reproductive collapse for the season (R. Francis, pers. comm.). In Cameroon's Waza-Logone floodplain, fishermen destroyed breeding colonies of Marabou Stork and Yellow-billed Stork—some as large as 250 nests—because they perceived them as competitors for fish (Scholte 2006). In addition to direct destruction, the poaching of chicks for consumption led to the abandonment of a Marabou Stork colony that had grown to 500 nests. Eight years after the restoration of the floodplain's hydrology, neither species had increased like the Saddlebill Stork and other waterbirds had (Scholte 2006). These scenarios represents the vulnerability of colonial breeders and the potential for local conservation issues to impact an entire region's population: the loss of the Waza-Logone colonies as sources of dispersers for the rest of West Africa may have impacted the region-wide population trend, and persistent failure of the Sierra Leone colony compounded with other threats could lead to extirpation in the country. These are especially critical points if a region's storks congregate in just a few colonies and some form of population

partitioning occurs. A population genetics study would answer questions about how range-wide populations are structured. Finally, the fact that most known persecuted colonies were not inside a national park or reserve demonstrates that conservation professionals must give more attention to unprotected areas, especially for colonial breeders.

The finding that all species are widespread from East to Southern Africa is certainly positive from a conservation perspective but does not necessarily indicate abundance. The abundance-occupancy hypothesis posits a positive relationship between distribution size and abundance (Lawton 1993; Gaston *et al.* 2000), and although there is evidence that this idea is true in many instances, it may fall short for species with limited ecological requirements (Jetz *et al.* 2008; Ocampo-Peñuela *et al.* 2016; Ramesh *et al.* 2017). For a species like the African Openbill, which is a presumed migrant and specialist feeder requiring abundant mollusks (Eriksson and Kautsky 1992), a large geographic distribution may not necessarily indicate it is abundant but rather its food sources are widely distributed. The overall range positions and patterns are somewhat similar between the wetland African storks yet variation in abundance that may be related to foraging, sociality, and breeding behavior is poorly understood. For example, although all are found throughout the Sudd, there is some contrast in the abundance of each species, especially seasonally (Table 1). The Saddlebill Stork reaches its greatest abundance in the Sudd yet it is still less abundant than more gregarious species. Following the approach of the abundance-occupancy hypothesis, their similar range sizes would indicate similar abundances, which is not the picture that emerges from wetland

counts across Africa. Environmental niche models for the wetland storks have showed similar responses to variation in annual precipitation and demonstrate there is a comparable optimal range for all species (see Chapter 2). This finding also indicates that a large geographic range alone cannot be used to infer abundance because abundance will be limited by spatial variation in precipitation. An empirical approach to assessing abundance patterns in African storks certainly is warranted for a complete understanding of spatial dynamics across the range in light of these complications in generalizing the abundance-occupancy hypothesis.

Although the mention of these six species throughout many pieces of literature and accounts in prominent sources would give the impression they are well-studied (e.g. Brown *et al.* 1982; Hancock *et al.* 1992; Hockey *et al.* 2005), it is not so and is similar to emerging patterns for storks elsewhere (Sundar 2020). Perhaps this study has best demonstrated the need for increased research on the endemic African storks and helped identify important knowledge gaps regarding each species. One clear need is an investigation into environmental requirements (see Chapter 2), seasonal movements, and how these might influence population dynamics, especially where declines are occurring. While breeding occurrence has been briefly described for some areas herein, there is a need for a separate, comprehensive assessment of breeding distribution for each species and how this has changed over time. This would be particularly valuable for colonial breeders in which entire regional populations may congregate seasonally.

There is an overlap in the drivers of decline among stork species, but species-specific

assessments should consider variations in ecology. For example, wetland degradation has impacted the African Openbill, Saddlebill Stork, Marabou Stork, and Yellow-billed Stork in the Inner Niger Delta (Zwarts *et al.* 2009), Waza-Logone floodplain (Scholte 2006), and White Volta and Oti Rivers (Dowsett-Lemaire and Dowsett 2014; 2019). However, why does it appear that the African Woollyneck has not responded similarly as far as range contraction and noticeable regional population declines? Perhaps there are some important differences in the African Woollyneck's ecology that warrant further investigation, such as use of agricultural habitats like the Asian Woollyneck *C. episcopus* (Katuwal *et al.* 2020; Kittur and Sundar 2020; Win *et al.* 2020)—a behavior only vaguely described in Africa from Sierra Leone (Field 1978). Apparent declines in the Abdim's Stork are not as easily explained either because they do not rely on wetlands. While some forms of agriculture and associated practices (e.g. maize farming, pesticide application, overgrazing) have been implicated in declines in some areas (Anderson 1997), these suggestions have never been investigated further. Clearing of woodlands may have actually created new habitat that could offset other habitat degradation. For the African Openbill it has already been found that small-scale distribution is related to mollusk abundance (Eriksson and Kautsky 1992), but similar ecological studies are absent for the piscivorous species, which were affected by depletion of fish stocks in the Inner Niger Delta (Zwarts *et al.* 2009). Thus, species-specific approaches to research and conservation are essential for assessing and conserving African storks.

Finally, this study has highlighted the dangers of overlooking poorly studied and inappropriately assessed species that would not seem to warrant conservation action. The

mainstream conservation narrative has focused on well-studied species, but has inexplicably also provided confident assessments that poorly studied species are faring well. This is not to say African storks are deserving of a threatened status or that threatened species should not be priority; rather, the lack of attention and resources allotted to species such as storks has likely caused the conservation community to miss important declines (Gula 2020). The findings herein should spur further research to ensure that such declines do not continue and that future assessments represent available information accurately.

2. SCALE-DEPENDENT ENVIRONMENTAL NICHE MODELS OF FIVE ENDEMIC AFRICAN STORKS

Introduction

Characterizing the ecological requirements of species for occupancy, survival, and reproduction is a basic yet integral part of wildlife ecology and conservation (Morrison *et al.* 2012). While these data alone are insufficient for assessing conservation status, they can provide some indication of extinction risk (Bland *et al.* 2015), which is especially critical in the face of ongoing environmental change. Environmental niche models (ENMs) are a widely used tool for spatial predictions of species distributions (Pearce and Lindenmayer 1998; Elith *et al.* 2006; Hernandez *et al.* 2008; Braunisch and Suchant 2010; Radović *et al.* 2015) and delineation of species-environment relationships (De Barros Ferraz *et al.* 2012; Espinosa *et al.* 2018; Farashi and Alizadeh-Noughani 2019; Yamada *et al.* 2019), although most studies fail to discuss the latter (Yackulic *et al.* 2013). Despite the statistical caveats that come with ENMs, including limitations of model evaluation metrics (Fourcade *et al.* 2018), potential for over- and under-estimation of suitability (Loiselle *et al.* 2003), and issues with spatial sampling bias (Leitão *et al.* 2011; Kramer-Schadt *et al.* 2013), they provide useful and preliminary information that can contribute to an understanding of rudimentary environmental requirements and enhance conservation strategies (Baker *et al.* 2020), especially of poorly studied species and populations (e.g. Kebede *et al.* 2014; Vale *et al.* 2014; Miró *et al.* 2017; Khosravi *et al.* 2019; Gula *et al.* 2020).

African storks remain a poorly studied group within the order Ciconiiformes despite recognition of the paucity of basic ecological and population information over three decades ago (Luthin 1987). While much research has focused on the migratory storks in Africa—the White Stork *Ciconia ciconia* (e.g. Gerkmann *et al.* 2008; Rotics *et al.* 2016; Chenchouni 2017; Fandos *et al.* 2020; Soriano-Redondo *et al.* 2020), Black Stork *C. nigra* (e.g. Bobek *et al.* 2008; Chevallier *et al.* 2008; Chevallier *et al.* 2011; Jiguet *et al.* 2011), and, to a lesser extent, Abdim's Stork *C. abdimii* (Adjakpa 2000; Jensen *et al.* 2006; Christensen *et al.* 2008; Petersen *et al.* 2008; Ivande *et al.* 2012)—relatively little attention has been given to the African Openbill *Anastomus lamelligerus*, African Woollyneck *Ciconia microscelis*, Saddlebill Stork *Ephippiorhynchus senegalensis*, Marabou Stork *Leptoptilos crumeniferus*, and Yellow-billed Stork *Mycteria ibis*. The Marabou Stork is the best studied of these five African endemics, primarily due to two long-term monitoring projects on nesting colonies in eSwatini and Uganda (Pomeroy 1973; Pomeroy 1977; Pomeroy 1978; Monadjem 2005; Monadjem *et al.* 2008; Monadjem *et al.* 2010; Monadjem *et al.* 2012; Pomeroy and Kibuule 2017). However, only three studies have empirically assessed how any of these species respond to environmental variation. In Zimbabwe, the African Openbill was more abundant when water levels were low and mussel density was high (Eriksson and Kautsky 1992). Breeding success at a Marabou Stork nesting colony in eSwatini declined as rainfall increased through the breeding season (Monadjem and Bamford 2009). And more recently, ENMs of the African Woollyneck found scale-dependent responses to environmental variables, although annual and seasonal precipitation were most notably influential for predicting distribution (Gula *et al.* 2020).

Habitat degradation and climate change are prominent threats to declining waterbirds in Africa (Simmons *et al.* 2004; Kirby *et al.* 2008; Tarakini *et al.* 2020), but the general lack of empirical studies on the environmental requirements of storks makes forecasting their susceptibility to these threats difficult. There is little doubt they are negatively affected by these threats as some population declines in West Africa particularly have been attributed to prey depletion, anthropogenic changes to hydrology, and drought (Zwarts *et al.* 2009; Dowsett-Lemaire and Dowsett 2014; 2019; Gula *et al.* 2019). However, there is not evidence of African Woollyneck declines in West Africa (Gula *et al.* 2020) despite long-term drought that almost certainly impacted the Saddlebill Stork, for example (Gula *et al.* 2019), which raises questions about variation in environmental sensitivity among species. This is particularly relevant because population changes in many countries across Africa have not been as precipitous so as to easily ascribe causal factors as in parts of West Africa.

Therefore, our aim was to use ENMs as a starting point for remedying knowledge gaps about African storks by predicting suitability across their geographic ranges and characterizing relationships with environmental variables. Besides developing the first ENMs for the African Openbill, Saddlebill Stork, Marabou Stork, and Yellow-billed Stork, we developed new models for the African Woollyneck that were spatially and quantitatively comparable to those of the other four species for assessing niche similarity and that account for temporal scale of locality data. While a similar study is needed for the Abdim's Stork, its migratory ecology requires different modeling methods to address questions about seasonal niches in breeding and nonbreeding ranges. In the absence of

population and ecological field data, we use outputs to characterize how each species may respond to environmental change moving forward and to inform prospects for future field research.

Methods

We developed species-specific ENMs at a resolution of 10 arcminutes (0.17°) at the range-wide and regional scales to predict potential suitable areas and examine responses to environmental variables. Regions were divided into East, Southern, and West Africa by visually assessing clustering of pooled locality data. Range-wide locality data for the African Openbill, African Woollyneck, Saddlebill Stork, Marabou Stork, and Yellow-billed Stork were collated and vetted from the following online databases: eBird (eBird 2020), the Global Biodiversity Information Facility (<https://www.gbif.org>), and the West African Bird Database (<https://www.wabdab.org>). Although bird atlases from the following countries mapped distribution at a coarser resolution than the ENMs, they provided some detailed records within the text: Benin and Togo (Dowsett-Lemaire and Dowsett 2019), Ethiopia and Eritrea (Ash and Atkins 2009), Ghana (Dowsett-Lemaire and Dowsett 2014), Malawi (Dowsett-Lemaire and Dowsett 2006), and Senegal/The Gambia (Morel and Morel 1990). Tanzania Bird Atlas data were also provided directly (N. Baker, pers. comm.), and because their resolutions are less than that of the ENMs, distributions from the Southern African Bird Atlas Project 2 (SABAP2; <http://sabap2.birdmap.africa>) and Nigeria Bird Atlas (<http://nigeriabirdatlas.adu.org.za>)—both ongoing efforts—were used as well. Many records for each species also came from the National Geographic Okavango Wilderness Project (M. Mills, unpub. data) and the

West African Ornithological Society's journal *Malimbus*. Finally, records were located by manually tracing citations in a variety of literature (see supplementary material in Gula *et al.* 2019) or provided directly by in-country experts. Because the primary data source for records from the Sudd in South Sudan came from comprehensive aerial surveys (Howell *et al.* 1988), only a random subset of these data was used so models were not overfit to conditions in Sudd given the spatial sampling bias there.

Unfortunately, a similar subsampling approach was not possible for other data. Records from all sources were filtered to one per 10-arcminute cell (Elith *et al.* 2006; Serrano-Rodríguez *et al.* 2018), which prevents false cross-validation in model replicate tests (see below).

Variables from the WorldClim 2.1 database (Fick and Hijmans 2017) and land cover from the GlobCover project (ESA and UCL 2010; Bontemps *et al.* 2011) were used as environmental input data in the models. The WorldClim database includes elevation and annual trends and extremes in precipitation and temperature from 1970–2000. GlobCover provides satellite-derived, categorical vegetation cover at a 1-km resolution, and so was resampled by the majority of values in a 10-arcminute cell to make its resolution congruent with the WorldClim layers. However, GlobCover data were from 2009 and were thus not temporally congruent with other model inputs. At the range-wide and regional scales, only WorldClim variables with Pearson correlation coefficients <0.75 were used (Table 2.1). Further variables were not incorporated into models because of the paucity of environmental layers for Africa at a range-wide scale. Thus, our models represent simple baselines that can be expanded upon as more data become available in

the future. Only stork records from 1970–2000 were used in models to ensure they were temporally congruent with climate inputs. As a peripheral exercise, we tested how outputs varied between models developed with and without the temporal restriction, as this methodological approach is scarcely addressed in ENM literature. However, the temporally-restricted model is most accurate and appropriate from an analytical standpoint, and so the comparisons of the two approaches are confined to Appendix 1.

To allow for appropriate comparison between the models for each species, they each required similar environmental extents. Therefore, a buffer was created around the most peripheral non-vagrant records of all species combined (excluded vagrant records included those north of 17° N) to define the model extent for all species. Although ENMs were already developed for the African Woollyneck (Gula *et al.* 2020), this process was repeated in this study to make the extents and temporal scales comparable to the other species. There are few data on movement of African storks (excluding long-distance migrants) with which to select a reasonable buffer of area available to storks in peripheral areas, so 300 km was selected as a coarse buffer by averaging the distance between tagged Marabou Stork resights that were less than 1,000 km in southern Africa (Monadjem *et al.* 2008).

Models were developed in MaxEnt, a machine-learning program that outperforms other tools in predicting species distributions (Elith *et al.* 2006; Phillips *et al.* 2006; Elith *et al.* 2010). MaxEnt's particular utility is its use of presence-only data while other methods also require absence data, which are more difficult to collect or confirm. The MaxEnt

algorithm uses the area under the receiver operating curve (AUC) to assess model predictive capacity by essentially providing a probability that a known presence record will be selected over a random background locality (Fielding and Bell 1997; Jorge et al. 2013). Therefore, a model that performs better than random has AUC values varying

Table 2.1. Environmental variables used in niche models. Each climate variable represents an average across the years 1970–2000. Note: not every variable was used in each model scale.

Variable	Description
<i>Annual precipitation (mm)</i>	Total amount of annual rainfall
<i>Precipitation in the warmest quarter (mm)</i>	Total amount of rainfall in the three consecutive months with the highest average temperature
<i>Precipitation in the driest quarter (mm)</i>	Total amount of rainfall in the three consecutive months with the lowest rainfall
<i>Precipitation in the coldest quarter (mm)</i>	Total amount of rainfall in the three consecutive months with the lowest average temperature
<i>Precipitation in the driest month (mm)</i>	Total amount of rainfall in the month with the lowest rainfall
<i>Precipitation seasonality (%)</i>	Ratio of the standard deviation of the monthly total precipitation to the mean monthly total precipitation (i.e. coefficient of variation)
<i>Annual mean temperature (°C)</i>	Average temperature in a year
<i>Maximum temperature in the warmest month (°C)</i>	Highest monthly temperature in a year
<i>Minimum temperature in the coldest month (°C)</i>	Lowest monthly temperature in a year
<i>Mean diurnal temperature range (°C)</i>	Average of the monthly temperature ranges (monthly maximum minus monthly minimum)
<i>Mean temperature in the driest quarter (°C)</i>	Average temperature in the three consecutive months with the lowest rainfall
<i>Temperature seasonality</i>	Standard deviation of mean monthly temperature $\times 100$
<i>Elevation (m)</i>	Altitude
<i>Land cover</i>	Vegetation categories derived from satellite imagery

from 0.50–1.0, with values closer to 1.0 indicating better predictive capacity (Phillips and Dudík 2008).

Ten replicate models were conducted in MaxEnt and averaged because the algorithm takes different learning paths in each run and can therefore exhibit some variation in output. Exploratory modeling found averages from ten model replicates did not differ from averages of fifty replicates. A benefit of conducting replicate models is that MaxEnt tests each replicate model's predictions against another using cross-validation (Phillips 2017) and then provides an average AUC. To determine the influence of each model input variable on predicting each species' distribution, jackknife tests of test gain (a measure of goodness of fit) were examined in MaxEnt in which each model was re-tested with one variable removed to assess the subsequent drop in gain. The importance of each variable is then measured by how much it contributes to the gain of the model when used as the sole input variable. Spatial predictions of distribution for each species incorporate the threshold for maximum test sensitivity plus specificity provided by MaxEnt as a lower probability cutoff (De Barros Ferraz et al. 2012; Jorge et al. 2013; Kebede et al. 2014), below which conditions are most likely unsuitable (Phillips 2017). Sensitivity is the probability that a model predicts a presence record correctly, and specificity is the probability it correctly predicts an absence (Liu et al. 2011).

Pairwise species niche similarity was quantified with the metric I calculated in ENMTools 1.3 using the average model for each species (Warren *et al.* 2008; 2010). Similar to Schoener's D (Schoener 1968) but without its biological assumptions, I is a

similarity index that ranges from 0–1 in which 0 indicates no overlap and 1 indicates identical niches (i.e. 100% overlap). Niche breadth of each species' average model was also quantified in ENMTools using the inverse concentration metric (B) developed by Levins (1968). B measures how each species discriminates among environmental variables, with smaller values indicative of narrower niche breadth and greater specialization and larger values of wider breadth and greater generalization (Colwell and Futuyma 1971).

Results

African Openbill

African Openbill models had high predictive capacity at all scales, with AUC values ranging from 0.84–0.86 (Table 2.2). Range-wide, annual precipitation was the most important variable for predicting distribution, and the modeled response indicated an optimum range similar to other species from *c.* 500–1,000 mm (Figure 2.1). The other top variables in the jackknife test were land cover, temperature seasonality, and precipitation in the warmest quarter of the year (Appendix 2.1). The species was most positively associated with artificial surfaces (>50% urban), regularly flooded grassland/woody vegetation, and water bodies, and had the lowest probability of occurrence in closed broadleaved evergreen/semi-deciduous forest (Appendix 3.1). The response to temperature seasonality and precipitation in the warmest quarter deviated from the other species significantly (Figure 2.1). It had the narrowest range-wide niche breadth of the five stork species (Table 2.3).

Table 2.2. Average AUC values and standard deviations of ten replicates of each species' model.

Species	Range-wide	East Africa	Southern Africa	West Africa
<i>African Openbill</i>	0.86 (0.03)	0.85 (0.04)	0.84 (0.04)	0.84 (0.06)
<i>African Woollyneck</i>	0.85 (0.03)	0.86 (0.05)	0.86 (0.05)	0.86 (0.05)
<i>Saddlebill Stork</i>	0.85 (0.03)	0.86 (0.04)	0.87 (0.03)	0.89 (0.05)
<i>Marabou Stork</i>	0.85 (0.02)	0.87 (0.03)	0.81 (0.04)	0.87 (0.06)
<i>Yellow-billed Stork</i>	0.84 (0.02)	0.87 (0.03)	0.82 (0.03)	0.88 (0.06)

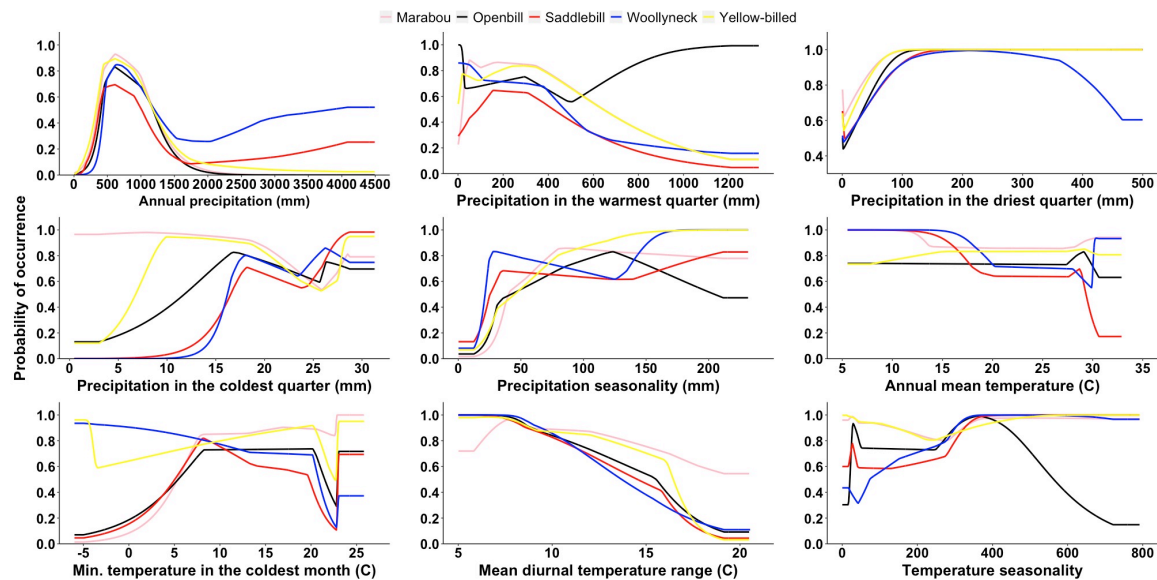


Figure 2.1. Range-wide model variable response curves for five African stork species. Note: all responses are when remaining variables are held constant at their means.

In the East African model, spatial suitability was less widespread than in the range-wide model (Appendix 4.1, 4.2). Land cover was the most important variable in the region, and the African Openbill was most positively associated with artificial surfaces (>50% urban), savannas, open needleleaved forest, and water bodies. The species had the lowest probability of occurrence in closed broadleaved evergreen/semi-deciduous forest (Appendix 3.6). Annual precipitation and precipitation in the coldest quarter of the year

were the next most important variables (Appendix 2.6). The species' response to precipitation in the warmest quarter most deviated from other species in that probability of occurrence declined more sharply as precipitation increased (Figure 2.2).

Table 2.3. Niche breadth (B) estimates from the averages of ten model replicates.

Species	Range-wide	East Africa	Southern Africa	West Africa
<i>African Openbill</i>	0.44	0.42	0.46	0.46
<i>African Woollyneck</i>	0.48	0.39	0.40	0.37
<i>Saddlebill Stork</i>	0.45	0.40	0.36	0.33
<i>Marabou Stork</i>	0.46	0.43	0.53	0.32
<i>Yellow-billed Stork</i>	0.50	0.39	0.52	0.31

In the East African model, spatial suitability was less widespread than in the range-wide model (Appendix 4.1, 4.2). Land cover was the most important variable in the region, and the African Openbill was most positively associated with artificial surfaces (>50% urban), savannas, open needleleaved forest, and water bodies. The species had the lowest probability of occurrence in closed broadleaved evergreen/semi-deciduous forest (Appendix 3.6). Annual precipitation and precipitation in the coldest quarter of the year were the next most important variables (Appendix 2.6). The species' response to precipitation in the warmest quarter most deviated from other species in that probability of occurrence declined more sharply as precipitation increased (Figure 2.2).

Spatial suitability was not as widespread in Zimbabwe and South Africa in the Southern African model compared to the range-wide model (Appendix 4.1, 4.3). Annual precipitation far out-ranked other variables as most important in predicting distribution in the region (Appendix 2.11), and responses to all variables were generally similar to other

species (Figure 2.3). It was most positively associated with regularly flooded grassland/woody vegetation and artificial surfaces (>50% urban), and had the weakest association with closed broadleaved deciduous forest (Appendix 3.11).

Spatial suitability predictions in the West African regional model varied the most from the range-wide model predictions (Appendix 4.1, 4.4). Land cover, annual precipitation, and mean temperature in the driest quarter were the top three most important variables (Appendix 2.16). The species was most positively associated with regularly flooded grassland/woody vegetation, water bodies, and rainfed croplands, and had the lowest probability of occurrence in savannas (Appendix 3.16). Although the species' response to annual precipitation was similar to other species, it deviated from others in its response to precipitation in the driest month and precipitation seasonality (Figure 2.4). Finally, it had the widest niche breadth of the five species in West Africa (Table 3).

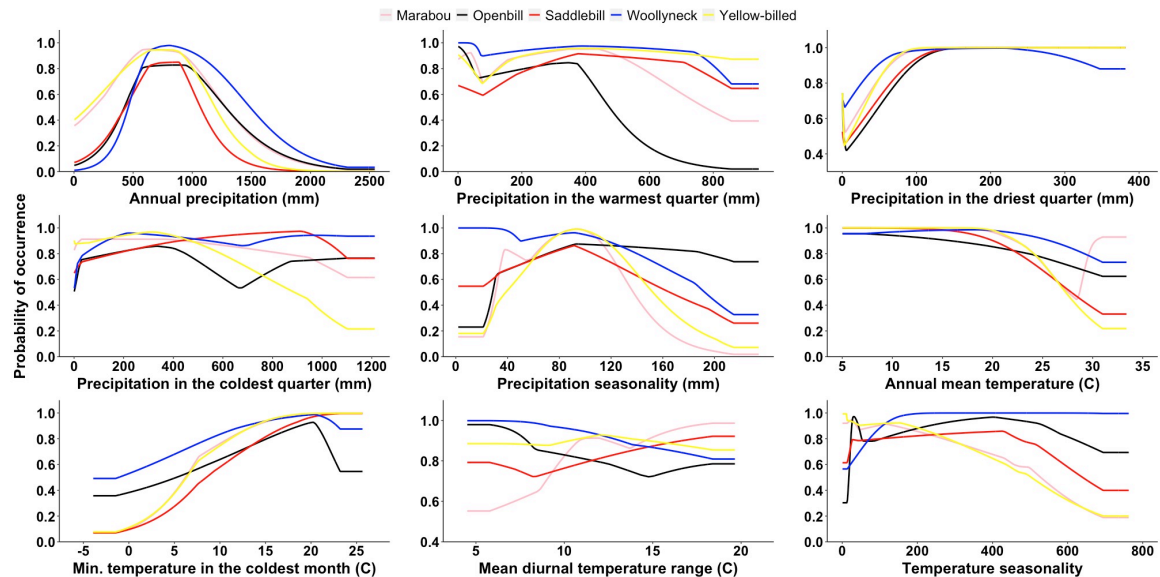


Figure 2.2. East African model variable response curves for five African stork species. Note: all responses are when remaining variables are held constant at their means.

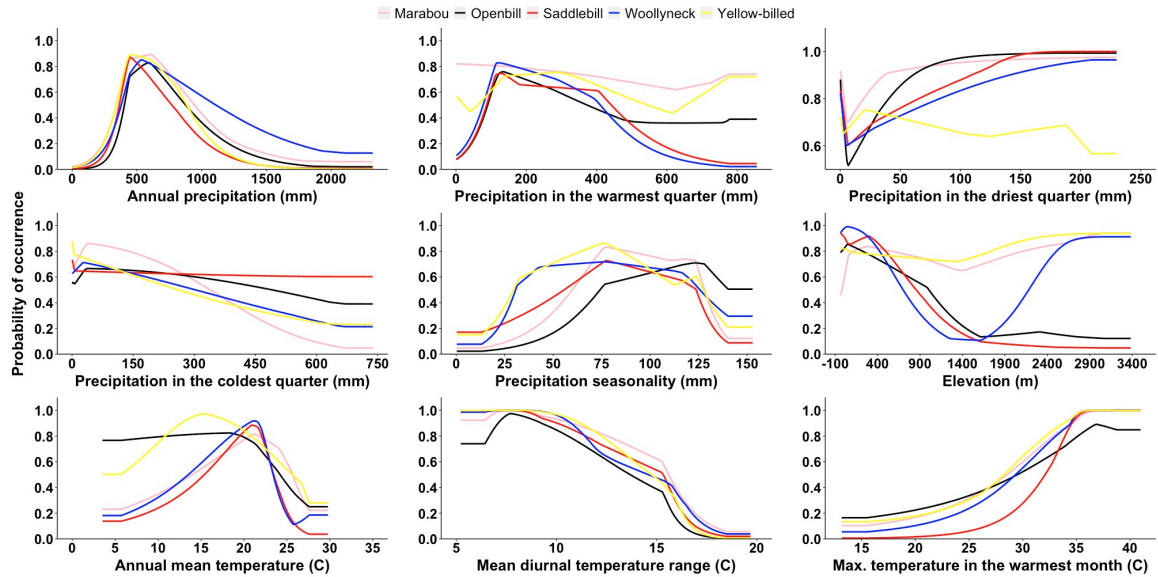


Figure 2.3. Southern African model variable response curves for five African stork species. Note: all responses are when remaining variables are held constant at their means.

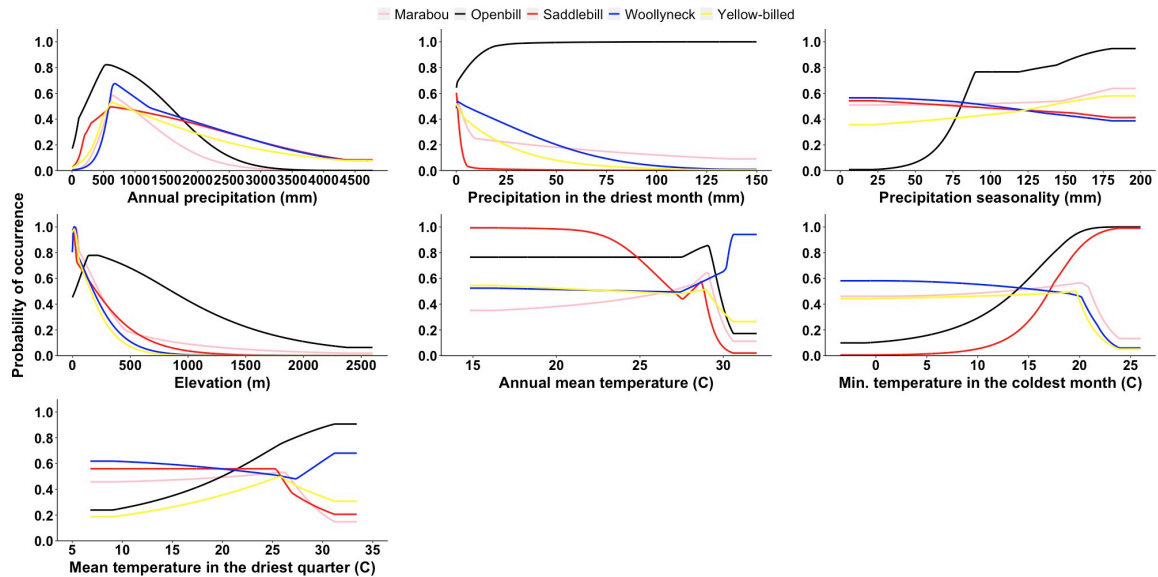


Figure 2.4. West African model variable response curves for five African stork species. Note: all responses are when remaining variables are held constant at their means.

African Woollyneck

Models had high predictive capacity at all scales for the African Woollyneck: the range-wide AUC was 0.85 and all regional models had an AUC of 0.86 (Table 2.2). The most important variable at the range-wide scale was annual precipitation (Appendix 2.2), for

which the modeled response indicated an optimum range similar to other species from *c.* 500–1,000 mm (Figure 2.1). However, it had a higher probability of occurrence at high levels of annual precipitation than other species. The next most important variables were precipitation in the warmest quarter, land cover, and temperature seasonality (Appendix 2.2). The species was most positively associated with permanently flooded, closed broadleaved forest/shrubland, regularly flooded grassland/woody vegetation, and artificial surfaces (>50% urban), and had the weakest association with closed broadleaved deciduous forest (Appendix 3.2). There was an overall negative relationship with minimum temperature in the coldest month and the response indicated a greater tolerance for cold temperatures than all other species but the Yellow-billed Stork (Figure 2.1). East African suitability predictions were more spatially limited than in the range-wide model (Appendix 4.5, 4.6). Annual precipitation and precipitation in the coldest and driest quarters were the most important variables in the region (Appendix 2.7). In contrast with the range-wide model response, there was a positive relationship with minimum temperature in the coldest month in East Africa (Figure 2.2). It was positively associated with nearly all land cover types but had the weakest association with mosaic cropland (50–70%)/vegetation (20–50%), broadleaved evergreen/semi-deciduous forest, and mosaic forest (50–70%)/grassland (20–50%; Appendix 3.7).

Spatial suitability predictions were more limited in the Southern African model than in the range-wide model, particularly from Namibia to Zambia. However, suitability was greater in central Mozambique in the regional model (Appendix 4.5, 4.7). Elevation and annual precipitation were the most important variables in the region (Appendix 2.12).

The species was most positively associated with regularly flooded grassland/woody vegetation, regularly flooded broadleaved forest, and mosaic forest (50–70%)/grassland (20–50%), and had the weakest association with water bodies (Appendix 3.12).

In West Africa, spatial suitability predictions were markedly different from the range-wide model, especially on the westernmost coast (Appendix 4.5, 4.8). Elevation, annual precipitation, and land cover were the most important variables (Appendix 2.17). The African Woollyneck was most positively associated with regularly flooded grassland/woody vegetation and artificial surfaces (>50% urban), and had the weakest association with the three land cover types that included cropland (Appendix 3.17).

Saddlebill Stork

Saddlebill Stork models had high predictive capacity at all scales, with AUC values ranging from 0.85–0.89 (Table 2.2). The most important variable in the range-wide model was annual precipitation, and there was an optimum range similar to other species from *c.* 500–1,000 mm (Figure 2.1). Land cover, precipitation in the warmest quarter, and temperature seasonality were the next most important variables (Appendix 2.3). The species had the highest probability of occurrence in permanently flooded, closed broadleaved forest and regularly flooded grassland/woody vegetation, and the lowest probability in broadleaved evergreen/semi-deciduous forest and bare areas (Appendix 3.3).

The East African model predicted more limited spatial suitability in the region than the

range-wide model (Appendix 4.9, 4.10). Annual precipitation was the most important variables followed by precipitation in the warmest quarter, land cover, and precipitation in the coldest quarter (Appendix 2.8). The species had similar probabilities of occurrence in most land cover types except broadleaved evergreen/semi-deciduous forest, which had the lowest probability (Appendix 3.8).

In Southern Africa, the regional model predicted greater spatial suitability in central Mozambique (Appendix 4.9, 4.11), and the Saddlebill Stork had the narrowest niche breadth of the five species in the region (Table 2.3). Annual precipitation was the single most important variable (Appendix 2.13), and the species was most positively associated with regularly flooded grassland/woody vegetation, sparsely vegetated, and bare areas. It had the weakest association with closed broadleaved forest (Appendix 3.13).

In West Africa, spatial suitability was markedly different than the range-wide model and was greater over a smaller geographic area (Appendix 4.9, 4.12). Land cover was the single most important variable in the region (Appendix 2.18). The species was most positively associated with regularly flooded grassland/woody vegetation, and had the weakest association with bare areas and the three land cover types that included cropland (Appendix 3.18). Finally, it exhibited the strongest negative response to precipitation in the driest month in West Africa compared to other species (Figure 2.4).

Marabou Stork

Marabou Stork models had high predictive capacity at all scales, with AUC values

ranging from 0.81–0.87 (Table 2.2). Annual precipitation was the most important variable in the range-wide model, and there was an optimum range similar to other species from *c.* 500–1,000 mm (Figure 2.1). Land cover and precipitation in the warmest cover ranked next in importance (Appendix 2.4). The species was most positively associated with regularly flooded grassland/woody vegetation, artificial surfaces (>50% urban), and water bodies, and had the weakest association with broadleaved evergreen/semi-deciduous forest (Appendix 3.4).

Niche breadth of the Marabou Stork was the widest of the five species in East Africa (Table 2.3). The East African model predicted less spatial suitability overall except in South Sudan, where suitability was greater than in the range-wide model (Appendix 4.13, 4.14). Precipitation seasonality, annual precipitation, and precipitation in the warmest quarter were the most important variables in the region (Appendix 2.9). The species was positively associated with most land cover types but had the weakest association with broadleaved evergreen/semi-deciduous forest and mosaic forest (50–70%)/grassland (20–50%; Appendix 3.9).

The Marabou Stork's niche breadth was also the widest of the five species in Southern Africa (Table 2.3), where the regional model predicted higher suitability in many areas compared to the range-wide model, especially in central Mozambique and southern Malawi (Appendix 4.13, 4.15). Annual precipitation was the single most important variable for predicting distribution in the region (Appendix 2.14). The species was most positively associated with regularly flooded grassland/woody vegetation, artificial

surfaces (>50% urban), bare areas, and water bodies. It was most weakly associated with broadleaved evergreen/semi-deciduous forest and closed broadleaved deciduous forest (Appendix 3.14).

The West African regional model predicted much higher suitability in the westernmost countries in the region compared to the range-wide model and patchy suitability elsewhere (Appendix 4.13, 4.16). Annual precipitation, land cover, and elevation were the most important variables in the regional model (Appendix 2.19). The Marabou Stork was most positively associated with sparsely vegetated areas, regularly flooded grassland/woody vegetation, and artificial surfaces (>50% urban), and had the lowest probabilities of occurrence in rainfed croplands, shrublands, and water bodies (Appendix 3.19).

Yellow-billed Stork

All models of Yellow-billed Stork distribution had high predictive capacity, with AUC values ranging from 0.82–0.88 (Table 2.2). At the range-wide scale, it had the widest niche breadth of the five species (Table 2.3). In the range-wide model, annual precipitation was the most important variable (Appendix 2.5). There was an optimum range from *c.* 500–1,000 mm, similar to other species (Figure 2.1). Land cover and precipitation in the warmest quarter were the next most important variables. The species was most positively associated with permanently flooded, close broadleaved forest, regularly flooded grassland/woody vegetation, and artificial surfaces (>50%) urban (Appendix 3.5). It had the weakest association with broadleaved evergreen/semi-

deciduous forest and mosaic grassland (50–70%)/forest (20–50%).

In East Africa, the regional model predicted lower overall suitability than the range-wide model (Appendix 4.17, 4.18). The most important variables were annual precipitation and precipitation in the warmest and coldest quarters (Appendix 2.10). The species was positively associated with most land cover types but was most weakly associated with broadleaved evergreen/semi-deciduous forest, closed and open broadleaved deciduous forest, and mosaic forest (50–70%)/grassland (20–50%; Appendix 3.10).

The Southern African model predicted lower suitability in South Africa and greater suitability in northern Botswana and the Zambezi River Valley than in the range-wide model (Appendix 4.17, 4.19). As in all other species but the African Woollyneck, annual precipitation was the most important variables predicting distribution in the region (Appendix 2.15). The species was most positively associated with artificial surfaces (>50% urban), regularly flooded grassland/woody vegetation, regularly flooded broadleaved forest, and open needleleaved forest. It had the weakest association with broadleaved evergreen/semi-deciduous forest and closed and open broadleaved deciduous forest (Appendix 3.15).

In West Africa, the regional model predicted greater suitability in the westernmost countries than the range-wide model; suitability was patchy elsewhere in the region (Appendix 4.17, 4.20). The Yellow-billed Stork had the narrowest niche breadth of the five species in West Africa (Table 2.3). The most important variables were elevation,

land cover, mean temperature in the driest quarter, and annual precipitation (Appendix 2.20). The highest probabilities of occurrence were in regularly flooded grassland/woody vegetation and artificial surfaces (>50% urban), and the lowest probability was in rainfed croplands (Appendix 3.20).

Niche overlap

All pairwise comparisons of species' niche predictions showed very high similarity: *I* ranged from 0.89–0.99 at all model scales, indicating near identical niches (Appendix 5). The least similar niches were that of the African Openbill and African Woollyneck in West Africa.

Discussion

Our models had high predictive capacity for five African stork species, regardless of scale, and demonstrated the importance of precipitation and land cover as predictors of distribution. The environmental niches of all species were highly similar, and each had an optimum range of annual precipitation predicted by both range-wide and regional models. Outside the optimum, probability of occurrence dropped sharply. Species-specific responses to environmental variation were scale-dependent, albeit generally similar among species, and were consistent overall with field studies that have demonstrated the importance of seasonal rainfall and hydrology for waterbird communities (Berruti 1983; González 1997; Zwarts *et al.* 2009; Wen *et al.* 2011; Cumming *et al.* 2012; Takekawa *et al.* 2015). The significance of fluctuating hydrology can be attributed to foraging ecology that requires seasonally low water levels in which aquatic prey become concentrated

during dry-down (Kushlan *et al.* 1975; Kushlan 1986; Maheswaran and Rahmani 2001; Gawlik 2002; Borkhataria *et al.* 2012). The modeled relationships with precipitation variables in African storks suggests what Gula *et al.* (2020) also described for the African Woollyneck, namely a certain balance between enough seasonal rain to refill depleted foraging areas and trigger aquatic prey reproduction, and yet not too much to decrease prey density and make foraging difficult. Indeed, although precipitation seasonality was not among the most important variables, the response curves in most models support this notion in that they either have an optimum or storks are most likely to occur where seasonality is highest. Field research on the Marabou Stork has confirmed seasonality can influence breeding success (Monadjem and Bamford 2009), and fluctuating water levels affect mollusk density and therefore African Openbill abundance (Eriksson and Kautsky 1992). However, our modeled responses of the African Openbill to precipitation during the driest and warmest times of the year deviated from the trend in other species except in Southern Africa. Range-wide and in West Africa, the African Openbill had a positive relationship with rainfall during the driest and warmest seasons whereas other species had negative relationships. In East Africa the species had a stronger negative relationship with high levels of rainfall during the driest periods. These differences may be indicative of more complex hydrological requirements than in piscivorous storks.

The importance of annual and seasonal precipitation to African storks warrants further research attention in light of the predictions for future climate scenarios. Decreased rainfall and increased dry spells are predicted in Southern Africa and parts of East Africa, as is an imminent change in overall climate in West Africa (Dosio *et al.* 2019; Gaetani *et*

al. 2020; Haile *et al.* 2020). The niche characterizations from our models suggest some level of sensitivity to changes in climate (Thuiller *et al.* 2005), and the predicted changes have the potential to affect stork populations that rely on varying levels of seasonality for breeding. Along with the slow life histories of some species (Hancock *et al.* 1992), this aspect of their ecologies could prevent already declining or low populations from rebounding in the face of climate change, especially when compounded with anthropogenic threats. The population trend of most species in East and Southern Africa has not been empirically assessed, which creates increased uncertainty of the degree to which they will be impacted by future climate change.

Unsurprisingly, all species were positively associated with flooded land cover types and had the weakest associations with most broadleaved forest types, which are largely limited to Central Africa and parts of West Africa. The positive association with artificial surfaces (>50% urban) for nearly all species and scales was unexpected, but the spatial sampling bias of stork records used in the models is likely to have influenced these results. That is, a high proportion of records came from areas with heavy visitation by birdwatchers or naturalists, such as national parks and game reserves, where road or structure densities may have influenced the remote-sensing results from which the land cover data were derived. One other consideration is that the land cover layer was based on conditions in 2009 while records and climate data were from 1970–2000. It is likely some of the areas characterized as urban in 2009 were not yet developed as heavily during the thirty years from which the occurrence data derive. Nevertheless, association with human-altered areas warrants further research attention, as the Marabou Stork and

African Woollyneck are known to closely associate with anthropogenic food sources in urban areas in some parts of their ranges (Pomeroy 1975; Thabethe and Downs 2018; Francis *et al.* 2021). It is curious, however, that the African Woollyneck and Marabou Stork have different population trends in West Africa. While there is no evidence of African Woollyneck declines (Gula *et al.* 2020; also see Chapter 1), the Marabou Stork has declined in much of the region, which could be related to differences in nesting biology: the African Woollyneck generally nests singly and the Marabou Stork is a colonial nester (Hancock *et al.* 1992). Colonial species are more vulnerable to persecution and populations can be more strongly impacted by nest destruction due to greater accessibility by humans (Scholte 2006; Chapter 1). Therefore, species may respond to encroachment differently and further field investigations are necessary to properly place into perspective our preliminary findings.

Use of agricultural areas remains unaddressed in research on African storks, but it is apparent that most species in West Africa are not associated with croplands. The African Openbill stands out again in its strong association with rainfed croplands in the region, where it has not experienced as significant declines as the Saddlebill Stork, Marabou Stork, and Yellow-billed Stork. However, a similar spatial sampling bias likely exists in which our records primarily come from protected areas; agricultural areas are just not properly represented in survey and citizens science data. In Asia, a number of stork species have been found to be successful in some unprotected, agricultural landscapes (Sundar 2004; 2011; Sundar and Kittur 2013; Yamada *et al.* 2019; Katuwal *et al.* 2020; Kittur and Sundar 2020; Sundar 2020; Win *et al.* 2020), so it would be prudent for the

African conservation community to expand its attentions to include agricultural areas to test if the same holds true in a region like West Africa where natural habitat has been replaced with croplands particularly rapidly (Zwarts *et al.* 2009). Without doing so, it is difficult to thoroughly assess the threats to the stork species in this study.

Our results demonstrate certain sensitivities to climate change, and the degree of niche conservatism among storks could have implications for their abilities to adapt to future change in Africa (Lavergne *et al.* 2013). The similarity in niches among species at all scales still suggests there are other factors unaccounted for in our rudimentary models that facilitate niche partitioning. We did not explore niche equivalency or similarity using randomization hypothesis testing, but this would be a beneficial follow-up analysis to address questions of niche conservatism (Lovette and Hochachka 2006; Losos 2008; Warren *et al.* 2008). Biotic interactions—with one another or other waterbirds—are obviously lacking in our models and further research into this aspect of their ecologies will likely inform what role competition plays in each species' niche (Custer and Osborn 1978; Kushlan 1981; Guisan and Thuiller 2005). In India, resource partitioning among the Asian Openbill *Anastomus oscitans*, Black-necked Stork *Ephippiorhynchus asiaticus*, and Painted Stork *Mycteria leucocephala*—congenerics of three of our study species—occurred through differential feeding behavior, prey selection, and preference for different fine-scale habitat features such as vegetation structure and water levels (Ishtiaq *et al.* 2010). These dynamics are unexplored in African storks but are likely similar given the close phylogenetic relationships.

Stork populations in West Africa may be most at risk of extinction because they have already suffered declines in the past half century due to habitat degradation, prey depletion, and drought (Zwarts *et al.* 2009); and they may be susceptible to demographic issues related to metapopulation dynamics (Hanski 1998; Anderson *et al.* 2009).

Although the West African models predicted fairly widespread suitability in the region, some species, such as the Saddlebill Stork, appear to remain in isolated metapopulations (see Chapter 1). If these findings are not an artifact of poor coverage in many areas, which is very possible in some countries, then dispersal among these metapopulations is key to their persistence (Slatyer *et al.* 2013). A study of genetic structure across the range would effectively address the need to understand dynamics of these populations for properly assessing extinction risk. As peripheral populations, they already likely suffer from decreased genetic variation relative to those at the core of the range (Hoffman and Blouin 2004). Clearly our models indicate some regional variation in environmental requirements. Thus, the extent of their genetic diversity could affect each species' ability to adapt to further environmental change if immigrants from core areas swamp peripheral populations with alleles representative of core environmental conditions that counteract natural selection at the range edge (Kawecki 2008; Kellermann *et al.* 2009; Sexton *et al.* 2009).

Environmental niche modeling has been a valuable first step in addressing knowledge gaps about the ecologies of the African storks. Namely, our robust and repeatable approach serves as a starting point for further research, which is especially warranted given the questions raised in this study and numerous threats these species face across

their range. It is clear that on larger scales these species have high niche overlap regardless of the extent of their phylogenetic relationships, so future work should investigate ecological questions at fine scales because this is where data about interspecific variation can best inform conservation. Past studies on the African Openbill (Eriksson and Kautsky 1992) and the Marabou Stork (Monadjem and Bamford 2009) represent examples of the kind of research that is very much needed for other species, particularly in vulnerable populations in West Africa. Perhaps most critical is to understand how exactly fine scale environmental variation has population-level effects, which has since confounded an ability to address regional causes of decline in our study species.

APPENDIX SECTION

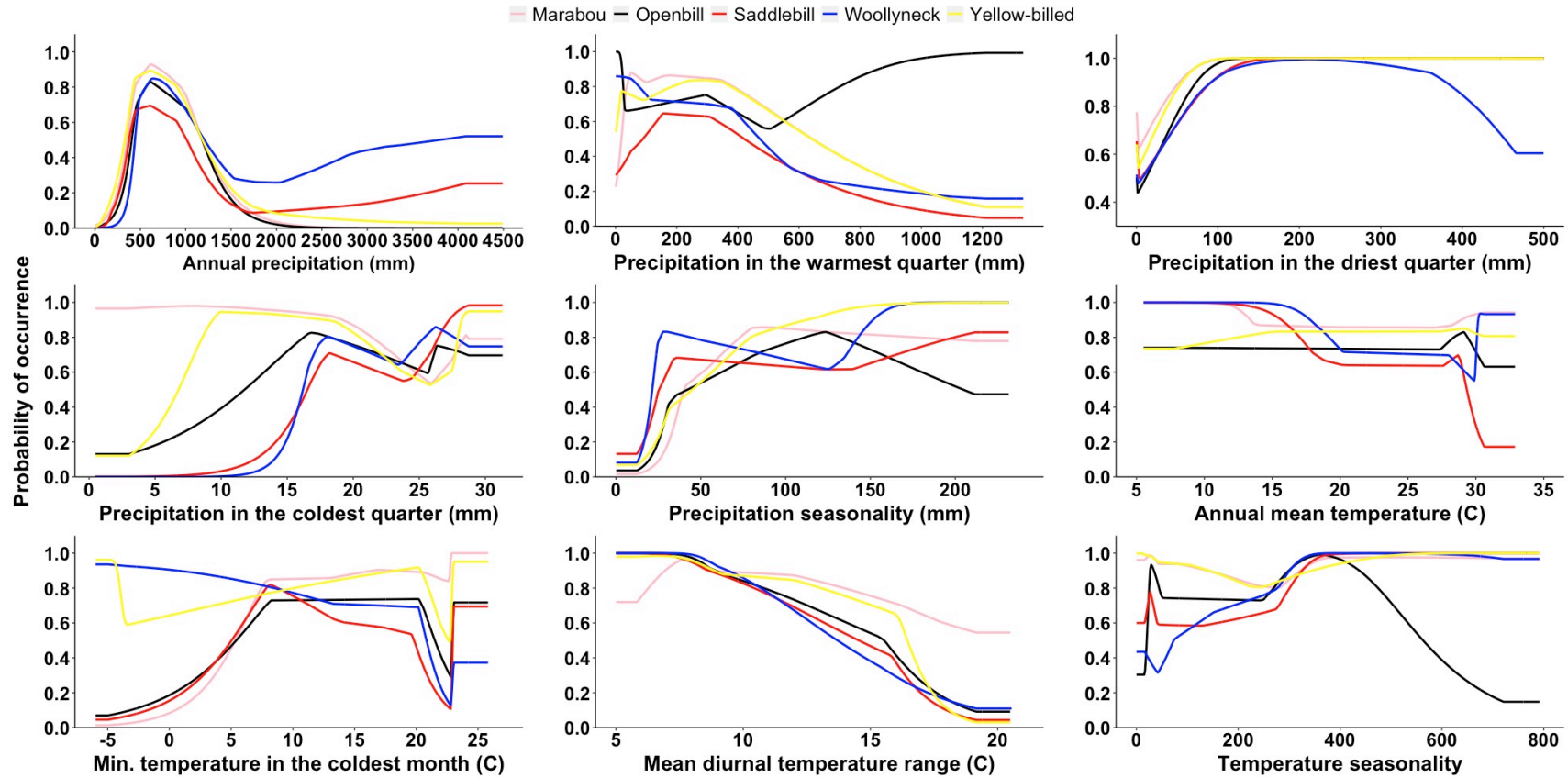
Appendix 1

Comparison of temporally-restricted and temporally-unrestricted model outputs

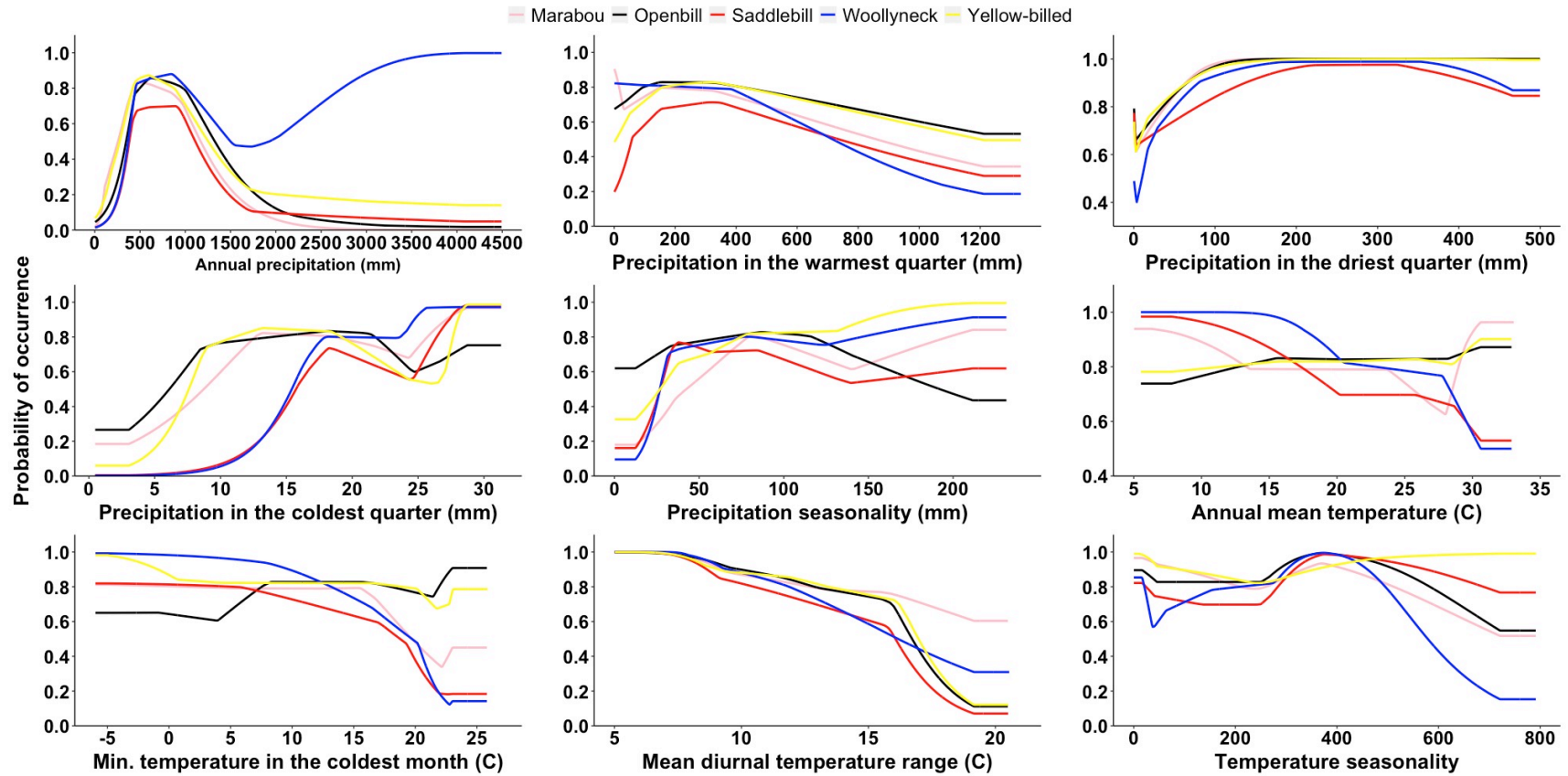
Because WorldClim data represented climate from 1970–2000, models at all scales were built using two approaches to test how temporally constrained input data affect outputs. Models were (1) trained using only 1970–2000 records (hereafter, “temporally-restricted model”) and (2) trained using all records with no year constraint (years ranging from 1867–2020; hereafter, “temporally-unrestricted model”). The temporally-restricted model is the most appropriate because the input data are temporally aligned with one another and therefore best represent the species’ relationship with the environmental variables. Thus, these results are the focus of this thesis. The purpose of the temporally-unrestricted model is to determine how the inclusion of locality data outside the temporal period of the environmental data can change the suitability predictions and characterization of environmental relationships, and we ultimately consider its outputs somewhat spurious. In this appendix, results from each model approach are presented and compared, including estimates of niche overlap (I) and niche breadth (B). The metric I was also used as a measure of similarity between the suitability predictions of each model approach as well.

1.1. Average AUC values and standard deviations of temporally-restricted (R) and temporally-unrestricted (U) models.

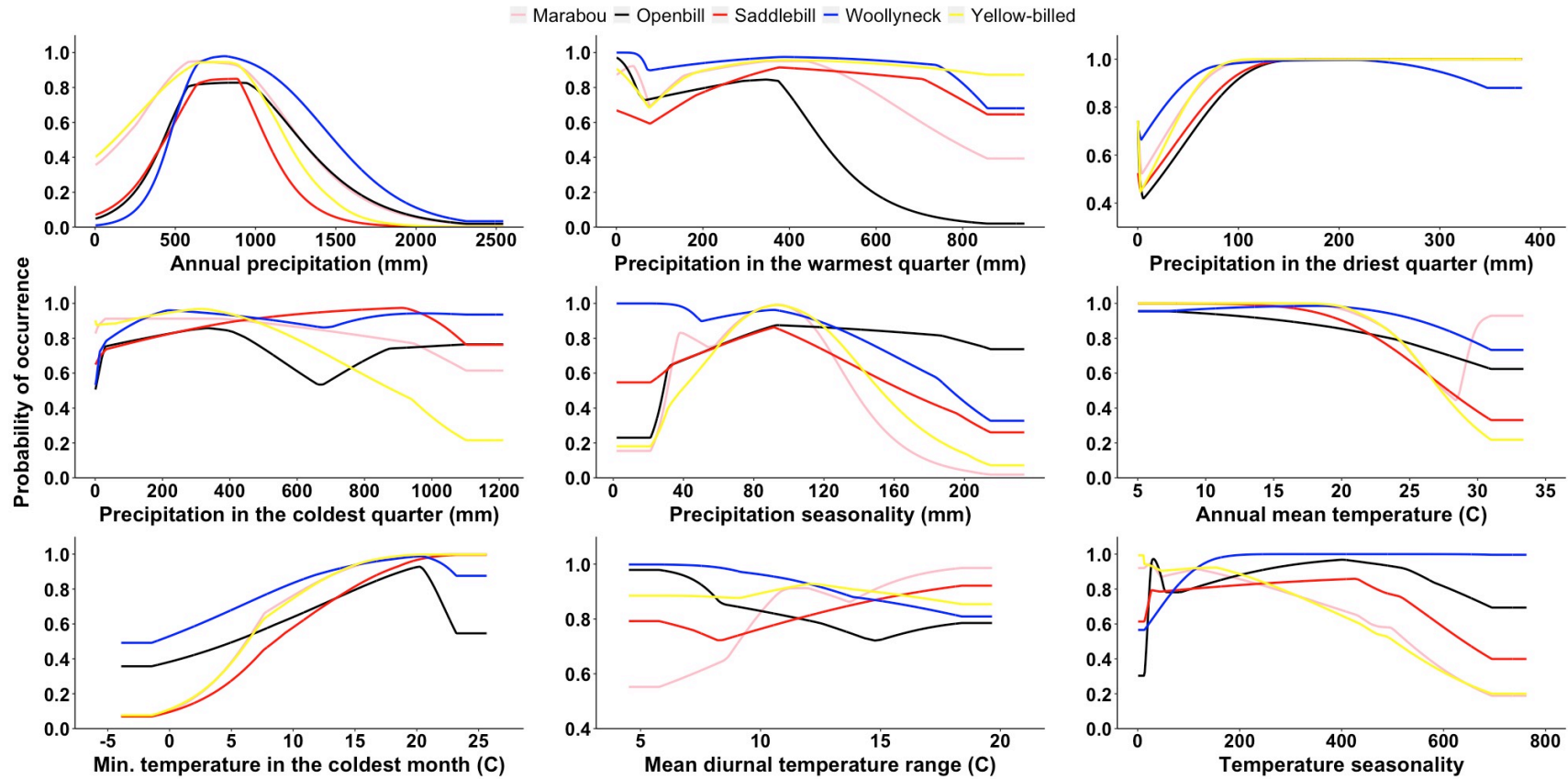
Species	Range-wide	East Africa	Southern Africa	West Africa
<i>African Openbill</i>	0.86 ±0.03 (R)	0.85 ±0.04 (R)	0.84 ±0.04 (R)	0.84 ±0.06 (R)
	0.81 ±0.01 (U)	0.84 ±0.02 (U)	0.80 ±0.04 (U)	0.83 ±0.07 (U)
<i>African Woollyneck</i>	0.85 ±0.03 (R)	0.86 ±0.05 (R)	0.86 ±0.05 (R)	0.86 ±0.05 (R)
	0.81 ±0.01 (U)	0.85 ±0.02 (U)	0.83 ±0.05 (U)	0.85 ±0.06 (U)
<i>Saddlebill Stork</i>	0.85 ±0.03 (R)	0.86 ±0.04 (R)	0.87 ±0.03 (R)	0.89 ±0.05 (R)
	0.83 ±0.02 (U)	0.84 ±0.02 (U)	0.82 ±0.04 (U)	0.89 ±0.05 (U)
<i>Marabou Stork</i>	0.85 ±0.02 (R)	0.87 ±0.03 (R)	0.81 ±0.04 (R)	0.87 ±0.06 (R)
	0.79 ±0.01 (U)	0.83 ±0.02 (U)	0.77 ±0.04 (U)	0.87 ±0.06 (U)
<i>Yellow-billed Stork</i>	0.84 ±0.02 (R)	0.87 ±0.03 (R)	0.82 ±0.03 (R)	0.88 ±0.06 (R)
	0.79 ±0.01 (U)	0.84 ±0.02 (U)	0.78 ±0.04 (U)	0.86 ±0.06 (U)



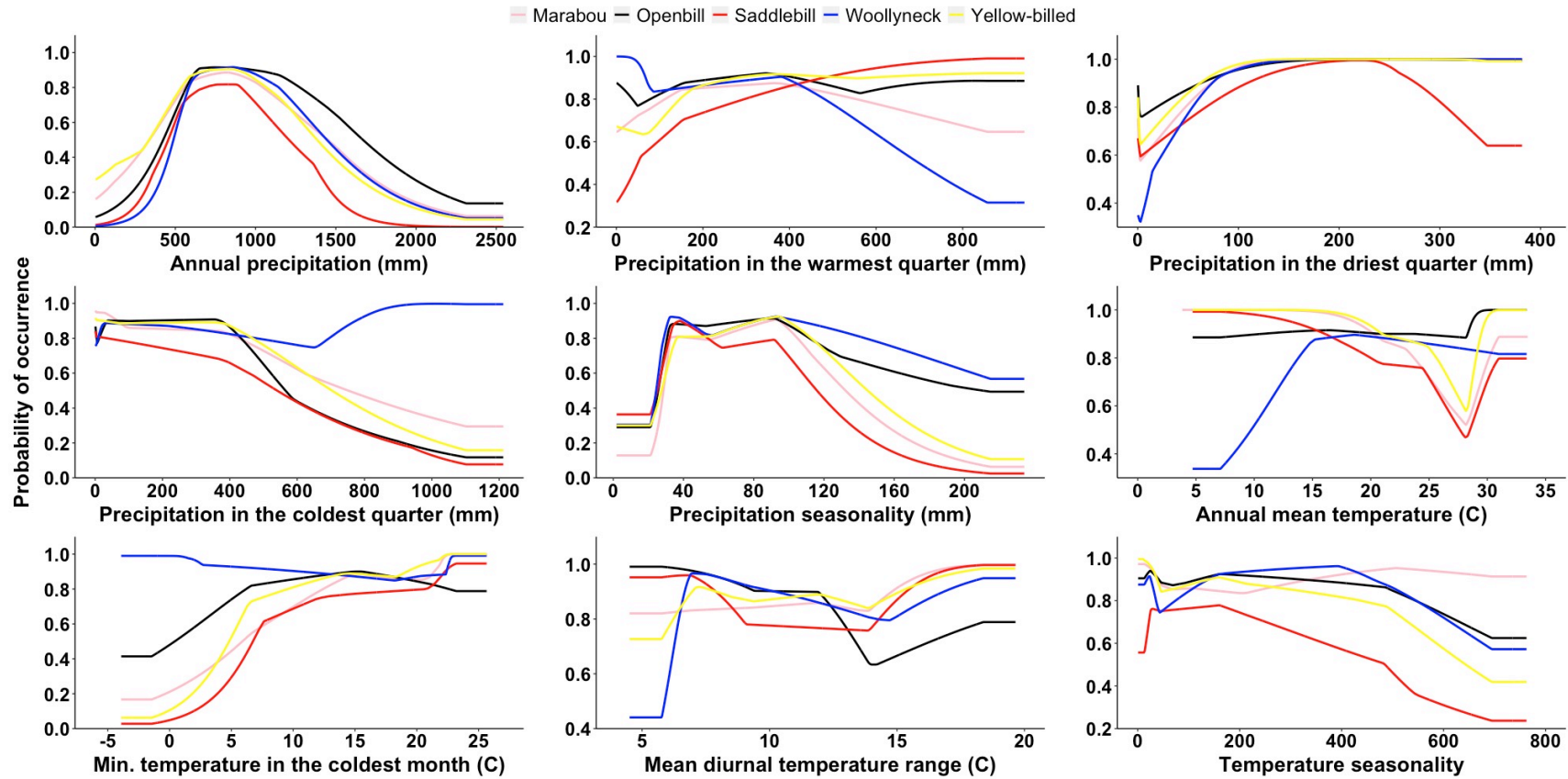
1.2. Range-wide variable response curves for the restricted models. Note: all responses are when remaining variables are held constant at their means.



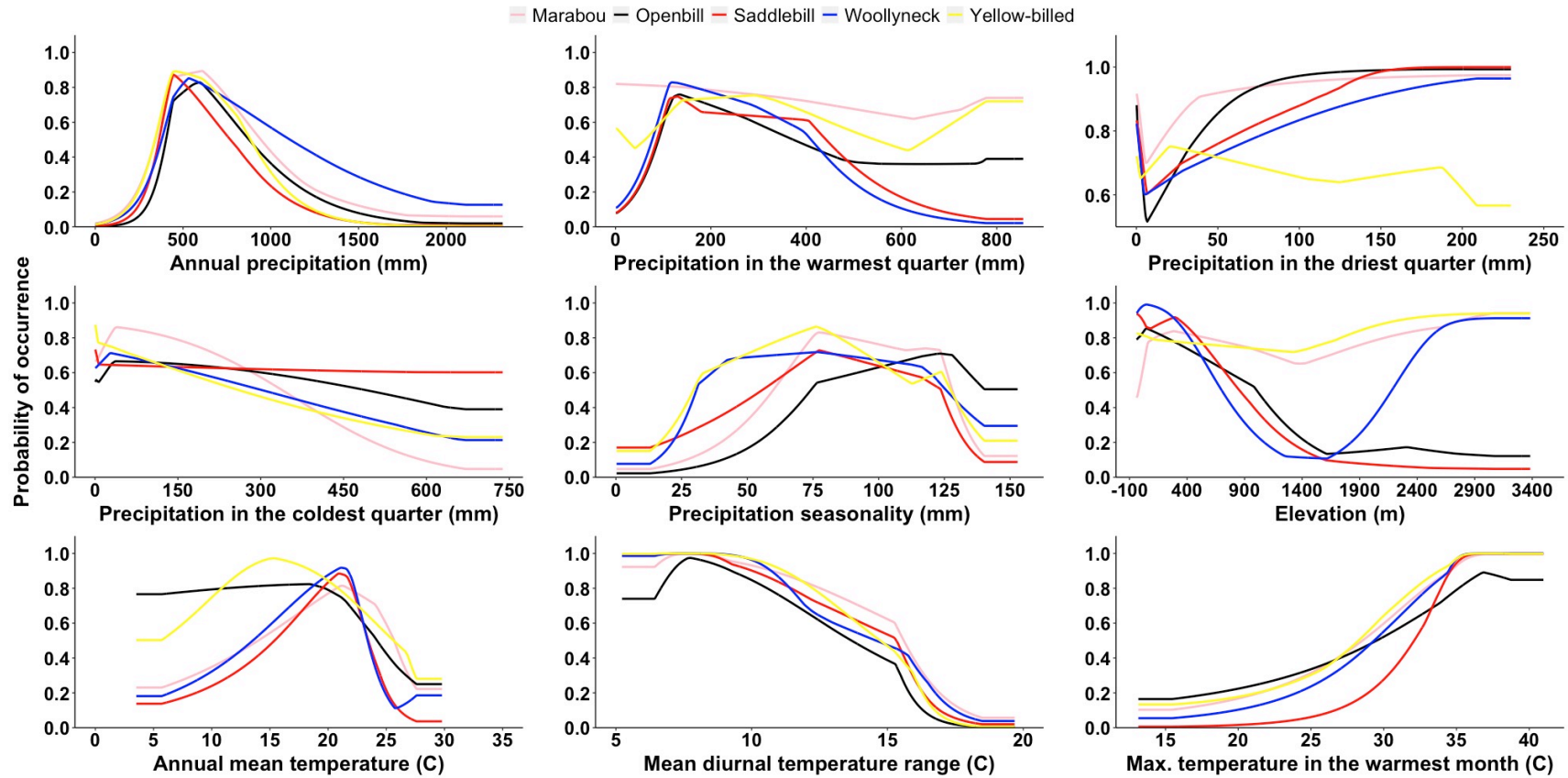
1.3. Range-wide response curves for the unrestricted models. Note: all responses are when remaining variables are held constant at their means.



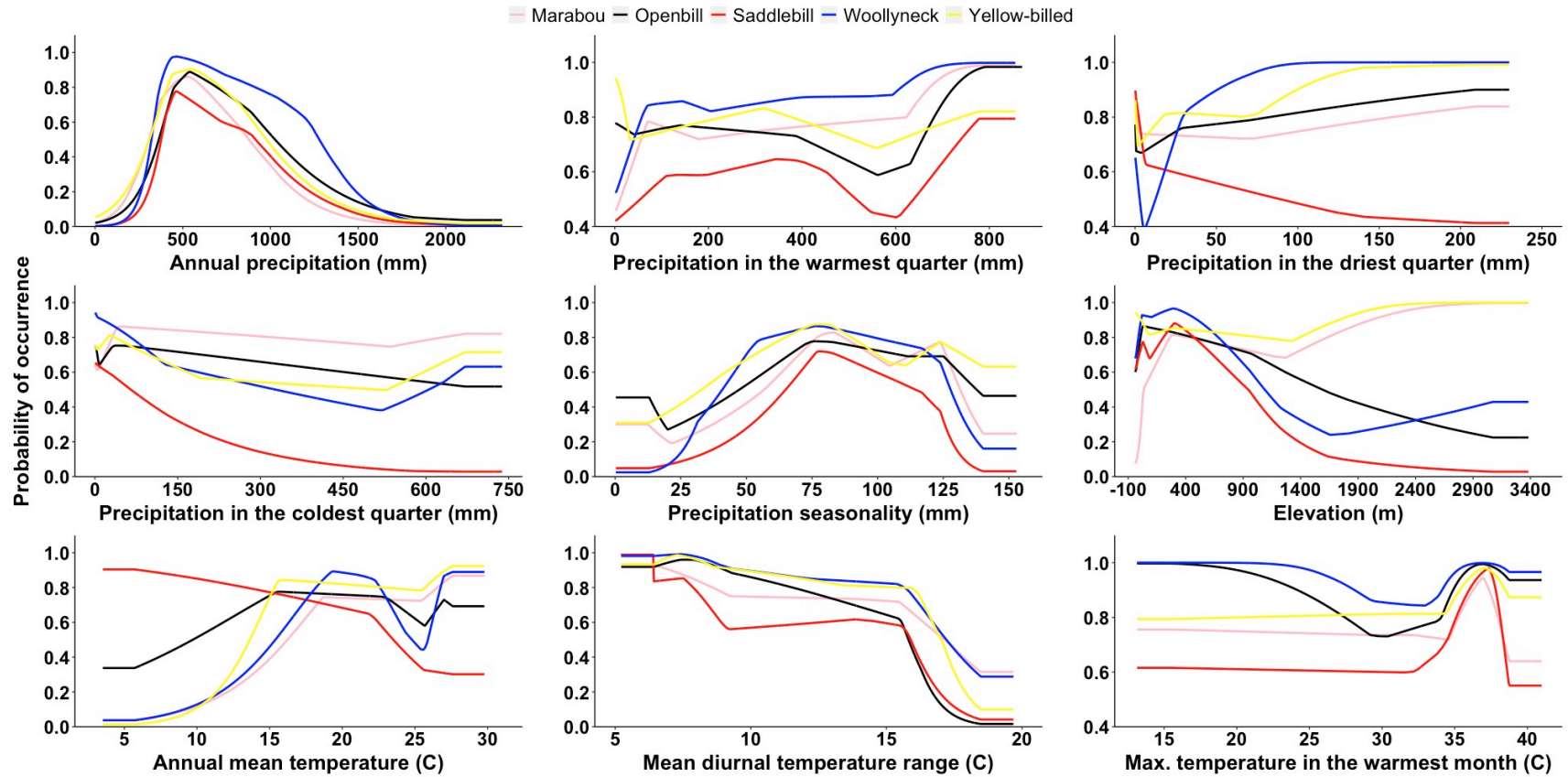
1.4. East African variable response curves for the restricted models. Note: all responses are when remaining variables are held constant at their means.



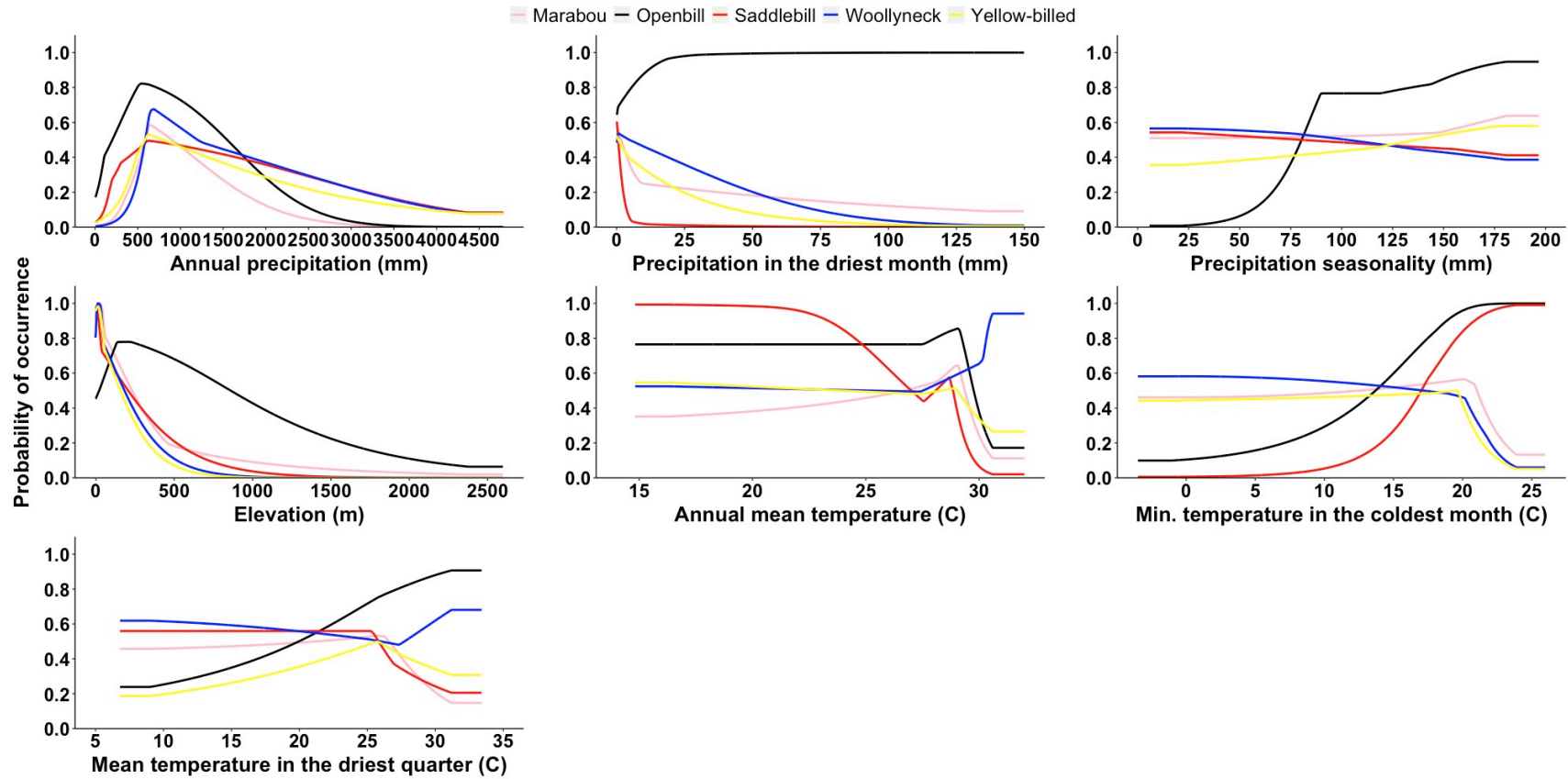
1.5. East African variable response curves for the unrestricted models. Note: all responses are when remaining variables are held constant at their means.



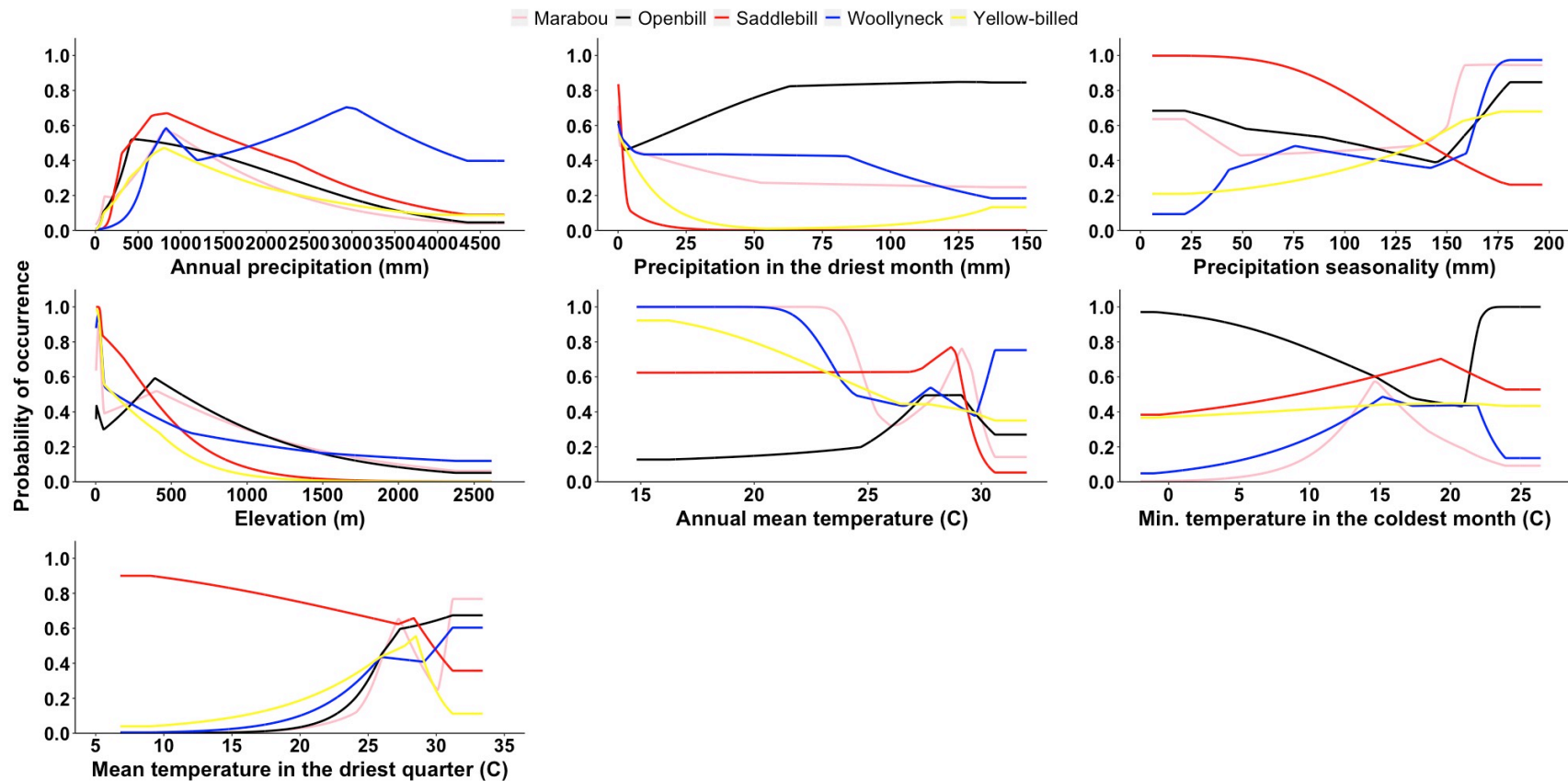
1.6. Southern African variable response curves for the restricted models. Note: all responses are when remaining variables are held constant at their means.



1.7. Southern African variable response curves for the unrestricted models. Note: all responses are when remaining variables are held constant at their means.

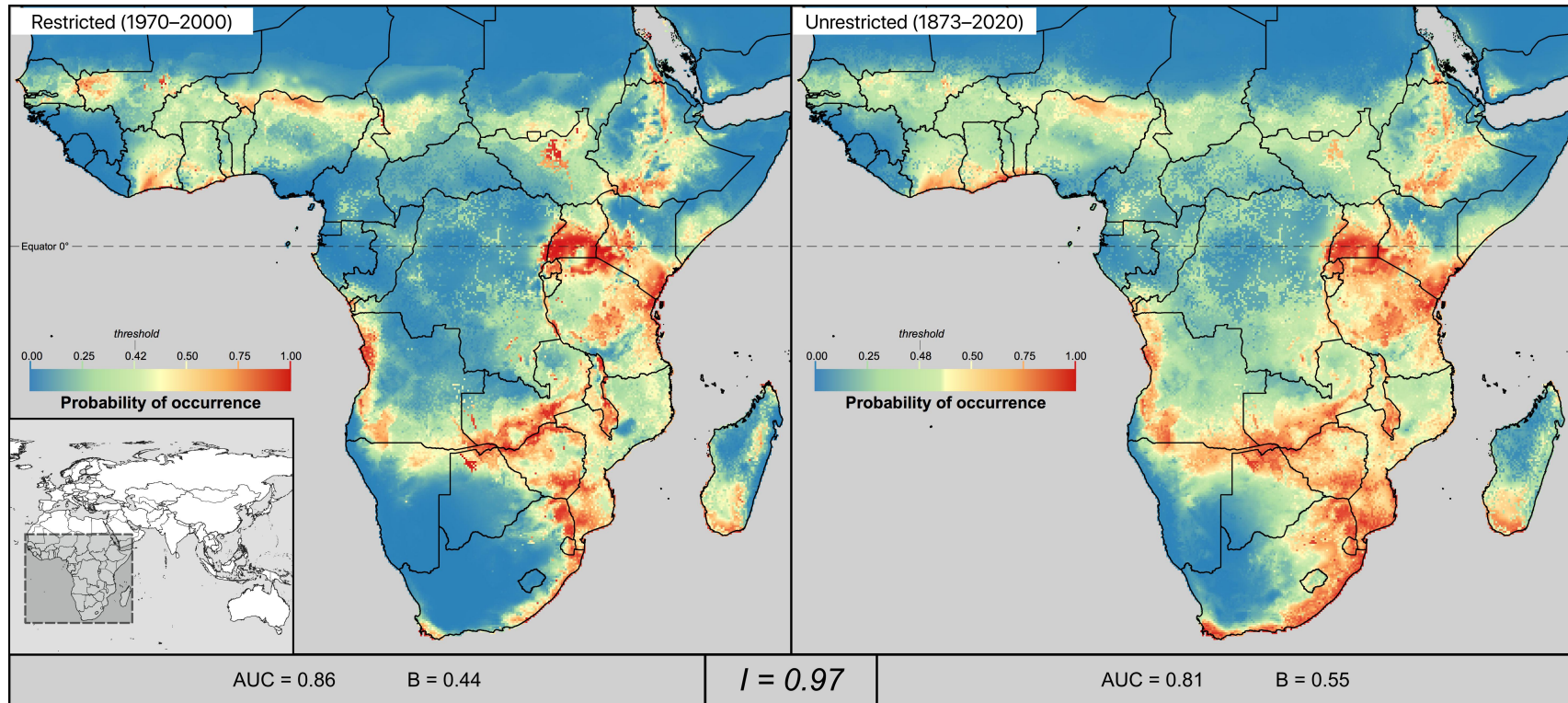


1.8. West African variable response curves for the restricted models. Note: all responses are when remaining variables are held constant at their means.

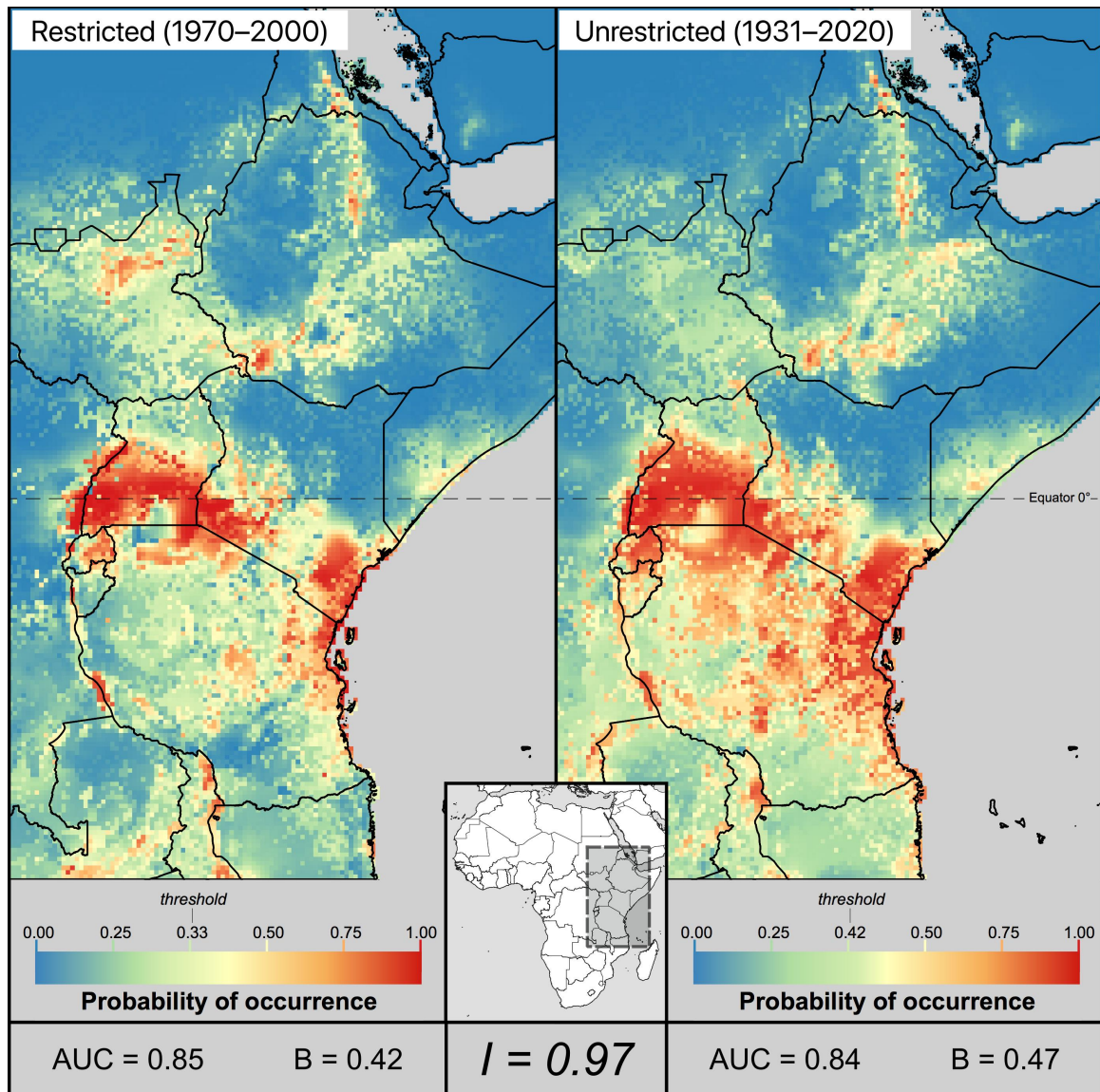


1.9. West African variable response curves for the unrestricted models. Note: all responses are when remaining variables are held constant at their means.

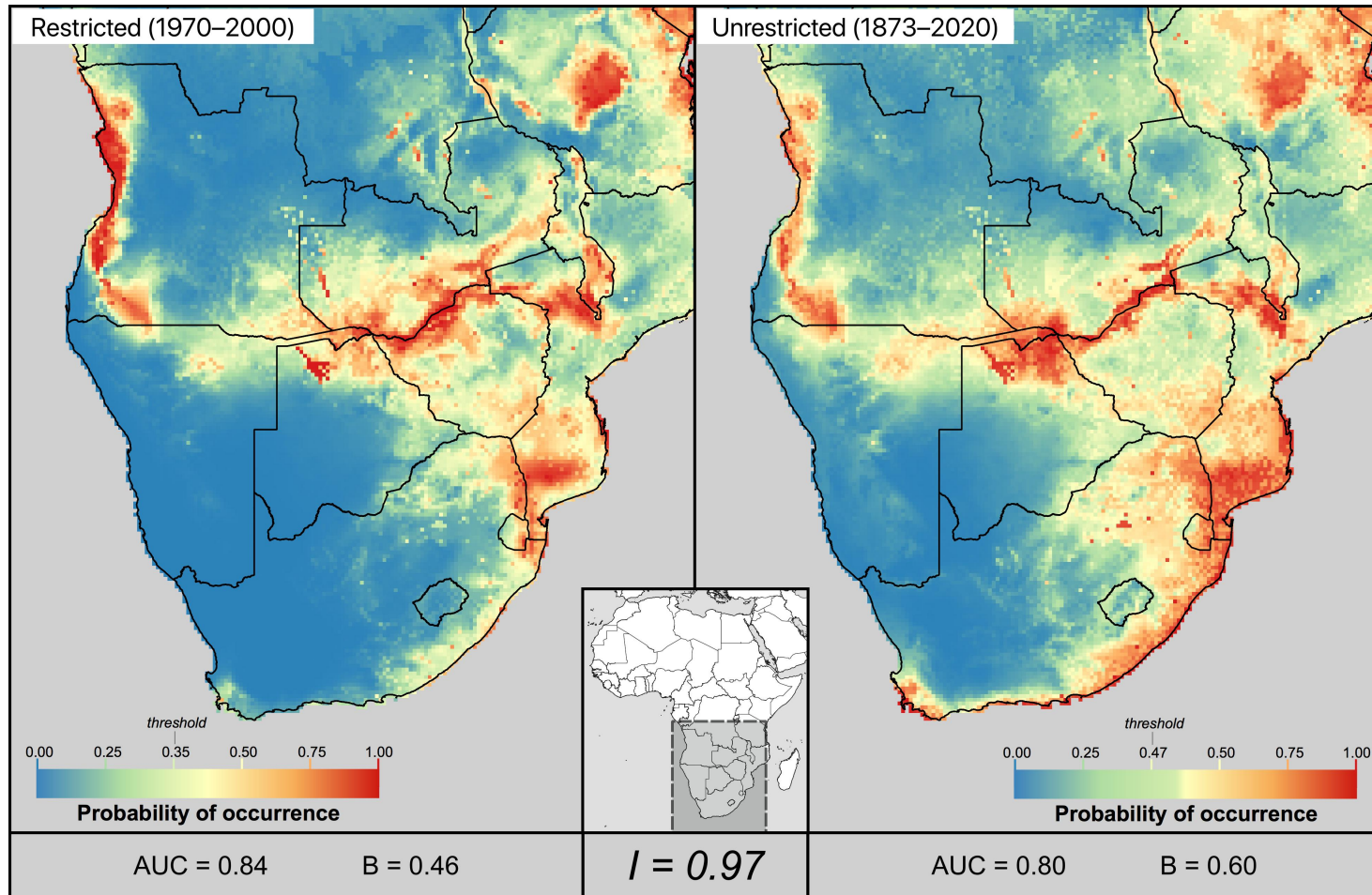
African Openbill



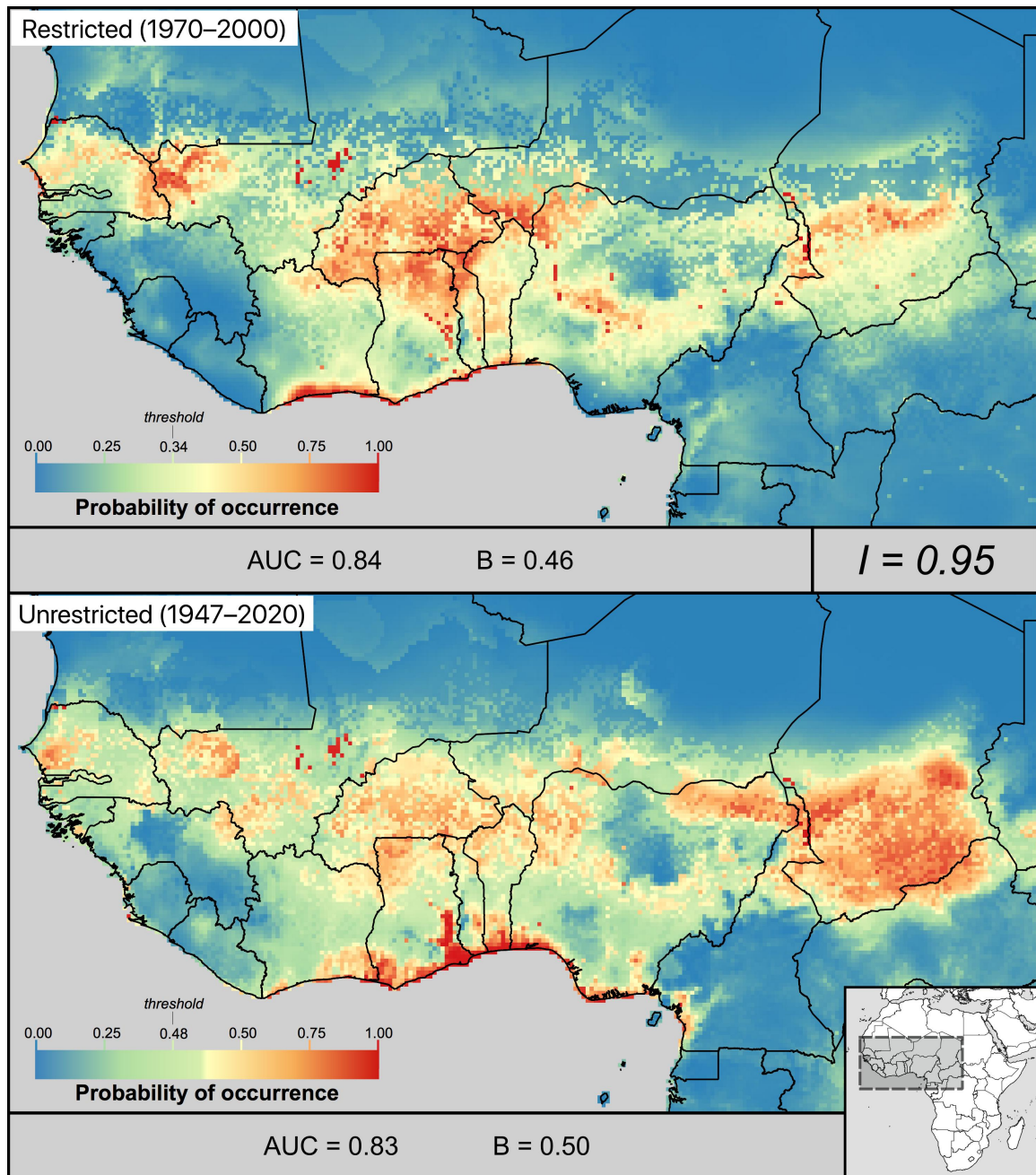
1.10. Average suitability predictions from ten replicates of the African Openbill temporally-restricted and temporally-unrestricted range-wide models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable. Similarity between the approach outputs is measured using I , which is essentially percent overlap in predictions. B is estimated niche breadth.



1.11. Average suitability predictions from ten replicates of the African Openbill temporally-restricted and temporally-unrestricted East African models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable. Similarity between the approach outputs is measured using I , which is essentially percent overlap in predictions. B is estimated niche breadth.

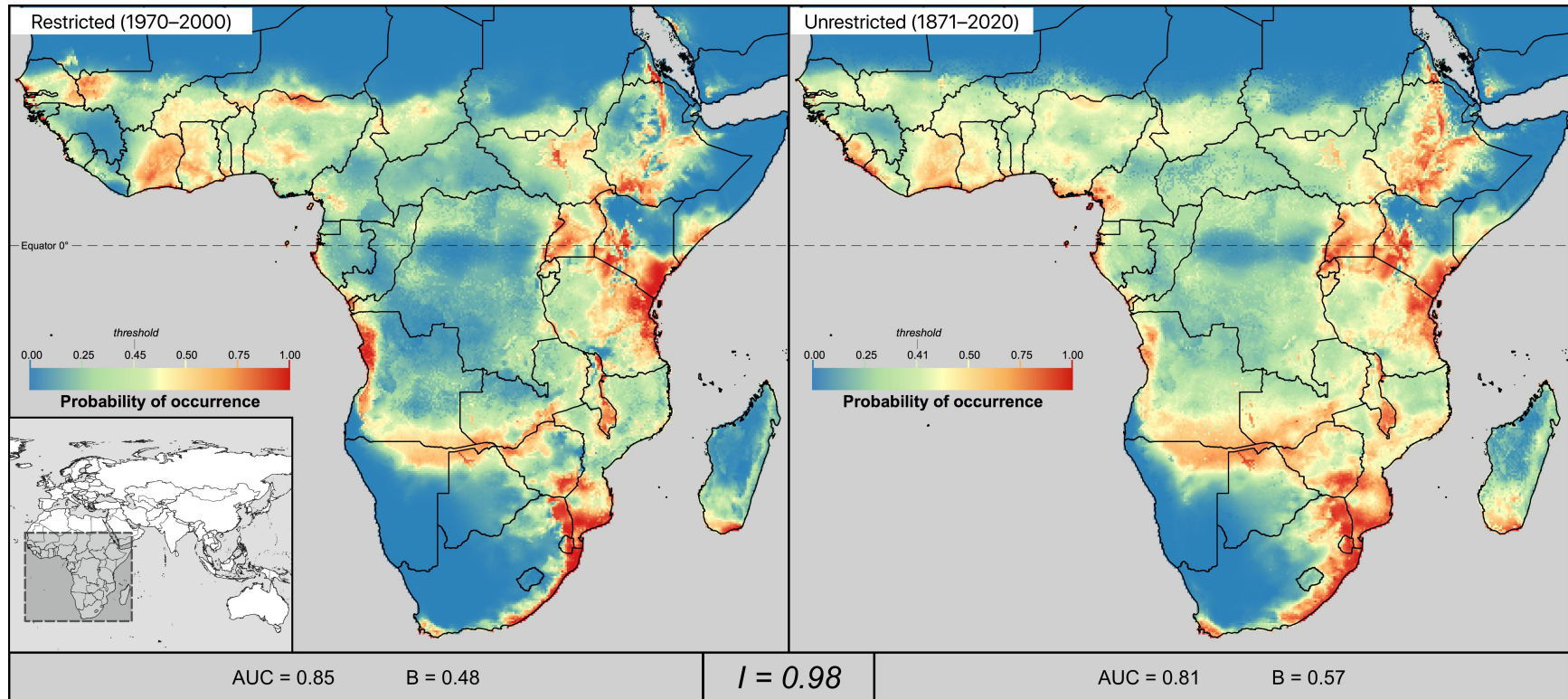


1.12. Average suitability predictions from ten replicates of the African Openbill temporally-restricted and temporally-unrestricted Southern African models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable. Similarity between the approach outputs is measured using I , which is essentially percent overlap in predictions. B is estimated niche breadth.

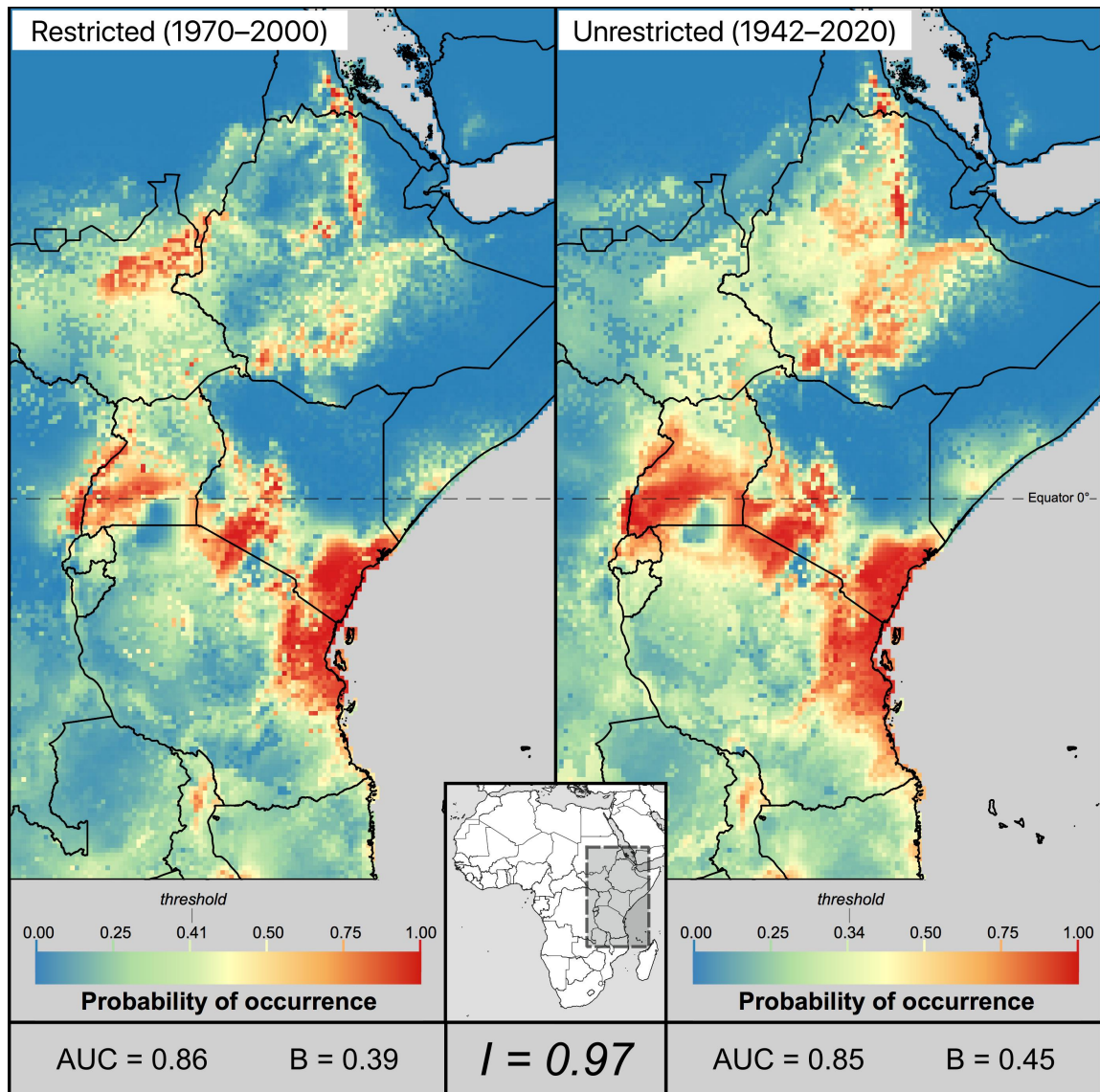


1.13. Average suitability predictions from ten replicates of the African Openbill temporally-restricted and temporally-unrestricted West African models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable. Similarity between the approach outputs is measured using I , which is essentially percent overlap in predictions. B is estimated niche breadth.

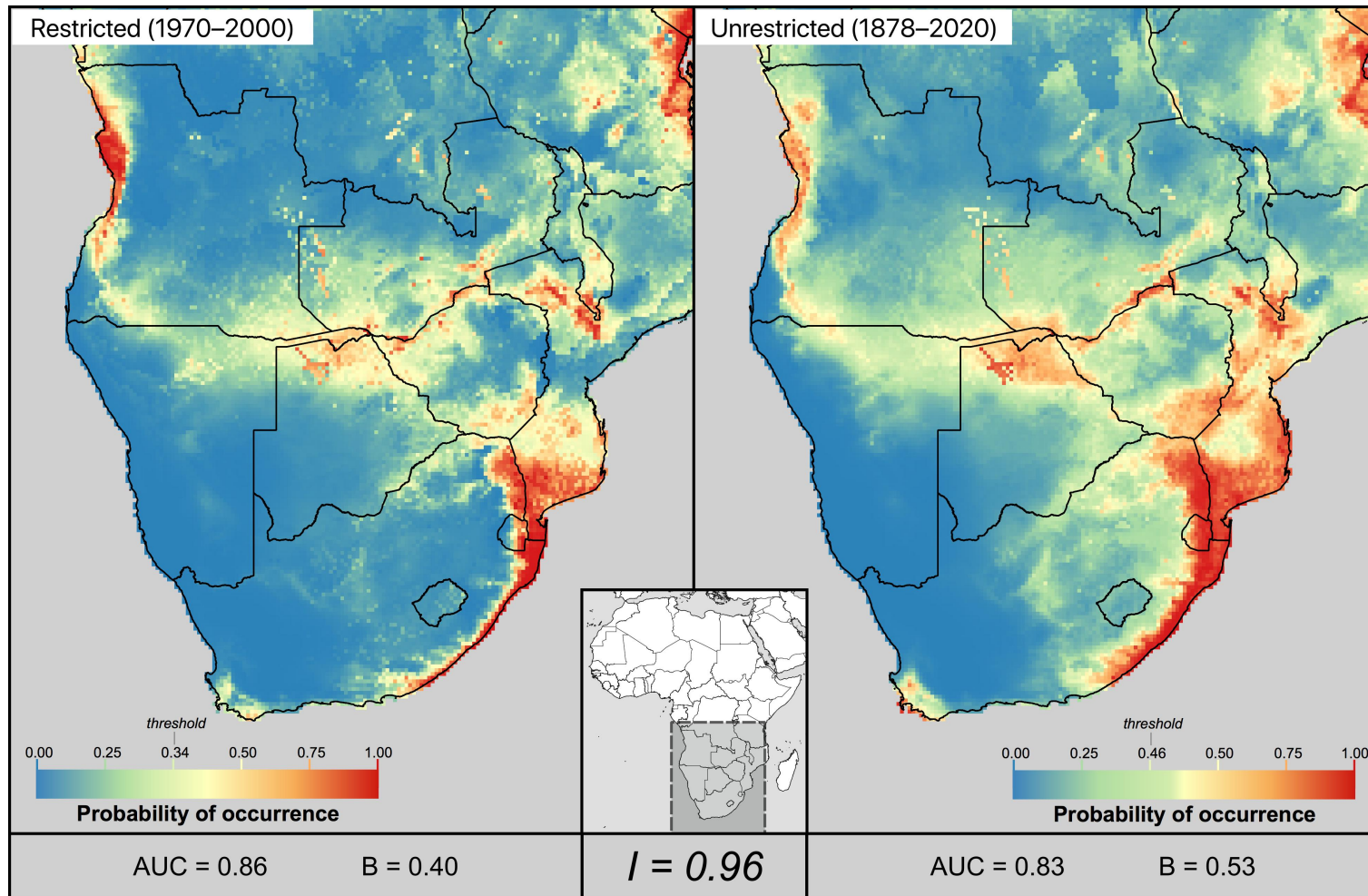
African Woollyneck



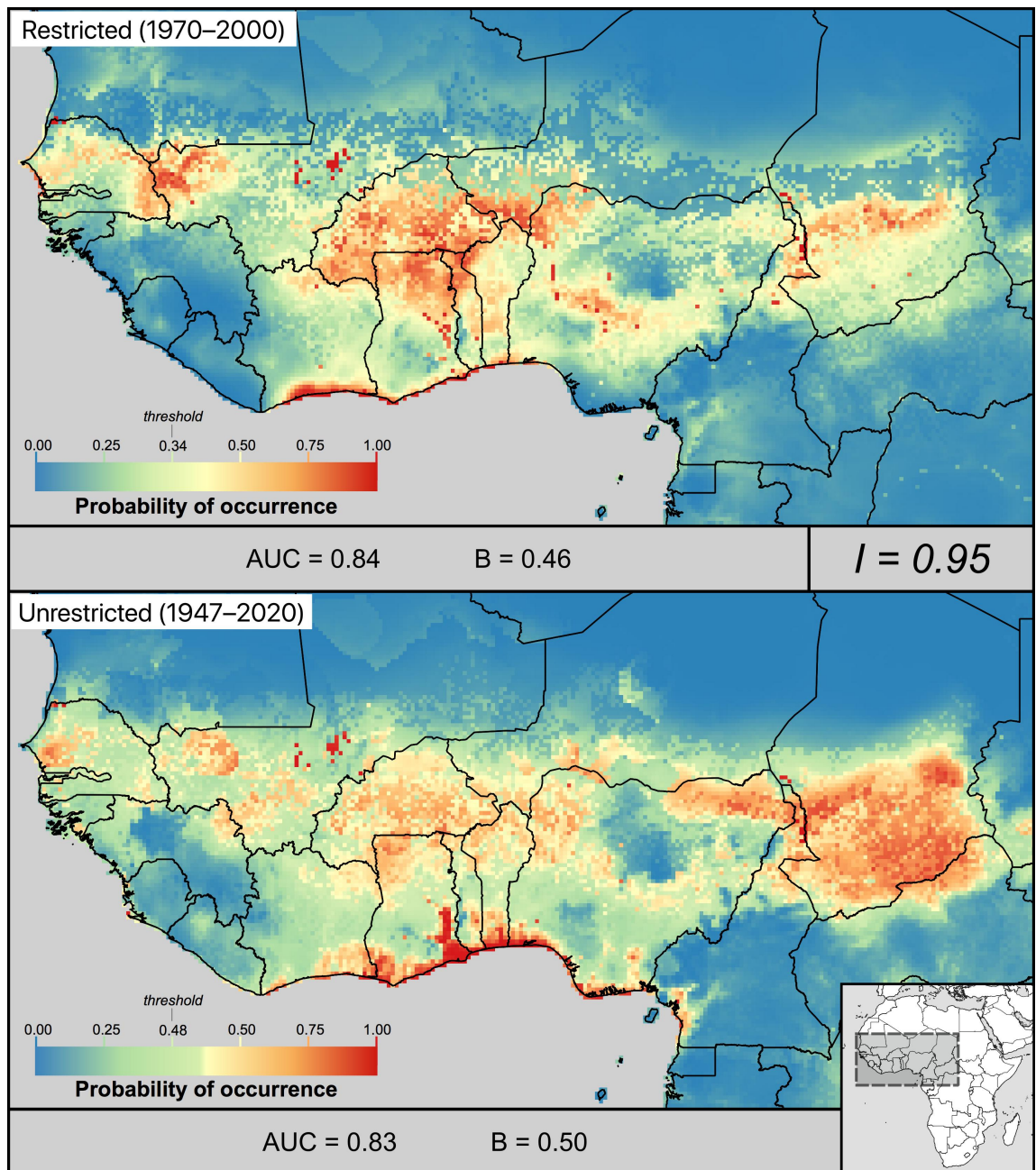
1.14. Average suitability predictions from ten replicates of the African Woollyneck temporally-restricted and temporally-unrestricted range-wide models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable. Similarity between the approach outputs is measured using I , which is essentially percent overlap in predictions. B is estimated niche breadth.



1.15. Average suitability predictions from ten replicates of the African Woollyneck temporally-restricted and temporally-unrestricted East African models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable. Similarity between the approach outputs is measured using I , which is essentially percent overlap in predictions. B is estimated niche breadth.

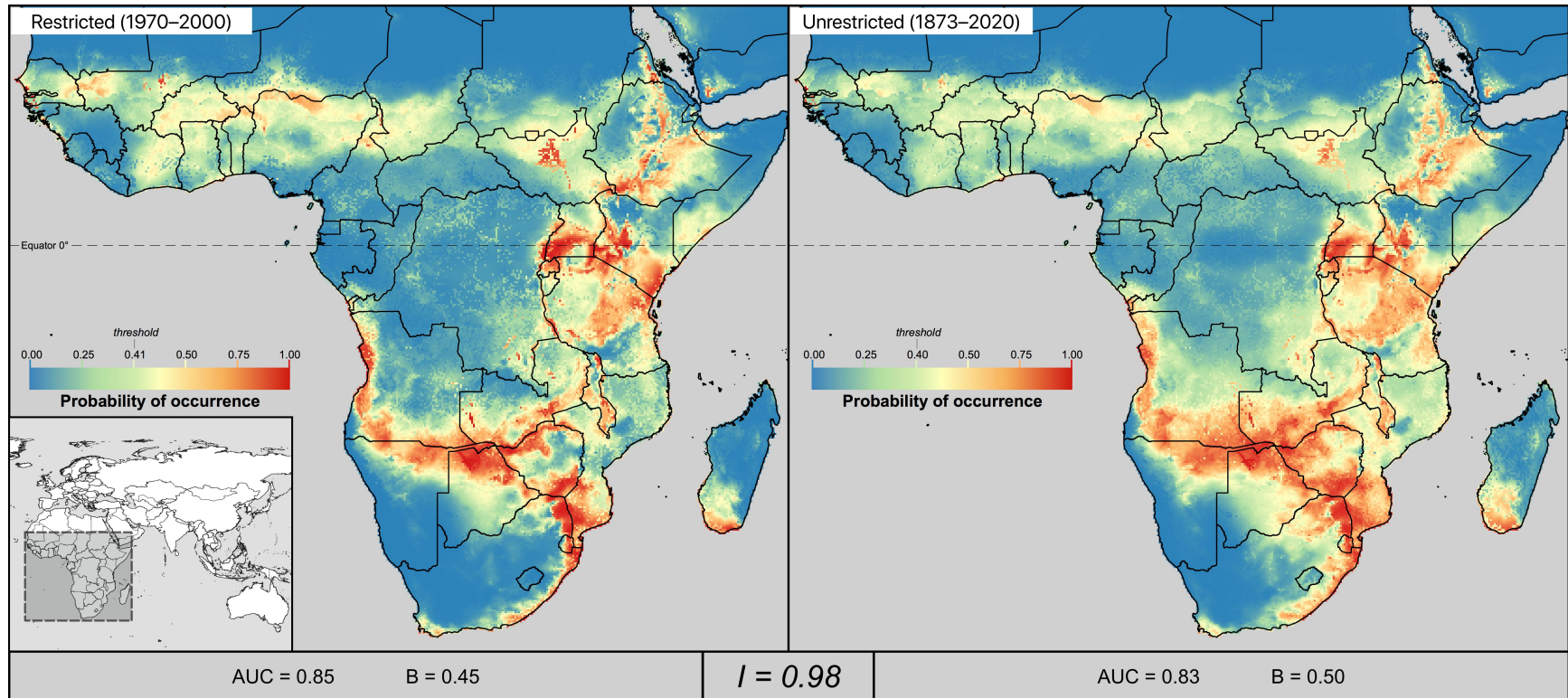


1.16. Average suitability predictions from ten replicates of the African Woollyneck temporally-restricted and temporally-unrestricted Southern African models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable. Similarity between the approach outputs is measured using I , which is essentially percent overlap in predictions. B is estimated niche breadth.

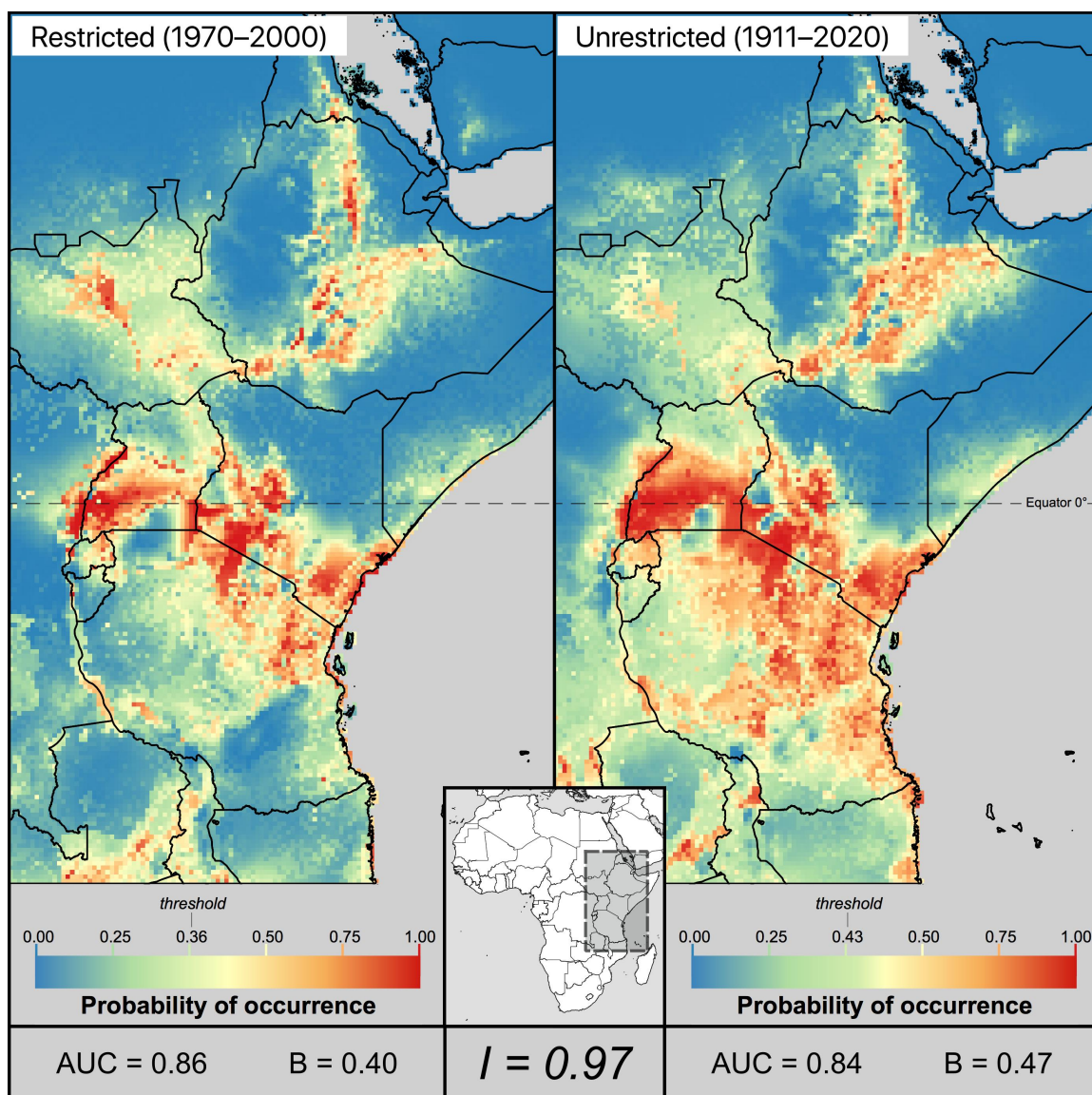


1.17. Average suitability predictions from ten replicates of the African Woollyneck temporally-restricted and temporally-unrestricted West African models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable. Similarity between the approach outputs is measured using I , which is essentially percent overlap in predictions. B is estimated niche breadth.

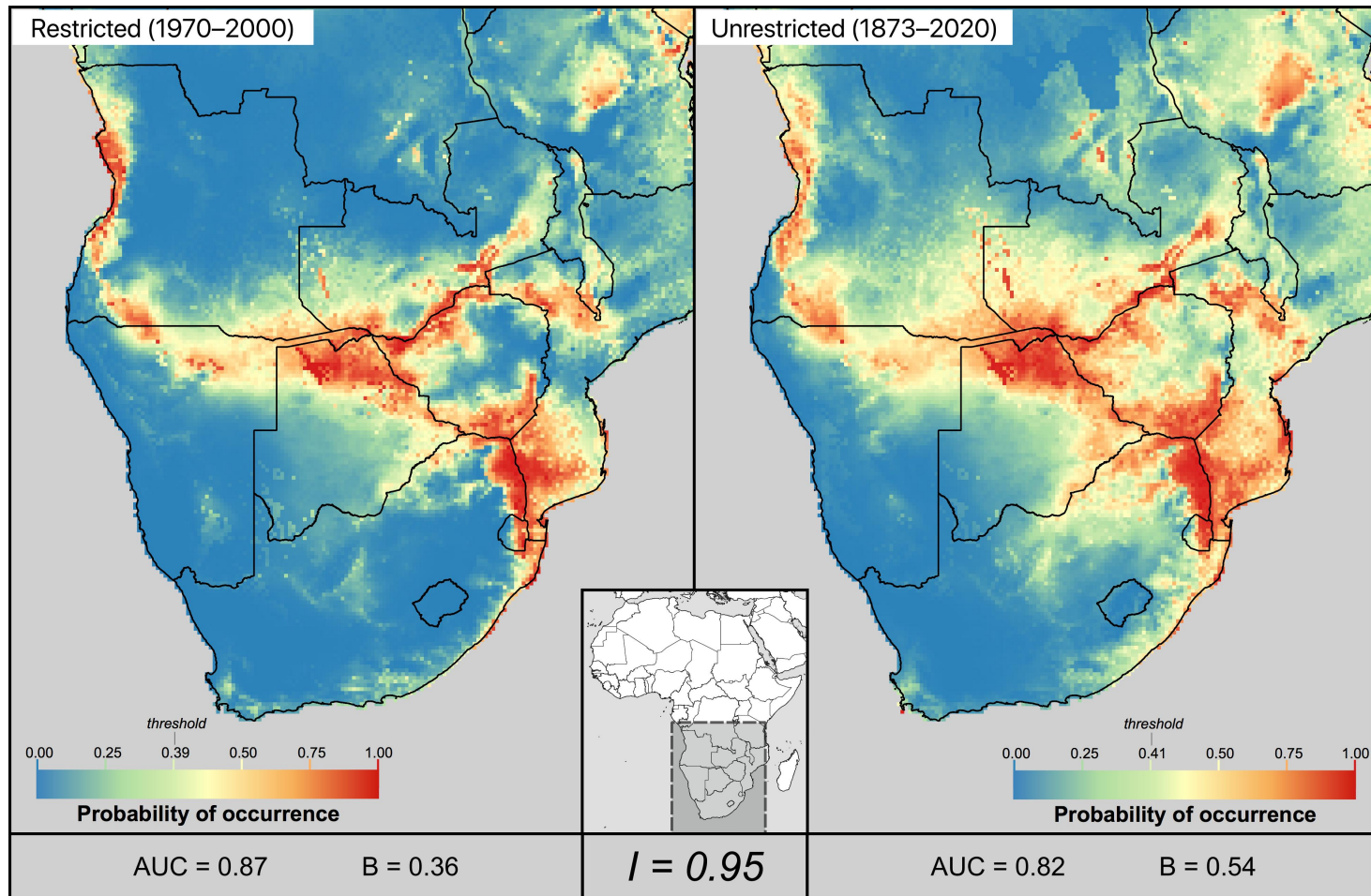
Saddlebill Stork



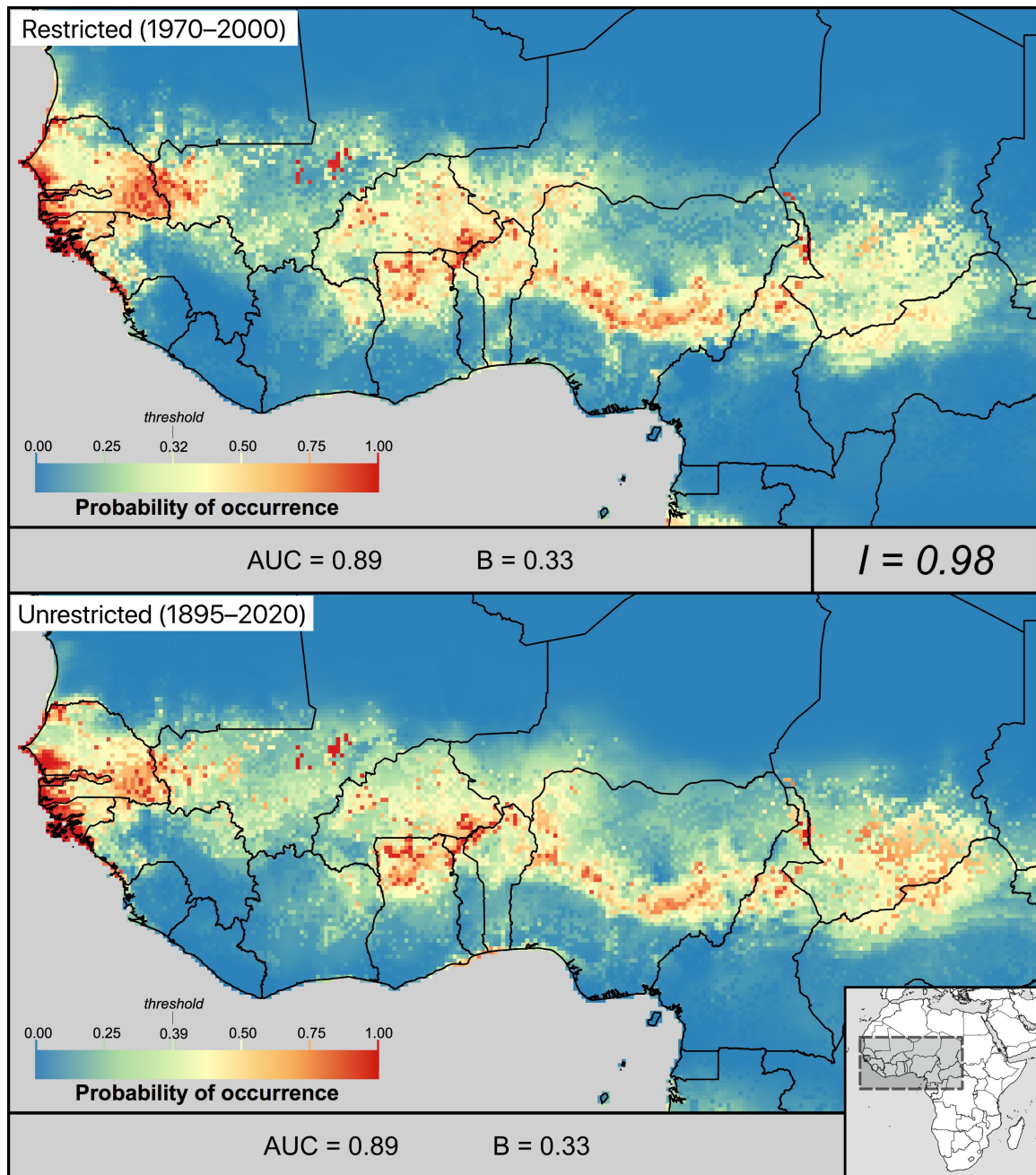
1.18. Average suitability predictions from ten replicates of the Saddlebill Stork temporally-restricted and temporally-unrestricted range-wide models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable. Similarity between the approach outputs is measured using I , which is essentially percent overlap in predictions. B is estimated niche breadth.



1.19. Average suitability predictions from ten replicates of the Saddlebill Stork temporally-restricted and temporally-unrestricted East African models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable. Similarity between the approach outputs is measured using I , which is essentially percent overlap in predictions. B is estimated niche breadth.

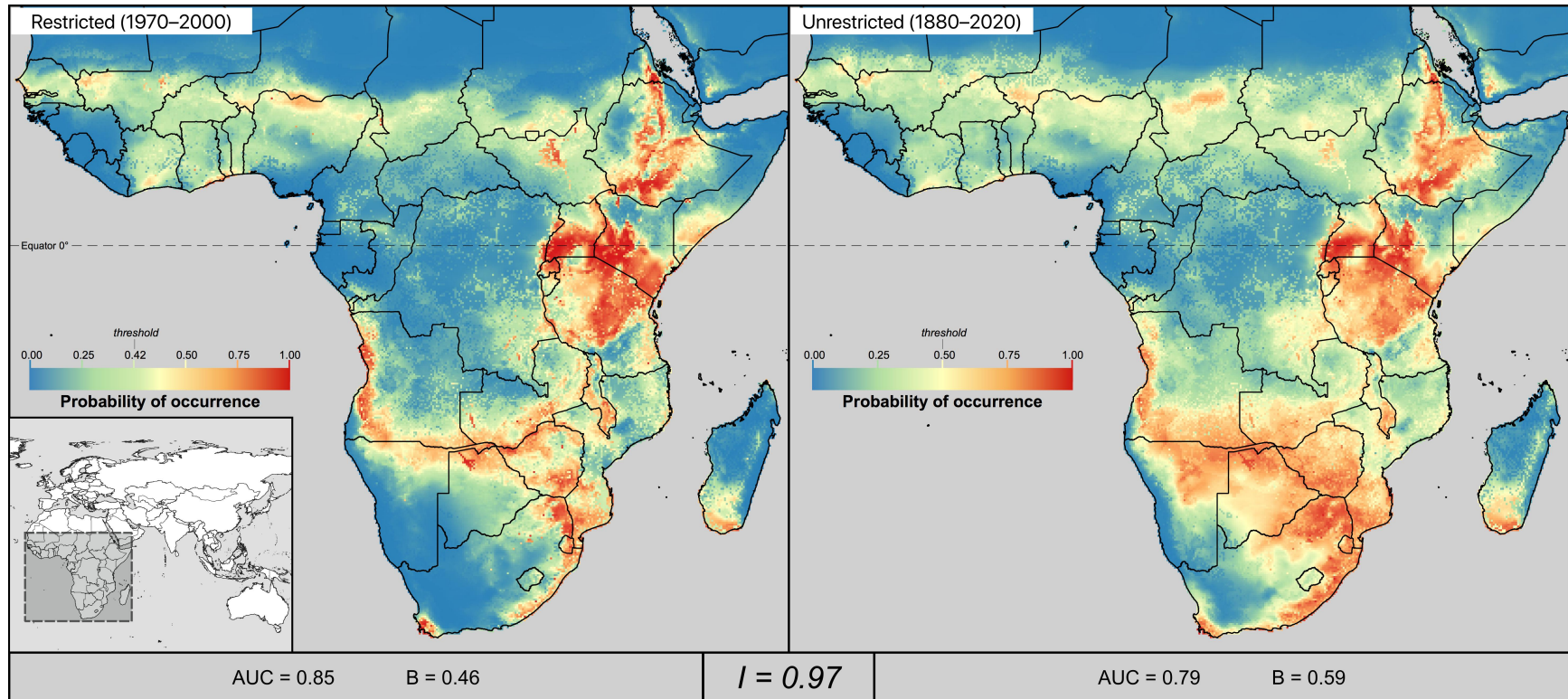


1.20. Average suitability predictions from ten replicates of the Saddlebill Stork temporally-restricted and temporally-unrestricted Southern African models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable. Similarity between the approach outputs is measured using I , which is essentially percent overlap in predictions. B is estimated niche breadth.

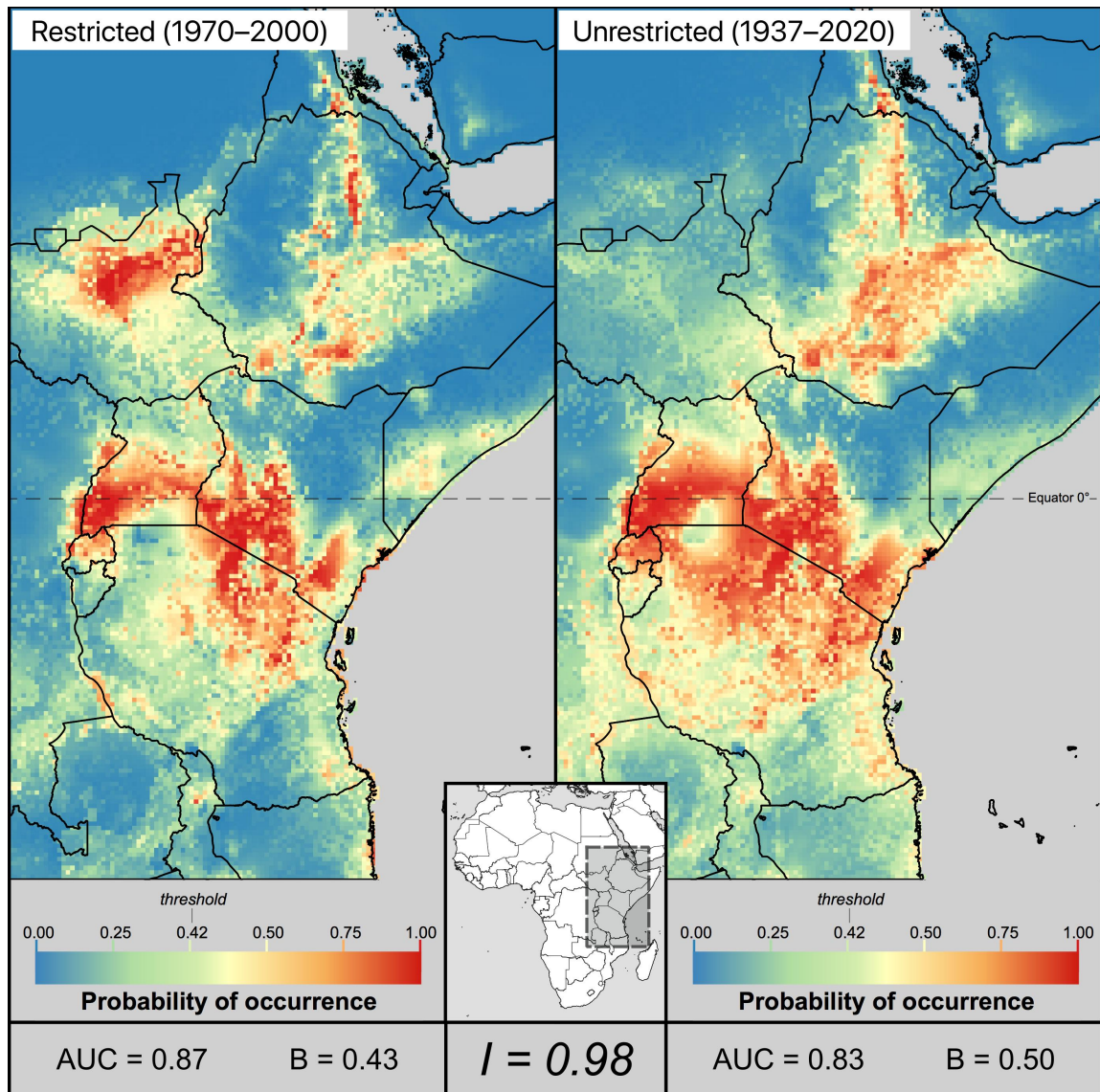


1.21. Average suitability predictions from ten replicates of the Saddlebill Stork temporally-restricted and temporally-unrestricted West African models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable. Similarity between the approach outputs is measured using I , which is essentially percent overlap in predictions. B is estimated niche breadth.

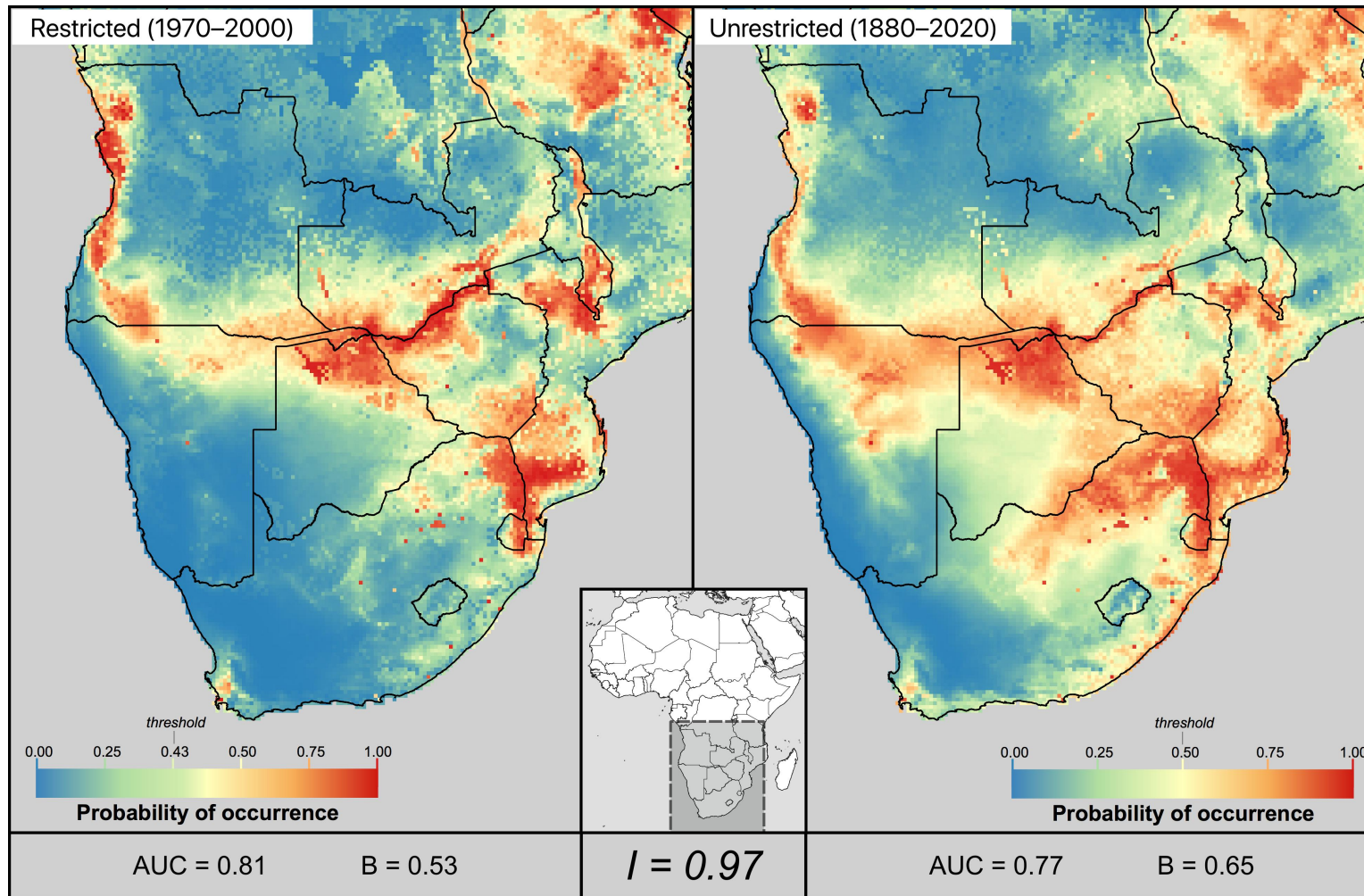
Marabou Stork



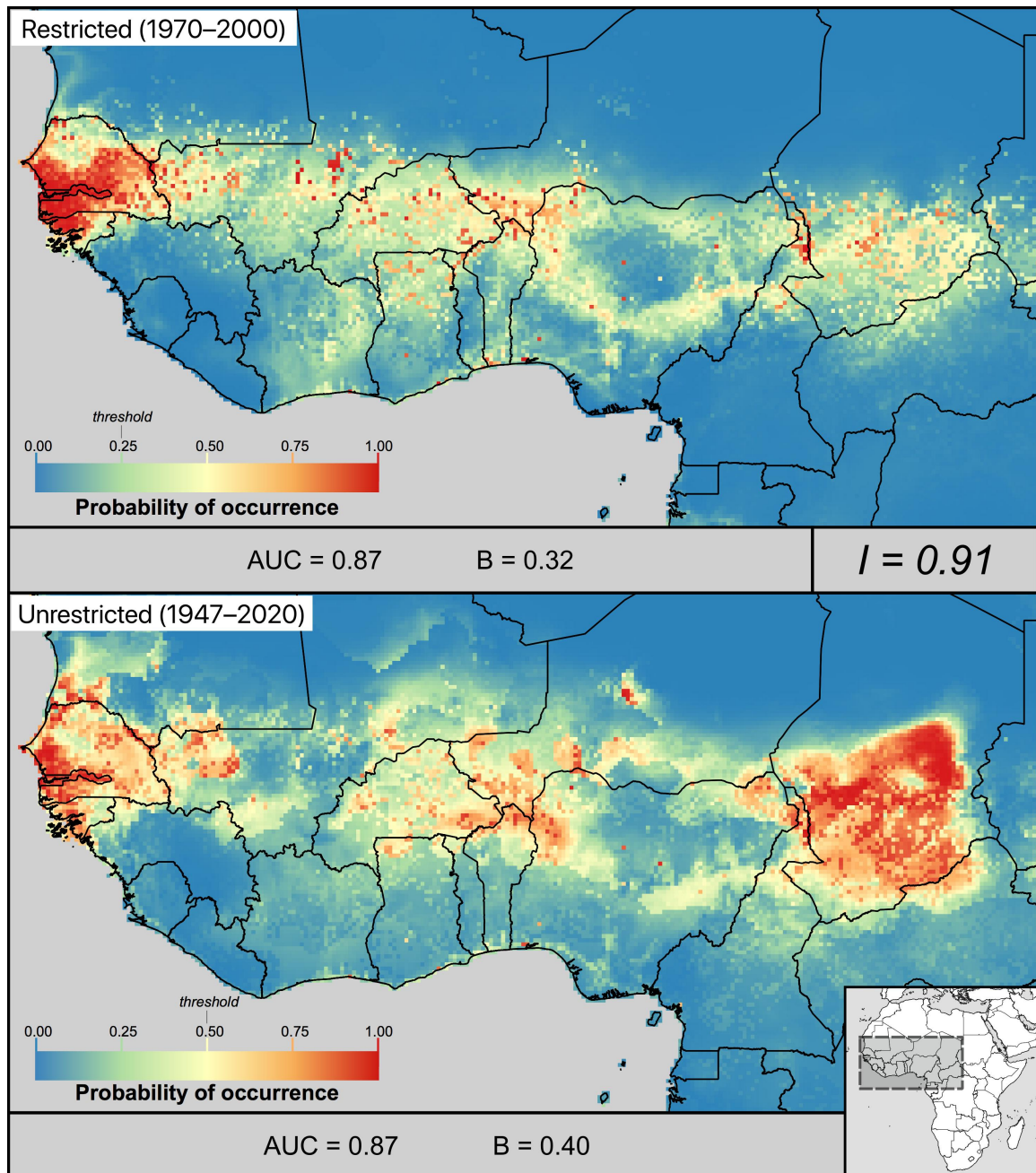
1.22. Average suitability predictions from ten replicates of the Marabou Stork temporally-restricted and temporally-unrestricted range-wide models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable. Similarity between the approach outputs is measured using I , which is essentially percent overlap in predictions. B is estimated niche breadth.



1.23. Average suitability predictions from ten replicates of the Marabou Stork temporally-restricted and temporally-unrestricted East African models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable. Similarity between the approach outputs is measured using I , which is essentially percent overlap in predictions. B is estimated niche breadth.

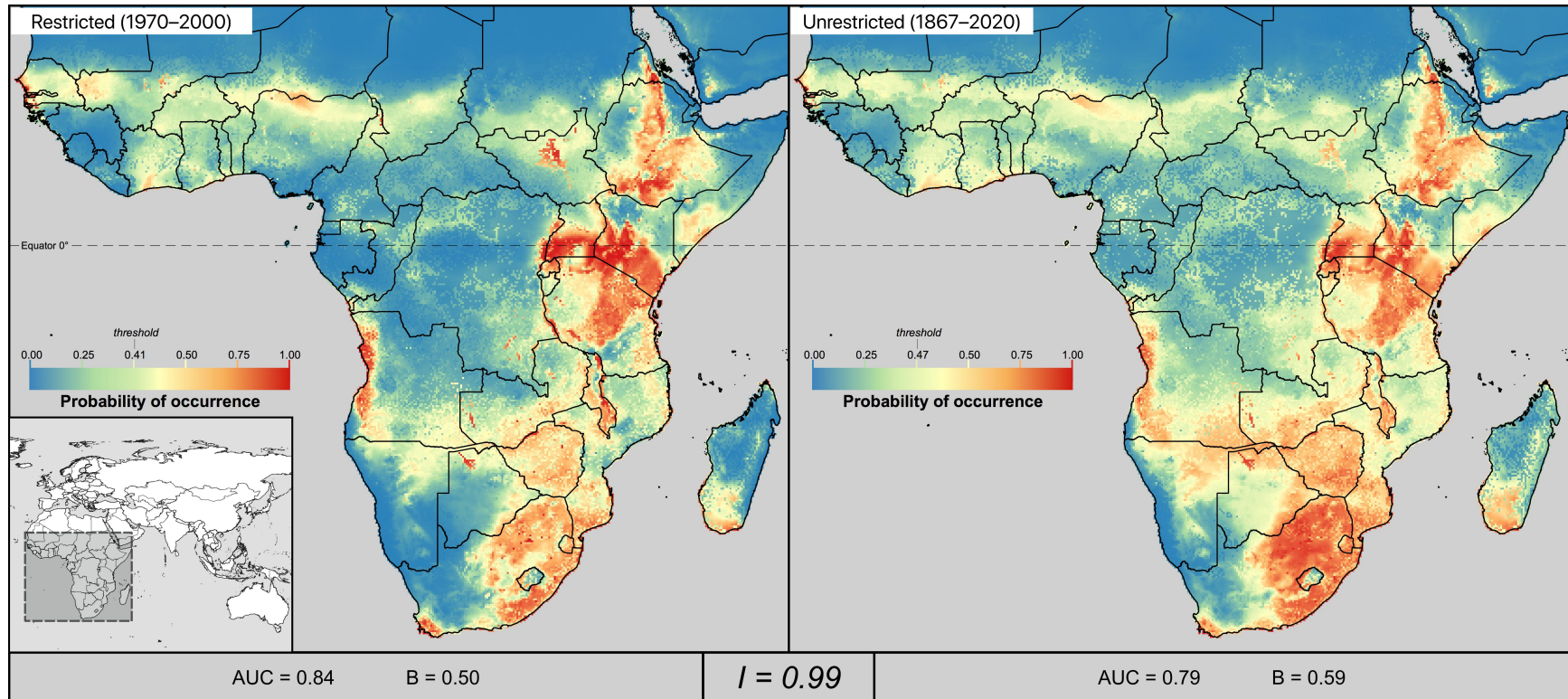


1.24. Average suitability predictions from ten replicates of the Marabou Stork temporally-restricted and temporally-unrestricted Southern African models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable. Similarity between the approach outputs is measured using I , which is essentially percent overlap in predictions. B is estimated niche breadth.

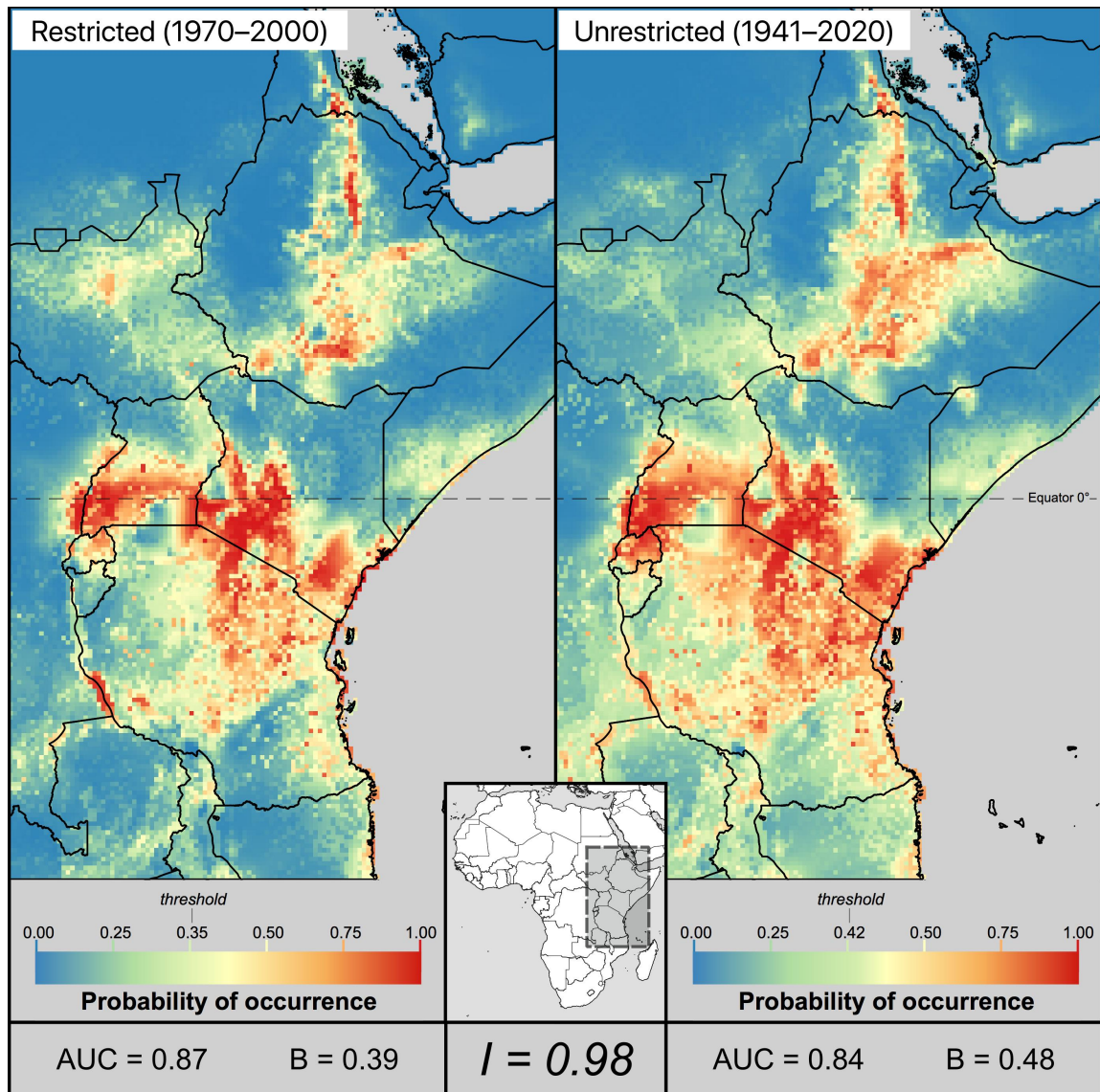


1.25. Average suitability predictions from ten replicates of the Marabou Stork temporally-restricted and temporally-unrestricted West African models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable. Similarity between the approach outputs is measured using I , which is essentially percent overlap in predictions. B is estimated niche breadth.

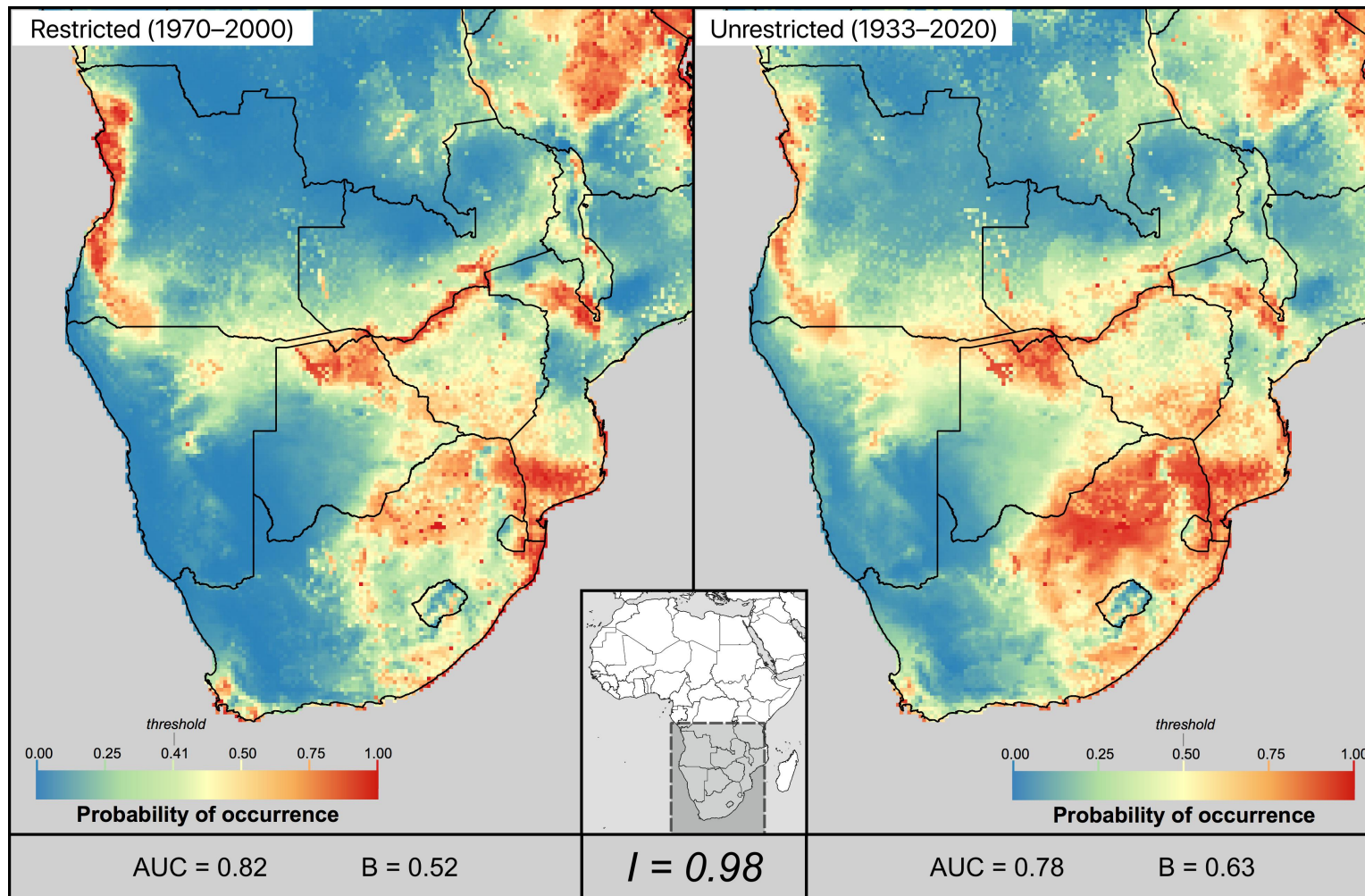
Yellow-billed Stork



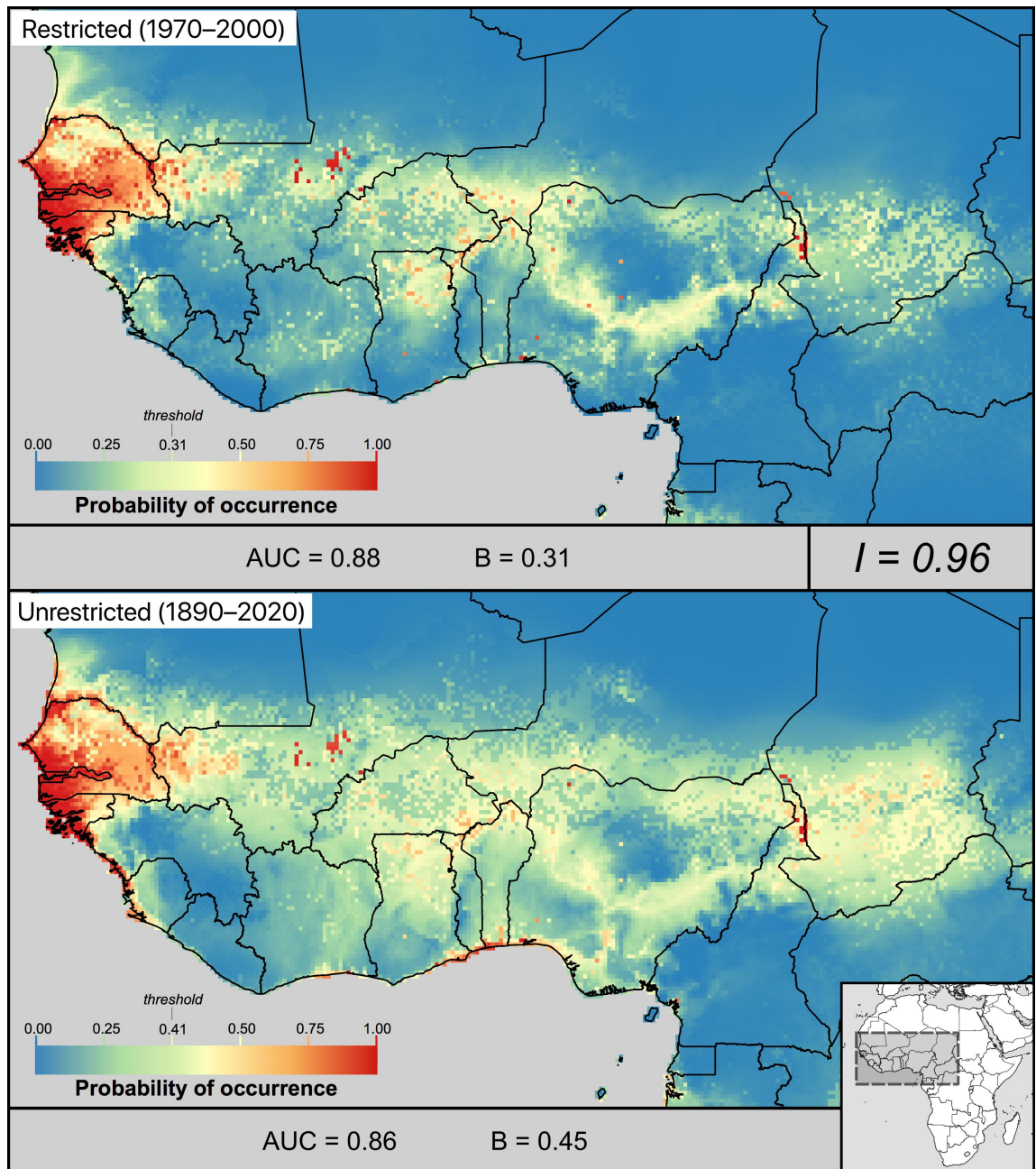
1.26. Average suitability predictions from ten replicates of the Yellow-billed Stork temporally-restricted and temporally-unrestricted range-wide models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable. Similarity between the approach outputs is measured using I , which is essentially percent overlap in predictions. B is estimated niche breadth.



1.27. Average suitability predictions from ten replicates of the Yellow-billed Stork temporally-restricted and temporally-unrestricted East African models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable. Similarity between the approach outputs is measured using I , which is essentially percent overlap in predictions. B is estimated niche breadth.



1.28. Average suitability predictions from ten replicates of the Yellow-billed Stork temporally-restricted and temporally-unrestricted Southern African models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable. Similarity between the approach outputs is measured using I , which is essentially percent overlap in predictions. B is estimated niche breadth.

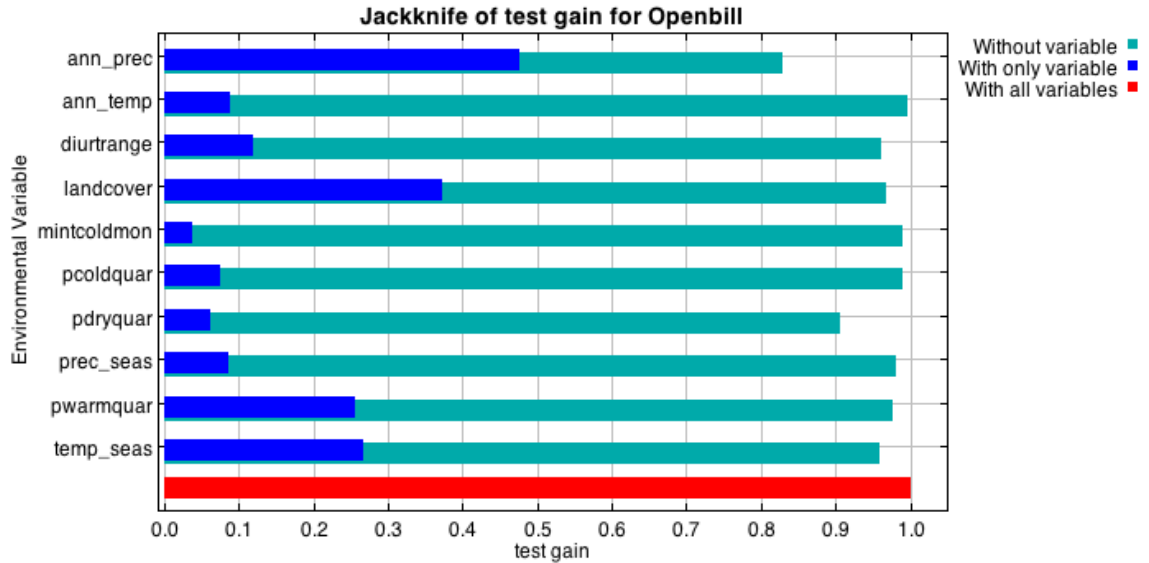


1.29. Average suitability predictions from ten replicates of the Yellow-billed Stork temporally-restricted and temporally-unrestricted West African models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable. Similarity between the approach outputs is measured using I , which is essentially percent overlap in predictions. B is estimated niche breadth.

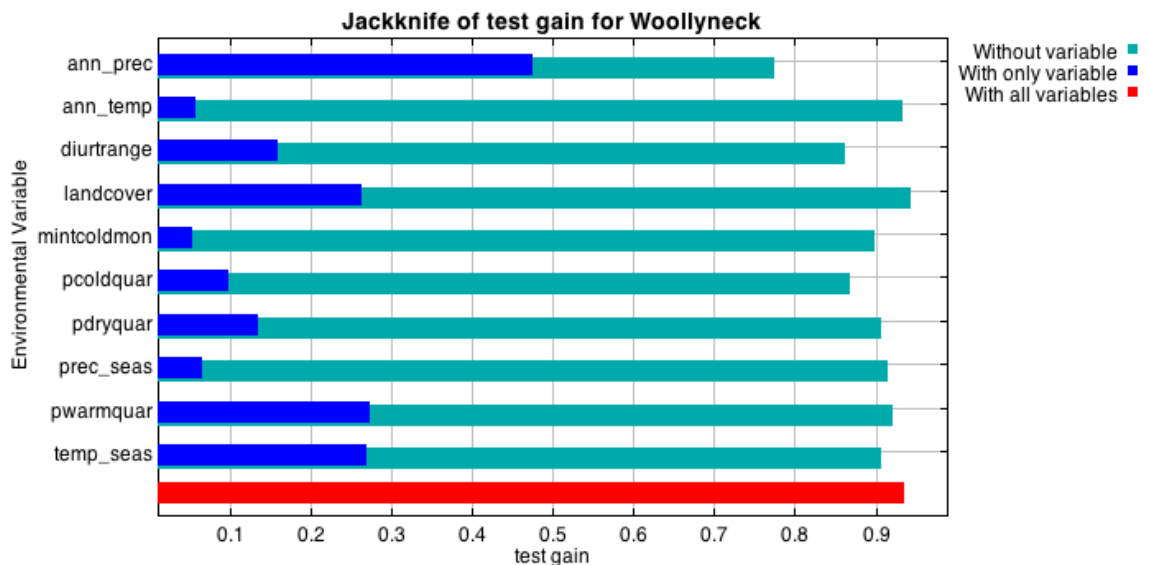
Appendix 2

Jackknife tests of test gain results

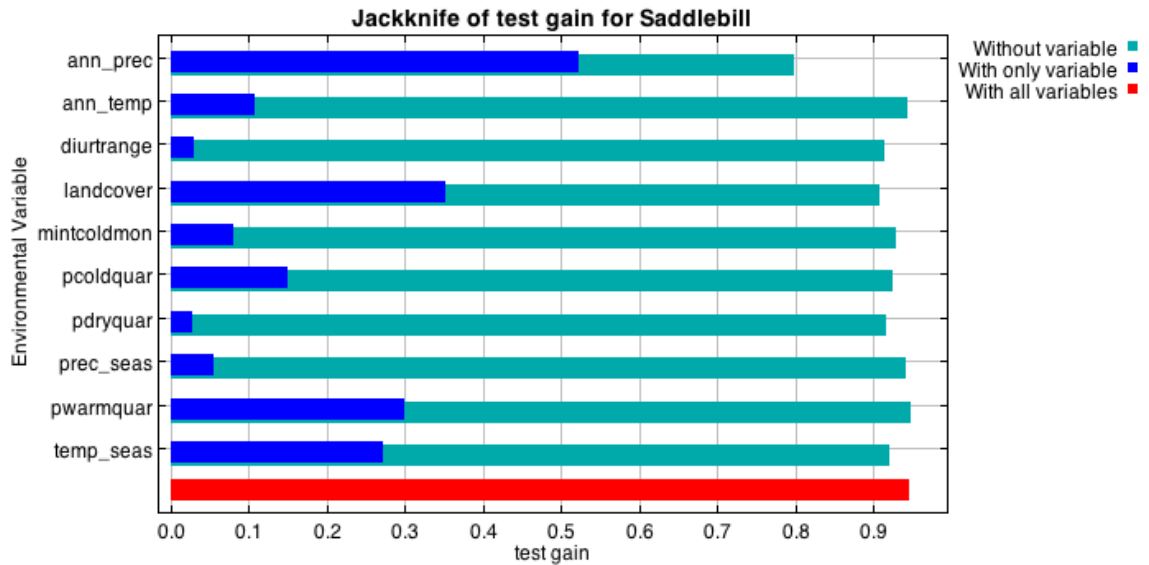
Range-wide models



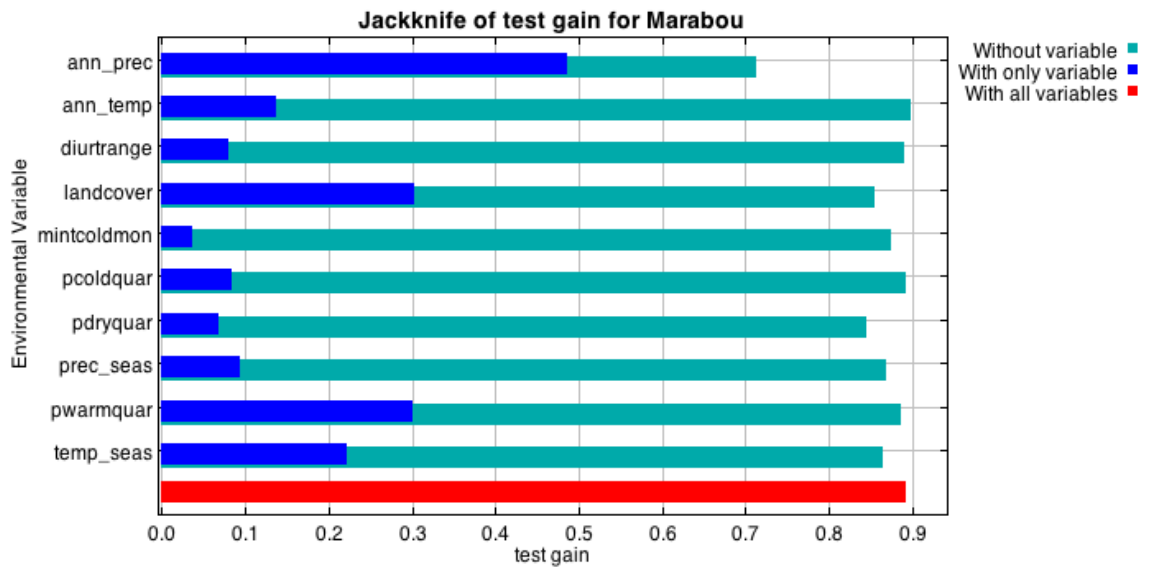
2.1. Jackknife test results for the range-wide African Openbill model. Variables with higher importance have greater test gain when used in a model on their own (blue).



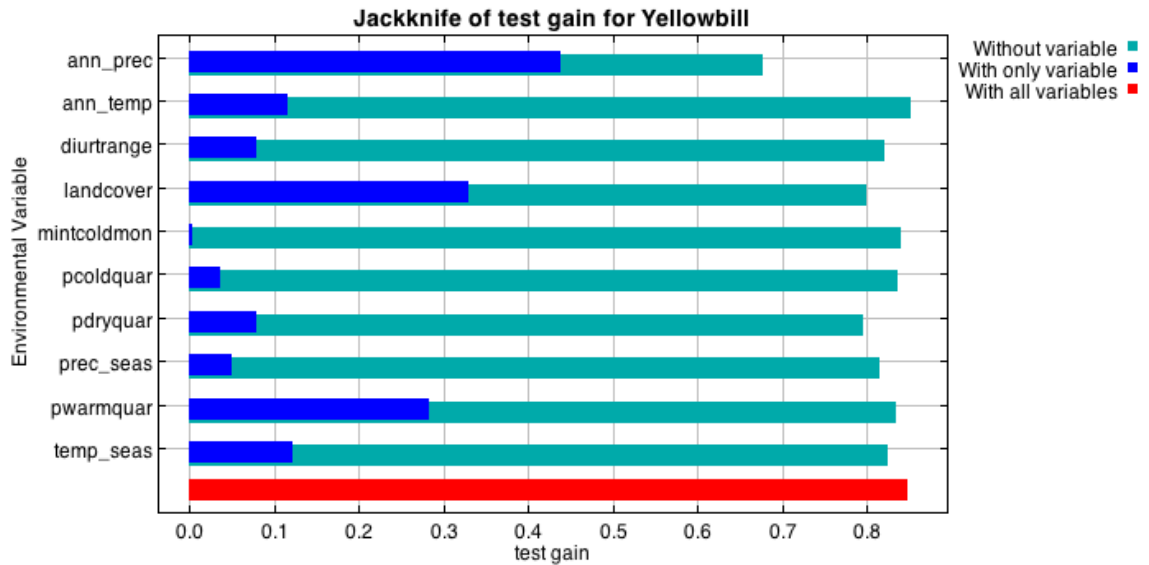
2.2. Jackknife test results for the range-wide African Woollyneck model. Variables with higher importance have greater test gain when used in a model on their own (blue).



2.3. Jackknife test results for the range-wide Saddlebill Stork model. Variables with higher importance have greater test gain when used in a model on their own (blue).

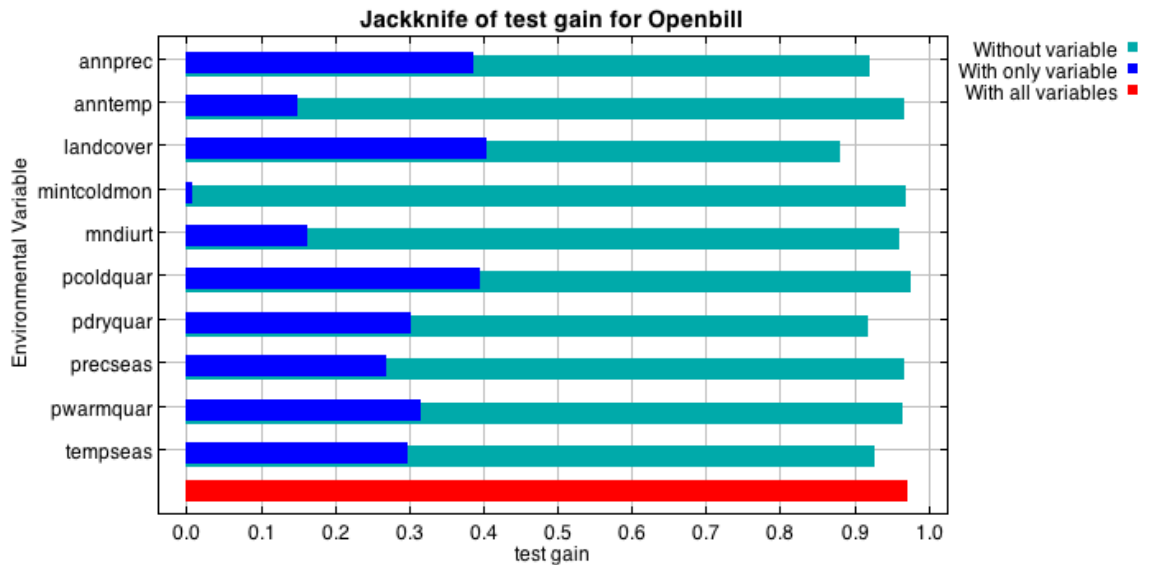


2.4. Jackknife test results for the range-wide Marabou Stork model. Variables with higher importance have greater test gain when used in a model on their own (blue).

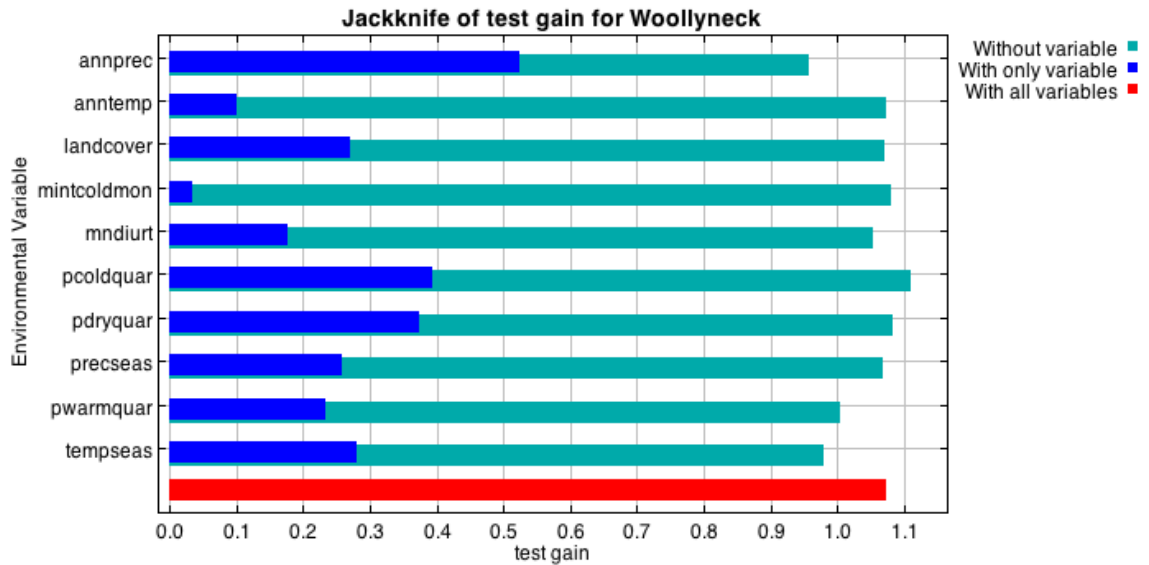


2.5. Jackknife test results for the range-wide Yellow-billed Stork model. Variables with higher importance have greater test gain when used in a model on their own (blue).

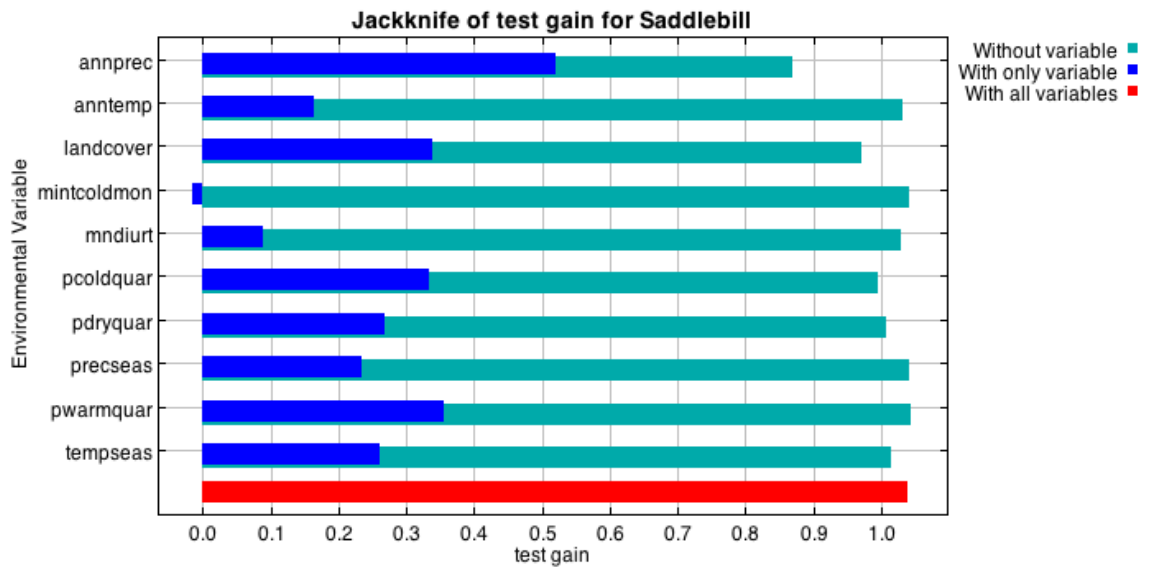
East African models



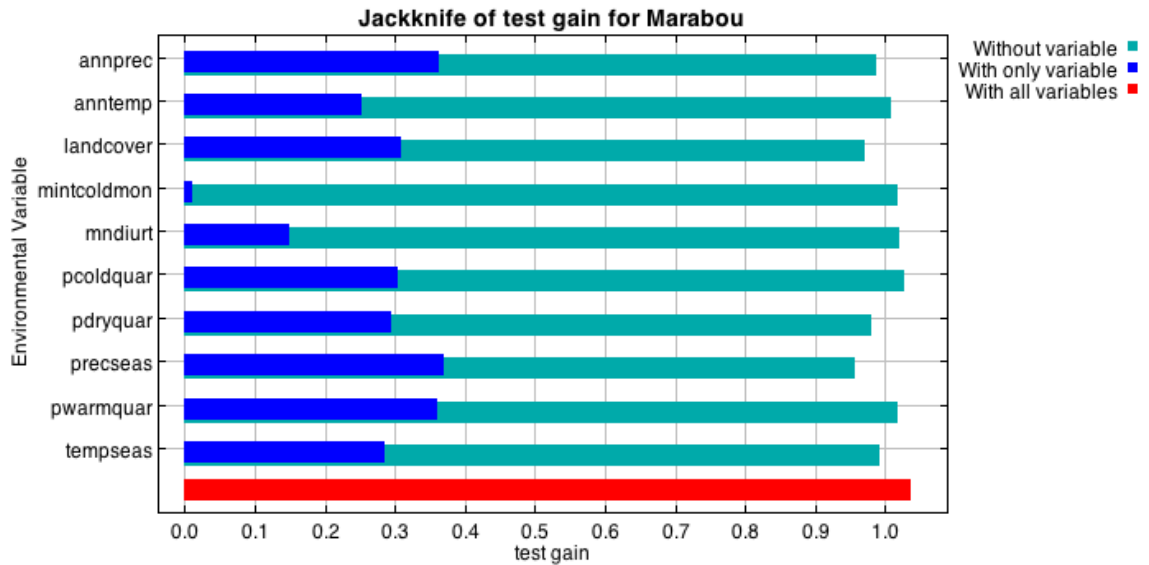
2.6. Jackknife test results for the African Openbill model in East Africa. Variables with higher importance have greater test gain when used in a model on their own (blue).



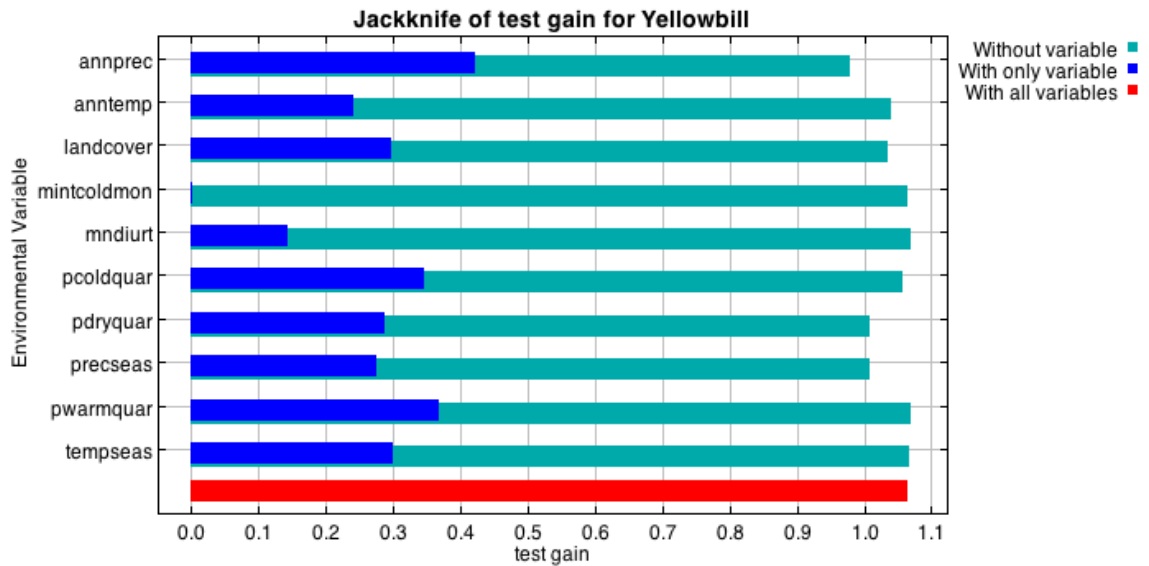
2.7. Jackknife test results for the African Woollyneck model in East Africa. Variables with higher importance have greater test gain when used in a model on their own (blue).



2.8. Jackknife test results for the Saddlebill Stork model in East Africa. Variables with higher importance have greater test gain when used in a model on their own (blue).

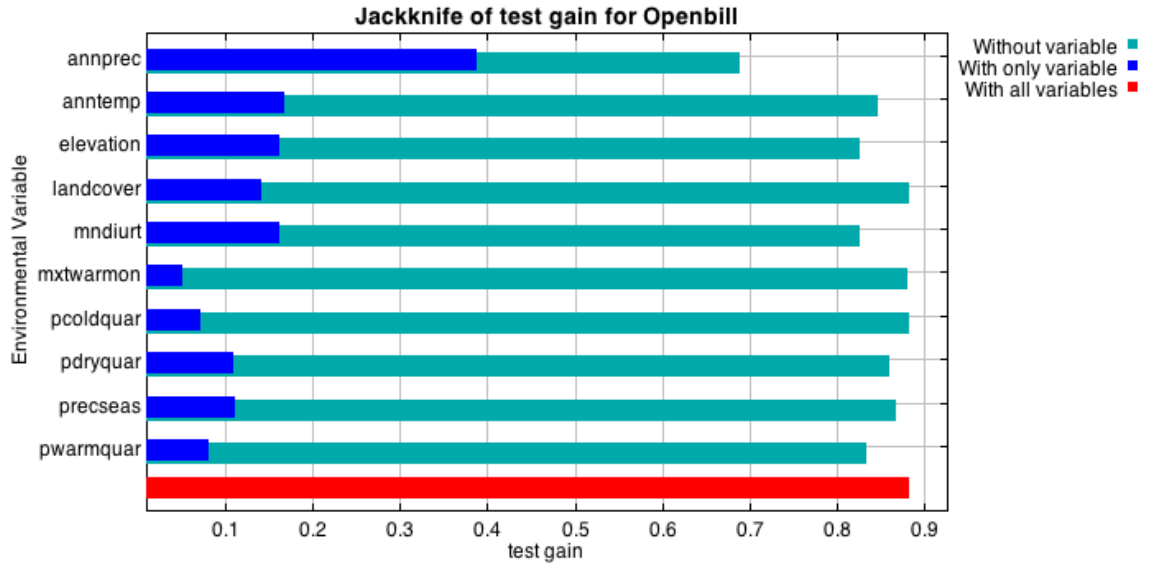


2.9. Jackknife test results for the Marabou Stork model in East Africa. Variables with higher importance have greater test gain when used in a model on their own (blue).

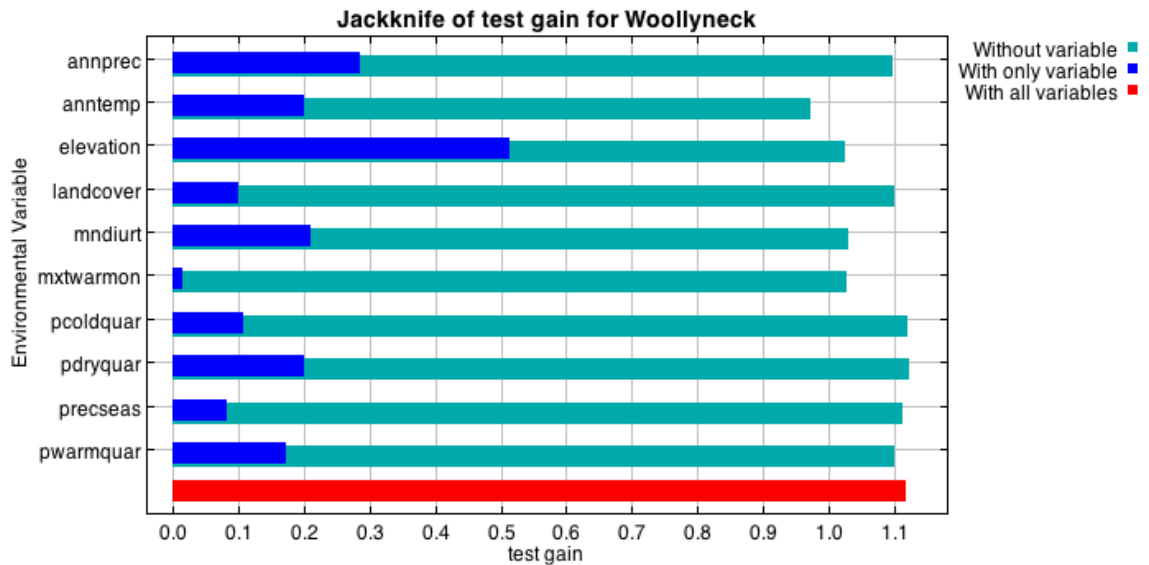


2.10. Jackknife test results for the Yellow-billed Stork model in East Africa. Variables with higher importance have greater test gain when used in a model on their own (blue).

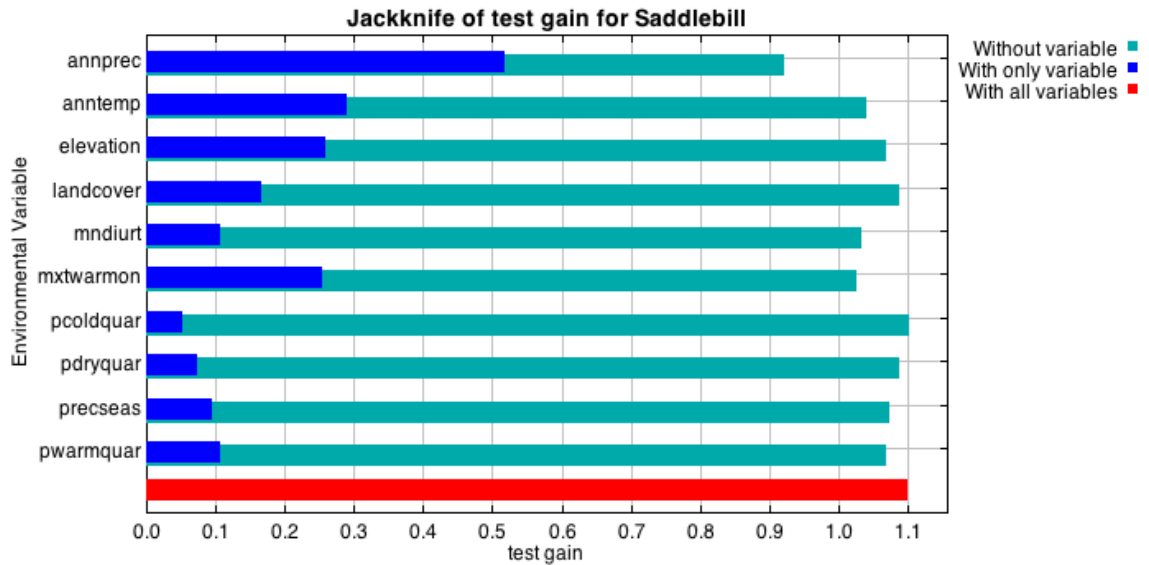
Southern African models



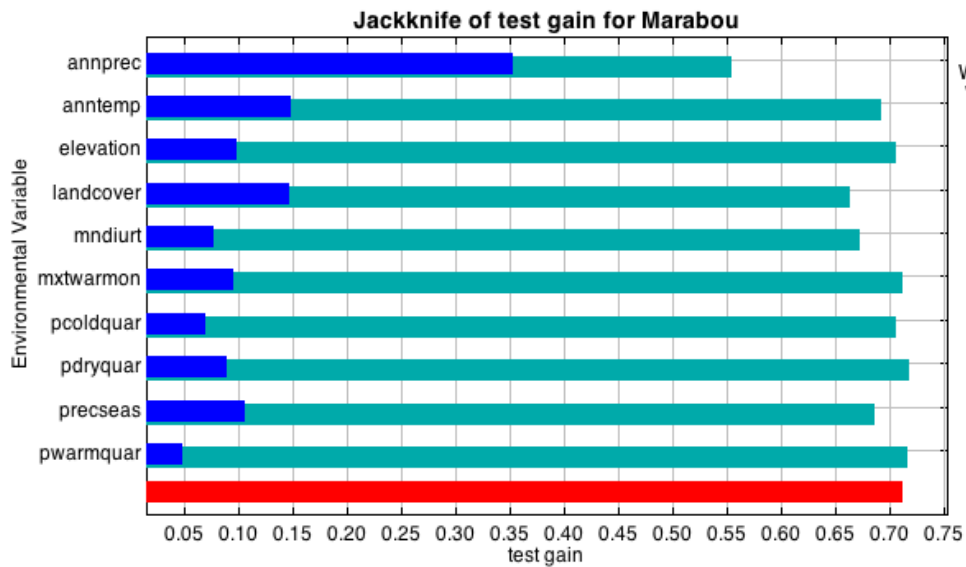
2.11. Jackknife test results for the African Openbill model in Southern Africa. Variables with higher importance have greater test gain when used in a model on their own (blue).



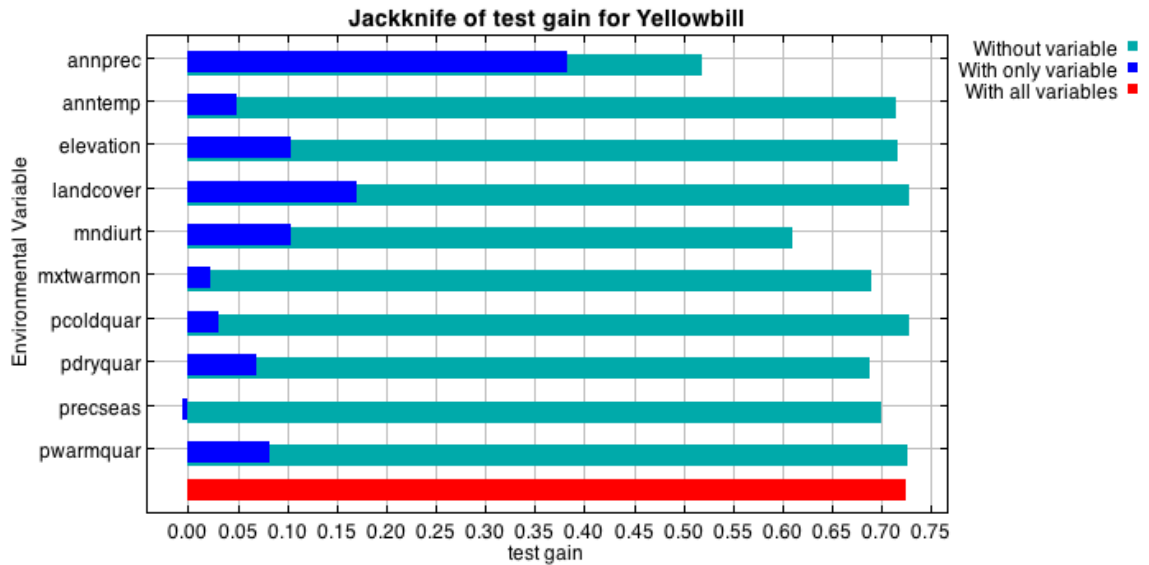
2.12. Jackknife test results for the African Woollyneck model in Southern Africa. Variables with higher importance have greater test gain when used in a model on their own (blue).



2.13. Jackknife test results for the Saddlebill Stork model in Southern Africa. Variables with higher importance have greater test gain when used in a model on their own (blue).

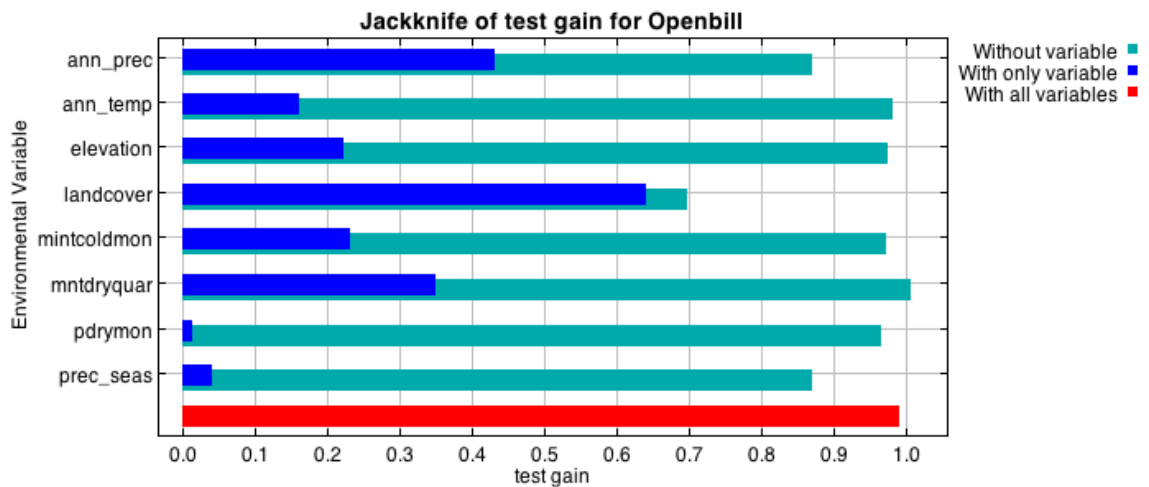


2.14. Jackknife test results for the Marabou Stork model in Southern Africa. Variables with higher importance have greater test gain when used in a model on their own (blue).

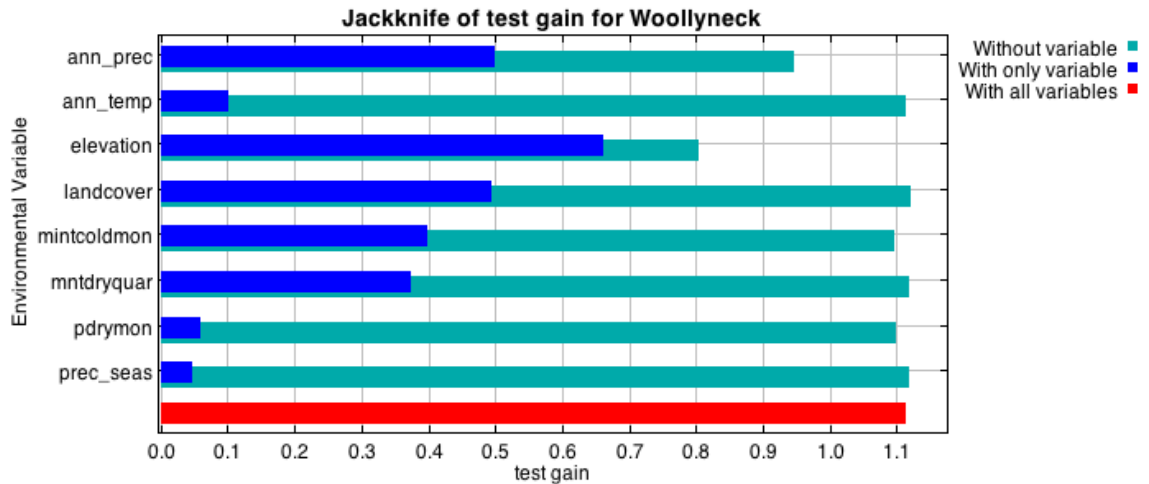


2.15. Jackknife test results for the Yellow-billed Stork model in Southern Africa. Variables with higher importance have greater test gain when used in a model on their own (blue).

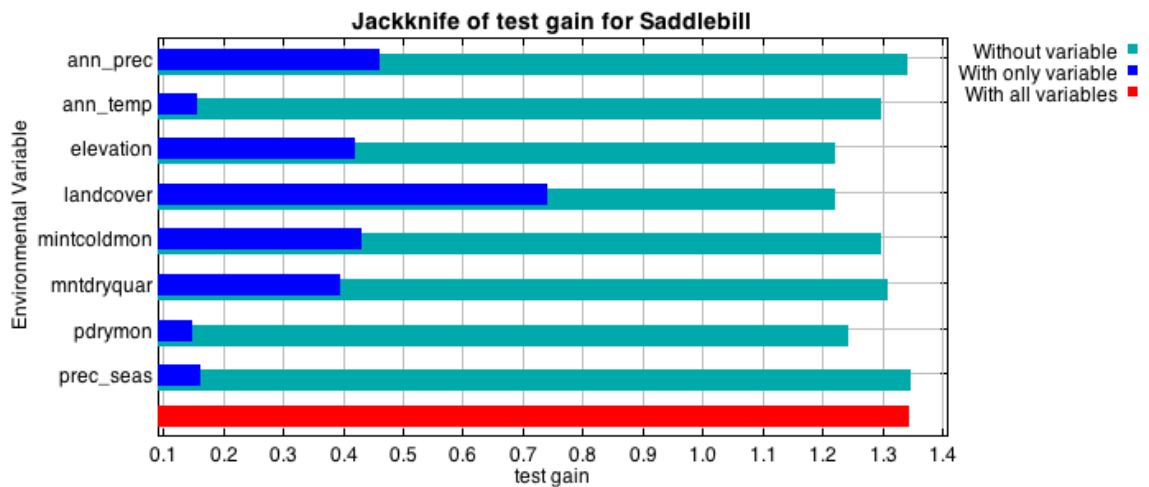
West African models



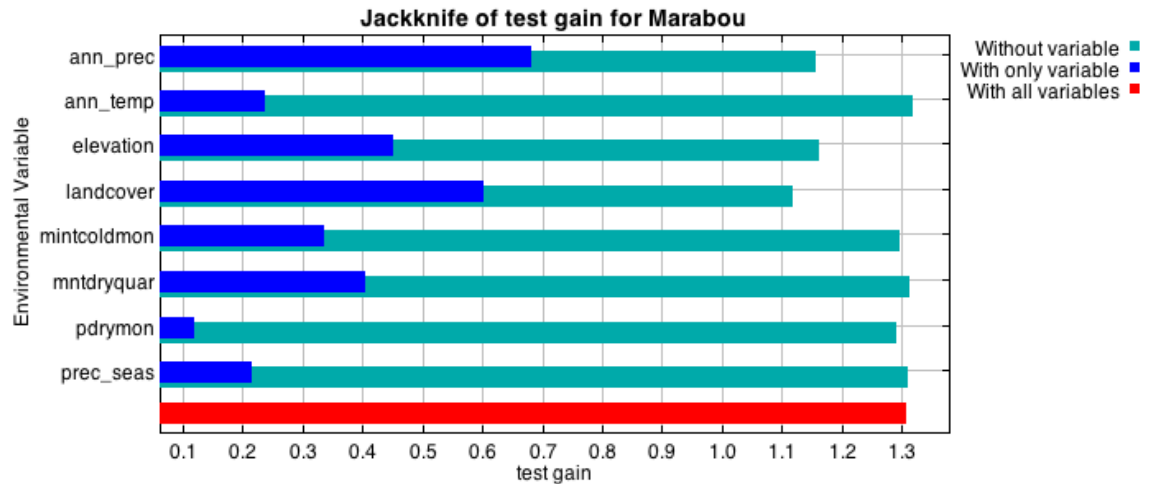
2.16. Jackknife test results for the African Openbill model in West Africa. Variables with higher importance have greater test gain when used in a model on their own (blue).



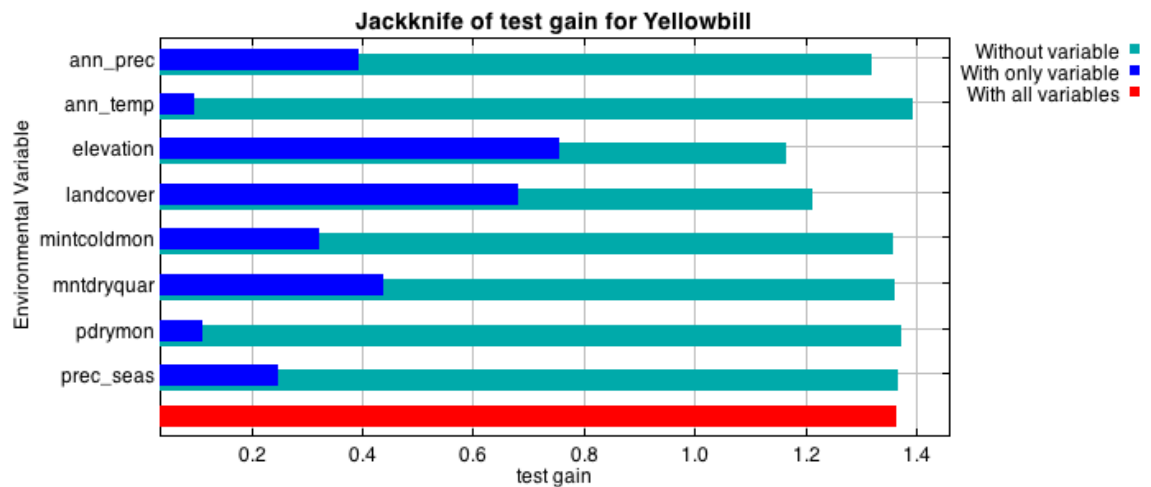
2.17. Jackknife test results for the African Woollyneck model in West Africa. Variables with higher importance have greater test gain when used in a model on their own (blue).



2.18. Jackknife test results for the Saddlebill Stork model in West Africa. Variables with higher importance have greater test gain when used in a model on their own (blue).



2.19. Jackknife test results for the Marabou Stork model in West Africa. Variables with higher importance have greater test gain when used in a model on their own (blue).



2.20. Jackknife test results for the Yellow-billed Stork model in West Africa. Variables with higher importance have greater test gain when used in a model on their own (blue).

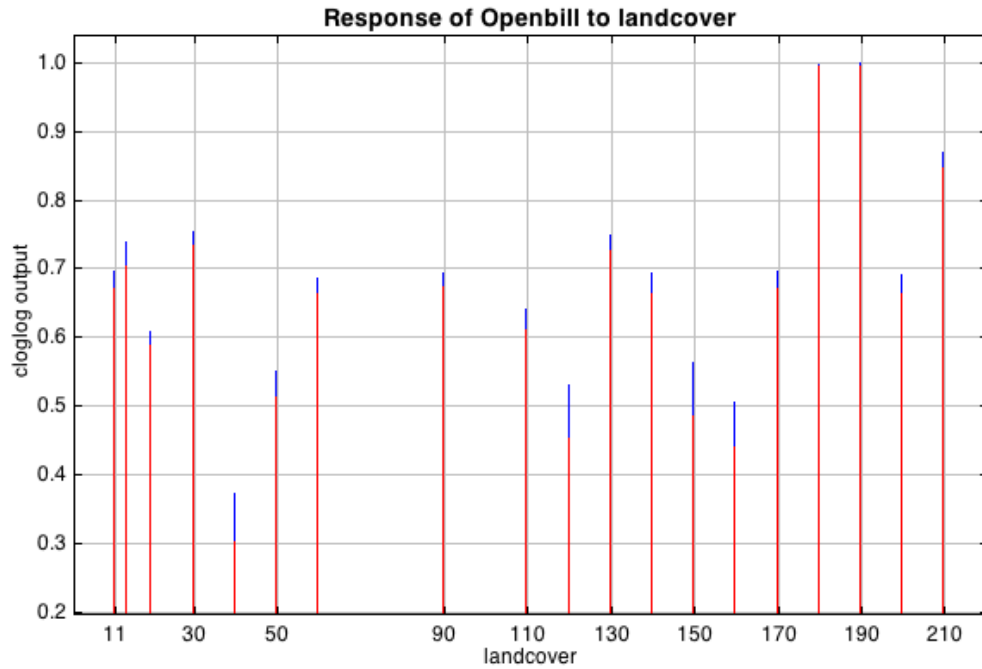
Appendix 3

Land cover categories and response plots

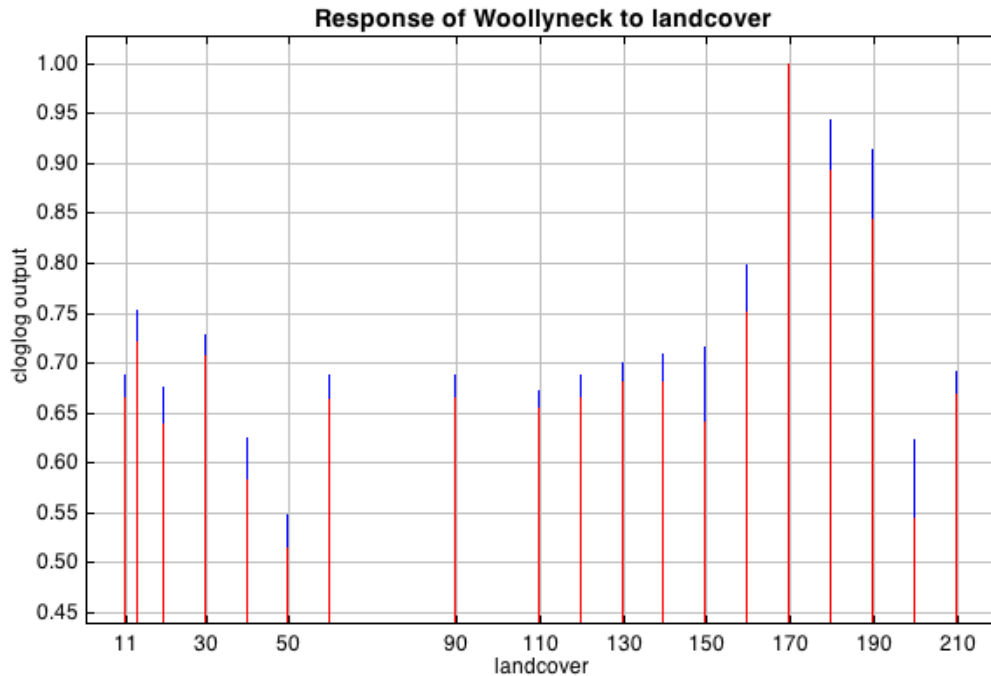
Land cover categories

Value	Description
11	Post-flooding or irrigated croplands (or aquatic)
14	Rainfed croplands
20	Mosaic cropland (50-70%) / vegetation (grassland/shrubland/forest) (20-50%)
30	Mosaic vegetation (grassland/shrubland/forest) (50-70%) / cropland (20-50%)
40	Closed to open (>15%) broadleaved evergreen or semi-deciduous forest (>5m)
50	Closed (>40%) broadleaved deciduous forest (>5m)
60	Open (15-40%) broadleaved deciduous forest/woodland (>5m)
90	Open (15-40%) needleleaved deciduous or evergreen forest (>5m)
110	Mosaic forest or shrubland (50-70%) / grassland (20-50%)
120	Mosaic grassland (50-70%) / forest or shrubland (20-50%)
130	Closed to open (>15%) (broadleaved or needleleaved, evergreen or deciduous) shrubland (<5m)
140	Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses)
150	Sparse (<15%) vegetation
160	Closed to open (>15%) broadleaved forest regularly flooded (semi-permanently or temporarily)
170	Closed (>40%) broadleaved forest or shrubland permanently flooded - Saline or brackish water
180	Closed to open (>15%) grassland or woody vegetation on regularly flooded or waterlogged soil
190	Artificial surfaces and associated areas (Urban areas >50%)
200	Bare areas
210	Water bodies

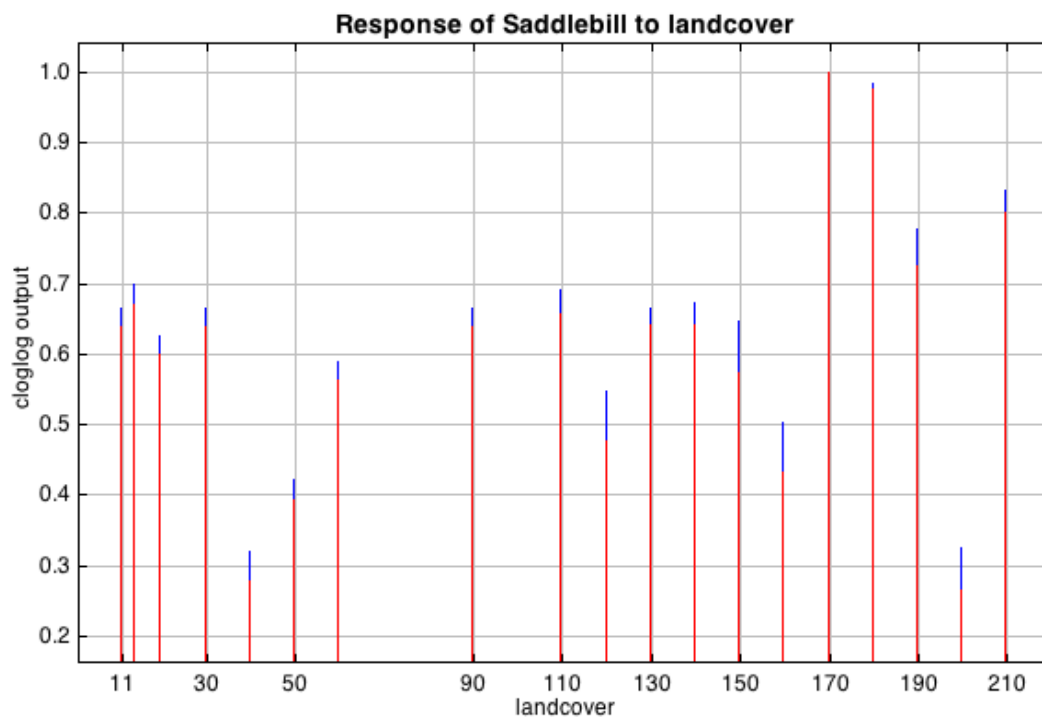
Range-wide models



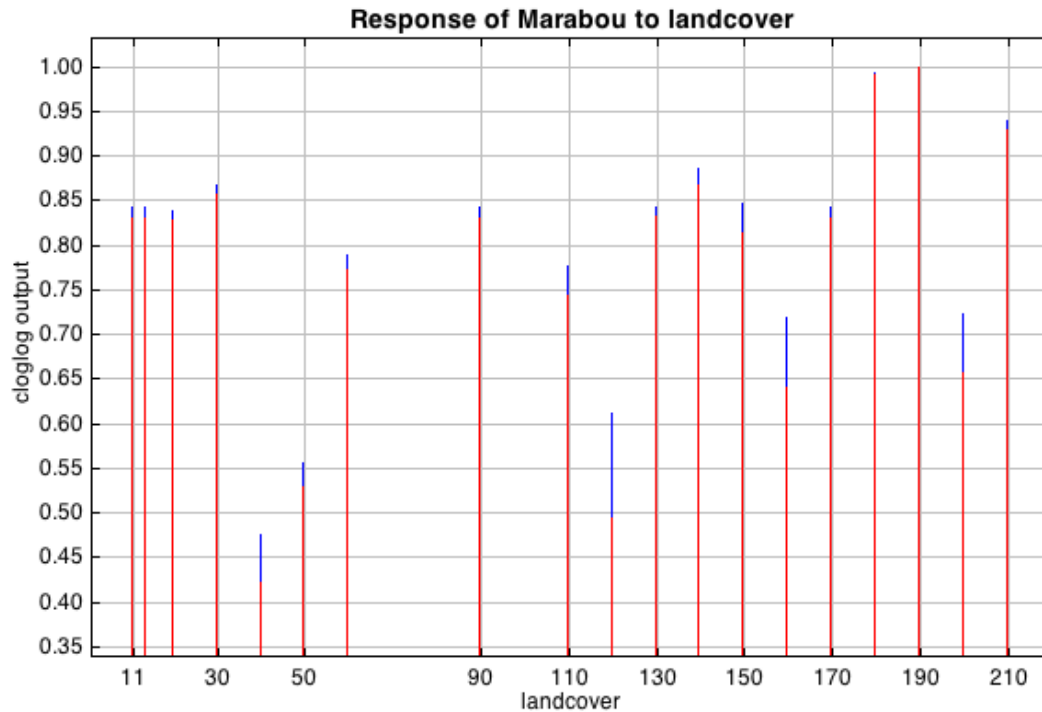
3.1. Response plot of African Openbill probability of occurrence (cloglog output) and land cover categories at the range-wide scale. Blue indicates standard deviation from ten model averages.



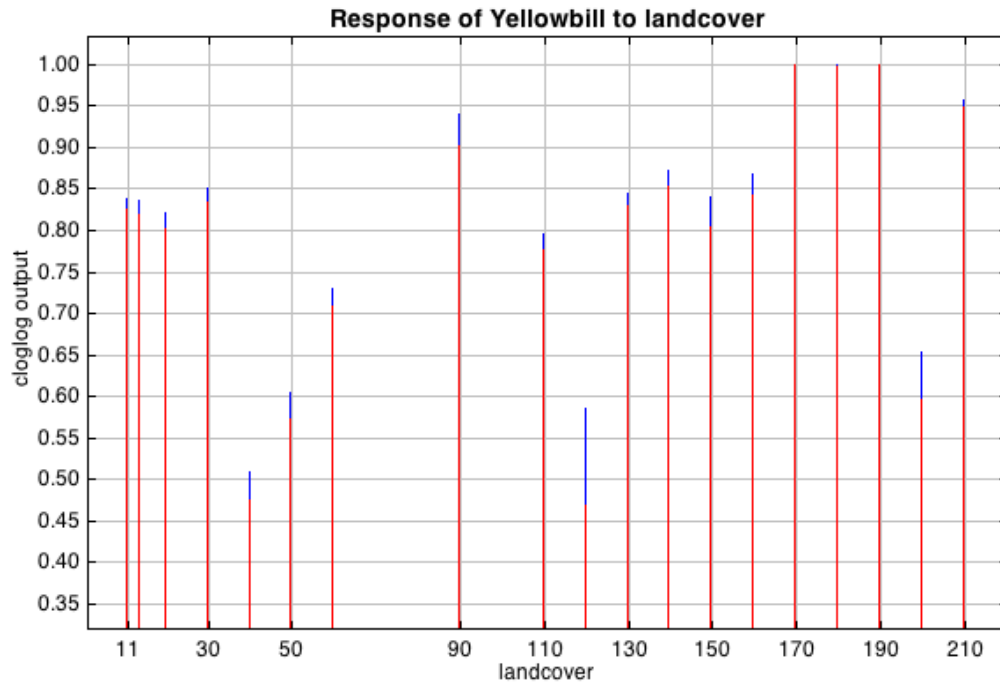
3.2. Response plot of African Woollyneck probability of occurrence (cloglog output) and land cover categories at the range-wide scale. Blue indicates standard deviation from ten model averages.



3.3. Response plot of Saddlebill Stork probability of occurrence (cloglog output) and land cover categories at the range-wide scale. Blue indicates standard deviation from ten model averages.

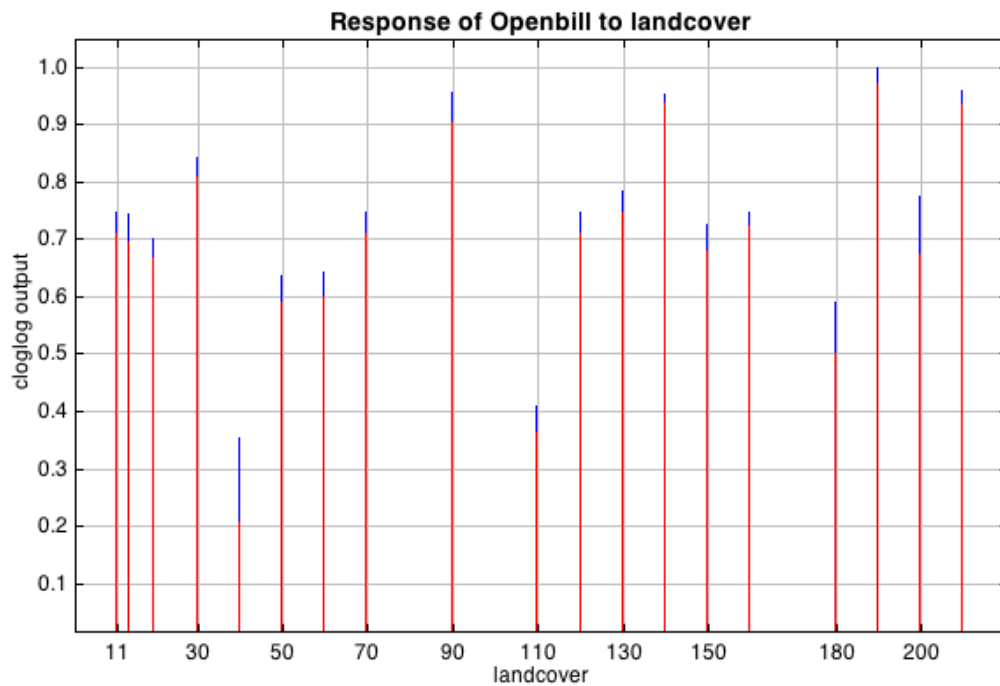


3.4. Response plot of Marabou Stork probability of occurrence (cloglog output) and land cover categories at the range-wide scale. Blue indicates standard deviation from ten model averages.

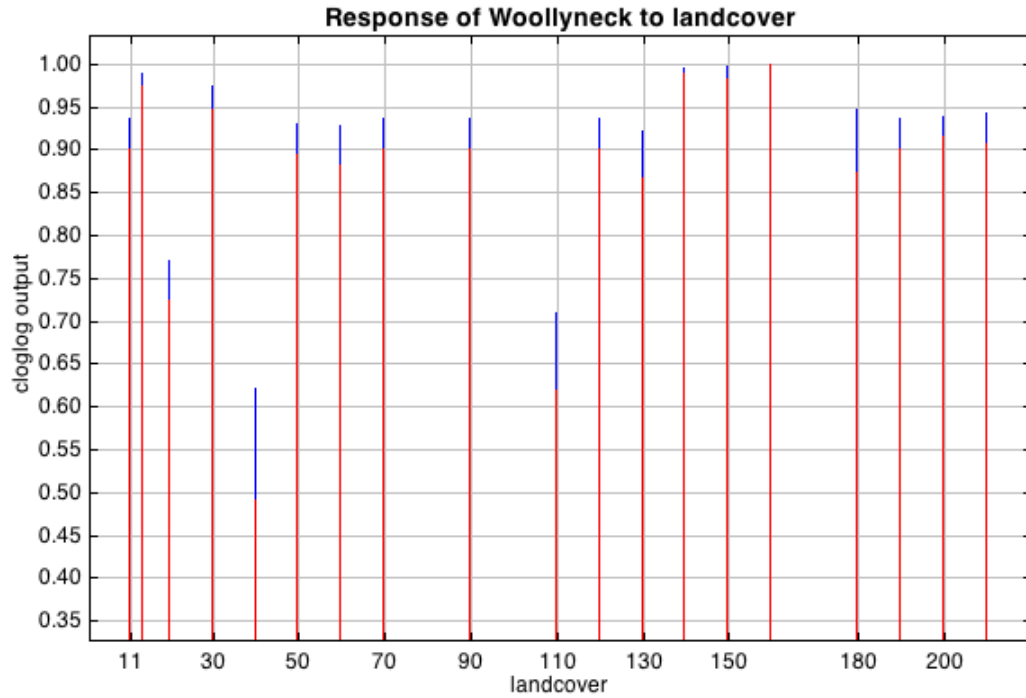


3.5. Response plot of Yellow-billed Stork probability of occurrence (cloglog output) and land cover categories at the range-wide scale. Blue indicates standard deviation from ten model averages.

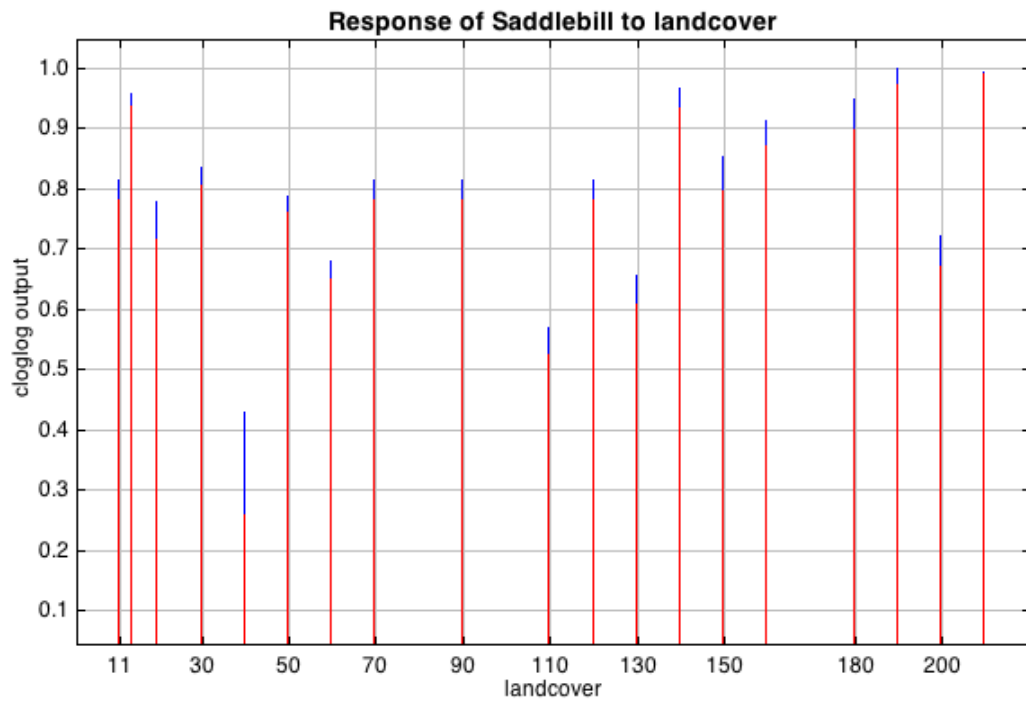
East African models



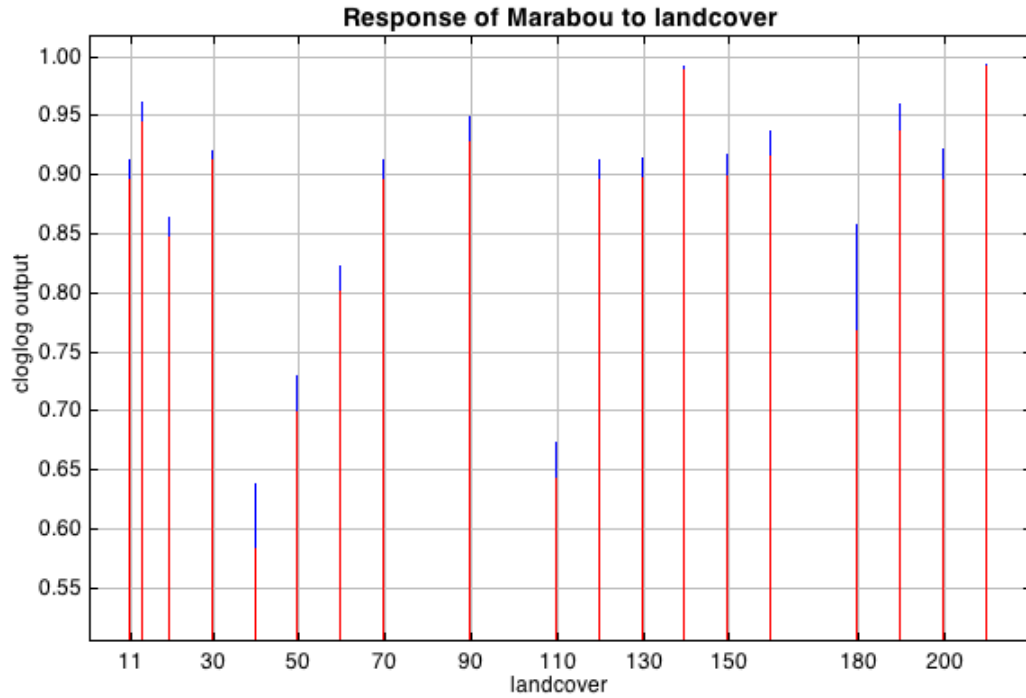
3.6. Response plot of African Openbill probability of occurrence (cloglog output) and land cover categories in East Africa. Blue indicates standard deviation from ten model averages.



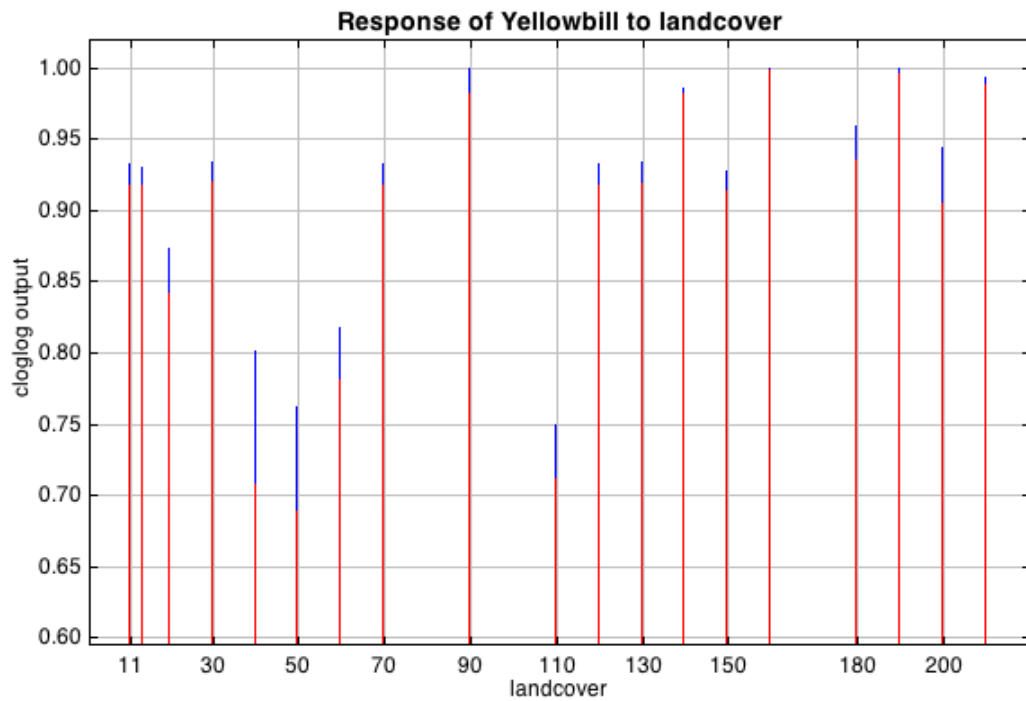
3.7. Response plot of African Woollyneck probability of occurrence (cloglog output) and land cover categories in East Africa. Blue indicates standard deviation from ten model averages.



3.8. Response plot of Saddlebill Stork probability of occurrence (cloglog output) and land cover categories in East Africa. Blue indicates standard deviation from ten model averages.

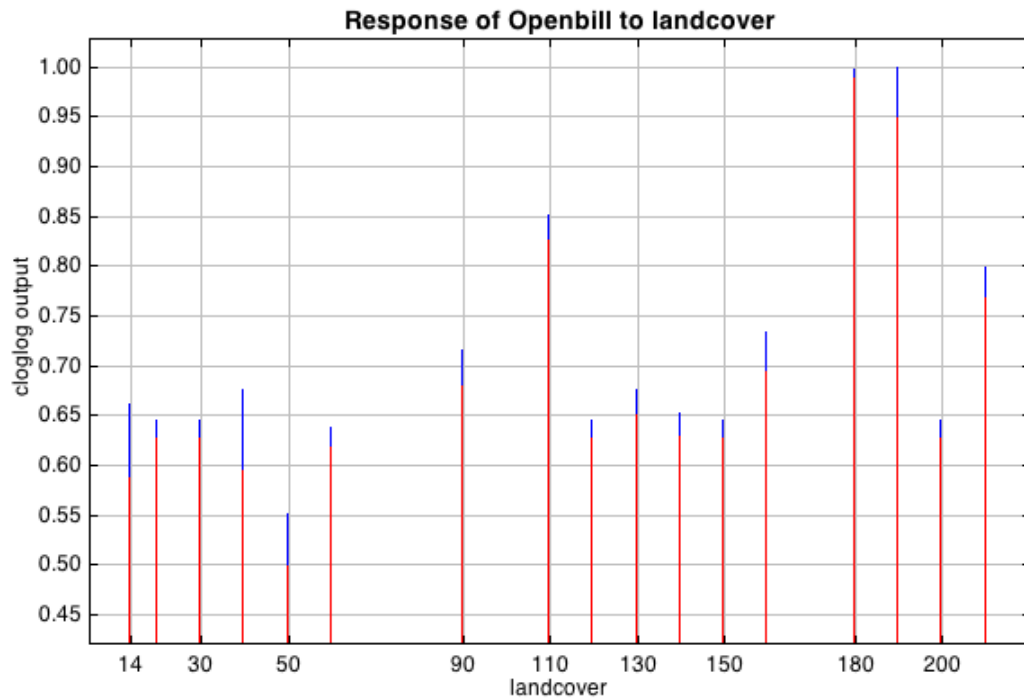


3.9. Response plot of Marabou Stork probability of occurrence (cloglog output) and land cover categories in East Africa. Blue indicates standard deviation from ten model averages.

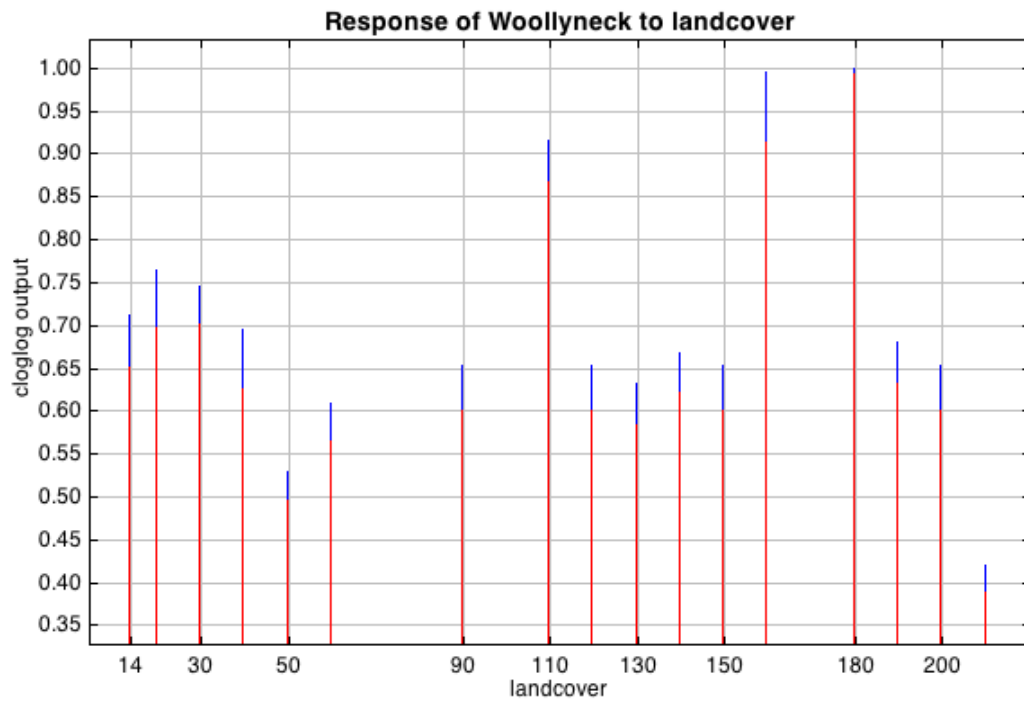


3.10. Response plot of Yellow-billed Stork probability of occurrence (cloglog output) and land cover categories in East Africa. Blue indicates standard deviation from ten model averages.

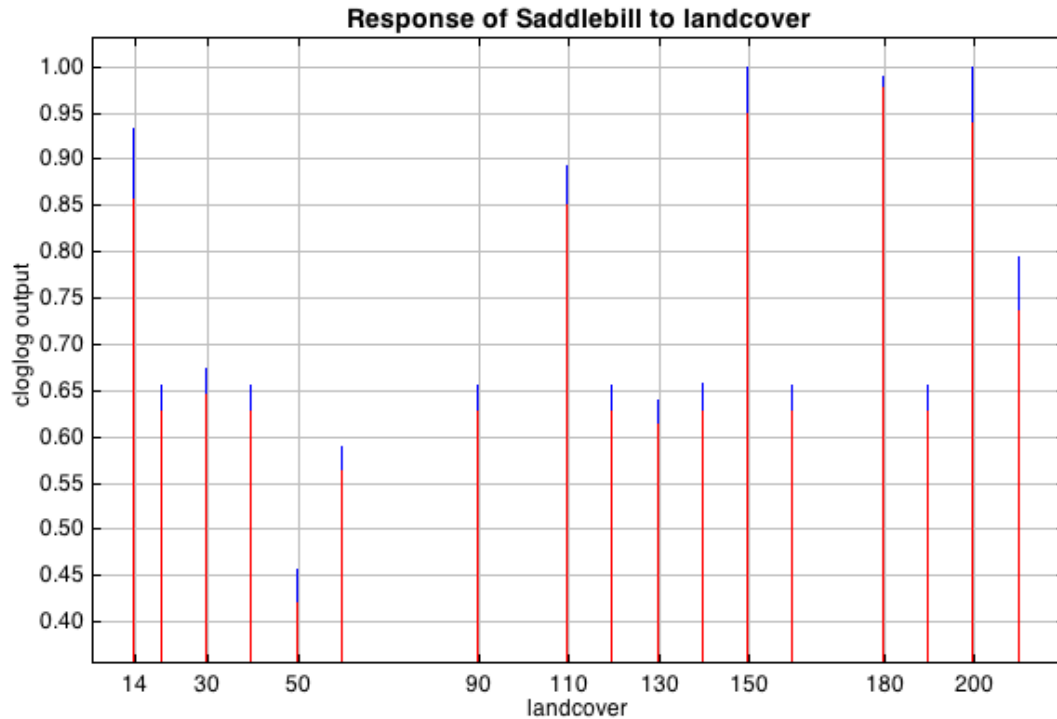
Southern African models



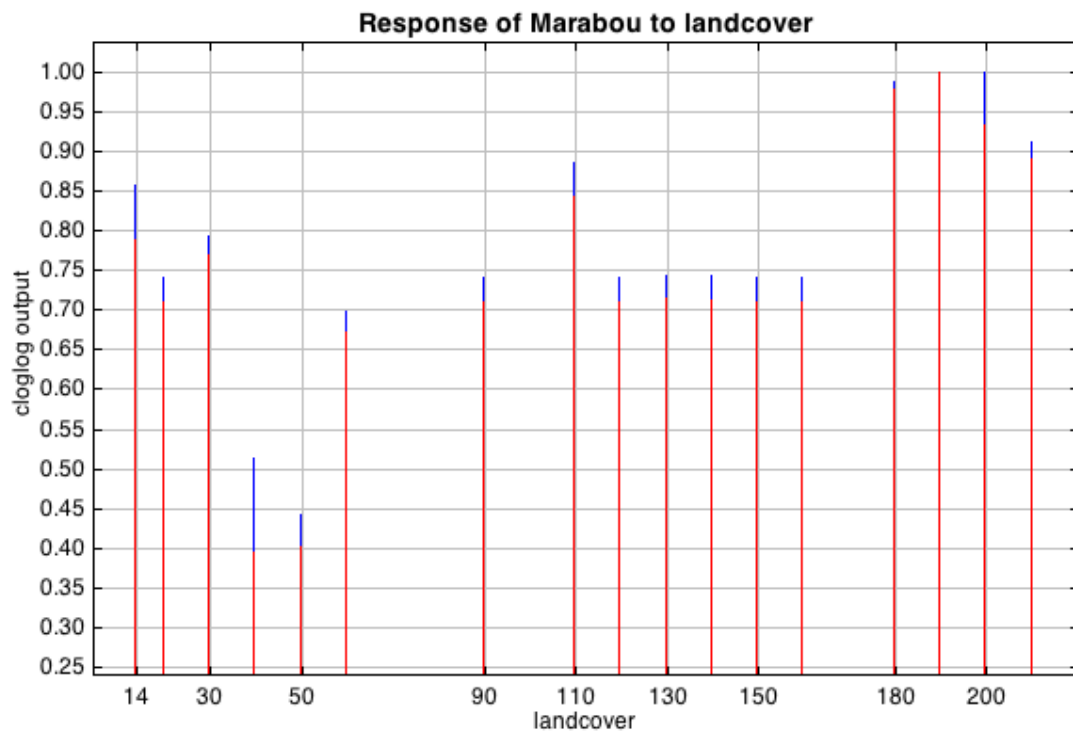
3.11. Response plot of African Openbill probability of occurrence (cloglog output) and land cover categories in Southern Africa. Blue indicates standard deviation from ten model averages.



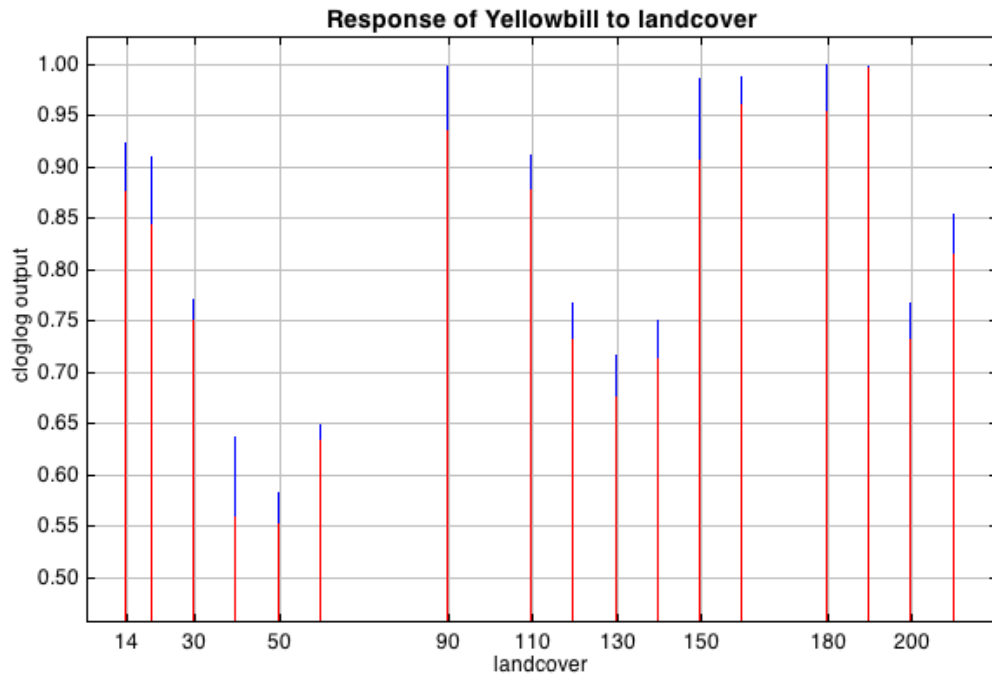
3.12. Response plot of African Woollyneck probability of occurrence (cloglog output) and land cover categories in Southern Africa. Blue indicates standard deviation from ten model averages.



3.13. Response plot of Saddlebill Stork probability of occurrence (cloglog output) and land cover categories in Southern Africa. Blue indicates standard deviation from ten model averages.

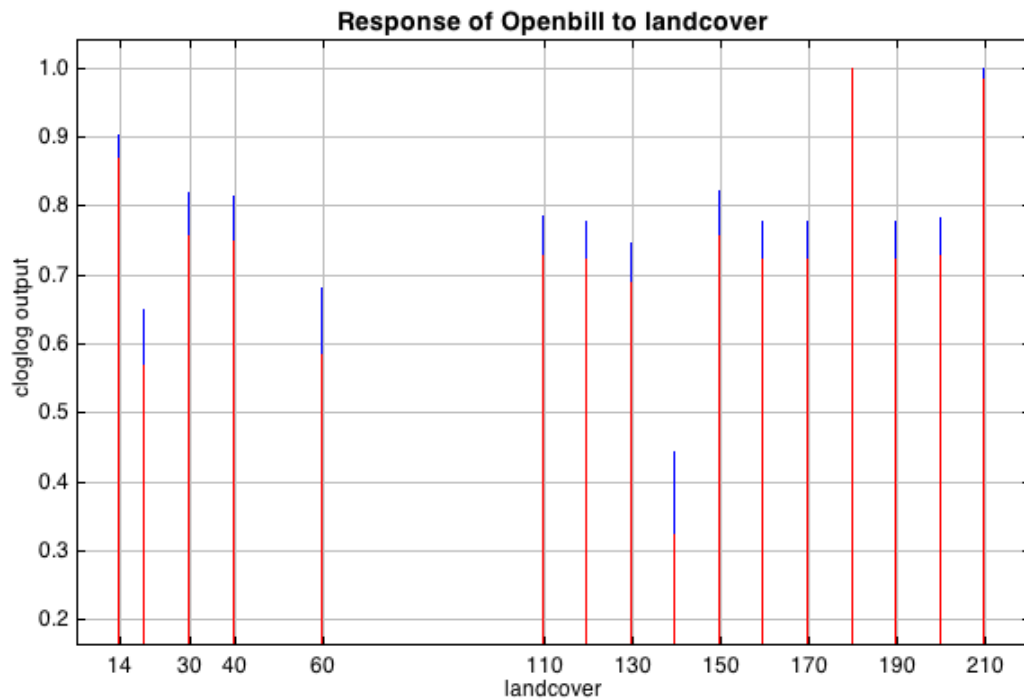


3.14. Response plot of Marabou Stork probability of occurrence (cloglog output) and land cover categories in Southern Africa. Blue indicates standard deviation from ten model averages.

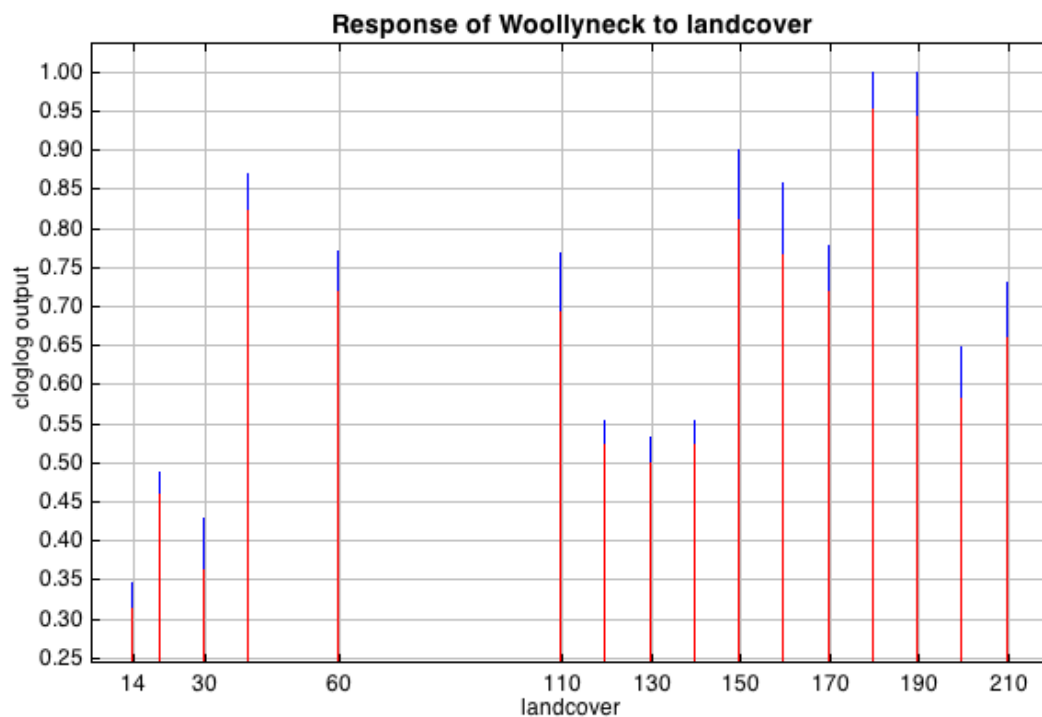


3.15. Response plot of Yellow-billed Stork probability of occurrence (cloglog output) and land cover categories in Southern Africa. Blue indicates standard deviation from ten model averages.

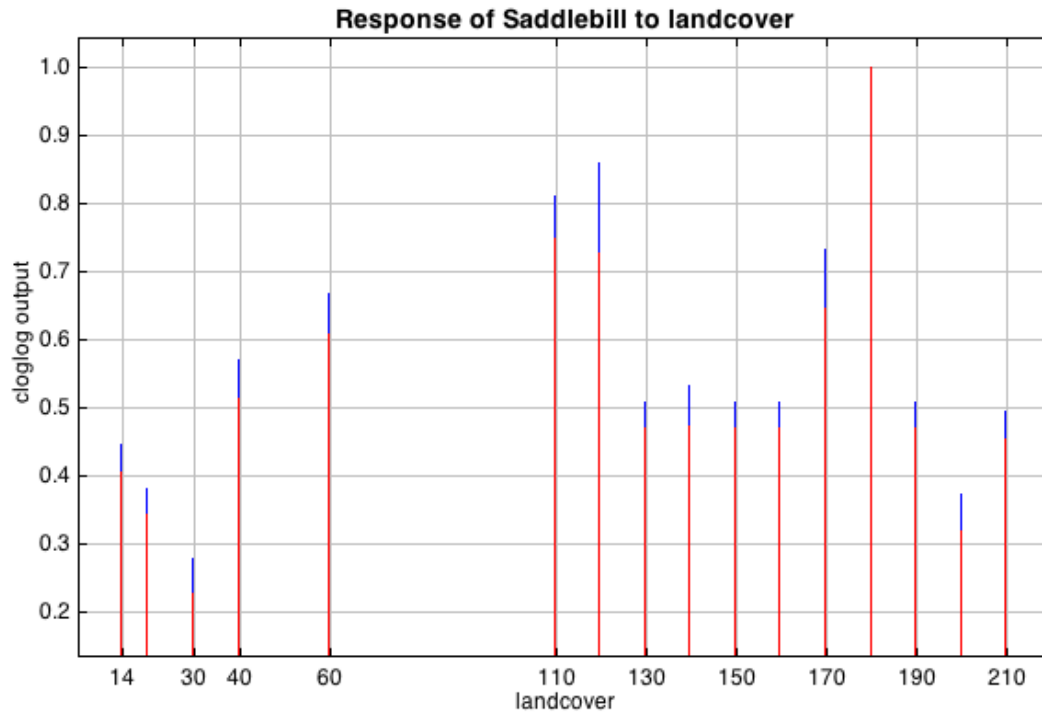
West African models



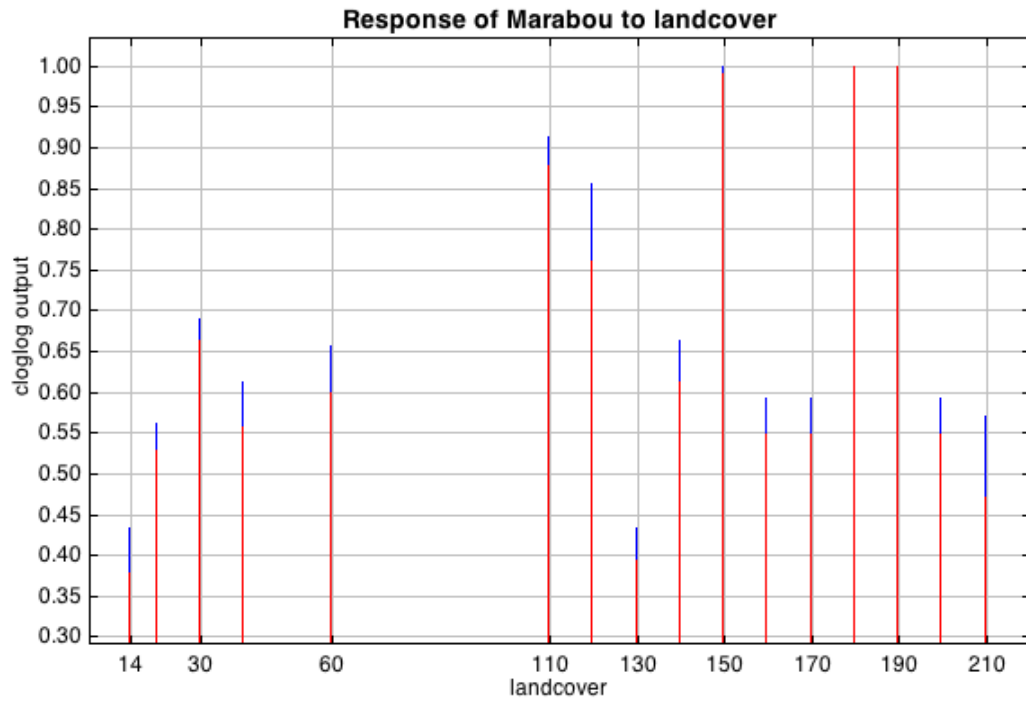
3.16. Response plot of African Openbill probability of occurrence (cloglog output) and land cover categories in West Africa. Blue indicates standard deviation from ten model averages.



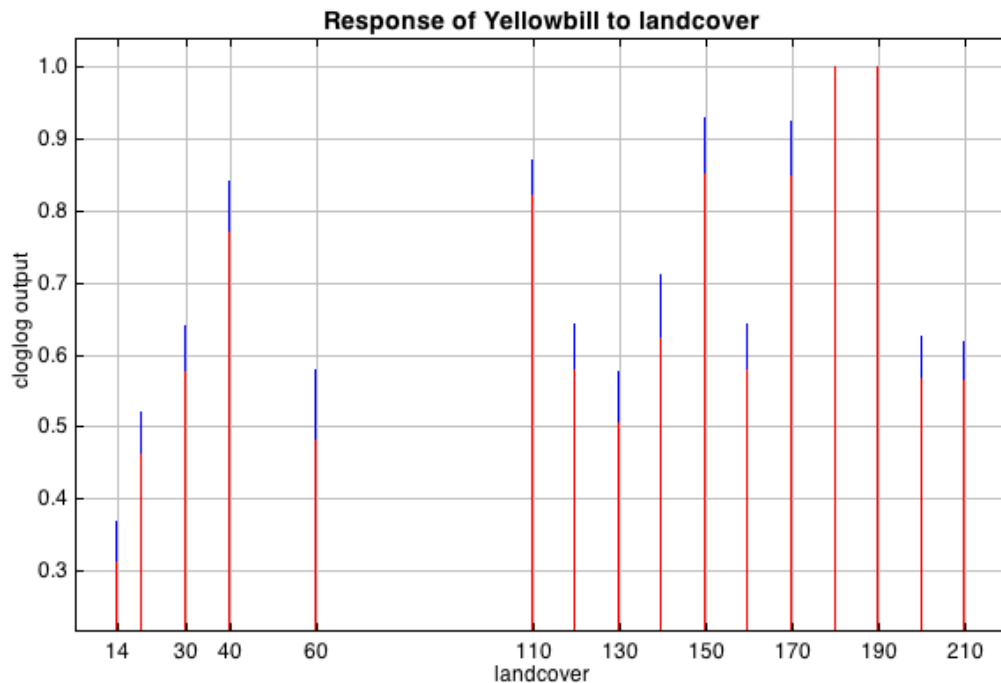
3.17. Response plot of African Woollyneck probability of occurrence (cloglog output) and land cover categories in West Africa. Blue indicates standard deviation from ten model averages.



3.18. Response plot of Saddlebill Stork probability of occurrence (cloglog output) and land cover categories in West Africa. Blue indicates standard deviation from ten model averages.



3.19. Response plot of Marabou Stork probability of occurrence (cloglog output) and land cover categories in West Africa. Blue indicates standard deviation from ten model averages.

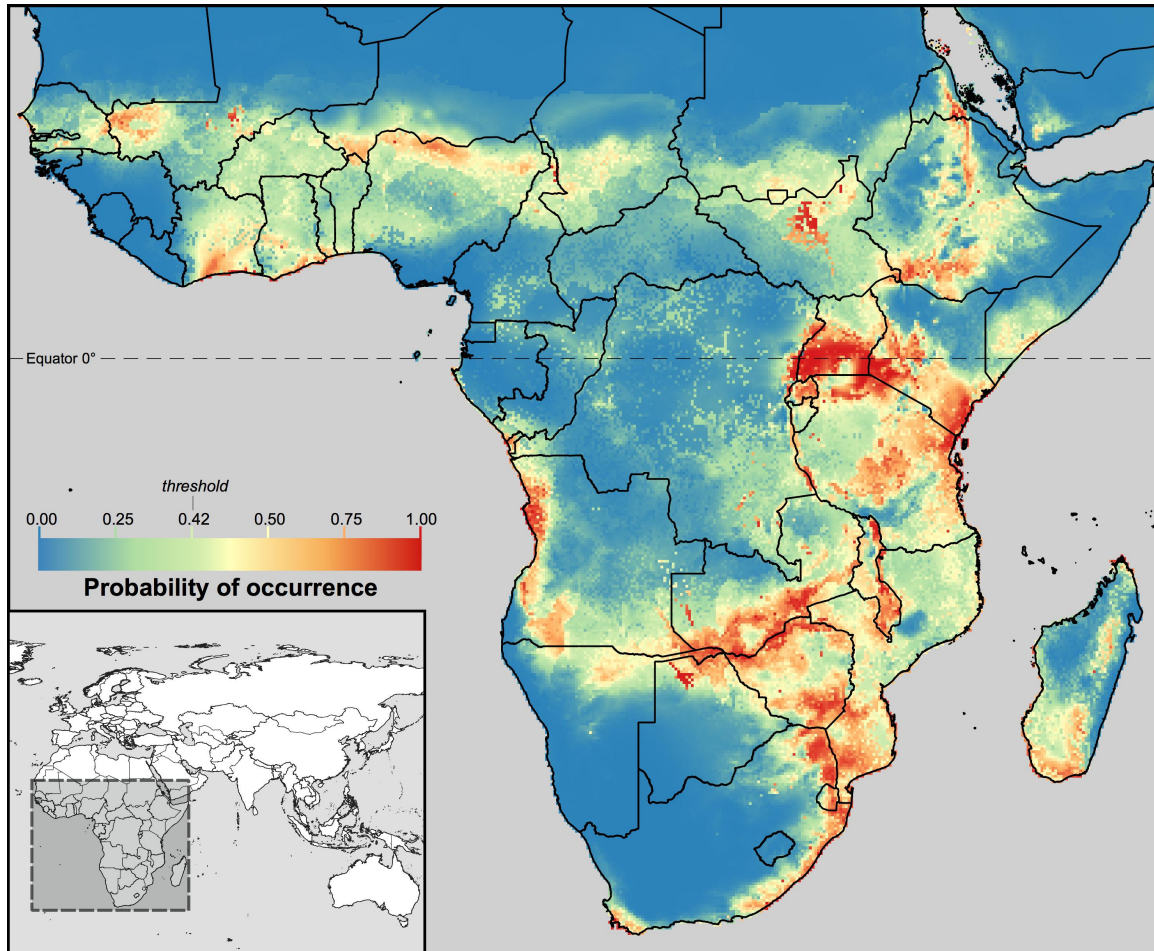


3.20. Response plot of Yellow-billed Stork probability of occurrence (cloglog output) and land cover categories in West Africa. Blue indicates standard deviation from ten model averages.

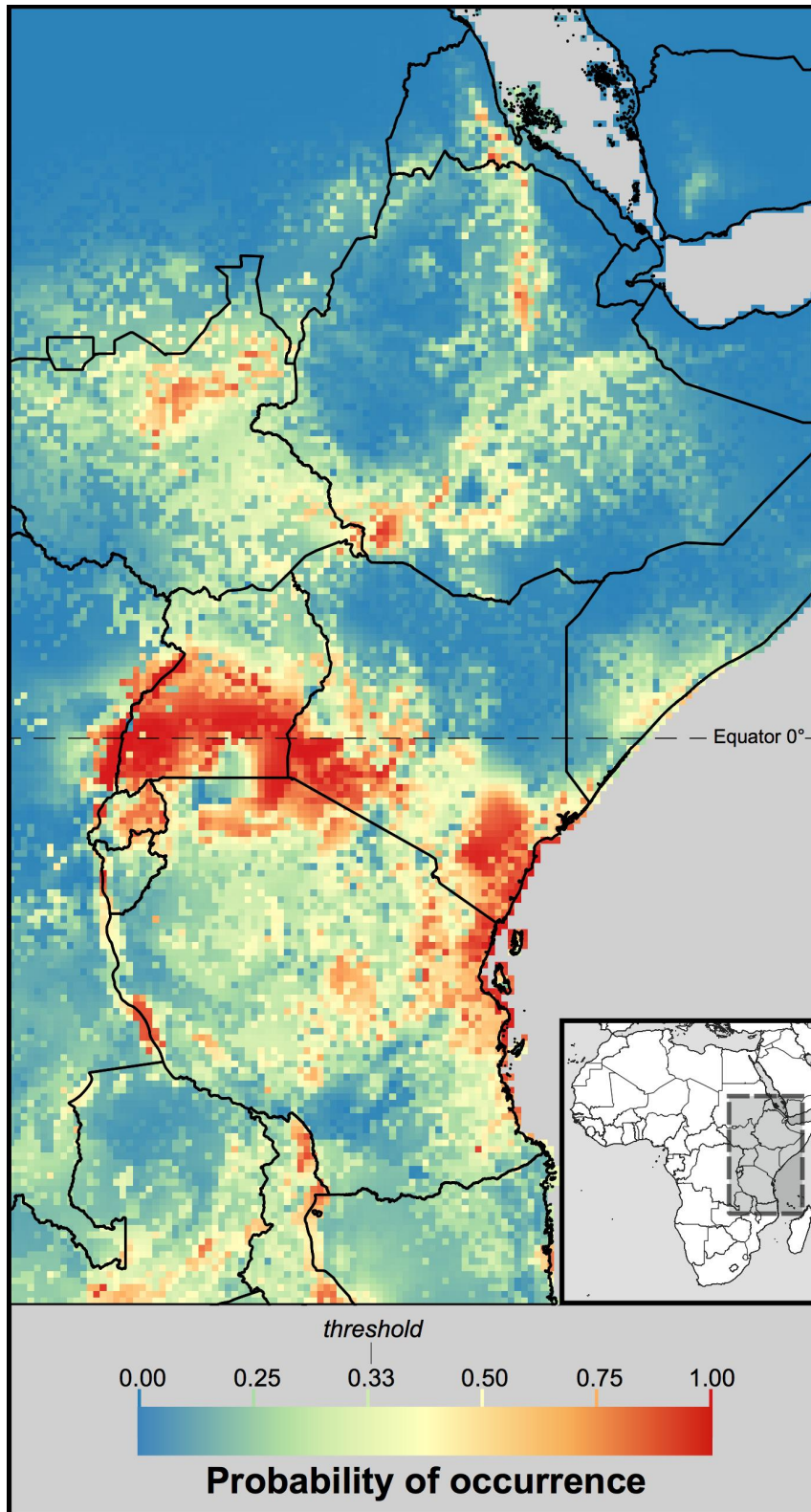
Appendix 4

Spatial suitability predictions

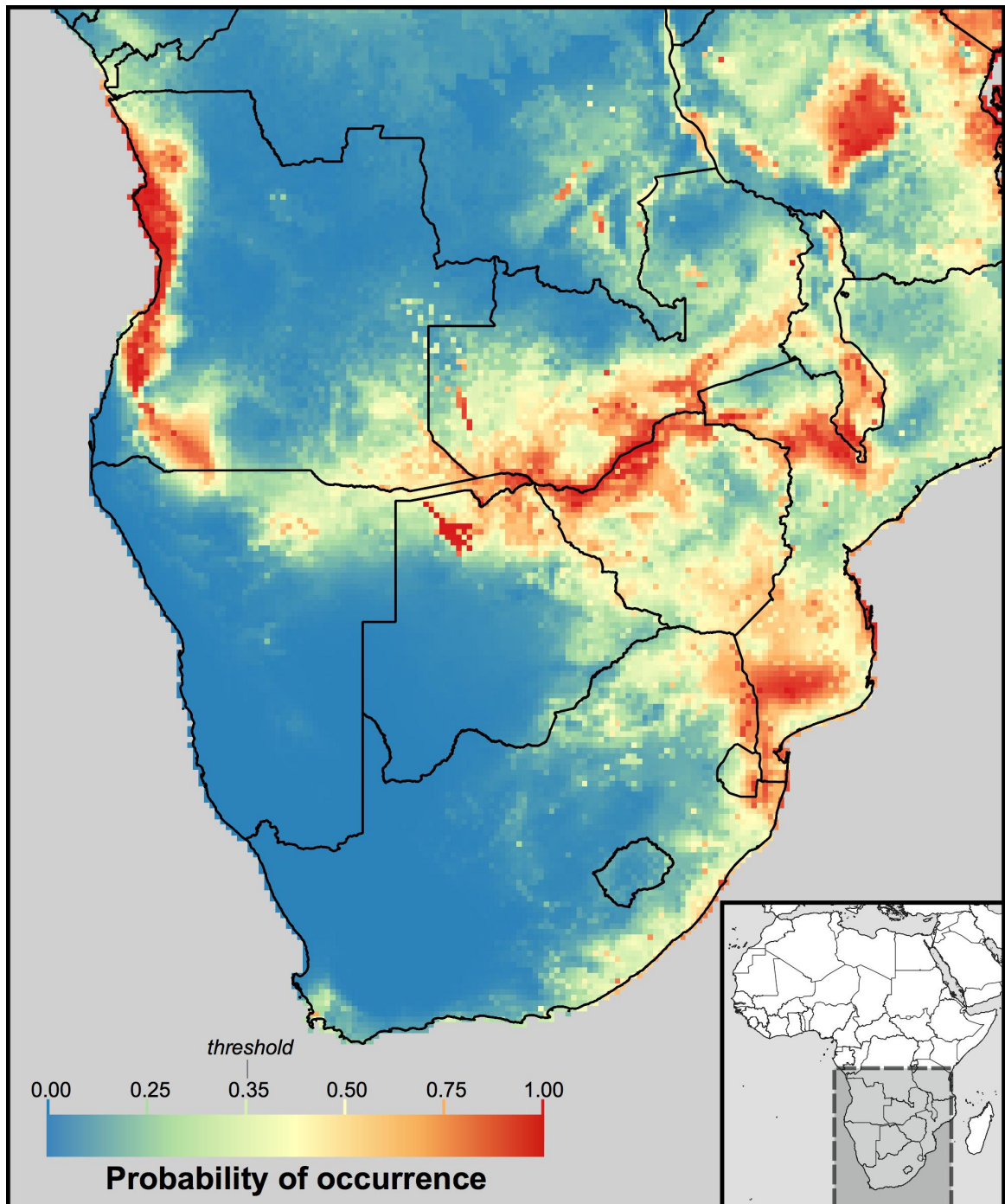
African Openbill



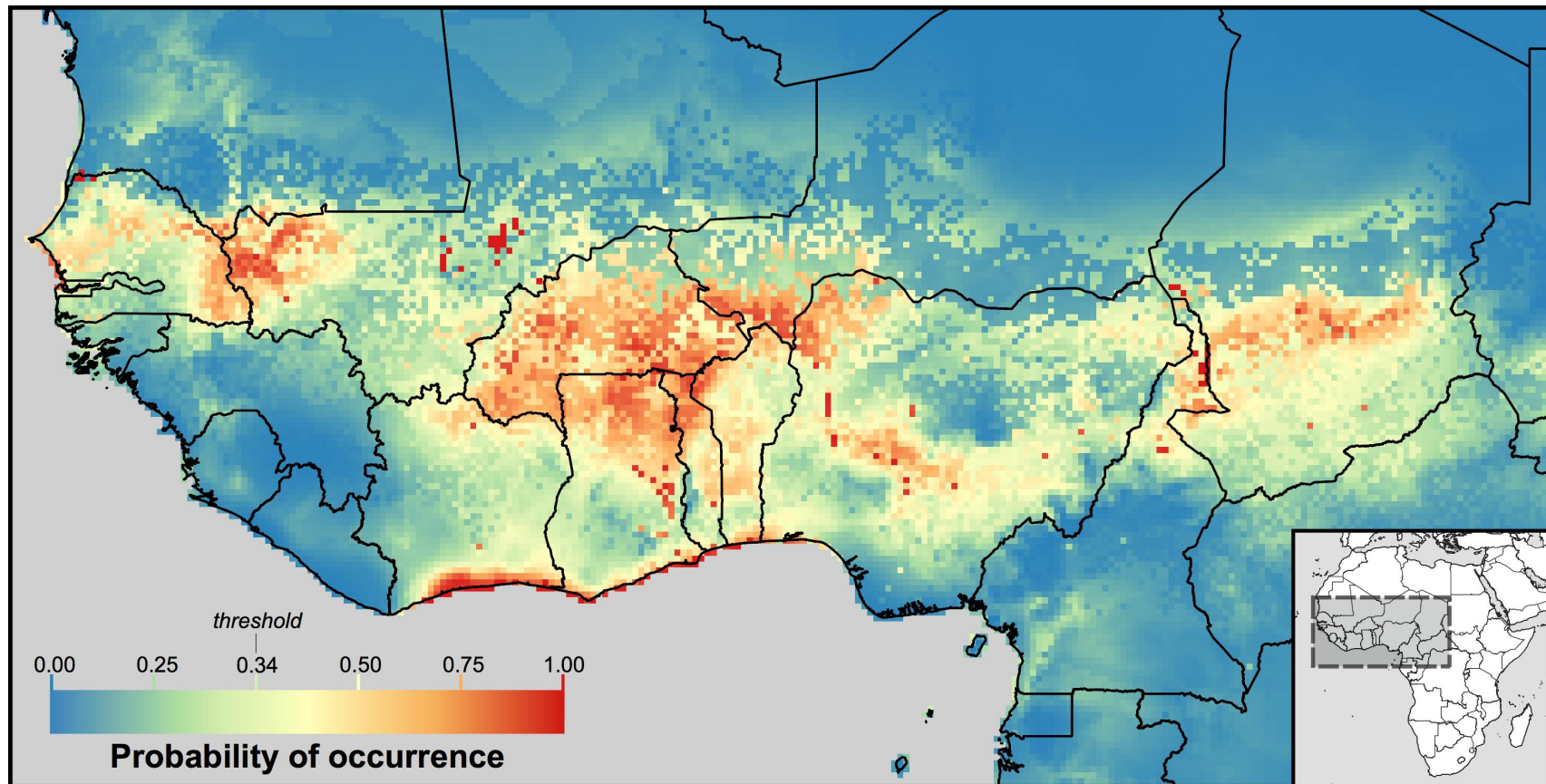
4.1. Average range-wide suitability predictions for the African Openbill from ten replicate models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable.



4.2. Average East African suitability predictions for the African Openbill from ten replicate models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable.

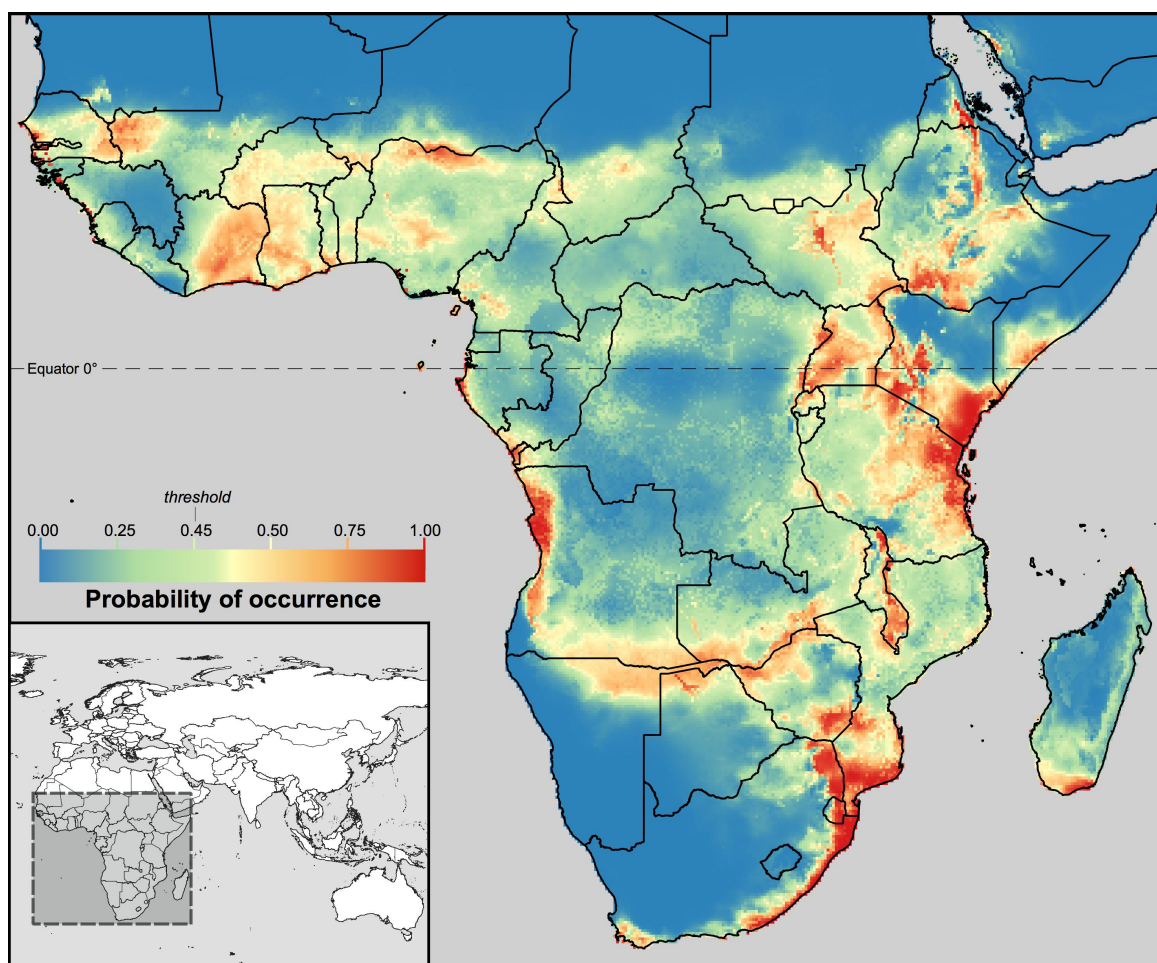


4.3. Average Southern African suitability predictions for the African Openbill from ten replicate models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable.

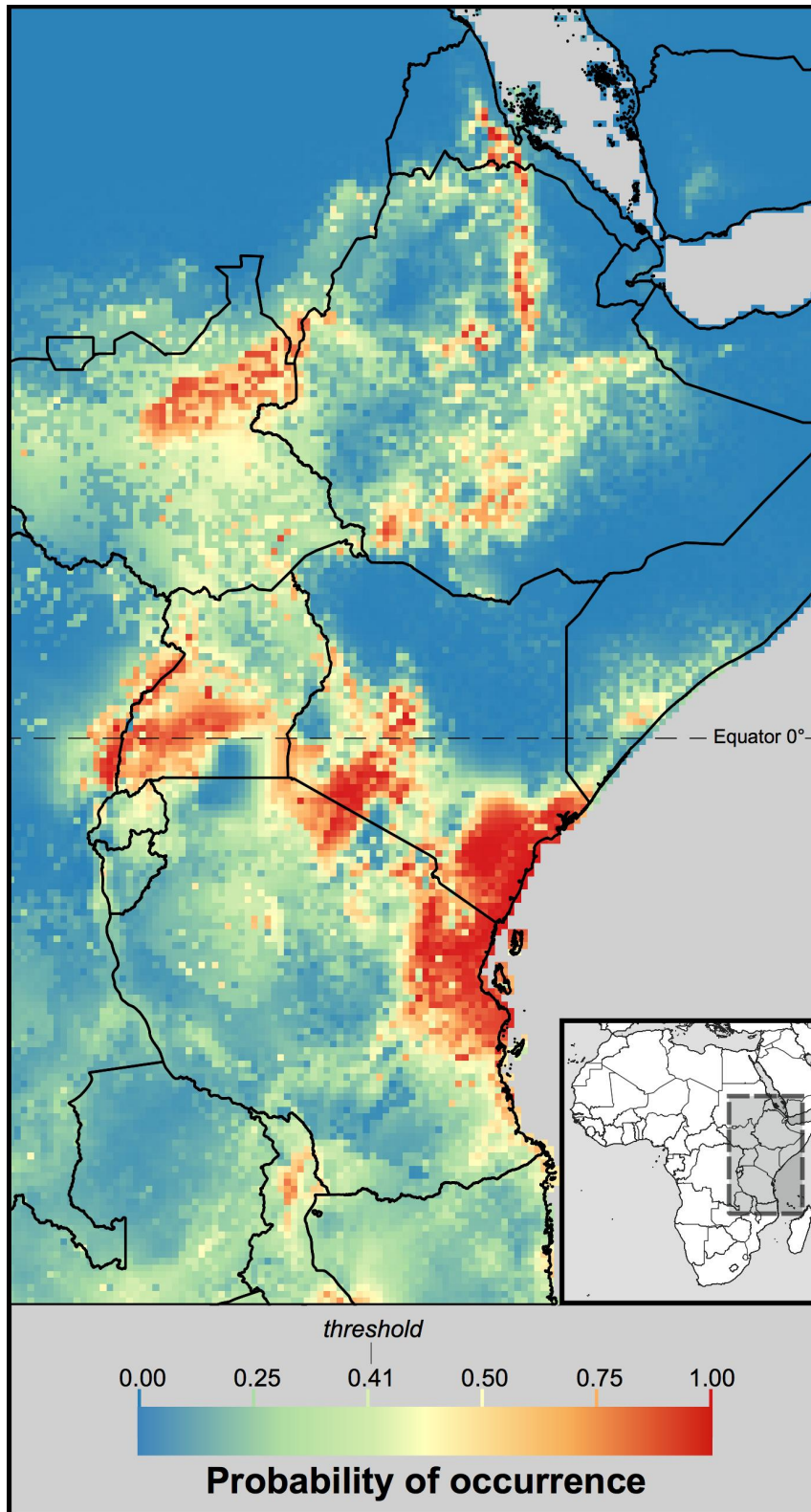


4.4. Average West African suitability predictions for the African Openbill from ten replicate models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable.

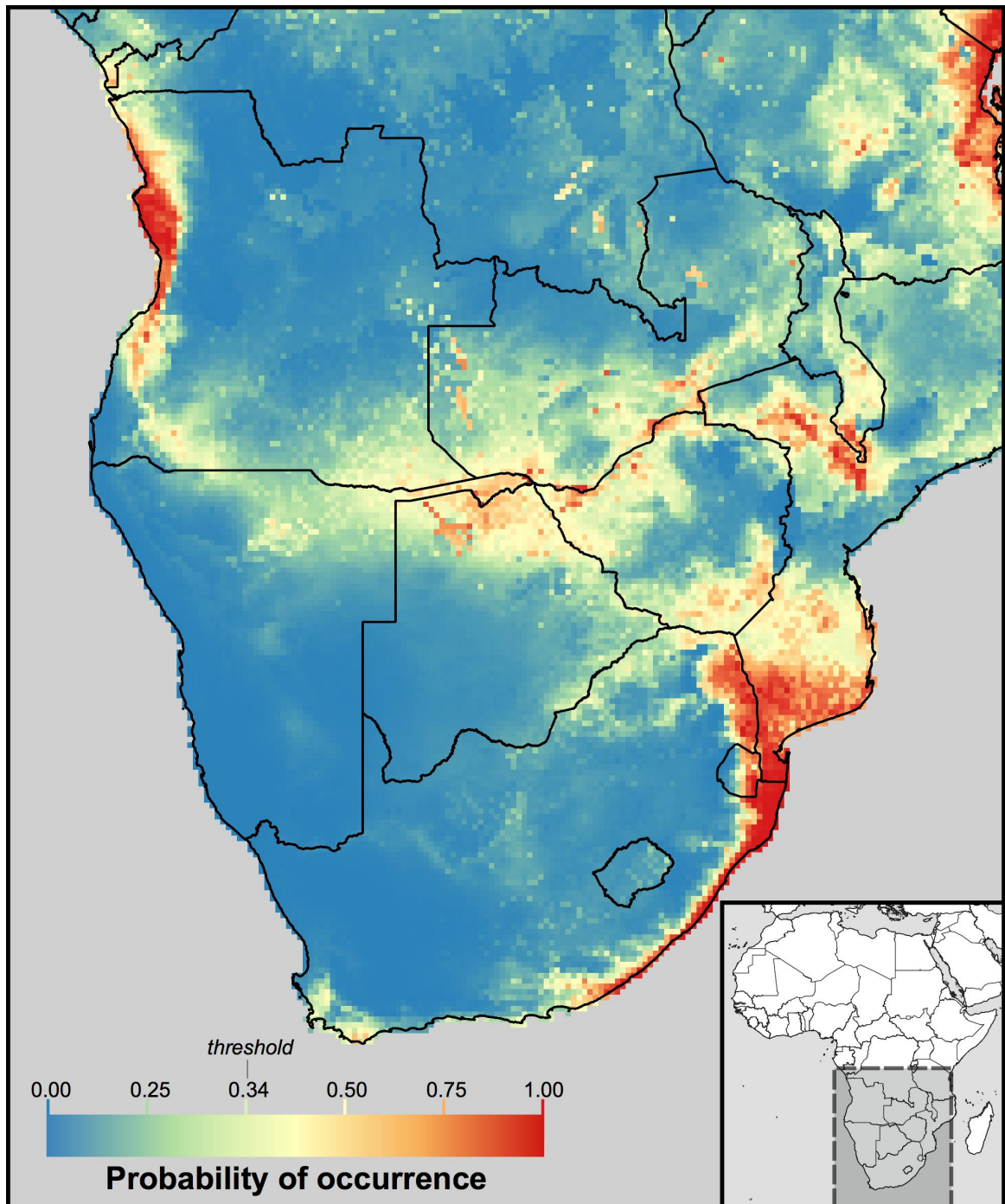
African Woollyneck



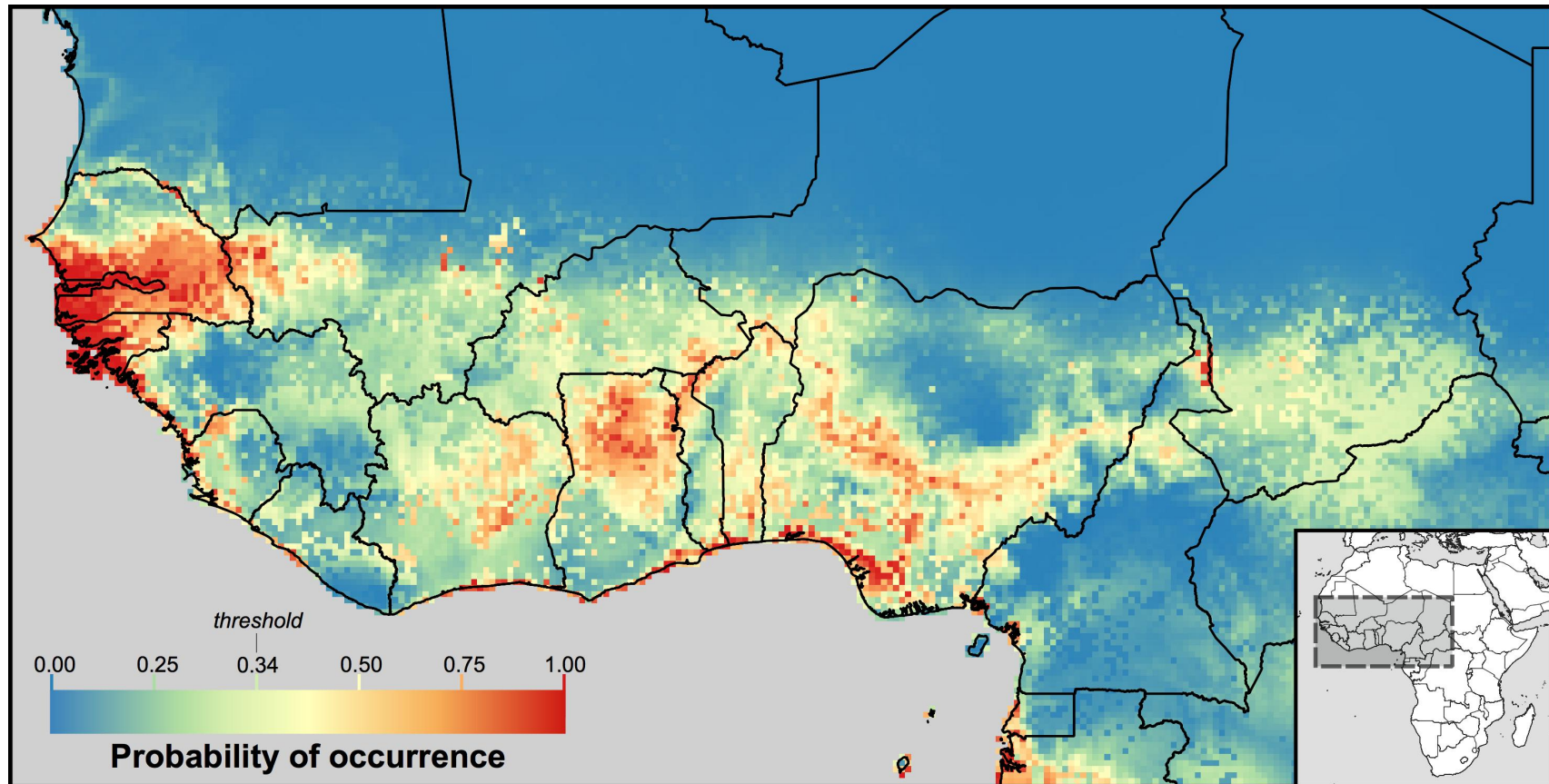
4.5. Average range-wide suitability predictions for the African Woollyneck from ten replicate models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable.



4.6. Average East African suitability predictions for the African Woollyneck from ten replicate models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable.

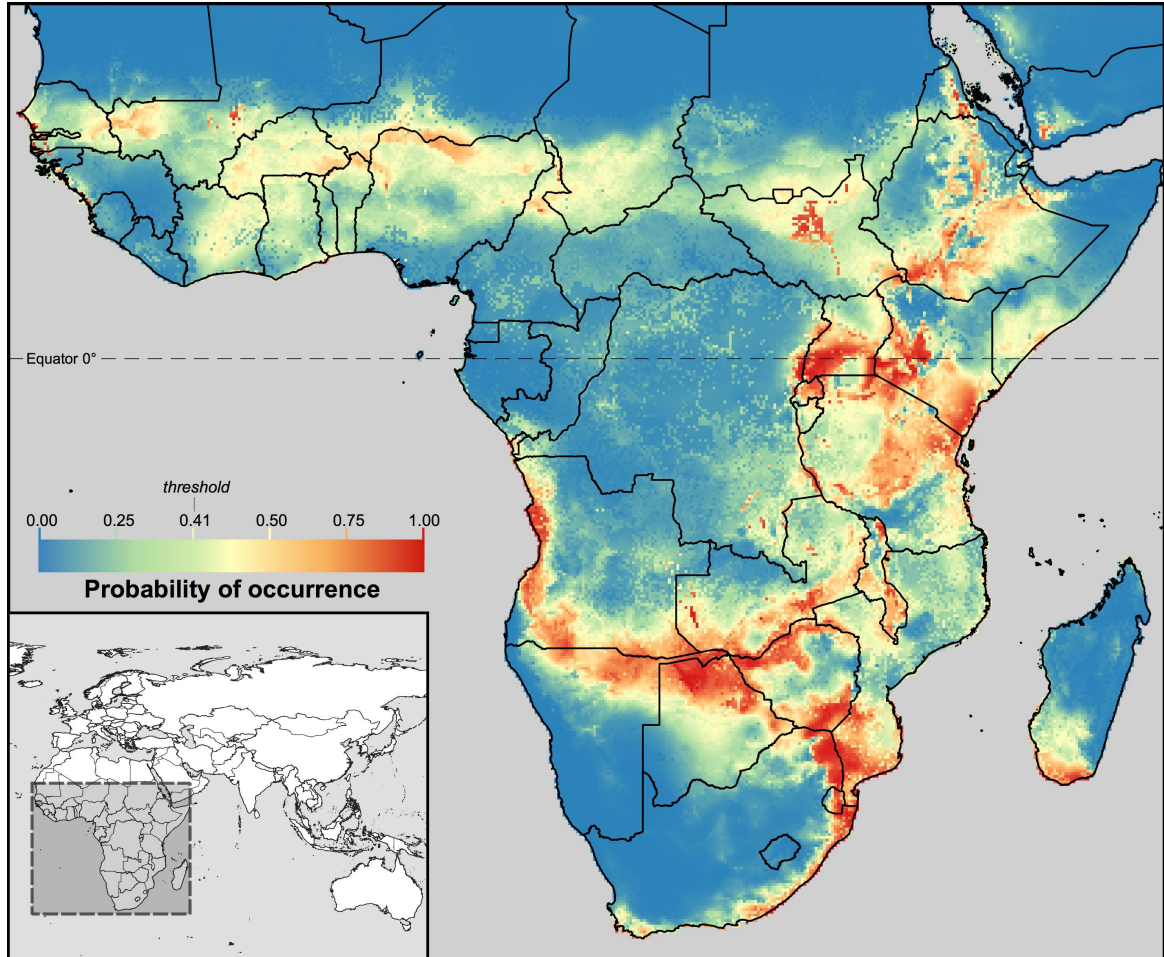


4.7. Average Southern African suitability predictions for the African Woollyneck from ten replicate models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable.

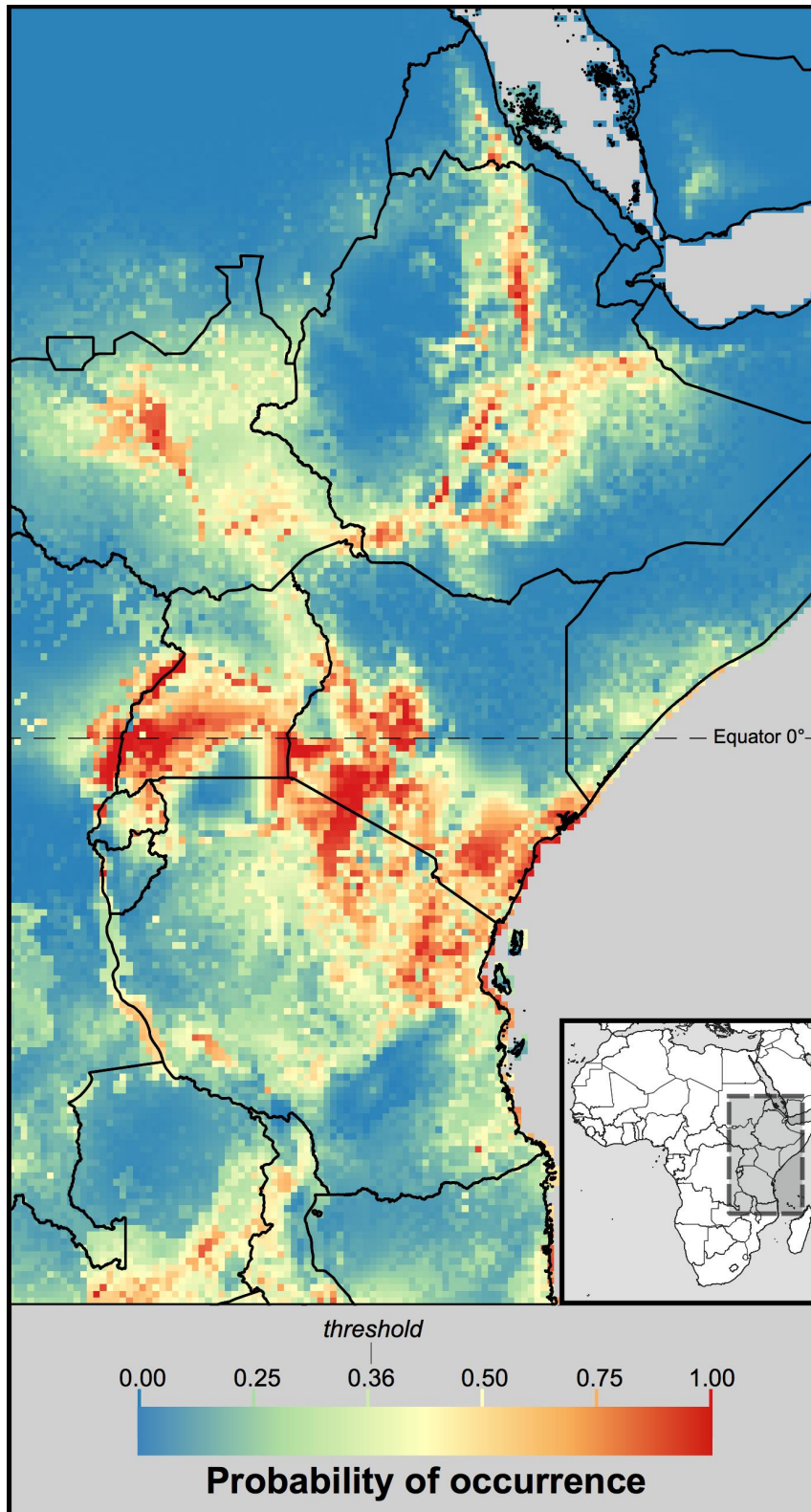


4.8. Average West African suitability predictions for the African Woollyneck from ten replicate models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable.

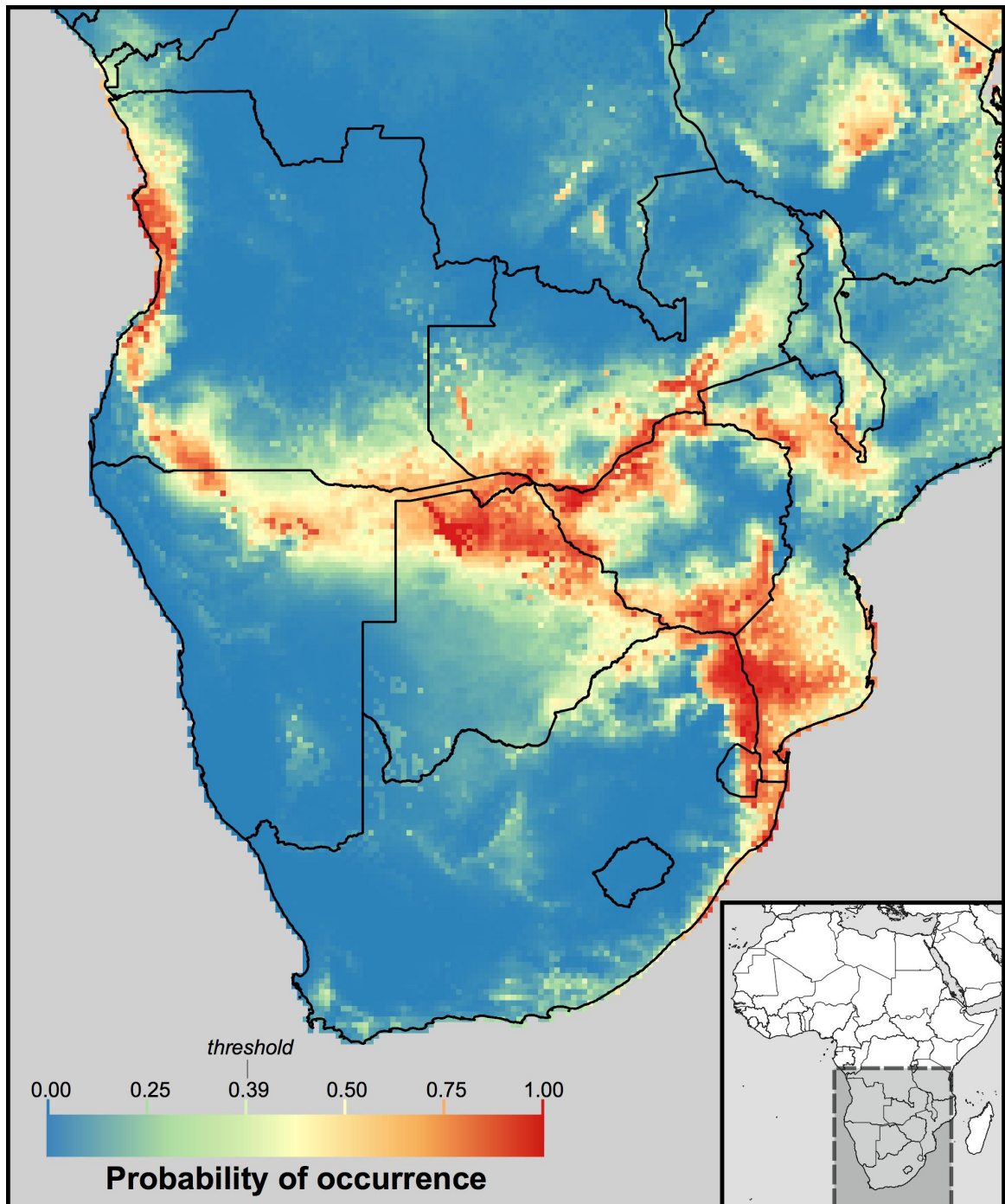
Saddlebill Stork



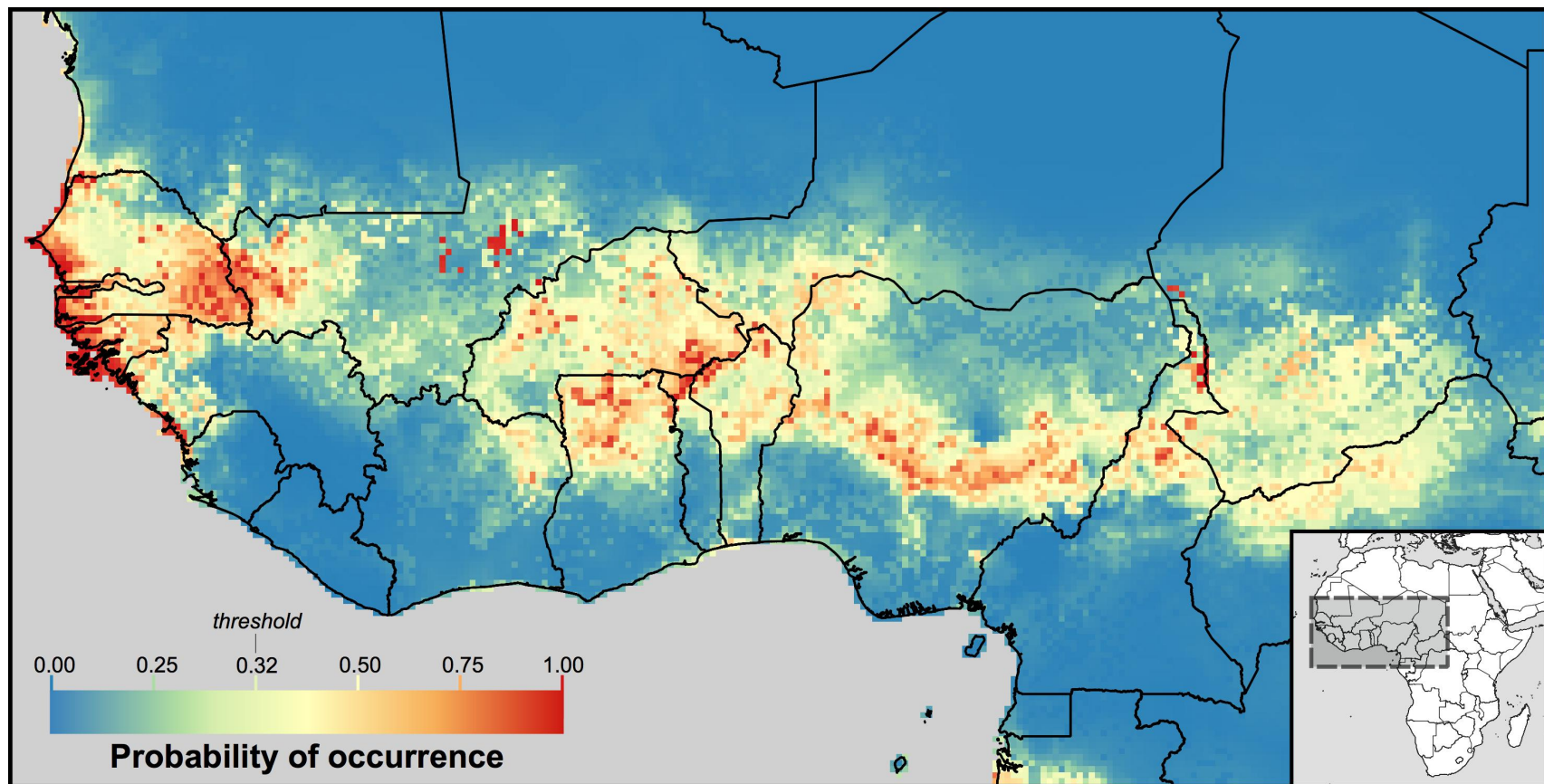
4.9. Average range-wide suitability predictions for the Saddlebill Stork from ten replicate models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable.



4.10. Average East African suitability predictions for the Saddlebill Stork from ten replicate models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable.

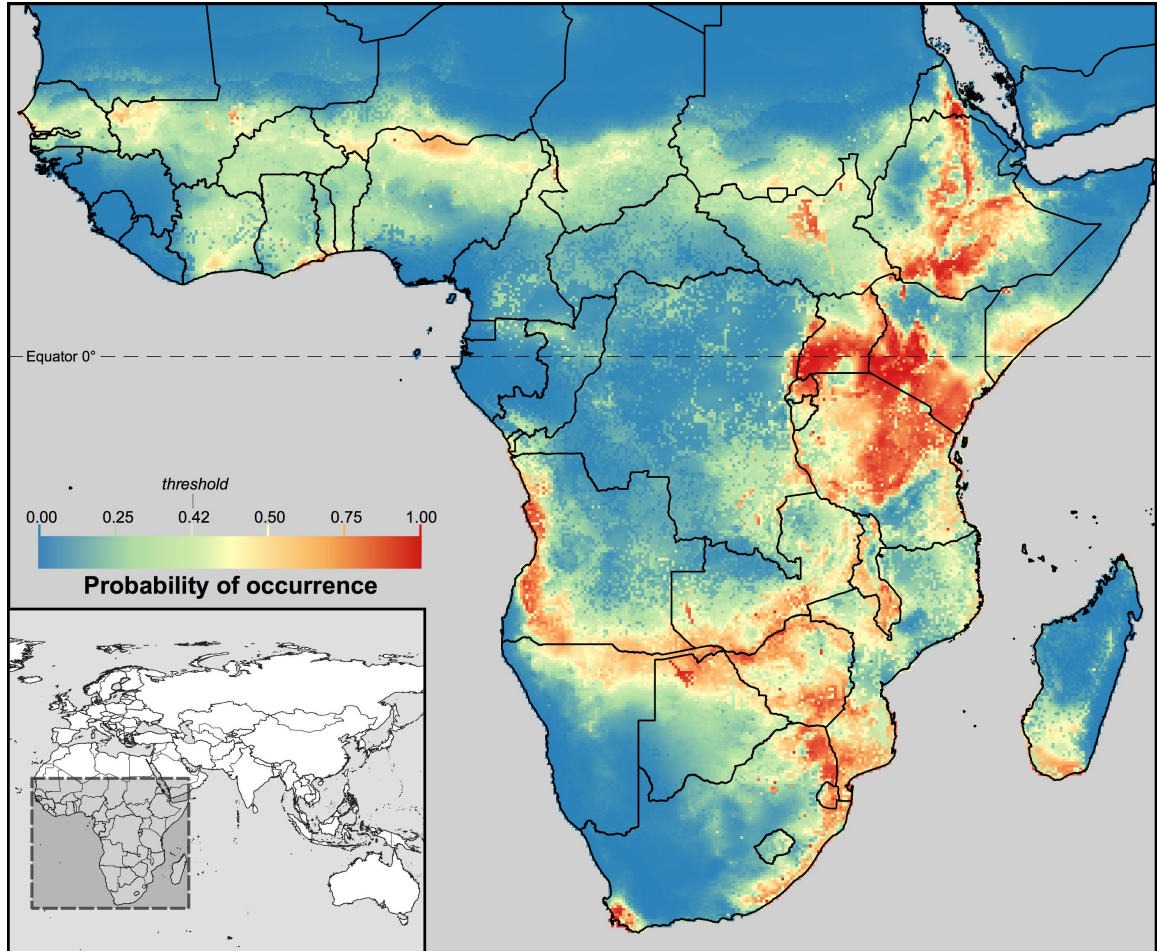


4.11. Average Southern African suitability predictions for the Saddlebill Stork from ten replicate models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable.

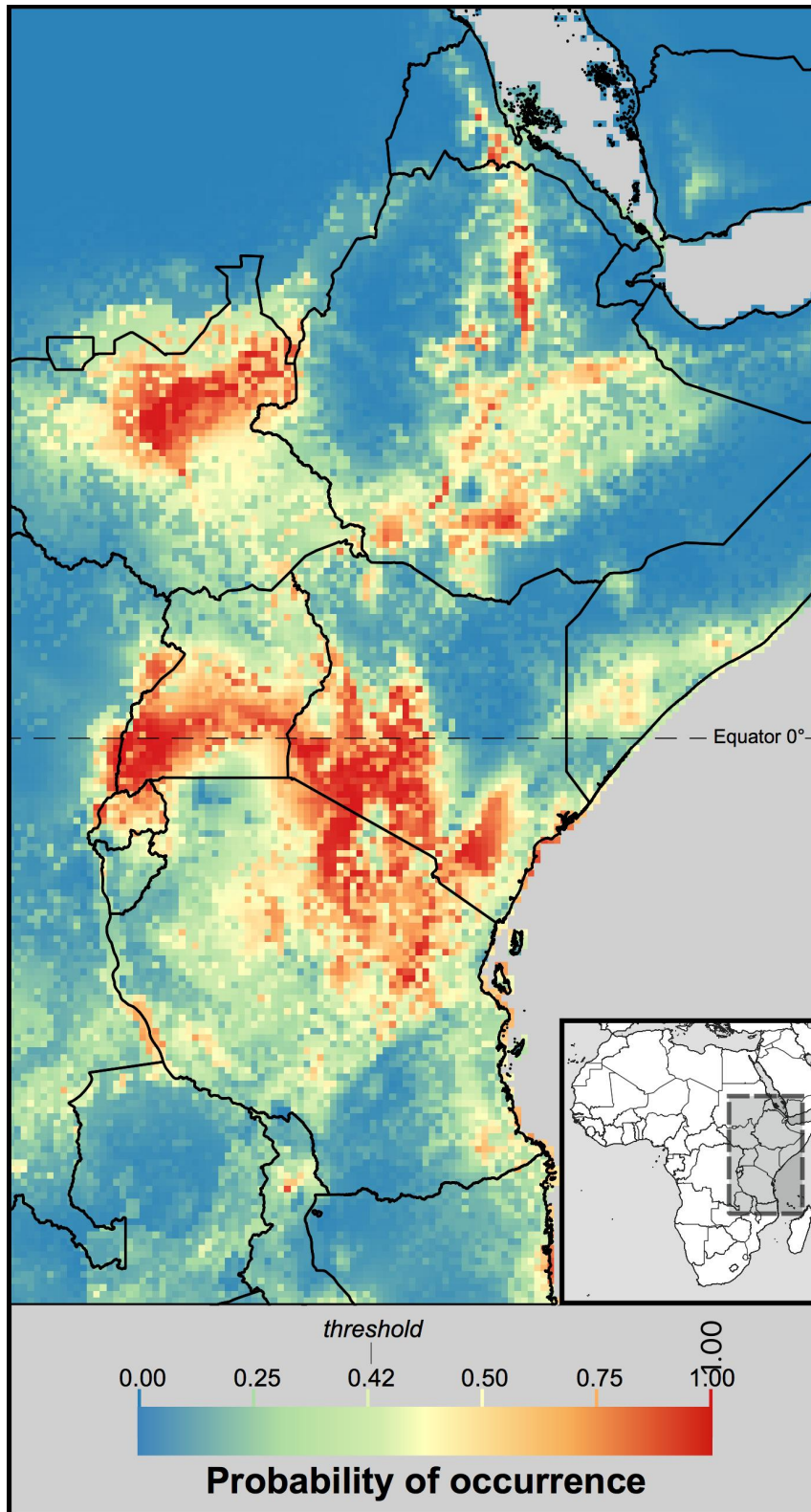


4.12. Average West African suitability predictions for the Saddlebill Stork from ten replicate models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable.

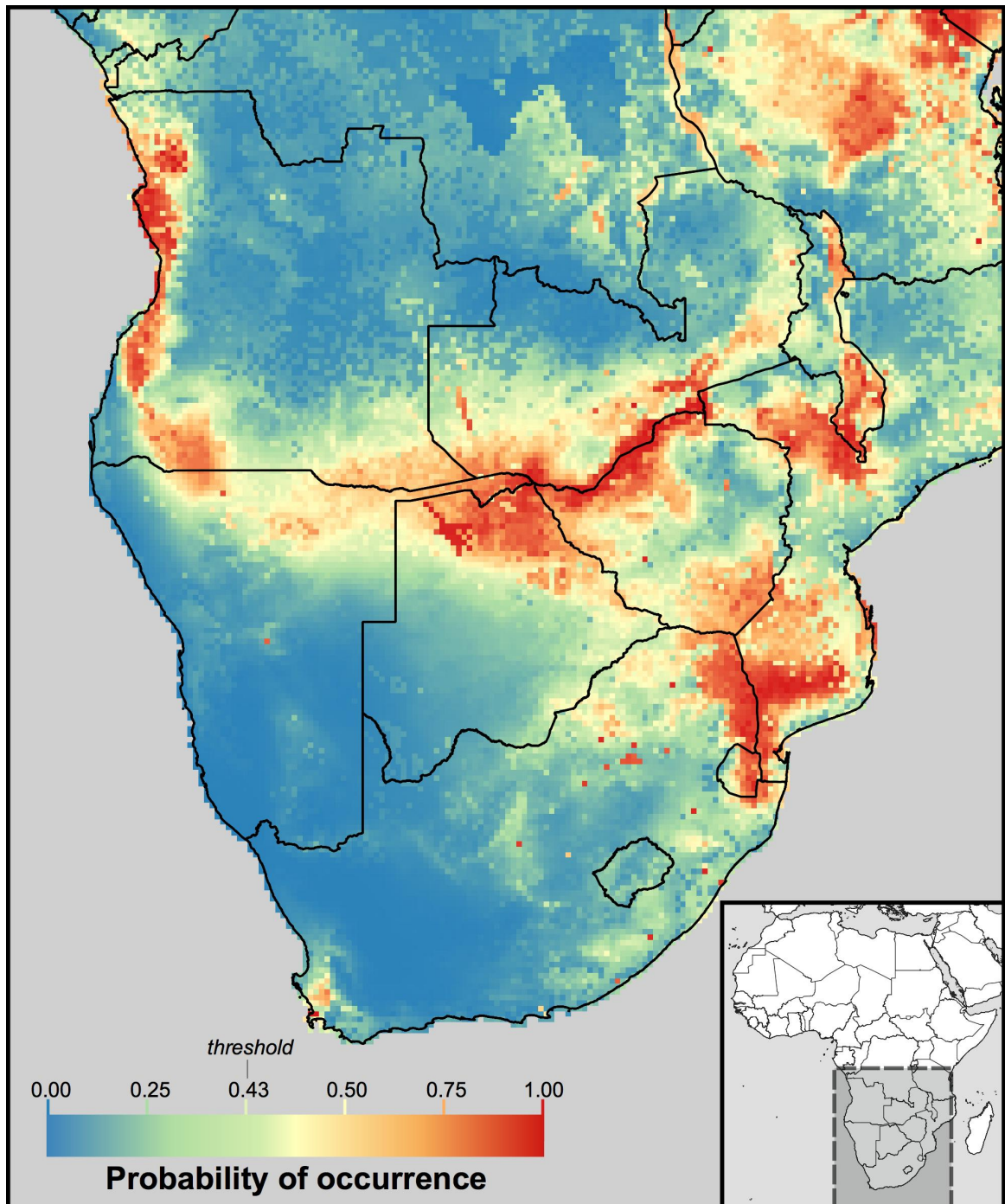
Marabou Stork



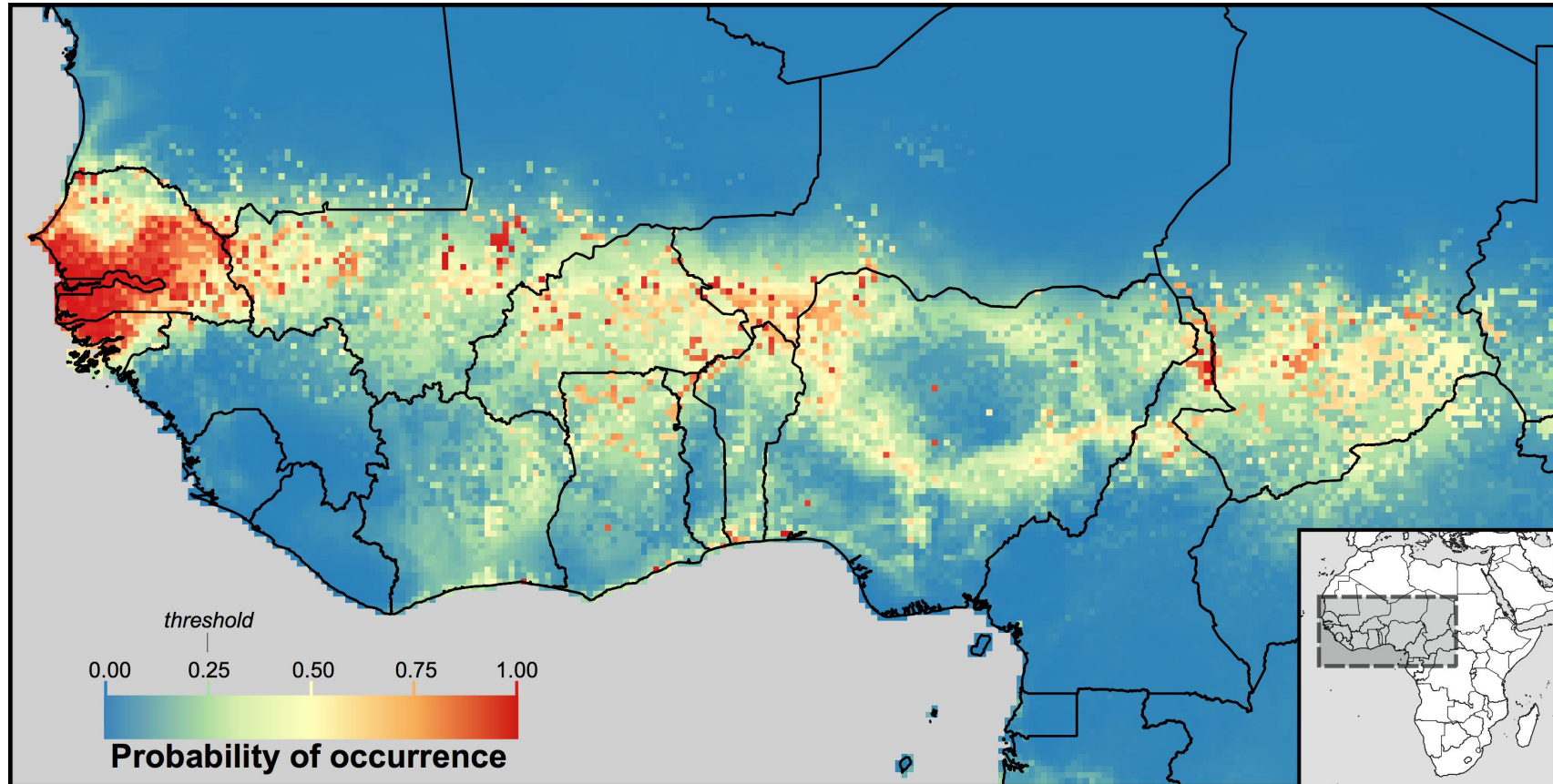
4.13. Average range-wide suitability predictions for the Marabou Stork from ten replicate models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable.



4.14. Average East African suitability predictions for the Marabou Stork from ten replicate models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable.

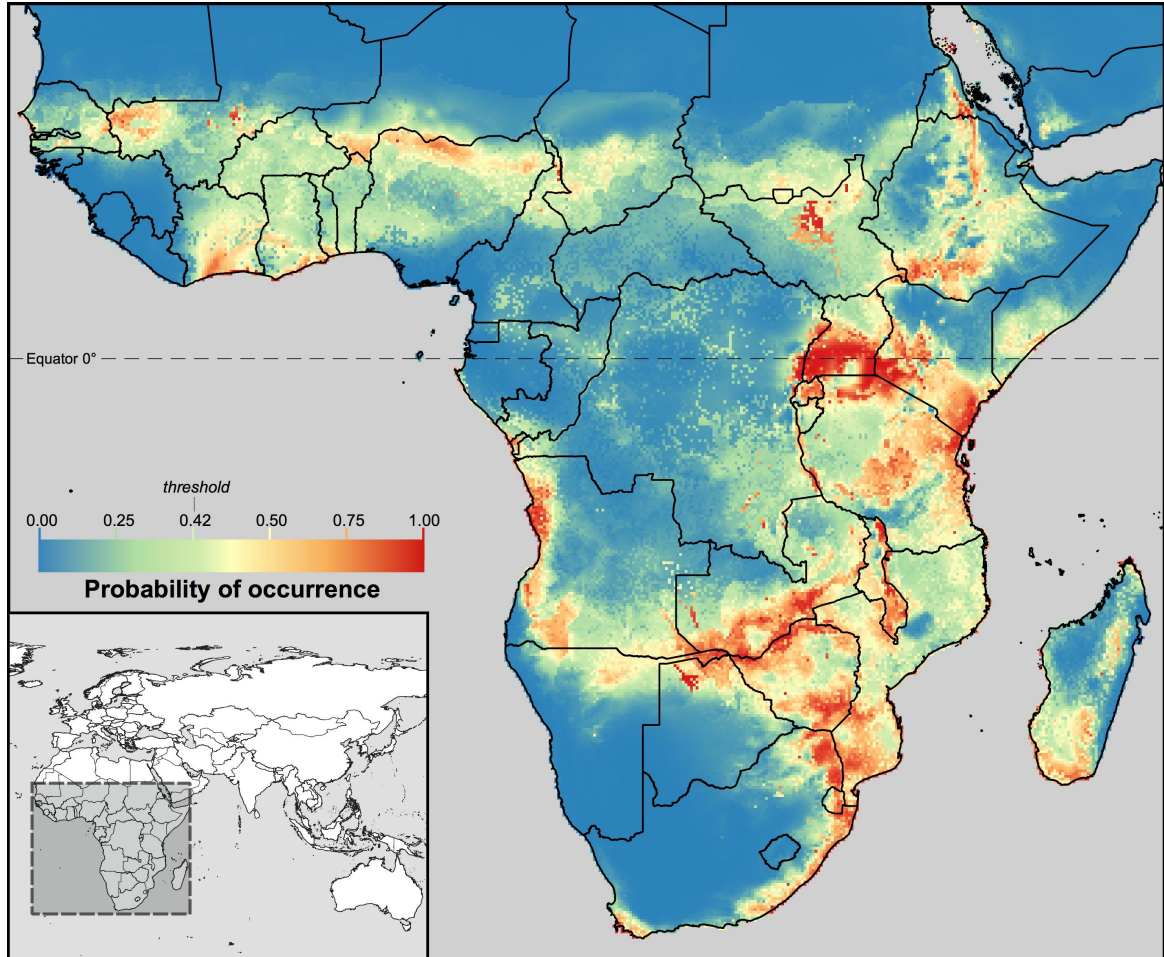


4.15. Average Southern African suitability predictions for the Marabou Stork from ten replicate models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable.

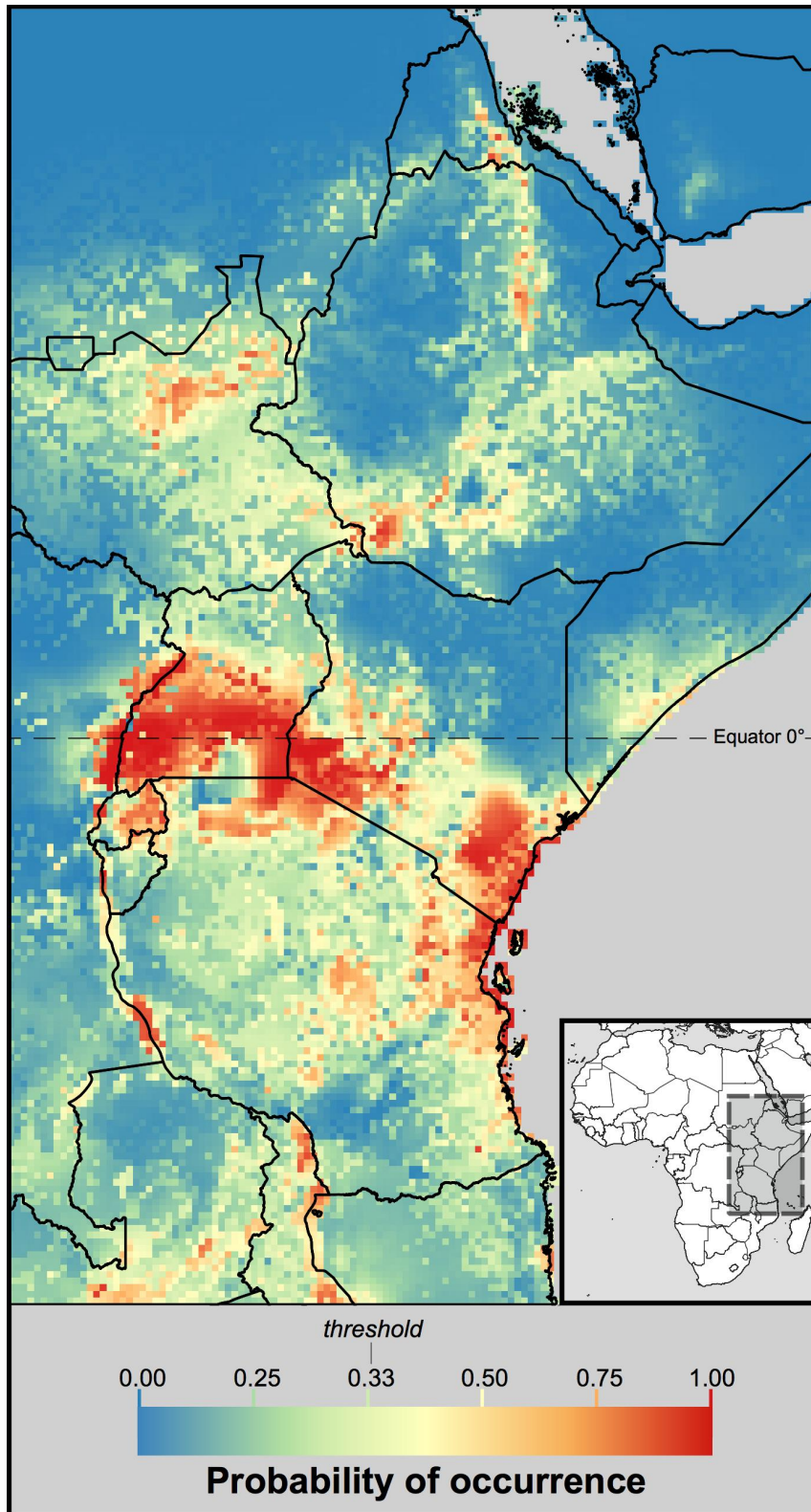


4.16. Average West African suitability predictions for the Marabou Stork from ten replicate models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable.

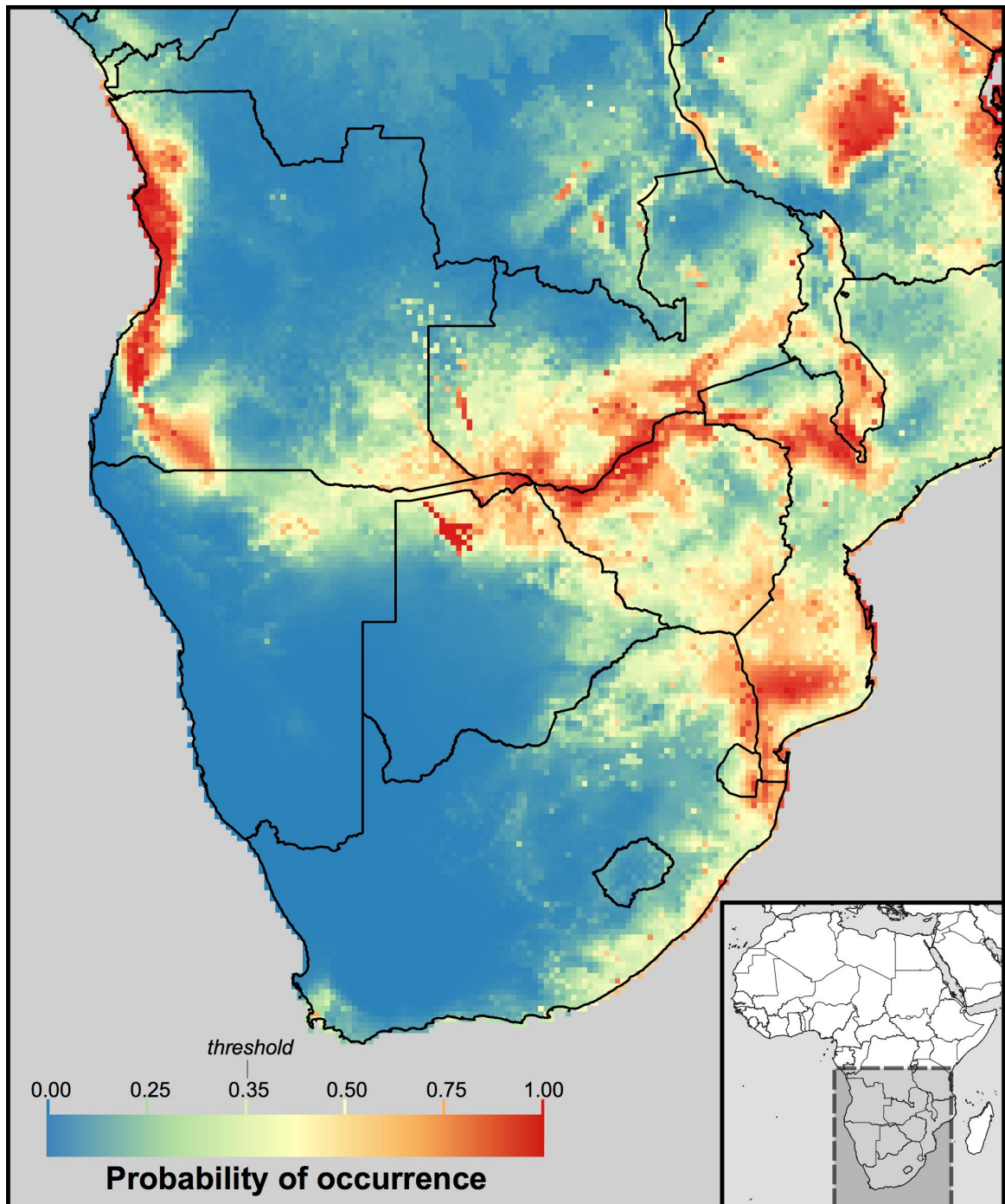
Yellow-billed Stork



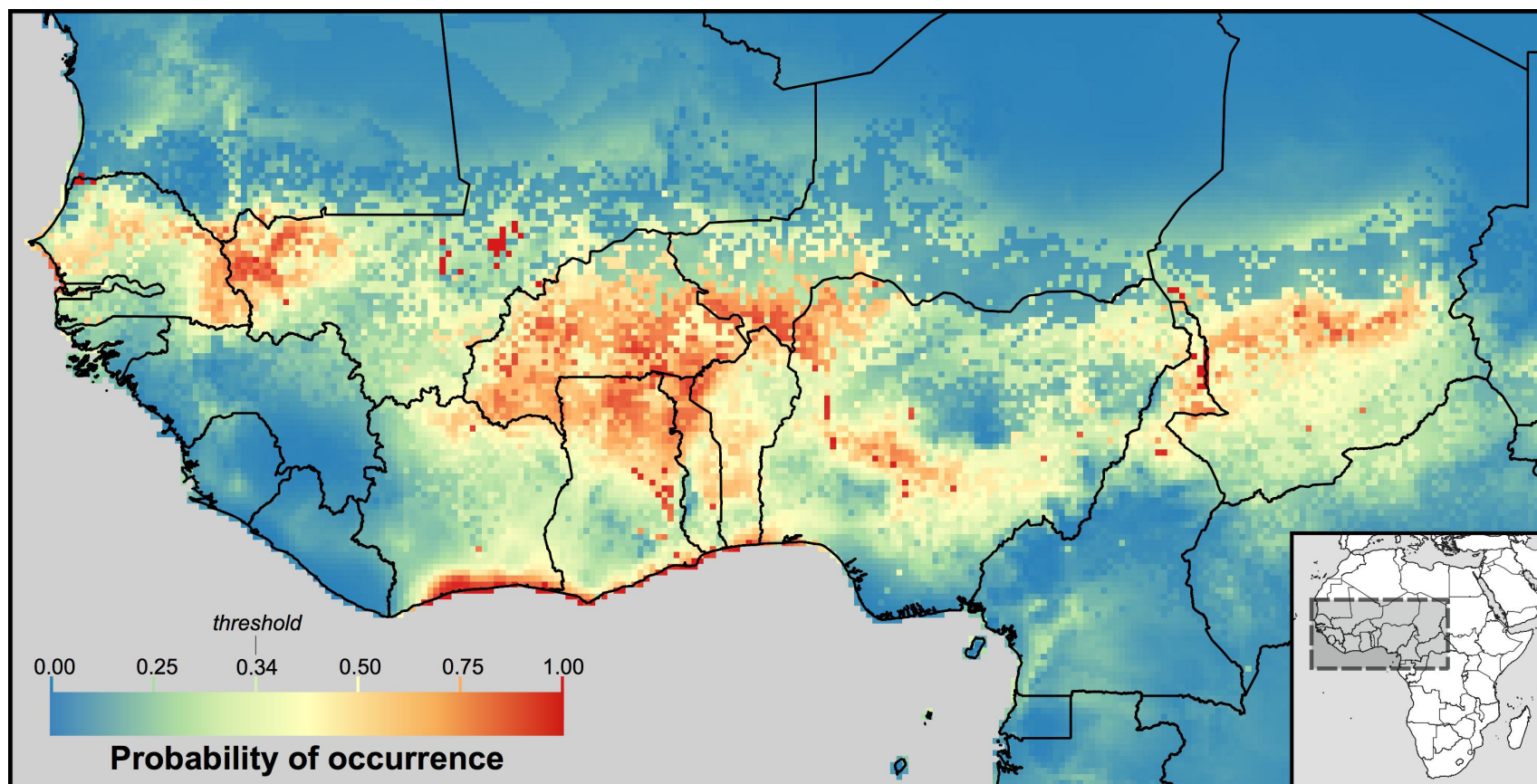
4.17. Average range-wide suitability predictions for the Yellow-billed Stork from ten replicate models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable.



4.18. Average East African suitability predictions for the Yellow-billed Stork from ten replicate models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable.



4.19. Average Southern African suitability predictions for the Yellow-billed Stork from ten replicate models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable.



4.20. Average West African suitability predictions for the Yellow-billed Stork from ten replicate models. Note thresholds for maximum test sensitivity plus specificity, below which conditions are likely unsuitable.

Appendix 5
Estimates of niche overlap (*I*) among species

5.1. Pairwise niche overlap (*I*) estimates for range-wide models.

Species	<i>African Openbill</i>	<i>African Woollyneck</i>	<i>Saddlebill Stork</i>	<i>Marabou Stork</i>	<i>Yellow-billed Stork</i>
<i>African Openbill</i>	–	0.96	0.97	0.98	0.96
<i>African Woollyneck</i>	–	–	0.96	0.95	0.94
<i>Saddlebill Stork</i>	–	–	–	0.98	0.96
<i>Marabou Stork</i>	–	–	–	–	0.98
<i>Yellow-billed Stork</i>	–	–	–	–	–

5.2. Pairwise niche overlap (*I*) estimates for East African models.

Species	<i>African Openbill</i>	<i>African Woollyneck</i>	<i>Saddlebill Stork</i>	<i>Marabou Stork</i>	<i>Yellow-billed Stork</i>
<i>African Openbill</i>	–	0.96	0.97	0.96	0.96
<i>African Woollyneck</i>	–	–	0.96	0.94	0.94
<i>Saddlebill Stork</i>	–	–	–	0.97	0.97
<i>Marabou Stork</i>	–	–	–	–	0.99
<i>Yellow-billed Stork</i>	–	–	–	–	–

5.3. Pairwise niche overlap (*I*) estimates for Southern African models.

Species	<i>African Openbill</i>	<i>African Woollyneck</i>	<i>Saddlebill Stork</i>	<i>Marabou Stork</i>	<i>Yellow-billed Stork</i>
<i>African Openbill</i>	–	0.96	0.94	0.97	0.94
<i>African Woollyneck</i>	–	–	0.96	0.95	0.94
<i>Saddlebill Stork</i>	–	–	–	0.95	0.92
<i>Marabou Stork</i>	–	–	–	–	0.96
<i>Yellow-billed Stork</i>	–	–	–	–	–

5.4. Pairwise niche overlap (*I*) estimates for West African models.

Species	<i>African Openbill</i>	<i>African Woollyneck</i>	<i>Saddlebill Stork</i>	<i>Marabou Stork</i>	<i>Yellow-billed Stork</i>
<i>African Openbill</i>	–	0.89	0.91	0.92	0.91
<i>African Woollyneck</i>	–	–	0.90	0.90	0.92
<i>Saddlebill Stork</i>	–	–	–	0.94	0.94
<i>Marabou Stork</i>	–	–	–	–	0.96
<i>Yellow-billed Stork</i>	–	–	–	–	–

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