Sounding out a continent: Seven decades of bioacoustics research in Africa

Word count: 7305

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Abstract

Bioacoustics has emerged as a useful method of data collection and analysis for diverse animals in a wide range of environments and has helped to describe, monitor, and conserve some of Africa's species biodiversity. However, little is known about how much it contributes to the continent's research corpus. We report results from a systematic review of bioacoustics applications in Africa that summarises the current state of the field and identifies research opportunities. Using keyword searches of bibliographic databases, scanning reference lists, and placing appeals to the bioacoustics community in Africa we identified 727 publications between 1953 and mid-2020. We documented variables ranging from publication type and author affiliation, geographic location, biome and habitat, biological groups, and research type. Most (69%) studies were focused on animal behaviour, with terrestrial species (88.6%), particularly mammals, substantially outweighing research on freshwater (4.8%) and marine (6.6%) habitats. The majority (74.3%) of authors who have contributed to this body of knowledge were non-African affiliates. Our review suggests that bioacoustics research in Africa has considerable room to expand institutionally, taxonomically, and thematically. We highlight the need and potential for more locally driven research and provide a roadmap for future bioacoustics applications across the continent.

Keywords: biodiversity monitoring, bioacoustics, systematic review, African continent, interdisciplinarity

Introduction

Acoustic signals represent a principal vehicle for communication in and among many species. Sounds are produced by many taxonomic groups including insects, crustaceans, fish, amphibians, reptiles, birds, and mammals (Prchalová et al. 2003; Diego-Rasilla and Luengo 2004; Patek et al. 2009; Yu et al. 2011; Rendon et al. 2015; Garcia and Favaro 2017). Auditory cues convey information about organisms' identity, reproductive status, habitat suitability, resource availability, and potential threats, underlining their role in reproductive success and survival (Wilson and Evans 2012; Allen et al. 2014; Warrington et al. 2014; Sibiryakova et al. 2017; Colla et al. 2018; Oliver et al. 2018). Given the importance of acoustic signals in a biological context and our ability to collect acoustic data more effectively through evolving technology, the investigation of animal-based sound production has emerged as a productive biological and ecological informant across a wide range of habitats and landscapes (Laiolo 2010; Blumstein et al. 2011). Increased interest in acoustic research has recently resulted in the establishment of an academic field solely dedicated to the investigation of sound utilisation in biological organisms and its application to monitoring and studying wildlife, generally termed bioacoustics (Mellinger 2018).

Traditionally, bioacoustics was used to contextualise animal vocal behaviour on a biological/ecological scale (Capranica 1967; Rosa and Andreone 2012; Köhler et al. 2017). However, as mechanisms to record animal sounds improved and reduced in cost, methods to take advantage of acoustic data were developed (Laiolo and Tella 2006; Alvarez-Berrios et al. 2016; Jeliazkov et al. 2016). Bioacoustics (and related subfields such as ecoacoustics, which treats sound as an indicative metric of ecological processes on large spatio-temporal scales, and soundscape ecology, which utilises landscape-scale ecological principles; see e.g., (Pijanowski et al. 2011; Sueur and Farina 2015; Farina and Gage 2017; Farina, 2018; Green et al. 2018)) is now used in applications as diverse as providing taxonomic descriptors

(Scherz et al. 2018), informing life history observations (Lowney et al. 2020), indicating the presence/absence of a species in a given area (Shabangu et al. 2019), and welfare monitoring of commercially farmed animals (Mcloughlin et al. 2019).

The uptake in data collection using acoustics has largely been driven by the development and commercialisation of automated recording units (ARUs) (Obrist et al. 2010, Darras et al. 2019). ARUs can be left unsupervised in an environment and record sound continuously or according to some pre-programmed schedule (i.e., 'passive acoustic monitoring,' or PAM) (Sousa-Lima et al. 2013; Mellinger 2018). Relatively cheap ARUs are readily available from a variety of suppliers across the globe (e.g., Whytock and Christie 2016; Hill et al. 2019; Wijers et al. 2021). The large sizes of acoustic datasets and lack of automatic analysis tools still present major management and analysis challenges (Kvsn et al. 2020), and by extension, obstacles to the uptake of such technology. However, sizable datasets have the potential for archiving and extracting valuable long-term biological and ecological information (Gibb et al. 2018), and PAM is now reported to provide a more cost-effective survey option than many other available methods (Sugai et al. 2018).

Africa boasts a huge number of unique species within exceptionally diverse habitats. For example, Madagascar holds approximately 3% of the world's endemic plants and vertebrates, while the Eastern Arc and coastal forests of Kenya and Tanzania register the highest species to area ratio (per 100 km^2) for endemic plants and vertebrates on the planet (Myers et al. 2000). However, as elsewhere, much of Africa's biodiversity is at risk. Further, decision-making processes around preserving African biodiversity are obstructed by several data-related barriers, ranging from unwillingness to collect and interrogate data to data availability and/or data quality (Stephenson et al. 2017; Farooq et al. 2021). Acoustic monitoring has been highlighted as a monitoring technique that can provide much-needed data (Stephenson 2020), and even facilitate monitoring of environmental threats that can be detected or assessed acoustically such as illegal hunting and logging (Pichegru et al. 2017; Mporas et al. 2020).

Despite this wide applicability, relatively little is known about how bioacoustics is used in Africa. Those reviews that have scrutinised the geographical distribution of bioacoustics applications (Shannon et al. 2016; Sugai et al. 2019; Jerem and Mathews 2021) suggest that dissemination of expertise and equipment has been disparately distributed along a global North-South axis. This is a transdisciplinary pattern (Maas et al. 2021) that mirrors historical and current global power structures. Geographical biases in the production and diffusion of knowledge are no novel phenomenon and are well established in fields such as medicine, with a heavy skew towards high-income countries (Skopac et al. 2020). Meijaard et al. (2015) found that high citation rates in conservation science, were strongly linked to per capita gross domestic product (GDP) and quality of governance – low rankings in which are usually (not necessarily justifiably) associated with the Global South.

Within bioacoustics, emphasis has largely been placed on habitat-, taxa-, and theme-specific reviews (Laiolo 2010; Lindseth and Lobel 2018; Teixeira et al. 2019). Given the paucity of Africa-based bioacoustics literature collations, we have identified a need to apply a regional filter and draw focus to knowledge flow and structures in the African context. We systematically review bioacoustics research undertaken in Africa and its territories to outline the focus and scope of historical research efforts within this domain. This relates particularly to a need for accurate and comprehensive biodiversity assessments (including threat detections) across African habitats, for which bioacoustics could be a useful source of data.

We thus present a baseline that we hope will help (1) further stimulate acoustics-based biodiversity data collection in Africa, (2) grow the continent's bioacoustics research capacity, and (3) inform future research directions by highlighting both gaps and opportunities.

Materials and methods

Between December 2019 and August 2020, we conducted a comprehensive search for literature on African bioacoustics research. We tried to adapt our synthesis based on recommendations outlined by Pullin and Stewart (2006) and Haddaway et al. (2020), to ensure diligence and minimise any potential bias, although due to the authors' linguistic predispositions, only English literature qualified for appraisal.

Our scope includes any use of acoustic signals from natural systems, and thus incorporates bioacoustics, ecoacoustics, and generic acoustic monitoring, and can be summarised by a definition by Mellinger (2011): "[animal] bioacoustics covers all matters related to the production, transmission, and reception of sound in nature, as well as the investigation and use of natural sound by people and impacts of anthropogenic sounds on animals". Our search parameters were based on varying combinations of the terms 'Africa(n)' OR individual African country names, AND 'bioacoustics', 'acoustic monitoring' OR 'ecoacoustics'. These search terms were run across the Web of Science Core Collection, Google Scholar, and the Victoria University of Wellington library. Search results were then refined based on the above definition for bioacoustics and whether any part of the study was conducted on African territory or endemic species. Studies on African species in non-African research facilities were included because they contribute to the understanding of the vocal repertoire and behaviour of African animals under different settings and environmental conditions and are intended to ultimately be applied in Africa.

We augmented our literature finding by scanning the reference lists of the papers we found and issued a call for submissions via the African Bioacoustics Community mailing list and social media platforms (https://africanbioacoustic.wixsite.com/abcommunity). As the aim was to provide a baseline data set, we did not apply any temporal limits to the publications identified. Where possible we replaced dissertations and theses with corresponding peer-reviewed publications preferring the peer-reviewed literature and aiming to avoid pseudo-replication.

Data extraction

For each paper we documented the variables listed in Table 1, which fall into the categories of publication type and authorship, geographic location, biome and habitat, biological groups, and research aims.

Affiliation data was standardised to account for institutional name changes over time. For example, the Gerhard Mercator University (formerly the University of Duisburg) merged with the University of Essen in 2003 to form the University of Duisburg-Essen. In this case, studies published under the auspices of any of these institutions were annotated 'University of Duisburg-Essen'.

One of our variables was the national affiliations of researchers involved in bioacoustics research in Africa. One challenge with this is that many authors report multiple affiliations, often one (or more) in Africa and one (or more) not. We identified primary and secondary affiliations (by order of presentation in the author list) and used these to differentiate between African and non-African affiliates. We also assessed how much each African country (based on affiliation address) has contributed to regional study output (based on the African Union's regional classifications).

Localities (or study sites) were initially transcribed from each publication and quantised to the scale of national park or similar (for example, Mount Kasigau was classified as part of the Eastern Arc Mountains). We also had to account for variations in names over time. A total of 34 localities were omitted, because the corresponding coordinates were not accessible through the respective publication or via internet searches.

Information on focal taxa was supplemented with appropriate Linnaean nomenclature, starting with taxonomic class. Here too, nomenclature adaptations over time were considered and corrected accordingly. Proportions of lower taxa (sub-class) are expressed as percentage of the respective taxonomic class. Records attributed to terrestrial habitats were further categorised into biomes as described by Olsen et al. (2001). These were extracted by overlaying our locality record with corresponding biome raster data in ArcGIS Pro 10.7.1 (Olsen et al. 2001).

Table 1: List of data descriptors extracted from each publication to inform trends in bioacoustics research emanating from the African continent and its territories.

Category	*Descriptor*	*Class*	*Description*
Publishing and authorship	Publication year		
	Publication type	Book chapter	
		Journal article	Research published in a peer-reviewed article

		Report	Studies published through governmental institutions or non-governmental organizations
		Thesis	Any published Bachelor's, Honour's, Master's or doctoral dissertation
	Journal	Name	
		Keywords	
	Author affiliation	Primary	First-listed institution the author was affiliated the production of the published study
		Secondary	Secondarily listed institution(s) the author was with during the production of the published stu
	Affiliation base	African	Nationality of each institution
		Non-African	
Geography	Localities		Specific location of study site
	Country	African country	Country where field research was carried out
		Ex-situ	Non-African location of studies investigating A species (e.g. zoos)
Biomes and habitat	Habitat/biome	Freshwater	
		Marine	
		Terrestrial	Subdivision into 14 biomes based on the classification by Olsen et al. (2001)
Biological groups	Taxa	Class	
		Order	
		Family	
		Genus	
		Species	
Research themes		Behavioural	Studies concerned with animal behaviour, relat production of and response to sound

Conservation	Studies investigating practical implementations bioacoustics to aid conservation efforts
Experimental	Studies experimenting with methodological protocols
Human impact	Studies assessing anthropophonic influences on animals and their acoustic environments
Physiological	Studies examining how certain physiological attributes impact sound production
Presence-absence	Studies focused on determining the presence or absence of a certain taxon
Taxonomic	Studies using bioacoustic classifiers to describe a taxonomic group

Table 2: Number of studies published per researcher affiliation base (by country) for each region in which the study was conducted. Regional categorisations are based on the African Union's delineation (www.au.int).

		Study region				
Affiliation region	Affiliation nationality	Central	Eastern	Northern	Southern	Western
Central	Cameroon	5	-	-	-	-
	Democratic Republic of the Congo	1	-	-	-	-
Eastern	Comoros	-	4	-	-	-
	Ethiopia	-	2	-	-	-
	Kenya	1	32	-	4	1
	Madagascar	-	28	-	1	-
	Sudan	-	1	-	-	-
	Tanzania	3	6	-	1	1
	Uganda	-	21	-	1	1

Northern	Algeria	-	-	1	-	-
	Morocco	-	-	3	-	-
	Tunisia	-	-	1	-	-
Southern	Botswana	-	-	-	4	-
	Eswatini	-	2	-	8	-
	Malawi	-	-	-	1	-
	Namibia	-	1	-	6	-
	South Africa	1	16	-	149	-
	Zimbabwe	-	1	-	3	-
Western	Ghana	-	-	-	-	1
	Ivory Coast	-	1	-	1	16
	Nigeria	-	-	-	2	-
	The Gambia	1	-	-	-	1

Categorisations among and within biological groups, geographies, habitats and research themes were treated without mutual exclusivity, meaning that more than one annotation could be assigned to one publication to reflect the fact that many bioacoustics studies are multi-purpose, and that the data collected can later be reanalysed to investigate other questions.

Data analyses

We used R (R Core Team 2020) for statistical analyses throughout. Differences in African vs non-African affiliation were investigated based on affiliation listing (primary or secondary), first authorship, and overall. Changes in time were analysed across 9-year intervals using Chi-square and Fisher's Exact tests (depending on the size of expected values), by evaluating them across sequential pairs (Table 2). For this analysis we excluded our first record (from

1953), due to the absence of affiliation details, meaning that our chronology begins in 1957. Data from 2020 were also omitted, because of the year's incomplete record.

Results

Our search yielded a total of 682,852 titles. After title screening these were reduced to 813, of which 766 abstracts met our criteria. Of these, 727 full-text documents were accessible to us and constituted this review's database. Table A1 provides a detailed overview of search parameters and outcomes. The first paper was published in 1953, one of two we found for that decade, with a further four from the 1960s.

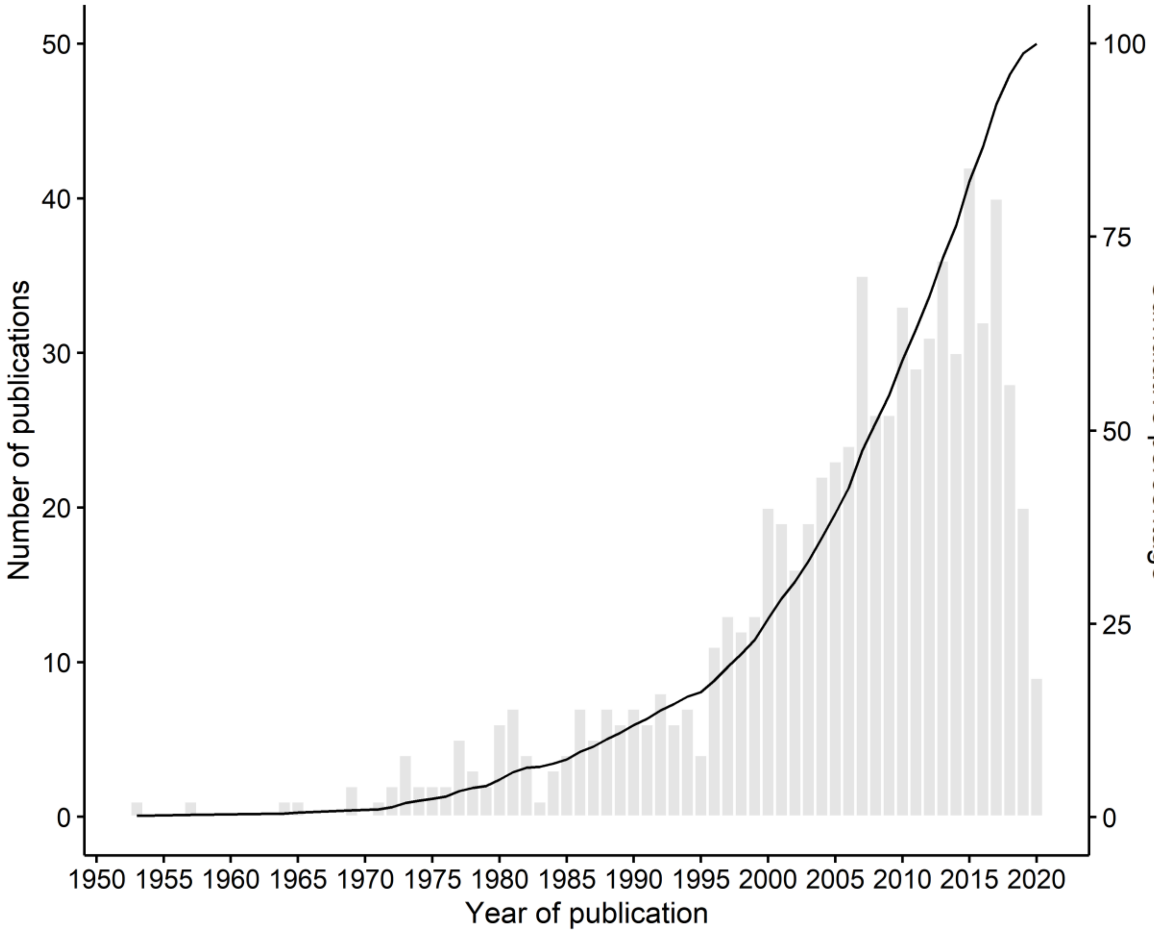

Figure 1: Publication output (bar plot) of African bioacoustics research over time. Our record starts in 1953, with the solid black line indicating the cumulative percentage since then. Records for 2020 are up to August.

As can be seen in Figure 1, the number of publications has been increasing exponentially over time: most research has been published relatively recently, with the cumulative percentage of our documented studies passing the halfway mark in 2007/2008, at an average publication rate increase of 14.1% per year; see Table A2.

Publishing and authorship

Most research outputs were published in peer-reviewed scientific journals (96.3%, n = 699), with book chapters, student theses (which were omitted if a peer-reviewed paper reporting the same results was available), and reports making up 2.2% (n = 16), 1.2% (n = 9), and 0.2% (n = 2), respectively. Note also that such ‘grey literature’ is generally more difficult to access, especially from pre-internet times, which may have resulted in under-detection. Our sample includes 174 different journals, with Animal Behaviour (10.5%, n = 76) being the most common publication venue (Table A3). More than two-thirds (69.2%, n = 503) of all publications have been open access, with a mean annual increase of open access publication of 23.8%.

Table 3: Differences in publication frequency among author affiliations.

	n (%)							
	First author		*All authors*		*First author*		*All authors*	
	AF	NAF	AF	NAF	χ^2	p-value	χ^2	p-value
Primary affiliation[b]	127 (17)	584 (82)	492 (21)	1804 (79)				
1957 -1965	1 (33)	2 (67)	3 (43)	4 (57)	-	-	-	-
1966 - 1974	4 (40)	6 (60)	4 (33)	8 (67)	-	1.000[a]	-	1.000[a]
1975 - 1983	4 (13)	28 (87)	9 (14)	57 (86)	-	0.075[a]	-	0.107[a]

1984 - 1992	8 (15)	45 (85)	20 (19)	89 (81)	-	1.000[a]	0.703	0.402
1993 - 2001	13 (12)	92 (88)	41 (16)	216 (84)	0.225	0.635	0.359	0.549
2002 - 2010	26 (12)	189 (88)	100 (15)	573 (85)	0.005	0.941	0.217	0.642
2011 - 2019	65 (23)	219 (77)	293 (26)	842 (74)	9.562	**0.002**	30.934	**0.000**
Secondary affiliation[b]	100 (54)	83 (46)	243 (49)	245 (51)				
1957 -1965	0	0	0	0	-	-	-	-
1966 - 1974	1 (20)	4 (80)	1 (20)	4 (80)	-	1.000[a]	-	1.000[a]
1975 - 1983	1 (50)	1 (50)	3 (50)	3 (50)	-	1.000[a]	-	0.206[a]
1984 - 1992	4 (100)	0 (0)	4 (100)	0 (0)	-	0.333[a]	-	1.000[a]
1993 - 2001	10 (67)	5 (33)	12 (52)	11 (48)	-	0.530[a]	-	0.123[a]
2002 - 2010	19 (50)	19 (50)	42 (48)	46 (52)	0.862	0.353	0.144	0.704
2011 - 2019	60 (54)	52 (46)	163 (48)	175 (52)	0.010	0.920	0.003	0.956
All affiliations[b]	227 (25)	667 (75)	735 (26)	2049 (74)				
1957 -1965	1 (33)	2 (67)	3 (43)	4 (57)	-	-	-	-
1966 - 1974	5 (33)	10 (67)	5 (29)	12 (71)	-	1.000[a]	-	0.647[a]
1975 - 1983	5 (15)	29	13	60 (83)	-	0.247[a]	-	0.308[a]

		(85)	(17)					
1984 - 1992	12 (21)	45 (79)	24 (21)	89 (79)	0.565	0.452	0.499	0.480
1993 - 2001	23 (19)	97 (81)	53 (19)	227 (81)	0.087	0.769	0.317	0.574
2002 - 2010	45 (18)	218 (19)	142 (19)	618 (81)	0.052	0.819	0.019	0.890
2011 - 2019	125 (32)	271 (68)	454 (31)	1017 (69)	14.249	**0.000**	39.397	**0.000**

AF = African; NAF = Non-African; n = number of occurrences; % = relative frequency expressed in percentages; χ^2 = Chi-square value; [a] = use of Fisher's Exact Test; [b] = include records from 2020; Bold values denote significant (*P* < 0.05) change in occurrences between corresponding and preceding time interval relative to affiliation proportions.

The articles included 1469 keywords (Table A4). Some of the most commonly used were 'bioacoustics' (2.0%, n = 50), 'communication' (1.3%, n = 33), 'vocalization' (1.3%, n = 32), 'acoustic communication' (0.9%, n = 23), 'echolocation' (0.8%, n = 21), 'vocal communication' (0.8%, n = 21), 'Madagascar' (0.8%, n = 19), 'vocalizations' (0.8%, n = 19), 'new species' (0.7%, n = 18), and 'taxonomy' (0.7%, n = 18).

We registered a total of 1181 authors, with 485 different affiliations, omitting 15 authors where we were unable to determine an affiliation. Non-African affiliations outweighed African affiliations by almost 3:1 (n = 363 vs n = 122; Table A5).

Among African institutions (primary and secondary) the University of Cape Town (13.7%, n = 101), the University of Pretoria (9.3%, n = 68), and Stellenbosch University (6.0%, n = 44) were most frequently documented. Of the 22 affiliation nationalities, 33.3% (n = 40) were South Africa, 13.1% (n = 16) Kenya, and 9.8% (n = 12) Madagascar based. The most represented non-African affiliations were the University of St Andrews (4.9%, n = 100), the University of Pennsylvania (4.7%, n = 97) and the University of California (3.9%, n = 79). Allowing for multiple affiliations (n = 2787), most researchers have been affiliates of the University of Cape Town (3.6%, n = 101), the University of St. Andrews (3.6%, n = 100), and the University of Pennsylvania (3.5%, n = 97).

In terms of regional research output from African affiliations, South African affiliates participated in the majority of research conducted in Southern Africa (Table 2). Kenya-based affiliates registered the most contributions towards studies done in East Africa.

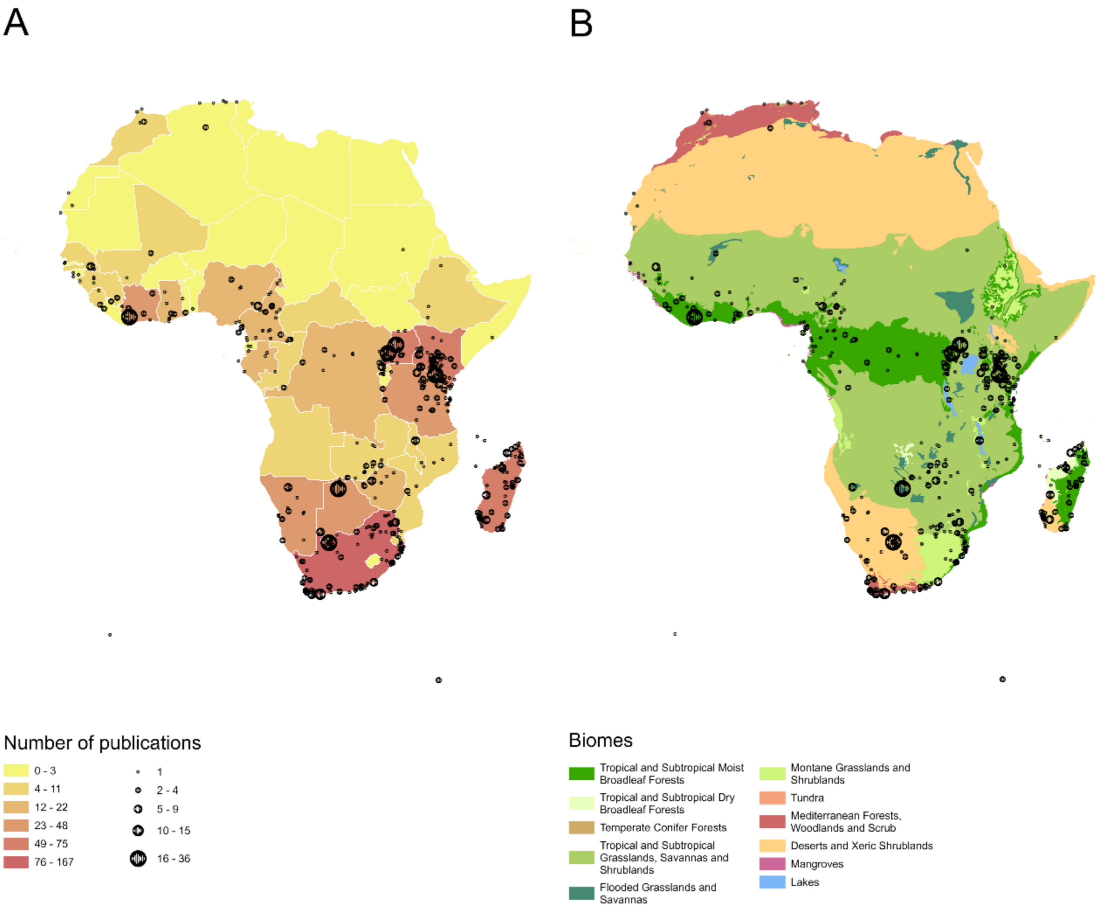

Figure 2: Distribution of bioacoustics publications across Africa, represented by a colour gradient (publications per country [left]) and graduated symbology (publications per study

site). Study sites of bioacoustics research across Africa, in relation to biome classification (Olsen et al. 2001) are depicted on the right. Increasing symbol size corresponds to higher number of research publications per site.

Overall, African-affiliated authorship increased over time (Table 3) but was only statistically significant between the most recent time intervals (2002–2010 to 2011–2019), both among first authors ($\chi^2 = 9.562$, $p < 0.05$, df = 1), and cumulatively ($\chi^2 = 30.934$, $p < 0.01$, df = 1). Similar observations were made among multiple affiliations, for both first ($\chi^2 = 14.249$, $p < 0.01$, df = 1) and all authors ($\chi^2 = 39.397$, $p < 0.01$, df = 1). No significant trends were documented for secondary affiliations. On average, significantly more non-African primary affiliates were listed per publication than African (Mann-Whitney U test: N1 = 227, N2 = 622, W = 49834, $p < 0.01$).

Geography

We documented study sites in 40 African countries. The most common were South Africa (20.1%, n =167), Kenya (9.0%, n = 75), and Madagascar (8.9%, n = 74) (Figure 2, Table A6). In addition, we identified 85 study sites (ex-situ) outside of Africa. We also identified 500 study localities across those 40 African countries. Of these, Taï National Park in the Ivory Coast was the most common site (3.7%, n = 36), followed by Uganda’s Budongo Central Forest Reserve (3.0%, n = 29) and South Africa’s Kuruman River Reserve (3.0%, n = 29). More than a tenth (10.2%, n = 85) of the studies we found were of African species but conducted overseas under laboratory/zoo conditions.

Biomes and habitats

Terrestrial systems have been the basis of the majority of bioacoustics studies (88.7%, n = 652, Figures 3&5). Among terrestrial habitats, we documented studies conducted across 10 different biomes (excluding lakes, Figure 2). More than one-third of bioacoustics research on the African continent has been conducted in tropical and subtropical grasslands, savannas and shrublands (34.3%, n = 305), and almost another third in tropical and subtropical moist broadleaf forests (31.8%, n = 283); see Table A7. Desert and xeric shrublands (n = 111) were the setting of 12.5% of all terrestrial studies. In contrast to terrestrial systems, marine (6.5%, n = 48) and freshwater (4.8%, n = 35) systems have been less explored. However, marine studies have experienced a relatively recent upturn in publication frequency and abundance. This is best illustrated by the fact that only 5 marine-based studies were published before 2000, whereas since the start of 2015 there were 24 (50.0%). We were unable to record any freshwater studies since 2015, while almost two-thirds (65.7%; n = 23) were published from 2000 to 2015.

Biological groups and research themes

We documented 6 taxonomic classes, 36 orders, 96 families, 204 genera, and 273 species (Figures 3 & 4, Table A8), amounting to 853 taxonomic records. Overall, 636 publications (87.5%) focussed on a single taxon. Mammals (Class Mammalia) have attracted 66.5% (n = 567) of the research focus, followed by birds (Class Aves) with 14.0% (n = 119). Insects (Class Insecta), ray-finned fishes (Class Actinopterygii), amphibians (Class Amphibia), and reptiles (Class Reptilia) make up 7.7% (n = 66), 5.7% (n = 49), 5.3% (n = 45), and 0.8% (n = 7) of the remaining record, respectively (Figure 3).

Terrestrial mammals (91.0%, n = 516) have been the basis of bioacoustics studies in Africa far more than marine mammals (9.0%, *n* = 51). The most studied mammal family has been Cercopithecidae (Old World monkeys, 26.3%, n = 149, Figure 5, while *Pan troglodytes* (9.2%, n = 52), *Loxodonta africana* (4.6%, n = 39), and *Papio ursinus* (3.4%, n = 29) have been the most explored mammal species in our record; overall studies on primates (Order Primates, n = 296) comprised more than half (52.3%) of the publications based on mammals. Marine mammals were only represented in the Order Artiodactyla. Members of Family Delphinidae have been the most studied marine mammalian subjects (4.6%, n = 26), while *Megaptera novaeangliae* (1.8%, n =10), *Tursiops aduncus* (1.1%, n = 6), and *Tursiops truncatus* (1.1%, n = 6) have been the most commonly studied marine mammal species.

The most studied avian order, Passerines (Order Passeriformes) have constituted 52.1% (n = 62) of the avifaunal record. Family-wise, most bird-related efforts were directed at Leiothrichidae (14.3%, n = 17), while the most researched species within this class have been *Turdoides bicolor* (13.5%, n = 16), *Dicrurus asimilis* (5.0%, n = 6), and *Phoeniculus* *purpureus* (5.0%, n = 6).

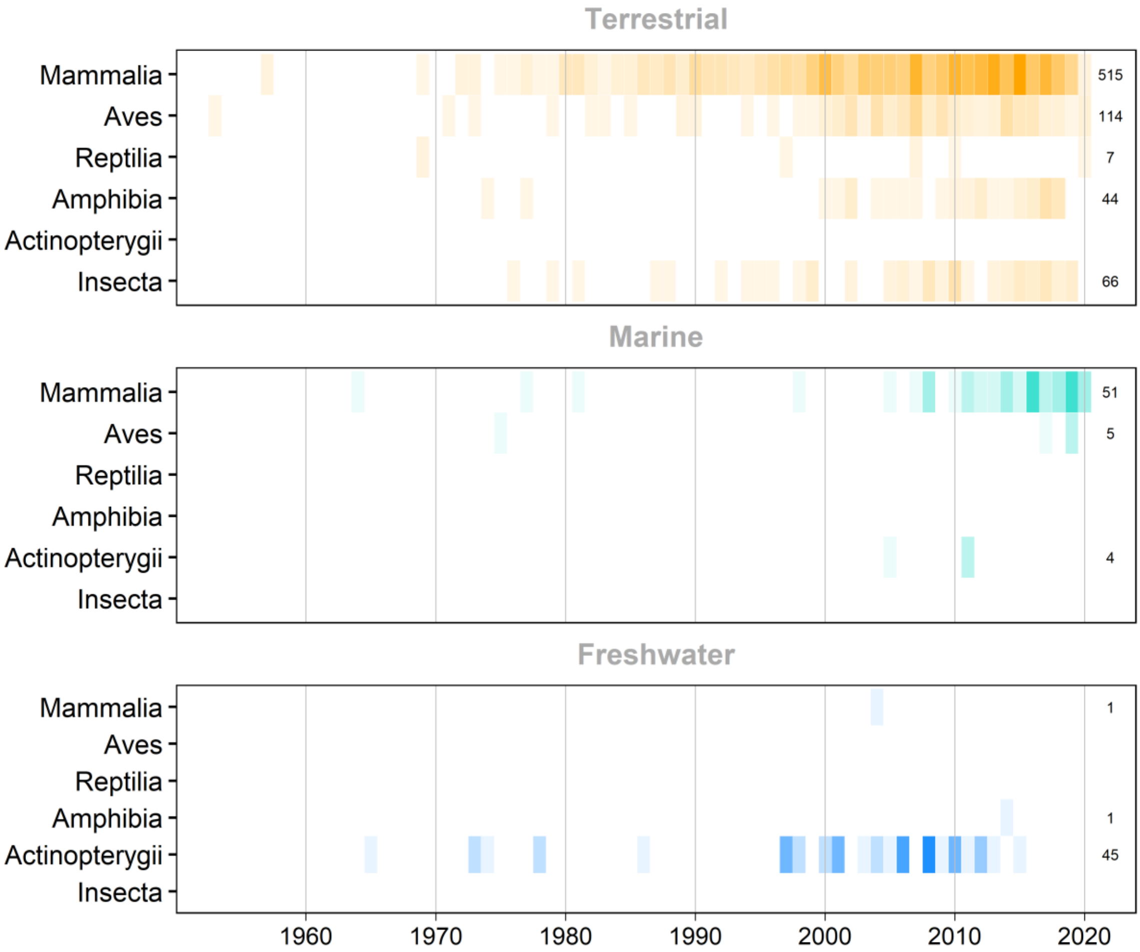

Figure 3: Publication record of African bioacoustics research based on taxonomic classes and subcategorised according to habitat. Filled plates indicate documented publication for a given year, while transparency gradient illustrates publication volume for respective years. Total numbers of publications documented per category are presented at the end of each row.

Of the other taxonomic classes, amphibians have all been from the order Anura, and no amphibian species that appears in more than one publication as a solo study subject. Within Class Actinopterygii (or ray-finned fish), Cichliformes and Cichlidae constituted the majority of research efforts on an order and family level, respectively, with 61.2% (n = 30), each. Orthoptera (63.6%, n = 42) and Tettigoniidae (54.6%, n = 36) have been the most investigated insect order and family, respectively. Reptiles have been the least represented taxonomic class in the literature, with Squamata (85.7%, n = 6) and Crocodilia (14.3%, n = 1) the only reptilian orders documented.

The research themes most commonly assigned to publications (n = 858) were ‘behaviour’ (69.0%, n = 592), ‘taxonomy’ (12.9%, n = 111), and ‘presence-absence’ (7.7%, n = 66).

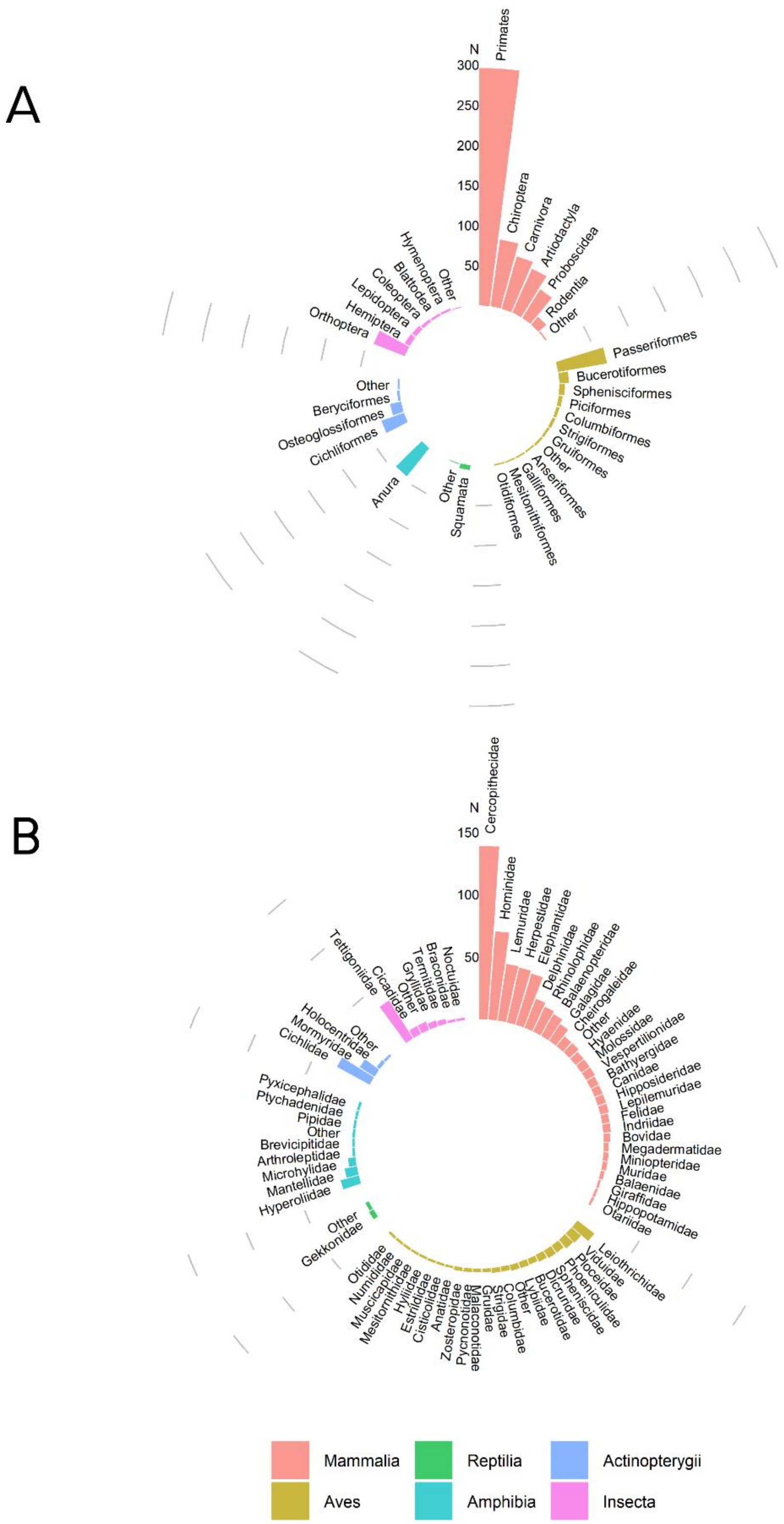

Figure 4: Documented study subjects based on number of publications per taxonomic (A) order and (B) family, categorised by class (Mammalia [n = 567], Aves [n = 119], Reptilia [n = 7], Amphibia [n = 45], Actinopterygii [n = 49], Insecta [n = 66]). Any order that only one publication was attributed to was classified as 'Other'. Grey grid lines correspond with main axis (N) indicating number of publications.

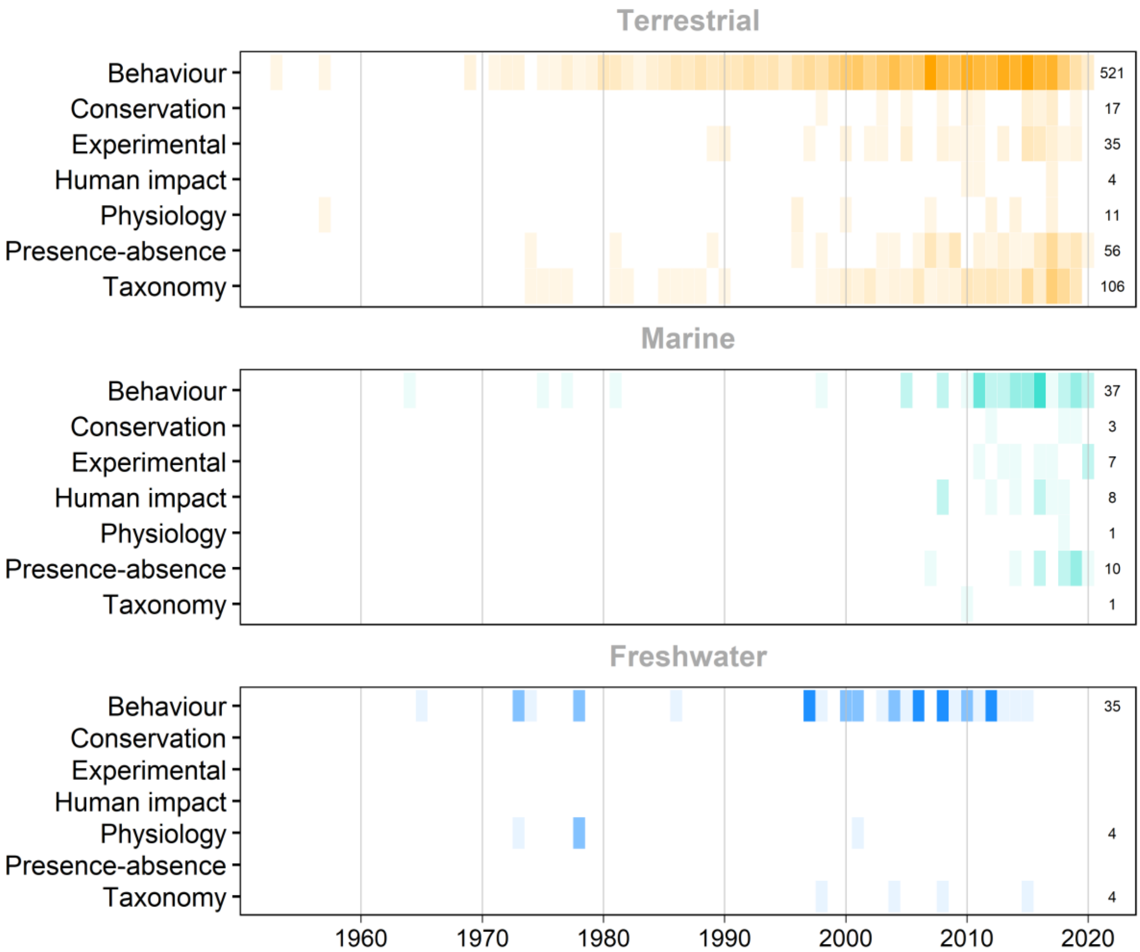

Figure 5: Publication record of African bioacoustics research based on research themes and subcategorised according to habitat. Filled plates indicate documented publication for a given year, while transparency gradient illustrates publication volume for respective years. Total numbers of publications documented per category are presented at the end of each row.

Discussion

Our comprehensive assessment of bioacoustics literature from Africa demonstrates that relevant publications have experienced an exponential upturn over the last decade, but still include some geographical, institutional, taxonomic, and thematic biases. Our review shows that the literature is skewed towards Eastern and Southern Africa, non-African affiliated authorship, mammalian subjects, and behaviour-based and terrestrial research.

The overall publication rate we observed is in line with related literature, presenting evidence of an exponential increase in publication of results globally (Sugai et al. 2019; Xie et al. 2020). Sugai et al. (2019), for example, found that almost two-thirds of PAM-based research has been restricted to the temperate zones of the Northern Hemisphere, while Northern Africa was highlighted as a primary geographical gap. This aligns with our own distribution map.

Bioacoustics research in Africa has been concentrated in Eastern and Southern Africa. This applies to study location, as well as institution base among African affiliated authors.

Concentration of research output seems to be a recurring theme, with Agha et al. (2018)

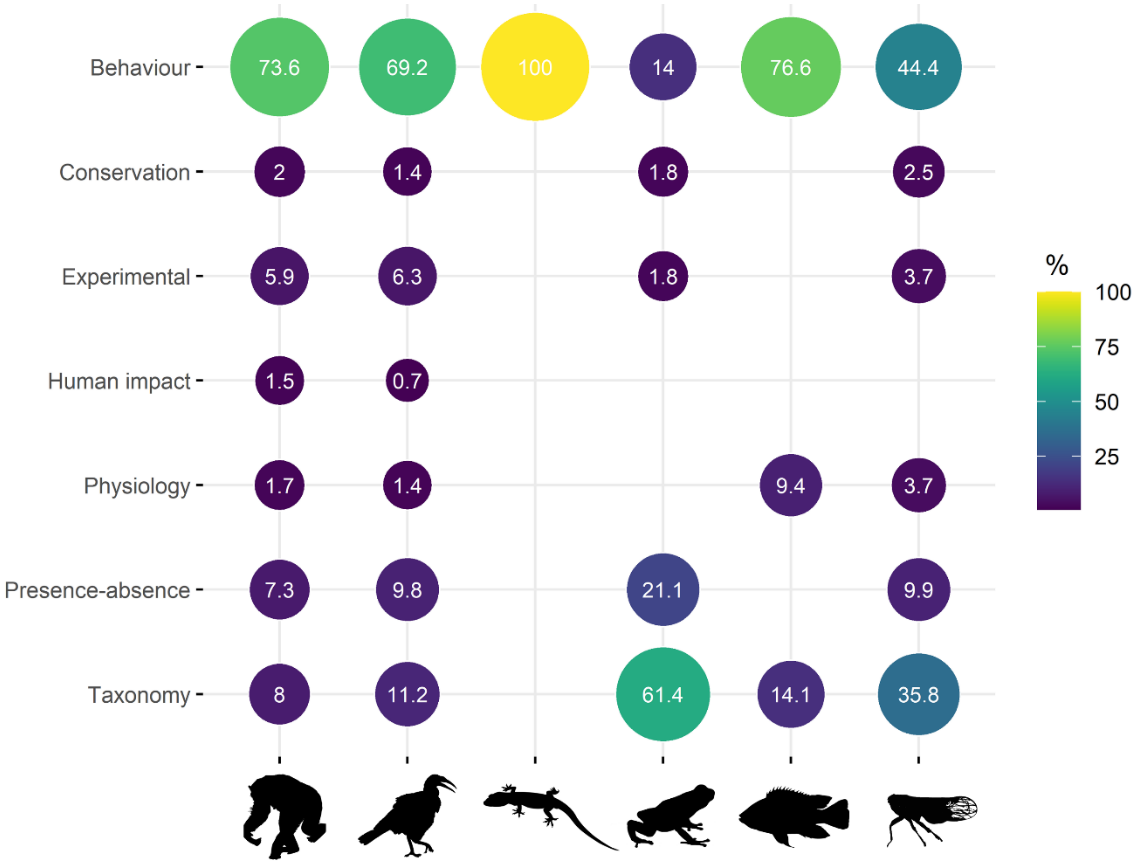

Figure 6: Distribution and volume of African bioacoustics publications across taxonomic classes and research themes. Numbers indicate percentages across themes per class. Colour and size of circles are proportionately scaled to percentages. From left to right, classes read as: Mammalia (n = 567), Aves (n = 119), Reptilia (n = 7), Amphibia (n = 45), Actinopterygii (n = 49), Insecta (n = 66).

reporting similar trends in the use of camera trapping technology on the continent. Western (2003) also highlights Eastern and Southern Africa as regions of more concentrated conservation science synergies – linking these, among other components, to disproportionate resource allocation in the establishment and activities of research institutions. An in-depth examination of historical drivers of these observed dynamics is beyond the scope of this review but adds a valuable contextual dimension (see Rodney [1972] for an introduction to this area).

More recently, Blom et al. (2016) reported improved impact of Science, Technology, Engineering and Mathematics (STEM) research outputs from Eastern and Southern Africa, as well as more international collaboration and higher researcher mobility, compared to Central and Western Africa. South Africa's contribution to this trend warrants particular attention, given its strong institutional representation. (Table 2; Table A5).

While globalisation has shaped modern research in a largely Anglocentric image, pre-independent African research efforts were often (and still are) published in the language congruent with respective (post-)colonial dynamics. This has resulted in a variable non-English publication record from across Africa throughout most of the 20th century. Hence, relevant review material may have been missed on the basis of language. We did attempt to consider this to the best of our ability via cross-examination of reference lists, and found it to be minimal, but those lists could themselves be subject to linguistic bias. Our own inability to conduct a multiple-language review should not discourage future reviews from taking a more expansive approach and help cultivate an intellectual environment that is more conducive to non-English domains (Nuñez and Amano 2021).

Protected areas such as Budongo Central Forest Reserve and Taï National Park have also attracted disproportionately high concentrations of research in some areas – contributing to most of Uganda's and the Ivory Coast's bioacoustics research output, respectively. This is primarily taxon-based. Taï National Park, for example, houses a large diversity of primate species (Bi et al. 2012), which, among other things, has attracted significant research interest and investment. For example, we documented the Taï Monkey Project as an affiliation 19 times during our review. While attached to an Ivorian address, the project was being administered and funded by the Swiss Centre for Scientific Research (CSRS). Project-based affiliations are particularly well-represented among the African-based affiliations we documented. The Kalahari Meerkat Project in South Africa's Kuruman River Reserve and the Budongo Conservation Field Station in Uganda's Budongo Central Forest Reserve appeared 36 and 34 times, respectively, but only four times as primary affiliations. This suggests that leadership of such projects remains outside African purview.

It seems that the sound-production capabilities of freshwater species has largely been overlooked in Africa, yet freshwater habitats hold a third of Earth's vertebrate species (Strayer & Dudgeon, 2010). Recent reviews drawing focus to freshwater-specific (Greenhalgh et al. 2020) and underwater soundscape- and fish-specific research (Lindseth and Lobel 2018) suggest that this is true internationally too. It has been suggested that well-informed soundscape scale research is becoming increasingly relevant with the growing anthropogenic influence on their freshwater and marine environments (Nabi et al. 2018; Duarte et al. 2021), and our understanding and interpretation of underwater soundscape-focused studies would greatly benefit from more comprehensive species-specific acoustic descriptions (Parmentier and Fine 2016; Rountree et al. 2018).

The common bias towards charismatic megafauna can be seen in the taxonomic groups that have been studied with bioacoustics (Bellon 2019; dos Santos et al. 2020); this is a common phenomenon around the globe (Clark and May 2002; Donaldson et al. 2016), with potentially detrimental implications for ecosystem management (Darwall et al. 2011). In Africa it has meant that primates are the focus: chimpanzee-related (*P. troglodytes*) studies alone, account for more than 6% of our entire record. The conservation status of the chimpanzee also encourages research into the species (Gerlach et al. 2014), which does not guarantee effective conservation intervention (Christie et al. 2020).

Two other groupings that have attracted bioacoustics applications are bats and amphibians, primarily as a taxonomic descriptor (Walters et al. 2012; Köhler et al. 2017). Bats generally attract heightened bioacoustics research interest, due to their echolocation behaviour (Sugai et al. 2018).

Our findings reaffirm the need and potential for human-impact-based acoustic studies, specifically in Africa: the first publication we found that explicitly investigated human-related impacts dates to 2008, but investigations into wildlife responses to anthropogenic noise date back to the early 1990s. This supports the conclusions of Shannon et al. (2016), who stressed the need for geographical expansion in a review of two decades worth of noise-related wildlife studies that found that over 80% of research was conducted in either Europe or North America. Acoustic devices can be employed to monitor environmental threats, posed by (unlawful) resource exploration and/or extraction (Astaras et al. 2017; Wrege et al. 2017; Astaras et al. 2020), both from anthropogenic noise and behavioural changes in the animals, such as variations in the movements of forest elephants in Gabon as a likely response to seismic prospecting (Wrege et al. 2010).

While conservation and human impact are often treated synonymously, we differentiated between the two for this review, to highlight an interest in direct anthropogenic impacts on the acoustic environment. The terms ‘ecoacoustics’ and ‘soundscape ecology,’ which more commonly incorporate multidisciplinary conservation and human-impact-related work (Ozga

2017; Teixeira et al. 2019; Burivalova et al. 2021) only appeared once (overall) in our keyword repository. Moreover, acoustic recordings can contribute to more than one research theme: for example, behavioural studies can establish an informative baseline for conservation practice including biodiversity assessments and human impact studies (Stephenson et al. 2017; Penar et al. 2020; Lewis et al. 2021).

Our review highlights the need to confer more African ownership of bioacoustics knowledge emanating from the African continent. It is encouraging that primary African affiliation among documented authors has experienced a significantly faster increase than non-African affiliation over the last two decades. However, the overall distribution of author affiliations remains heavily skewed towards non-African institutions, which is further compounded by the fact that many institutions with African addresses are administered and/or funded by non-African entities.

While international collaborations are to be encouraged, capacity building within the African bioacoustics community is needed, as are regional collaborations (which would initially entail transferring knowledge more effectively from South African institutions, in particular, to other African regions). The emergence and exponential growth of the field has been encouraged by the establishment of the African Bioacoustics Community in 2018 – a forum designed to facilitate collaboration and capacity building within the discipline. Such capacity building could be catalysed by obligatory acoustic monitoring for certain assessments/species or reducing costs and increasing accessibility of acoustic equipment through local manufacturing enterprises.

The scope of this review was inherently expansive due to bioacoustics' many applications. This versatility makes the discipline increasingly relevant in the Anthropocene (Snaddon et al. 2013; Sugai and Llusia 2019; Stephenson 2020). Based on our findings we offer the following recommendations to help facilitate the continental expansion of bioacoustics:

- Promote and stimulate African-led bioacoustics research – particularly through capacity building at African institutions
    i. Increase availability of cost-effective/low-cost equipment (especially underwater) – aided by local/regional research and development of such equipment to overcome budget constraints
    ii. Job creation for acoustics expertise – particularly in academia and the public sector
    iii. More intentional drive of science communication campaigns of bioacoustics research in Africa
    iv. Obligate acoustic elements for species-specific and applied research – especially for threatened species
- Focussed research on non-terrestrial habitats and/or non-mammalian taxa - notably fish, invertebrates, and amphibians
- Direct more attention towards research relating to species, habitat or landscape conservation and by extension, human impact
    i. Greater inclusion of acoustic impacts in policy and environmental impact assessment frameworks
- Give greater consideration for the inclusion of acoustic components in ecological research, with an emphasis on more concerted incorporations of ecoacoustics and soundscape ecology

- Explore opportunities to help collate and scale up standardised continent-wide acoustic monitoring networks and repositories, based on taxa and locality – paying particular attention to freshwater and marine habitats.

Systematically describing and investigating African bioacoustics literature has underlined the potential to expand the discipline on several levels across the continent. Employing bioacoustics across a wider geographic, taxonomic and thematic range could benefit some of the challenges African habitats, landscapes and species are facing. Our review also suggests a lacking representation of African affiliated researchers involved in the production of the literature we extracted. We hope that this along with bioacoustics' potential as an effective monitoring technique can help incentive bioacoustics capacity building on the African continent.

Acknowledgements

We thank C. Keanly for helping with the literature search and the African Bioacoustics Community for offering us access to their platform. Our gratitude also goes out to all researchers who shared their work with us. F.B. was supported by a National Geographic Okavango Wilderness Project/Wild Bird Trust grant (OWP003). T.G. was supported by a University of Stellenbosch sub-committee B post-doctoral fellowship. We would also like to extend our thanks to the two anonymous reviewers.

Disclosure statement

The authors of this paper declare no conflict in interests.

Appendices

Detailed results from our literature search across different databases (Table A1; citations and titles of all publications included in our analyses (Table A2); frequency of journal names of peer-reviewed literature (Appendix Table A3); frequency of keywords extracted from journal publications (Table A4); frequency of author affiliations subdivided into African and non-African institutions, as well as African countries and regions (Table A5); research host countries, ranked according to number of publications (Table A6); list of biomes associated with documented study sites, ranked according to number of publications (Table A7); all study species documented, ranked according to number of publications (Table A8) are available online.

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