



Original Research Article

How effective are the protected areas of East Africa?

Jason Riggio^{a,*}, Andrew P. Jacobson^{b,c}, Robert J. Hijmans^d, Tim Caro^a^a Department of Wildlife, Fish and Conservation Biology, University of California, Davis, CA, 95616, USA^b Nicholas School of the Environment, Box 90328, Duke University, Durham, NC, 27708, USA^c Center for the Environment, Catawba College, Salisbury, NC, USA^d Department of Environmental Science and Policy, University of California, Davis, CA, 95616, USA

ARTICLE INFO

Article history:

Received 3 November 2018

Received in revised form 19 February 2019

Accepted 20 February 2019

Keywords:

Biodiversity

Conservation prioritization

Effectiveness

Endemic species

National parks

Representativeness

ABSTRACT

Protected areas are the cornerstone of *in situ* conservation and their effective management is critical for maintaining biodiversity in the long term. In East Africa (Burundi, Kenya, Rwanda, Tanzania and Uganda) there are 1,776 protected areas (including 186 “strict” protected areas with IUCN management categories I through IV) covering more than 27% of its terrestrial area. Here we document the extent to which East African protected areas encompass ecoregions and endemic terrestrial vertebrate taxa, and using new land conversion data derived from medium to high spatial resolution satellite images, we assess how they have been encroached upon by agriculture and other land use. We find that East African protected areas cover 86% of ecoregions well (>10% threshold of ecoregion representativeness set by the Convention on Biological Diversity’s Aichi Target 11), some very well (>90% - Rwenzori-Virunga montane moorlands and East African montane moorlands). In contrast, Masai xeric grasslands and shrublands, Somali Acacia-Commiphora bushlands and thickets, and Southern Swahili coastal forests and woodlands are poorly represented. Protected areas cover at least 10% of the distribution of 256 of 303 East African endemic and near-endemic terrestrial vertebrate species (the latter defined here as having 90% or more of their range in East Africa). However, 37% of these species’ ranges do not have at least 10% coverage by strict PAs and only 26% of endemic species have at least half of their range covered by PAs. Encouragingly, we find that only 6.8% of East African protected areas has been converted to agriculture or other human use since gazettelement. Only 1.6% of strict protected areas have been converted providing very strong evidence that strict protection is the most enduring way of safeguarding habitat.

© 2019 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Protected areas (PAs) are the cornerstone of *in situ* conservation and their effective management is critical for maintaining biodiversity in the long term (Chape et al., 2005; Gaston et al., 2008; Joppa and Pfaff, 2011; Rodrigues et al., 2004; Watson et al., 2018, 2014). East Africa (Burundi, Kenya, Rwanda, Tanzania and Uganda totaling 1,722,114 km² in terrestrial area [calculated using the Global Administrative Areas boundaries (GADM, 2018)], excluding large lakes and reservoirs using the Global Lakes and Wetlands Database (Lehner and Döll, 2004)) has a large and famous network of PAs. Many of these PAs were

* Corresponding author. Department of Wildlife, Fish and Conservation Biology, 1088 Academic Surge, University of California, Davis One Shields Avenue, Davis, CA, 95616-8627, USA..

E-mail address: jriggio@ucdavis.edu (J. Riggio).

originally established as game reserves used by colonial hunters that were converted into national parks around or following independence (Caro, 2003). This establishment strategy, with a species-focus, differs from other patterns of PA establishment elsewhere that were often set up in regions of low agricultural value (Venter et al., 2018). East African PAs provide a significant contribution to the economy of this region through photographic and hunting tourism (Lindsey et al., 2007).

Currently according to the World Database on Protected Areas, there are 1,776 nationally designated PAs in East Africa covering more than 27% of its terrestrial area, including 186 PAs in IUCN management categories I through IV (i.e., “strict” PAs primarily managed for biodiversity conservation) (UNEP-WCMC and IUCN, 2018) that cover about half the area under protection (Fig. 1; Table 1). Protected area coverage varies by nearly a factor of 10 in this region, between 5.1% and 48.2% of the terrestrial surface of the five African nations, while strict protected areas encompass between 4.7% and 20.4% (Table 1). Tanzania contains the greatest number, highest percent coverage, and highest overall areal extent of PAs, while Burundi has the lowest PA coverage (Table 1). The total regional coverage by PAs drops from 27.4% to 12.2% when Tanzania is excluded (and from 13.7% to 6.9% coverage by strict PAs) (Table 1).

Although more than 200 PAs in East Africa have been downgraded, downsized or degazetted (i.e., lost their designation altogether) (Mascia et al., 2014), PAs continue to be expanded, established or upgraded through the region. For example, in the past two decades Tanzania has created three new national parks, upgraded two game reserves to national parks (with another five approved for upgrade), and enlarged five existing national parks (Table 2).

In this paper, we evaluate the representativeness and effectiveness (specifically habitat conversion) of this PA network in order to address three questions. First, are East African PAs representative of the ecoregions in the region as a whole? Most PAs in the region were established without considering conservation planning techniques to optimize reserves based on particular criteria (Ball and Possingham, 2000; Margules and Pressey, 2000; Venter et al., 2014). Instead, their establishment was largely formulated on whether they contained large mammal populations (e.g., Tsavo National Parks, Kenya) or particular charismatic species such as gorillas *Gorilla gorilla* (e.g., Virunga Mountains National Park, Rwanda) or chimpanzees *Pan troglodytes* (e.g., Gombe Stream National Park, Tanzania) (Caro, 2010).

Second, where in East Africa are there unprotected hotspots of vertebrate endemism? While we recognize that national boundaries rarely line up with biogeographic boundaries, conservation decisions are often made at a national or regional-levels. Identifying hotspots of vertebrate endemism can help guide national or regional efforts to establish future PAs to enhance biodiversity conservation in the face of rapidly advancing land conversion.

Third, what is the current extent of human encroachment into East African PAs? East Africa is experiencing rapid human population growth of nearly 3% per year (UN, 2017) and, together with economic development, this is leading to agriculture, mining, settlements and infrastructure (i.e., land conversion). As a consequence, many PAs are under threat and such information might improve understanding about the effectiveness of different forms of PA management (see Stoner et al., 2007a) and where countries should target conservation effort.

In this paper we examine each of these three issues using ecoregion, species distribution, and land cover data for the whole of East Africa's five countries. We present quantitative evidence to show that while East African PAs encompass a somewhat uneven sample of ecoregions and endemic species, they have largely escaped land conversion, and lastly we show that there are now relatively few possibilities for establishing new PAs in hotspots of vertebrate endemism.

2. Methods

2.1. Representativeness of protected areas (ecoregions)

To understand the extent to which the East African PA network conserves different vegetation types, we combined the boundaries of PAs in the 2018 World Database on Protected Areas (UNEP-WCMC and IUCN, 2018) with the Ecoregions 2017 spatial database (Dinerstein et al., 2017). We used a modified PA dataset for Tanzania from the Tanzania Wildlife Research Institute (TAWIRI). For all spatial analyses we excluded large lakes and reservoirs using the Global Lakes and Wetlands Database (GLWD-1; Lehner and Döll, 2004). Using ArcGIS software (ESRI, Redlands, California), we calculated the percentage of each of the ecoregions found in East Africa that was encompassed by all PAs and strict PAs (IUCN categories I-IV) using the Tabulate Intersection tool. We compared the resulting values to the Convention on Biological Diversity Aichi Biodiversity Target 11 goal of 10% protected representation for each ecoregion by 2020 (Leadley et al., 2014), and a goal of 50% protection as a proxy for the Half-Earth (Wilson, 2016) and Nature Needs Half (Locke, 2014) targets. We also compared the land conversion dataset (explained below) by ecoregion to examine the remaining amount of habitat.

2.2. Representativeness of protected areas (endemism)

To determine the extent to which East African PAs contain a representative sample of endemic and near-endemic vertebrate species (the latter defined here as having 90% or more of their range in East Africa, hereafter referred to simply as endemic species [e.g., Thomas et al., 2004]), we examined which amphibian, bird and mammal species are found in PAs and strict PAs in the region using the IUCN Red List of Threatened Species Version 2018-2 range maps (IUCN, 2018). We calculated the percentage of each endemic species' range covered by all PAs and strict PAs. We then converted each species' range to a raster and summed the resulting raster layers to create a vertebrate endemic species richness map for East Africa showing the number of endemic species occurring within each 1 km² raster cell of the region. We designated areas in the top quartile of

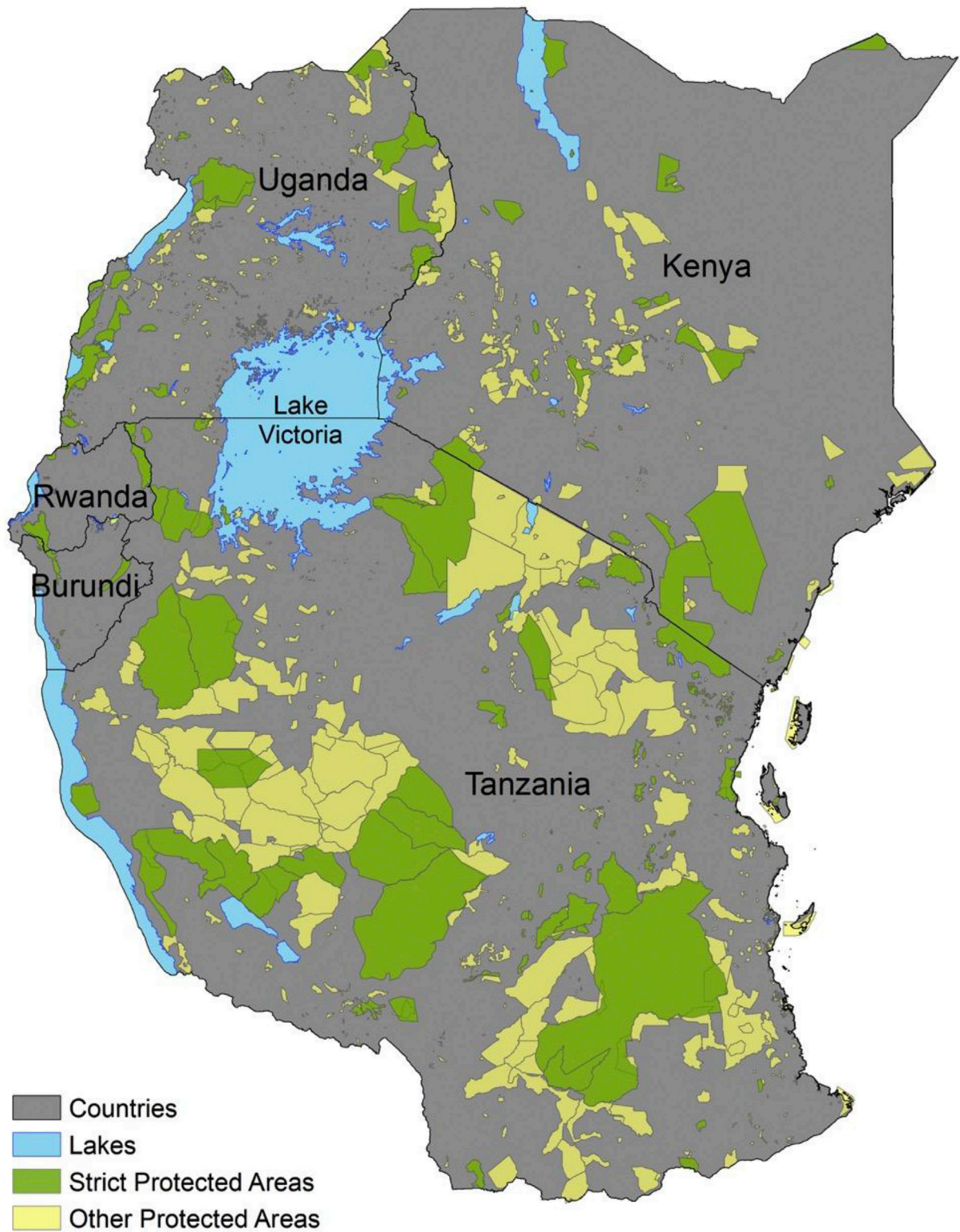


Fig. 1. Strict (IUCN category I – IV) and other protected areas in East Africa (Burundi, Kenya, Tanzania, Rwanda and Uganda).

Table 1

The percentage of terrestrial area in East Africa covered by protected areas and by strict protected areas (IUCN Category I – IV).

Country	Protected Areas (%)	Strict Protected Areas (%)
Burundi	5.1	4.7
Kenya	11.4	5.9
Rwanda	8.9	8.9
Tanzania	48.2	20.4
Uganda	17.8	9.5
East Africa	27.4	13.7
East Africa w/o Tanzania	12.2	6.9

Table 2

Year of establishment of national parks in Tanzania.

Name	Year of Establishment
Serengeti	1951
Arusha	1960 ^a
Lake Manyara	1960 ^a
Mikumi	1964 ^a
Ruaha	1964 ^a
Gombe Stream	1968
Tarangire	1970
Mount Kilimanjaro	1973
Katavi	1974 ^a
Rubondo Island	1977
Mahale Mountains	1985
Udzungwa Mountains	1994
Kitulo Plateau	2002
Saadani	2002
Jozani-Chwaka Bay	2004
Mkomazi	2006
Saanane Island	2013
Biharamuro	Approved in 2018
Burigi	Approved in 2018
Ibanda	Approved in 2018
Kimisi	Approved in 2018
Rumanyika	Approved in 2018

^a Expanded since establishment.**Table 3**

The terrestrial area of each East African ecoregion that is conserved as a (strict) protected area, converted to human use, or neither.

Ecoregion	Area (km ²)	Protected (%)	Strictly Protected (%)	Converted (%)	Not Converted Nor-Protected (%)
Rwenzori-Virunga montane moorlands	379	98.2	98.2	4.0	2.7
East African montane moorlands	3,110	92.8	68.9	4.0	5.1
Serengeti volcanic grasslands	126	88.0	0.0	0.0	12.0
Northern Congolian forest-savanna	386	58.3	55.2	17.1	26.5
Zambezian flooded grasslands	32,289	57.0	37.0	18.1	29.2
East African halophytics	1,628	53.3	3.5	13.2	34.4
Dry miombo woodlands	320,242	51.0	24.3	24.6	27.5
East African mangroves	1,706	49.8	1.0	14.7	42.0
Central Zambezian wet miombo woodlands	170,691	36.4	18.9	32.6	34.4
Southern Acacia-Commiphora bushlands and thickets	234,959	35.9	16.0	40.1	26.1
Eastern Arc forests	11,224	28.9	20.6	43.3	31.0
East African montane forests	57,139	27.3	5.0	58.6	20.6
Northern Swahili coastal forests	76,399	23.1	11.1	30.5	47.6
Itigi-Sumbu thicket	6,225	21.7	5.5	43.4	42.2
East Sudanian savanna	72,108	18.5	10.9	33.2	48.9
Northern Acacia-Commiphora bushlands and thickets	322,909	17.7	10.0	11.8	70.9
Albertine Rift montane forests	56,351	13.2	8.4	73.3	13.5
Southern Rift montane forest-grassland	17,786	11.0	7.6	61.4	30.2
Victoria Basin forest-savanna	160,003	10.1	6.7	59.0	32.2
Southern Swahili coastal forests and woodlands	16,121	6.0	0.7	39.1	56.0
Masai xeric grasslands and shrublands	71,002	3.7	3.1	0.1	96.2
Somali Acacia-Commiphora bushlands and thickets	89,331	1.0	1.0	1.8	97.2

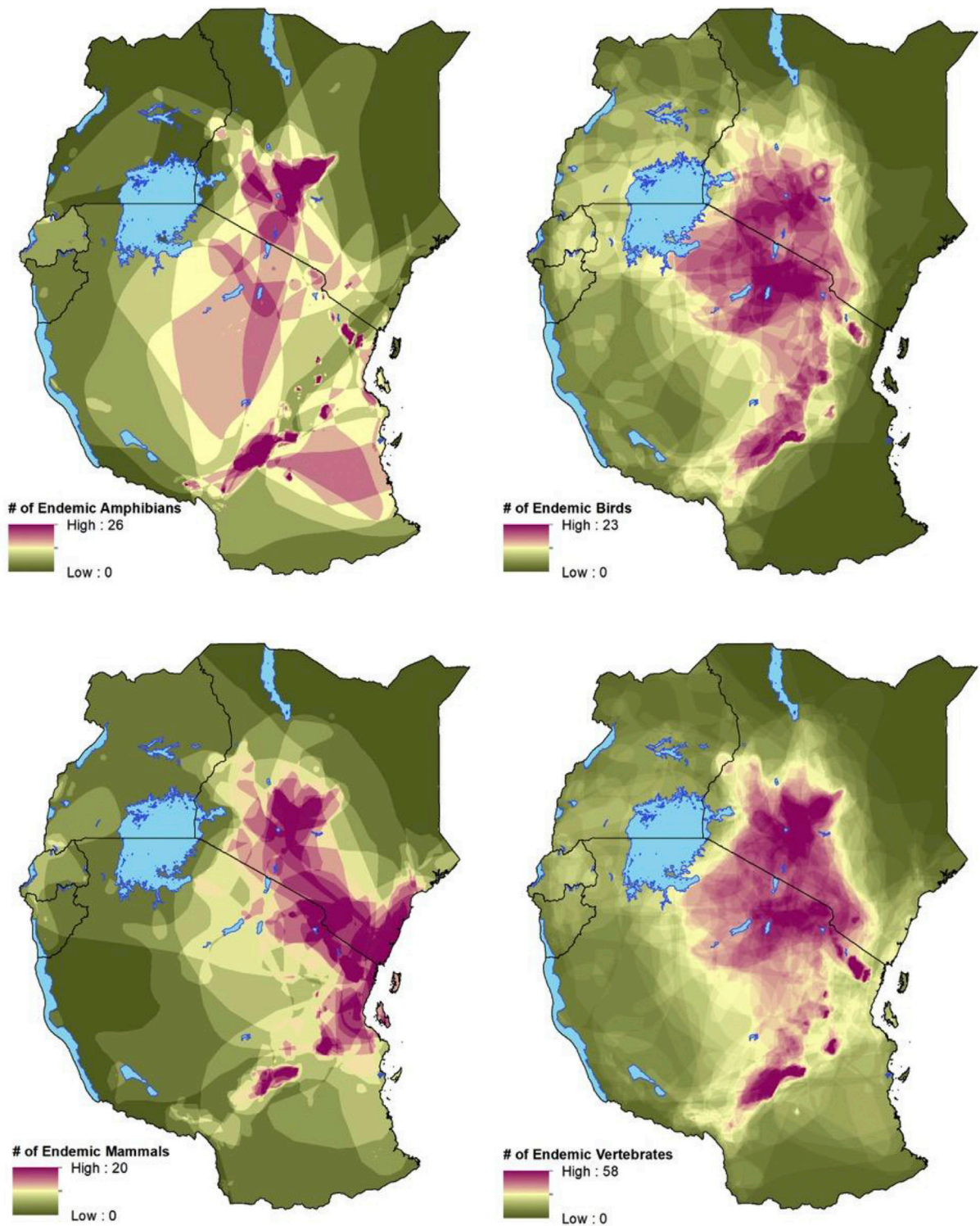


Fig. 2. Distribution and number (per 1 km² raster cell) of endemic and near-endemic (top left) amphibian, (top right) bird, (bottom left) mammal and (bottom right) combined vertebrate species across East Africa. High values represent the maximum number of endemic species found in the 1 km² raster cell.

endemic species richness as hotspots of vertebrate endemism, which translated to raster cells containing the ranges of more than 16 endemic species.

2.3. Effectiveness of protected areas

We examined the effectiveness of PAs in protecting wildlife habitat by assessing the extent of land conversion within these areas. We used a $0.01^\circ \times 0.01^\circ$ raster dataset (projected cell size of ~1 km at the equator) of anthropogenic land conversion that was created by visually establishing the presence of converted land on ~10 m or higher spatial resolution satellite data for all of East Africa (Jacobson et al., 2015). Analyzed imagery was dated between 2001 and 2016 with more than 90% from 2010 onwards. We updated this dataset by re-evaluating areas for which previously only Landsat imagery with 30 m spatial resolution was available or could not be assessed due to cloud cover (Riggio and Caro, 2017). We used this dataset to calculate the percentage of conversion by PA type (all or strict) and country.

2.4. The location of future protected areas

Finally, we considered which locations might be best protected in the near future in order to help meet the conservation goal of the Convention on Biological Diversity Aichi Biodiversity Target 11 goal of 10% protected representation for each ecoregion. This was done by mapping locations of (i) ecoregions with less than 10% PA coverage, along with (ii) East African endemic vertebrate species that are similarly under-protected (set at the Aichi Target 11 goal of less than 10% of their range covered by protected areas). We also considered which regions contained (iii) unprotected hotspots of vertebrate endemism (as defined earlier as containing more than 16 endemic species per 1 km² raster cell). To determine where protection may be most feasible, we assessed for all three conservation priorities the extent to which they are in lands that are either currently protected or converted to human use.

3. Results

3.1. Representativeness of protected areas (ecoregions)

There are 22 ecoregions within East Africa (Table 3). All but three, (a) Masai xeric grasslands and shrublands, (b) Somali Acacia-Commiphora bushlands and thickets, and (c) Southern Swahili coastal forests and woodlands meet the Aichi Target 11 goal of 10% protection by 2020, but only half ($n = 11$) meet that goal within strict PA status (Table 3). Nearly a third ($n = 7$) achieve the “Half-Earth/Nature Needs Half” target of having at least half of their area under some form of protection, and three ecoregions (a) East African montane moorlands, (b) Rwenzori-Virunga montane moorlands, and (c) Northern Congolian forest-savanna have achieved the “Half-Earth/Nature Needs Half” goals within strict PA status. In contrast, (a) Albertine Rift and East African montane forests, (b) Southern Rift montane forest-grassland, and (c) Victoria Basin forest-savanna each have more than half of their area converted to human use, indicating that restoration would be required to achieve a 50% protection target (Table 3).

Table 4

The percent of each East African ecoregion covered by hotspots of vertebrate endemism.

Ecoregion	% of Area Covered by Hotspots of Vertebrate Endemism
Serengeti volcanic grasslands	100.0%
Eastern Arc forests	88.8%
East African montane moorlands	88.7%
East African montane forests	74.0%
Southern Acacia-Commiphora bushlands and thickets	72.3%
East African halophytics	65.7%
Northern Acacia-Commiphora bushlands and thickets	26.0%
Zambezian flooded grasslands	25.2%
Southern Rift montane forest-grassland	14.9%
Dry miombo woodlands	12.7%
Itigi-Sumbu thicket	10.9%
Victoria Basin forest-savanna	3.1%
Northern Swahili coastal forests	1.7%
Central Zambezian wet miombo woodlands	1.6%
Albertine Rift montane forests	0.0%
East African mangroves	0.0%
East Sudanian savanna	0.0%
Masai xeric grasslands and shrublands	0.0%
Northern Congolian forest-savanna	0.0%
Rwenzori-Virunga montane moorlands	0.0%
Somali Acacia-Commiphora bushlands and thickets	0.0%
Southern Swahili coastal forests and woodlands	0.0%

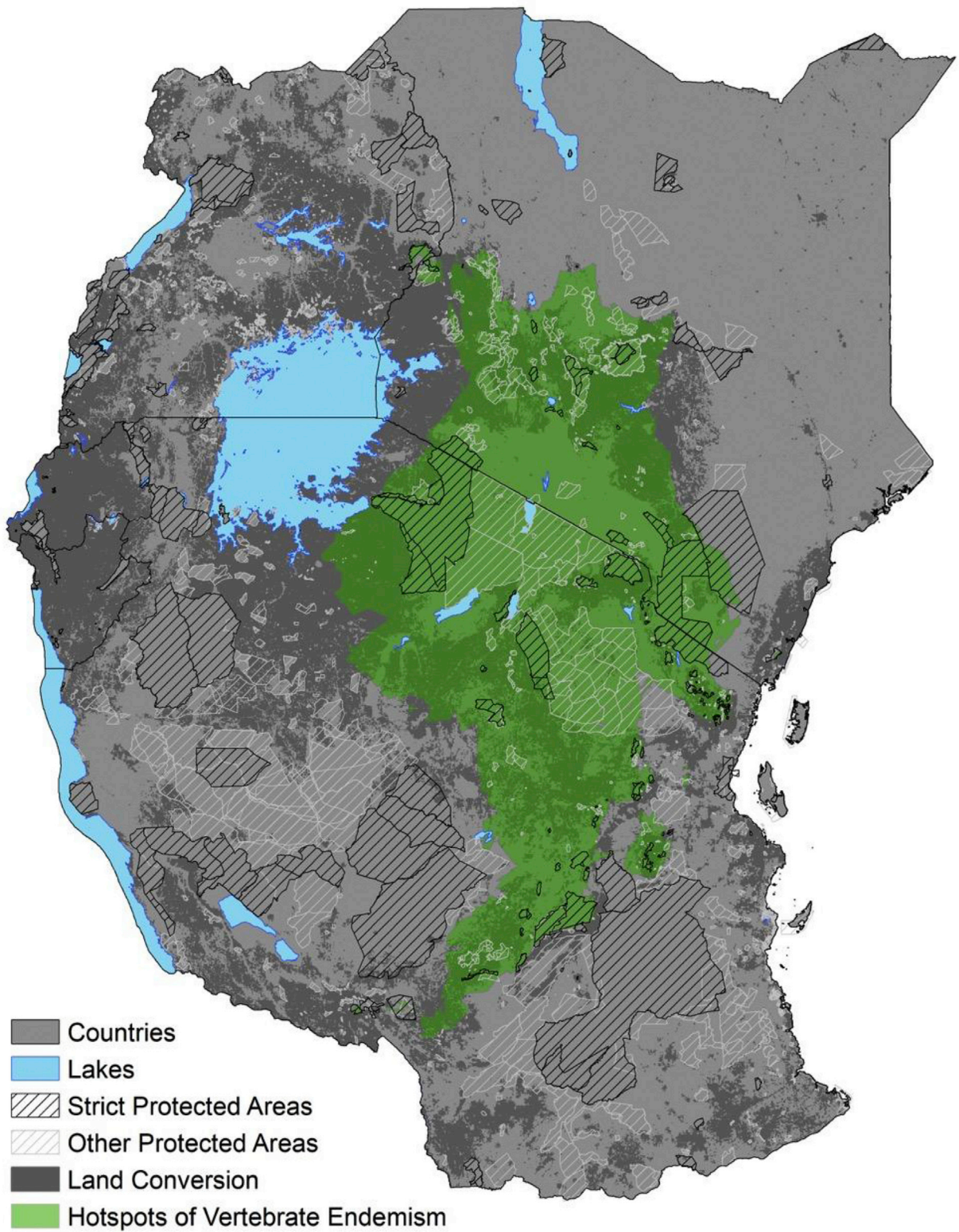


Fig. 3. Distribution of protected areas and hotspots of vertebrate endemism across East Africa in relation to land conversion.

3.2. Representativeness of protected areas (endemism)

Based on IUCN range maps, there are 125 endemic and 11 near-endemic amphibians, 66 endemic and 16 near-endemic birds, and 69 endemic and 16 near-endemic mammal species (303 total) in East Africa (Fig. 2; Table S1). Protected areas cover at least 10% of the distribution of 256 of these 303 endemic species (85% of endemic species) (Table S1). However, 37% of these species' ranges ($n = 111$) do not have at least 10% coverage by strict PAs and only 26% of endemic species ($n = 78$) have at least half of their range covered by PAs.

Six ecoregions have more than half of their area covered by hotspots of vertebrate endemism (as defined earlier as containing more than 16 endemic species per 1 km^2 raster cell): East African halophytics, East African montane forests, East African montane moorlands, Eastern Arc forests, Serengeti volcanic grasslands, and Southern Acacia-Commiphora bushlands and thickets (Table 4). The majority of PAs and strict PAs, however, are located outside of these areas of high vertebrate endemism (77% and 52% respectively) (Fig. 3).

3.3. Effectiveness of protected areas

Overall, 6.8% of protected areas (all categories) in East Africa have been converted (Fig. 3, Table 5). Burundi has the most impacted PAs, with 16.3% of their area affected, whereas PAs in the remaining four East African countries have suffered less than 10% conversion to agriculture or human settlement. In all East African countries, the proportion of land conversion in the subset of strict PAs was smaller than across all protected (Table 5) with only 1.6% converted to human use. In some parts of the region, for example around the Moyowosi-Kigosi Game Reserve complex in northwest Tanzania, the western boundary of Serengeti National Park in northern Tanzania, and in Burundi, Rwanda and Uganda, PAs are the *only* places where land has not been converted (Fig. 3).

3.4. The location of future protected areas

Three ecoregions are currently under-protected in terms of the 10% representation goal of Aichi Target 11. These are the largely unconverted (a) Masai xeric grasslands and shrublands and (b) Somali Acacia-Commiphora bushlands and thickets in northern Kenya and (c) the more impacted Southern Swahili coastal forests and woodlands in southeastern Tanzania (yellow, brown and light green regions respectively; Fig. 4). Turning now to endemic species, unconverted regions with under-protected endemic species (<10% of their range covered by protected areas) occur primarily in Marsabit, Garissa, and Kajiado counties of Kenya, and the Central and Western regions of Uganda (red regions; Fig. 4). Unprotected and unconverted hotspots of vertebrate endemism are scattered throughout south-central Kenya and northern and central Tanzania (green regions; Fig. 3). These are the areas where conservation efforts could focus.

4. Discussion

At the regional level, the number of PAs within East Africa is high compared to many other countries (UNEP-WCMC and IUCN, 2016) and the PA network at a regional level exceeds the Convention of Biodiversity Aichi Target 11 of 17% protection of terrestrial lands (nearly achieving this with respect to strict PAs). Moreover, PAs are still being established in these countries (Table 2) although protected area downgrading, downsizing and degazettement is also an issue (Mascia et al., 2014). However, the positive regional figures obscure important country-level differences. The largest country in terms of area, Tanzania, also contains the greatest coverage of strict PAs (20%) and hence drives the impressive regional conservation trend. In contrast, no other East African country has designated more than 10% of its land as strict PAs, and Burundi has designated only 4.7%.

Our analyses uncovered a number of issues regarding the extent to which habitats and species are being protected by this PA network. First, some ecoregions are disproportionally protected by East African PAs with (a) Rwenzori-Virunga and East African montane moorlands and (b) Northern Congolian forest-savanna being well covered by the network (>50% coverage by strict PAs), but (c) Somali Acacia-Commiphora bushlands and thickets, (d) Masai xeric grasslands and shrublands and (e) Southern Swahili coastal forests and woodlands being poorly represented (<10% protection regardless of IUCN category; Fig. 4). The lack of PA coverage in Southern Swahili coastal forests and woodlands is particularly concerning as this ecoregion is highly threatened, much of it already converted to human use (39.1%).

In regards to vertebrate species endemism, ecoregions with at least half of their area covered by hotspots of vertebrate endemism include (a) East African montane moorlands (93% coverage by PAs), (b) Serengeti volcanic grasslands (88%), (c) East

Table 5
Land conversion within the boundaries of protected areas in East Africa by protected area type.

	Protected Areas Converted by Reserve Type (%)					
	Burundi	Kenya	Rwanda	Tanzania	Uganda	East Africa
Protected Areas	16.3	7.2	4.0	6.7	7.1	6.8
Strict Protected Areas	11.3	0.5	3.2	1.8	1.2	1.6

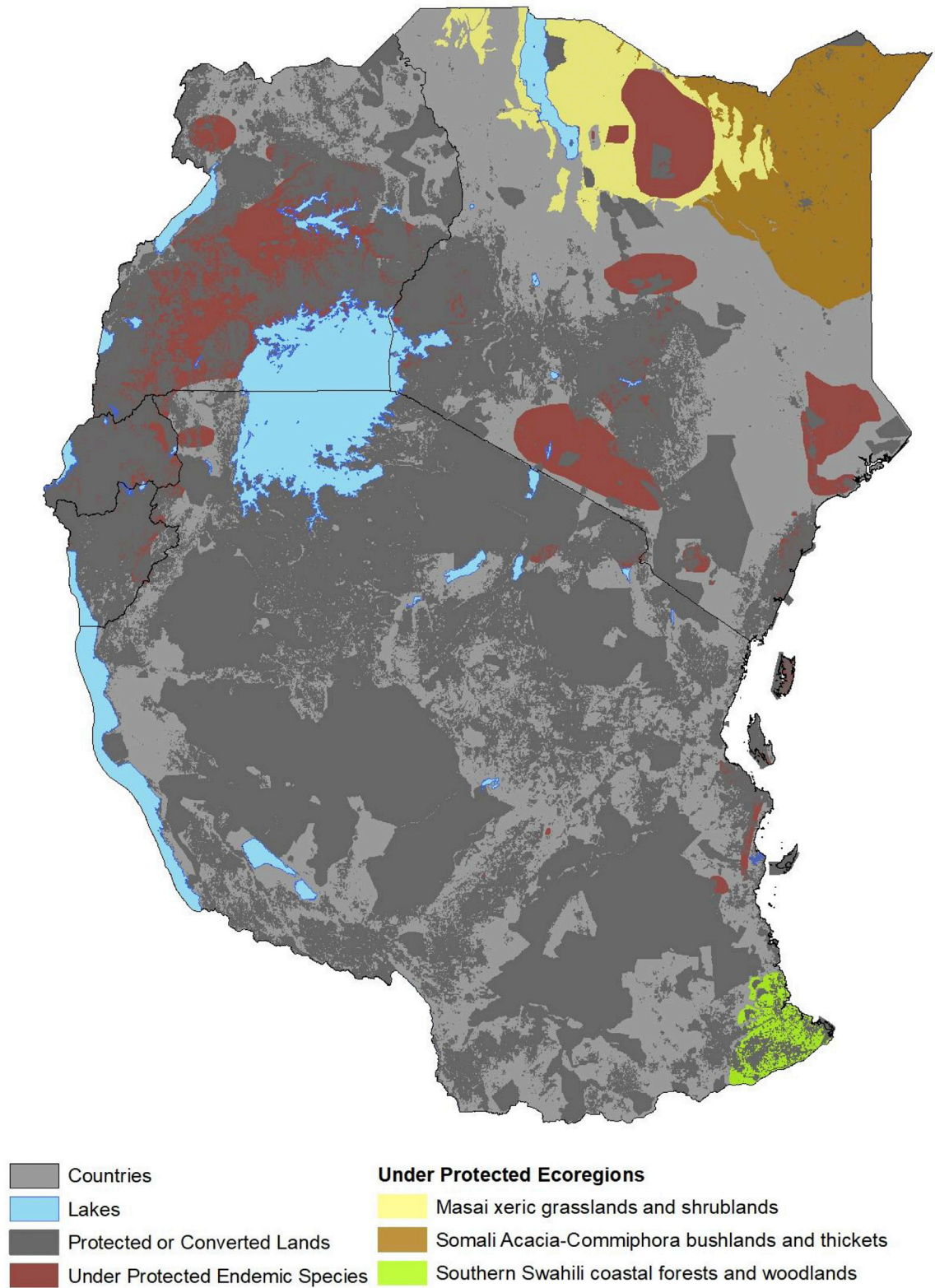


Fig. 4. Potential locations of future protected areas in East Africa represented by colored areas showing hotspots of vertebrate endemism and under-protected endemic species or ecoregions (<10% protected).

African halophytics (53%), (d) Southern Acacia-Commiphora bushlands and thickets (36%), (e) Eastern Arc forests (29%), and (f) East African montane forests (27%). However, 16% of the 303 East African endemics have less than 10% of their distribution covered by strict PAs (Fig. 4). In essence then, the scoresheet is mixed for East African PAs. There are many of them, they cover a significant portion of the terrestrial surface of the region, but they fall short on conserving certain habitats, endemic vertebrate hotspots and endemic species.

With rapidly growing economies and a population growth rate nearly two and half times the global average (2.71% versus 1.09%; UN, 2017), more natural land in East Africa will be converted to agriculture and settlements in the coming decades. Indeed, a global analysis showed that East Africa is a hotspot for future conflict between agricultural expansion and intensification and biodiversity (Shackelford et al., 2015). Yet we find the degree to which habitat within PAs (as of ~2015) has been converted for human use is encouragingly low (6.8%) (although some of the most impacted likely have been downsized or degazetted since establishment). Strict PAs in particular have experienced little encroachment, amounting to less than 2% overall. This compares favorably to national parks in Zambia (2% of their area have been converted to human land uses; Lindsey et al., 2014), and forested protected areas globally (3% of their area was deforested between 2000 and 2012; Heino et al., 2015), and substantially better than PAs in South Asia where a quarter of the area inside of their boundaries have been converted to human use (Clark et al., 2013). Protected areas in East Africa have therefore largely avoided undesirable land use change. These data strongly and convincingly support the need for full protection (preferably by protected area types classified by the IUCN in categories I to IV) in preventing land being converted to agriculture. Multiple studies now show that while pastoralism, an important land use in the area (Kideghesho et al., 2013), can have neutral or even positive biodiversity effects (Little, 1996; Reid et al., 2004), transition to agriculture or settlements does not (Kiffner et al., 2015; Msuha et al., 2012; Tilman et al., 2001).

Approximately 30% of East Africa has been converted to anthropogenic land cover (Burundi, 86%, Rwanda 82%, Uganda 44%, Tanzania 32%, Kenya 17% [Jacobson et al., 2015]) leaving limited opportunities for new large-scale PAs. The largest contiguous regions of unprotected and unconverted natural landscapes are in central Uganda and northern and eastern Kenya (Fig. 3). However, these are not generally located within areas of high endemism. Because of the low rainfall in these areas, it is unlikely that much of these lands will be converted to agriculture in the near future.

Opportunities for specifically protecting hotspots of vertebrate endemism are now limited to portions of central and south-central Kenya and central Tanzania (Fig. 4). It is important to note that the lack of land conversion does not mean these landscapes are unpeopled as they may contain pastoral communities with large numbers of livestock. Nevertheless, small, targeted reserves may be easier to set up than larger ones, and they may be appropriately sized for small-ranged endemics such as the Udzungwa forest-partridge (*Xenoperdix udzungwensis*). That said, small protected areas may be less effective at preventing encroachment and species decline (Woodroffe and Ginsberg, 1998). Upgrading protected areas along with increased funding may also be effective in protecting habitat or species (Lindsey et al., 2017; Pfeifer et al., 2012; Pringle, 2017; Tranquilli et al., 2014). In south-central Kenya and northern Tanzania, where a significant portion of the region is already set aside as PAs and the remaining areas are in pastoral systems, more innovative forms of protection may be needed.

We acknowledge some caveats to this analysis and its focus on government-operated PAs at the national or regional level. Focusing on local efforts such as conserving 10% of each East African ecoregion might preclude globally efficient conservation solutions like prioritizing areas of high vertebrate endemism, as endemic species are not distributed equally throughout the ecoregions (Table 4; Pouzols et al., 2014). For example, very few of the endemic species ranges coincide with the desert ecoregions of northern and eastern Kenya (also the most underrepresented ecoregion in the PA network). In addition, land cover change is only one form of human disturbance. We did not consider such impacts as hunting/poaching, livestock encroachment, illegal logging, or altered fire regimes (but see Bowker et al., 2017; Caro et al., 2016; Pfeifer et al., 2012). Indeed, while biodiversity protection is one of the key objectives of PA establishment, wildlife populations are declining rapidly throughout East Africa, even within the PA network (Caro and Scholte, 2007; Craigie et al., 2010; Newmark, 1996; Ogutu et al., 2016; Stoner et al., 2007b; Western et al., 2009). Thus, even though East African PAs largely escaped direct habitat loss, protection of vertebrate populations seems less than effective within these areas. Increasing human and financial resources (Brooks et al., 2004; Leverington et al., 2010) could improve the effectiveness in reducing threats such as poaching, illegal grazing, and fuel wood extraction (Lindsey et al., 2014).

In conclusion, our analyses indicate that the East African network of PAs is extensive in both number and area, that it protects most natural habitats effectively, and that further expansion of PAs to cover some priority biodiversity conservation areas is still possible and necessary. We recommend that PA expansion be focused on increasing representation in the xeric ecoregions of northern Kenya, and the Southern Swahili coastal forests and woodlands in southeastern Tanzania, and on targeted reserves covering under-protected endemic species in Kenya, and the Central and Western regions of Uganda.

Acknowledgements

J.R. and R.H. were partly supported by the USAID Feed the Future Sustainable Intensification Innovation Lab grant AID-OOA-L-14-00006. A.J. was supported by a fellowship from National Geographic Society's Big Cats Initiative (grant SP08-11), and the Mohamed bin Zayed Species Conservation Fund (#10251555). We thank A. Lobora at the Tanzania Wildlife Research Institute (TAWIRI) for his assistance with obtaining updated protected area boundary files for Tanzania. We also thank S. Pimm and C. Jenkins for their input on earlier drafts of this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00573>.

References

- Ball, I.R., Possingham, H.P., 2000. *Marxan (V 1.8.6): Marine Reserve Design Using Spatially Explicit Annealing*. User manual, Brisbane, Australia.
- Bowker, J.N., De Vos, A., Ament, J.M., Cumming, G.S., 2017. Effectiveness of Africa's tropical protected areas for maintaining forest cover. *Conserv. Biol.* 31, 559–569. <https://doi.org/10.1111/cobi.12851>.
- Brooks, T.M., Da Fonseca, G.A.B., Rodrigues, A.S.L., 2004. Protected areas and species. *Conserv. Biol.* 18, 616–618. <https://doi.org/10.1111/j.1523-1739.2004.01836.x>.
- Caro, T., 2010. *Conservation by Proxy: Indicator, Umbrella, Keystone, Flagship and Other Surrogate Species*. Island Press, Washington, DC. <https://doi.org/x>.
- Caro, T., Charles, G.K., Clink, Dena, J., Riggio, J., Weill, A.M., Whitesell, C., 2016. Protected areas under threat. In: Sample, V.A., Bixler, R.P., Miller, C. (Eds.), *Forest Conservation in the Anthropocene: Science, Policy, and Practice*. The University Press of Colorado, Boulder, CO, pp. 83–98. <https://doi.org/10.5876/9781607324591.c006>.
- Caro, T., Scholte, P., 2007. When protection falters. *Afr. J. Ecol.* 45, 233–235. <https://doi.org/10.1111/j.1365-2028.2007.00814.x>.
- Caro, T.M., 2003. Umbrella species: critique and lessons from East Africa. *Anim. Conserv.* 6, 171–181. <https://doi.org/10.1017/S1367943003003214>.
- Chape, S., Harrison, J., Spalding, M., Lysenko, I., 2005. Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. *Philos. Trans. R. Soc. B Biol. Sci.* 360, 443–455. <https://doi.org/10.1098/rstb.2004.1592>.
- Clark, N.E., Boakes, E.H., McGowan, P.J.K., Mace, G.M., Fuller, R.A., 2013. Protected areas in south Asia have not prevented habitat loss: a study using historical models of land-use change. *PLoS One* 8, e65298. <https://doi.org/10.1371/journal.pone.0065298>.
- Craigie, I.D., Baillie, J.E.M., Balmford, A., Carbone, C., Collen, B., Green, R.E., Hutton, J.M., 2010. Large mammal population declines in Africa's protected areas. *Biol. Conserv.* 143, 2221–2228. <https://doi.org/10.1016/j.biocon.2010.06.007>.
- Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E.C., Jones, B., Barber, C.V., Hayes, R., Kormos, C., Martin, V., Crist, E., Sechrest, W., Price, L., Baillie, J.E.M., Weeden, D., Suckling, K., Davis, C., Sizer, N., Moore, R., Thau, D., Birch, T., Potapov, P., Turubanova, S., Tyukavina, A., De Souza, N., Pintea, J.C., Brito, J.C., Llewellyn, O.A., Miller, A.G., Patzelt, A., Ghazanfar, S.A., Timberlake, J., Klöser, H., Shennan-Farpon, Y., Kindt, R., Lillesø, J.P.B., Van Breugel, P., Graudal, L., Voge, M., Al-Shammari, K.F., Saleem, M., 2017. An ecoregion-based approach to protecting half the terrestrial realm. *Bioscience* 67, 534–545. <https://doi.org/10.1093/biosci/bix014>.
- GADM, 2018. *Global Administrative Areas: Version 3.6 [WWW Document]*.
- Gaston, K.J., Jackson, S.F., Cantú-Salazar, L., Cruz-Piñón, G., 2008. The ecological performance of protected areas. *Annu. Rev. Ecol. Evol. Syst.* 39, 93–113. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173529>.
- Heino, M., Kumm, M., Makkonen, M., Mulligan, M., Verburg, P.H., Jalava, M., Räsänen, T.A., 2015. Forest loss in protected areas and intact forest landscapes: a global analysis. *PLoS One* 10, e0138918. <https://doi.org/10.1371/journal.pone.0138918>.
- IUCN, 2018. *The IUCN Red List of Threatened Species: Version 2018-2*.
- Jacobson, A., Dhanota, J., Godfrey, J., Jacobson, H., Rossman, Z., Stanish, A., Walker, H., Riggio, J., 2015. A novel approach to mapping land conversion using Google Earth with an application to East Africa. *Environ. Model. Softw.* 72, 1–9. <https://doi.org/10.1016/j.envsoft.2015.06.011>.
- Joppa, L.N., Pfaff, A., 2011. Global protected area impacts. *Proc. R. Soc. B Biol. Sci.* 278, 1633–1638. <https://doi.org/10.1098/rspb.2010.1713>.
- Kideghesho, J., Rija, A., Mwamende, K., Selemani, I., 2013. Emerging issues and challenges in conservation of biodiversity in the rangelands of Tanzania. *Nat. Conserv.* 6, 1–29. <https://doi.org/10.3897/natureconservation.6.5407>.
- Kiffner, C., Wenner, C., Lavoilet, A., Yeh, K., Kioko, J., 2015. From savannah to farmland: effects of land-use on mammal communities in the Tarangire-Manyara ecosystem, Tanzania. *Afr. J. Ecol.* 53, 156–166. <https://doi.org/10.1111/aje.12160>.
- Leadley, P., Krug, C.B., Alkemade, R., Pereira, H.M., Sumaila, U.R., Walpole, M., Marques, A., Newbold, T., Teh, L.S.L., van Kolck, J., Bellard, C., Januchowski-Hartley, S.R., Mumby, P.J., 2014. *Progress towards the Aichi Biodiversity Targets: an Assessment of Biodiversity Trends, Policy Scenarios and Key Actions*. Montreal.
- Lehner, B., Döll, P., 2004. Development and validation of a global database of lakes, reservoirs and wetlands. *J. Hydrol.* 296, 1–22. <https://doi.org/10.1016/j.jhydrol.2004.03.028>.
- Leverington, F., Costa, K.L., Pavese, H., Lisle, A., Hockings, M., 2010. A global analysis of protected area management effectiveness. *Environ. Manag.* 46, 685–698. <https://doi.org/10.1007/s00267-010-9564-5>.
- Lindsey, P.A., Nyirenda, V.R., Barnes, J.I., Becker, M.S., McRobb, R., Tambling, C.J., Taylor, W.A., Watson, F.G., T'Sas-Rolfes, M., 2014. Underperformance of African protected area networks and the case for new conservation models: insights from Zambia. *PLoS One* 9, e94109. <https://doi.org/10.1371/journal.pone.0094109>.
- Lindsey, P.A., Petracca, L.S., Funston, P.J., Bauer, H., Dickman, A., Everatt, K., Flyman, M., Henschel, P., Hinks, A.E., Kasiki, S., Loveridge, A., Macdonald, D.W., Mandisodza, R., Mgoola, W., Miller, S.M., Nazerali, S., Siegel, L., Uiseb, K., Hunter, L.T.B., 2017. The performance of African protected areas for lions and their prey. *Biol. Conserv.* 209, 137–149. <https://doi.org/10.1016/j.biocon.2017.01.011>.
- Lindsey, P.A., Roulet, P.A., Romanach, S.S., 2007. Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. *Biol. Conserv.* 134, 455–469. <https://doi.org/10.1016/j.biocon.2006.09.005>.
- Little, P.D., 1996. Pastoralism, biodiversity, and the shaping of savanna landscapes in East Africa. *Africa* 66, 37–51. <https://doi.org/10.2307/1161510>.
- Locke, H., 2014. Nature needs half: a necessary and hopeful new agenda for protected areas. *Nat. New South Wales* 58, 7–17.
- Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. *Nature* 405, 243–253.
- Mascia, M.B., Pailler, S., Krithivasan, R., Roshchanka, V., Burns, D., Mlotha, M.J., Murray, D.R., Peng, N., 2014. Protected area downgrading, downsizing, and degazettement (PADDD) in Africa, Asia, and Latin America and the Caribbean, 1900–2010. *Biol. Conserv.* 169, 355–361. <https://doi.org/10.1016/j.biocon.2013.11.021>.
- Msuha, M.J., Carbone, C., Pettorelli, N., Durant, S.M., 2012. Conserving biodiversity in a changing world: land use change and species richness in northern Tanzania. *Biodivers. Conserv.* 21, 2747–2759. <https://doi.org/10.1007/s10531-012-0331-1>.
- Newmark, W.D., 1996. Insularization of Tanzanian parks and the local extinction of large mammals. *Conserv. Biol.* 10, 1549–1556. <https://doi.org/10.1046/j.1523-1739.1996.10061549.x>.
- Ogutu, J.O., Piepho, H.P., Said, M.Y., Ojwang, G.O., Njino, L.W., Kifugo, S.C., Wargute, P.W., 2016. Extreme wildlife declines and concurrent increase in livestock numbers in Kenya: what are the causes? *PLoS One* 11. <https://doi.org/10.1371/journal.pone.0163249>.
- Pfeifer, M., Burgess, N.D., Swetnam, R.D., Platts, P.J., Willcock, S., Marchant, R., 2012. Protected areas: mixed success in conserving East Africa's evergreen forests. *PLoS One* 7, e39337. <https://doi.org/10.1371/journal.pone.0039337>.
- Pouzols, F.M., Toivonen, T., Minin, E. Di, Kuikkala, A.S., Kullberg, P., Kuustera, J., Lehtomäki, J., Tenkanen, H., Verburg, P.H., Moilanen, A., 2014. Global protected area expansion is compromised by projected land-use and parochialism. *Nature* 516, 383–386. <https://doi.org/10.1038/nature14032>.
- Pringle, R.M., 2017. Upgrading protected areas to conserve wild biodiversity. *Nature* 546, 91–99. <https://doi.org/10.1038/nature22902>.
- Reid, R.S., Thornton, P.K., Kruska, R.L., 2004. Loss and fragmentation of habitat for pastoral people and wildlife in east Africa: concepts and issues. *Afr. J. Range Forage Sci.* 21, 171–181. <https://doi.org/10.2989/10220110409485849>.
- Riggio, J., Caro, T., 2017. Structural connectivity at a national scale: wildlife corridors in Tanzania. *PLoS One* 12 (11), e0187407. <https://doi.org/10.1371/journal.pone.0187407>.

- Rodrigues, A.S.L., Andelman, S.J., BAKAN, M.I., Boitani, L., Brooks, T.M., Cowling, R.M., Fishpool, L.D.C., Da Fonseca, G.A.B., Gaston, K.J., Hoffmann, M., Long, J.S., Marquet, P.A., Pilgrim, J.D., Pressey, R.L., Schipper, J., Sechrest, W., Stuart, S.H., Underhill, L.G., Waller, R.W., Watts, M.E.J., Yan, X., 2004. Effectiveness of the global protected area network in representing species diversity. *Nature* 428, 640–643. <https://doi.org/10.1038/nature02422>.
- Shackelford, G.E., Steward, P.R., German, R.N., Sait, S.M., Benton, T.G., 2015. Conservation planning in agricultural landscapes: hotspots of conflict between agriculture and nature. *Divers. Distrib.* 21, 357–367. <https://doi.org/10.1111/ddi.12291>.
- Stoner, C., Caro, T., Mduma, S., Mlingwa, C., Sabuni, G., Borner, M., 2007a. Assessment of effectiveness of protection strategies in Tanzania based on a decade of survey data for large herbivores. *Conserv. Biol.* 21, 635–646. <https://doi.org/10.1111/j.1523-1739.2007.00705.x>.
- Stoner, C., Caro, T., Mduma, S., Mlingwa, C., Sabuni, G., Borner, M., Schelten, C., 2007b. Changes in large herbivore populations across large areas of Tanzania. *Afr. J. Ecol.* 45, 202–215. <https://doi.org/10.1111/j.1365-2028.2006.00705.x>.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira De Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. *Nature* 427, 145–148. <https://doi.org/10.1038/nature02121>.
- Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., Swackhamer, D., 2001. Forecasting agriculturally driven global environmental change. *Science* (80-.) 292, 281–284. <https://doi.org/10.1126/science.1057544>.
- Tranquilli, S., Abedi-Lartey, M., Abernethy, K., Amsini, F., Asamoah, A., Balangtaa, C., Blake, S., Bouanga, E., Breuer, T., Brncic, T.M., Campbell, G., Chancellor, R., Chapman, C.A., Davenport, T.R.B., Dunn, A., Dupain, J., Ekobo, A., Eno-Nku, M., Etoga, G., Furuichi, T., Gatti, S., Ghiurghi, A., Hashimoto, C., Hart, J.A., Head, J., Hega, M., Herlinger, I., Hicks, T.C., Holbech, L.H., Huijbregts, B., Köhl, H.S., Imong, I., Yeno, S.L.D., Linder, J., Marshall, P., Lero, P.M., Morgan, D., Mubalama, L., N'Goran, P.K., Nicholas, A., Nixon, S., Normand, E., Nzoguyimpa, L., Nzooh-Dongmo, Z., Ofori-Amanfo, R., Ogunjemite, B.G., Petre, C.A., Rainey, H.J., Regnaut, S., Robinson, O., Rundus, A., Sanz, C.M., Okon, D.T., Todd, A., Warren, Y., Sommer, V., 2014. Protected areas in tropical Africa: assessing threats and conservation activities. *PLoS One* 9, e114154. <https://doi.org/10.1371/journal.pone.0114154>.
- UNEP-WCMC, IUCN, 2018. Protected Planet. The World Database on Protected Areas (WDPA).
- UNEP-WCMC, IUCN, 2016. Protected Planet Report 2016. Cambridge, UK and Gland, Switzerland.
- United Nations, D. of E., Social Affairs, P.D., 2017. World Population Prospects: the 2017 Revision, Key Findings and Advance Tables. Working Paper No. ESA/P/WP/248.
- Venter, O., Fuller, R.A., Segan, D.B., Carwardine, J., Brooks, T., Butchart, S.H.M., Di Marco, M., Iwamura, T., Joseph, L., O'Grady, D., Possingham, H.P., Rondinini, C., Smith, R.J., Venter, M., Watson, J.E.M., 2014. Targeting global protected area expansion for imperiled biodiversity. *PLoS Biol.* 12. <https://doi.org/10.1371/journal.pbio.1001891>.
- Venter, O., Magrath, A., Outram, N., Klein, C.J., Possingham, H.P., Di Marco, M., Watson, J.E.M., 2018. Bias in protected-area location and its effects on long-term aspirations of biodiversity conventions. *Conserv. Biol.* 32, 127–134. <https://doi.org/10.1111/cobi.12970>.
- Watson, J.E.M., Dudley, N., Segan, D.B., Hockings, M., 2014. The performance and potential of protected areas. *Nature* 515, 67–73. <https://doi.org/10.1038/nature13947>.
- Watson, J.E.M., Venter, O., Lee, J., Jones, K.R., Robinson, J.G., Possingham, H.P., Allan, J.R., 2018. Protect the last of the wild. *Nature* 563, 27–30. <https://doi.org/10.1038/d41586-018-07183-6>.
- Western, D., Russell, S., Cuthill, I., 2009. The status of wildlife in protected areas compared to non-protected areas of Kenya. *PLoS One* 4. <https://doi.org/10.1371/journal.pone.0006140>.
- Wilson, E.O., 2016. Half-Earth: Our Planet's Fight for Life. W.W. Norton & Company, New York. <https://doi.org/10.1149/1.3635578>.
- Woodroffe, R., Ginsberg, J.R., 1998. Edge effects and the extinction of populations inside protected areas. *Science* (80-.) 280, 2126–2128. <https://doi.org/10.1126/science.280.5372.2126>.