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RESEARCH ARTICLE

Representation of biodiversity and ecosystem services in East Africa's protected area network

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Abstract The dramatic increase in anthropogenic activity severely threatens the biodiversity and life-support services that underpin human well-being. The broadened focus of protecting ecosystem services (ESs) better aligns the interests of people and biodiversity conservation. In this study, we used species richness as a surrogate for biodiversity and mapped the key ESs in East Africa with the goal to assess the spatial congruence between biodiversity and ESs, and evaluate the representation of current protected areas (PAs) network for biodiversity and ESs. The results showed that PAs well represented for species richness and regulating services but underrepresented for provisioning services. The PAs network occupies 10.96% of East Africa's land surface, and captures 20.62–26.37% of conservation priorities for vertebrate and plant species. It encompasses more than 16.23% of priority areas for three regulating services, but only 6.17% and 5.22% for crop and livestock production, respectively. Strong correlations and high overlaps exist between species richness and regulating services, particularly for carbon storage, water yield and plants. Thus, we believe that actions taken to conserve biodiversity also will protect certain ESs, which in turn will create new incentives and funding sources for the conservation of biodiversity. Overall, our results have wide-ranging policy implications and can be used to optimize conservation strategies for both biodiversity and multiple ESs in East Africa.

Keywords Biodiversity · Conservation priority area · East Africa · Ecosystem management · Ecosystem services · Protected areas (PAs)

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INTRODUCTION

Natural ecosystems sustain biodiversity and fundamental life-support services that are indispensable to humanity (Summers et al. 2012). Recently, with continually increasing human pressure, biodiversity and certain key ecosystem services (ESs) that underpin human well-being have declined dramatically (Archer et al. 2018). Protected areas (PAs) have been the primary mechanism in biodiversity conservation, rehabilitation and sustainable management (Naughton-Treves et al. 2005; Rands et al. 2010). Efforts to conserve natural systems have traditionally focused on biodiversity. More recently, society has increasingly focused on managing nature for the ES it provides people (Balvanera et al. 2001; Naidoo et al. 2008; Tallis et al. 2008; Manhaes et al. 2016). Incorporating ES in PAs networks and biodiversity conservation policies appear to promote relevant policy sectors committed to biodiversity conservation (Armsworth et al. 2007; Haslett et al. 2010; Wittmer and Gundimeda 2012; Castro et al. 2015).

Biodiversity plays a multi-layered role in the delivery of ES (Mace et al. 2012). Relations between biodiversity conservation actions and ES delivery on a large spatial scale are ambiguous, with negative (trade-offs) and positive (synergies) correlations (Naidoo et al. 2008; Strassburg et al. 2010; Eastwood et al. 2016; Xu et al. 2017b). Indeed, this ambiguity can influence optimal management decisions (Dee et al. 2017). If biodiversity underpins these key services, and these services are found in PAs more than in non-PAs (Castro et al. 2015; Eastwood et al. 2016), then it is more likely to develop political and financial support for conservation (Haslett et al. 2010; Xu et al. 2017b). However, the direct evidence base for this argument is weaker than might be expected. To better integrate ES into planned or existing conservation programmes and maximize the representation of conservation targets, we need to more broadly evaluate the spatial concordance between areas that produce ES and those that support biodiversity (Manhaes et al. 2016).

In practice, funding for conservation action is constrained, and thus, identifying priority areas for biodiversity conservation and the biophysical supply of ES is essential to allocate conservation resources and guide sustainable development (Zagonari 2016). Therefore, there is an urgent need to quantify and map the spatial distribution pattern of biodiversity and ES. A well-designed PAs network is expected to achieve both conservation and development goals. However, relatively little is known about the extent to which the current PAs network captures biodiversity and ES (Scott et al. 2001; Jenkins et al. 2013; Xu et al. 2017b), as well as the gap between conservation demand and supply (Chapa-Vargas and Monzalvo-Santos 2012).

Representation, a core concept and criterion in systematic conservation planning that has important implications for the effectiveness of PAs, can be measured by the presence or absence of important conservation features (Kukkala and Moilanen 2013; Lu et al. 2017). Thus, the levels of current PAs systems devoted to biodiversity and ES can be revealed effectively through representation analysis (Manhaes et al. 2016).

East Africa is rich in wildlife resources and has been a focus of biodiversity conservation (Withers and Hosking 2002). Over the past decades, a large number of PAs have been established to protect biodiversity and support livelihoods, and cover nearly 11% of East Africa's land surface today (Fig. 1) (Watson et al. 2014). Further, people in East Africa regard farming, logging, grazing, and hunting as their main sources of livelihood, and thus the conflict between biodiversity conservation and local livelihoods has become increasingly prominent. Therefore, the need for research to identify conservation priority areas of biodiversity and ES and evaluate the extent to which the current PAs network captures biodiversity and ES is of utmost urgency in East Africa.

In this study, we aimed to answer the following questions: (1) Where are the conservation priority areas for species richness and the biophysical supply of services (the upper 20th percentile of each) located in East Africa, and are these areas spatially concordant? (2) How well-represented are biodiversity and ES in the current PAs network? To address above questions, we first mapped the spatial distribution of species richness and key ES in East Africa. Second, we analysed the interactions (trade-offs or synergies) among multiple variables related to species richness and services. Third, we identified the conservation priority areas for species richness and the biophysical supply of services. Finally, we calculated the percentage of priority areas within the current PAs network to provide a snapshot of how well the PAs network encompasses biodiversity and ES. Our results can provide guidance for conservation and ecosystem management in East Africa.

MATERIALS AND METHODS

Ecosystem service assessment

In this study, we assessed three key regulating ESs: carbon storage, water yield and soil retention, and two key provisioning ES: crop and livestock production. These services were selected based on their significance to East Africa and the availability of data. All spatial analyses were conducted and maps generated using ESRI ArcGIS 10.1 software.

Water yield was estimated using the water balance equation derived from the Integrated Valuation of Ecosystem Services and Trade-offs (INVEST) model, indicating the difference between the amount of precipitation and evapotranspiration (Xu et al. 2017b). Soil retention was measured using the revised universal soil loss equation, indicating the difference between potential and actual soil erosion in ecosystems (Ouyang et al. 2016). Vegetation carbon storage refers to carbon stored by living vegetation (aboveground and belowground biomass), which was estimated by assigning the associated carbon value (Table S1) to each land cover, stratified by ecoregion (Ruesch and Gibbs 2008). Crop production was approximated as the relative cropland percentage instead of the absolute value (Fritz et al. 2015). For livestock production, we used tropical livestock units (TLUs) to combine cattle (TLU = 0.7), goats (TLU = 0.1) and sheep (TLU = 0.1) densities into a single map of livestock density, which can be an indicator for livestock production (Manhaes et al. 2016; Andela et al. 2017). Then, we resampled all ES to a resolution of 1/120° using the nearest neighbor method. More specific details about the assessment of the five key ES can be found in *SI Text*. Finally, for each ES type, we normalized the biophysical supply value directly to a scale that ranges from 0 to 100 using the minimum–maximum normalization method and defined a priority area for ES provision as the top 20% of the cumulative area (Qiu and Turner 2013; Xu et al. 2017b) (Fig. S2).

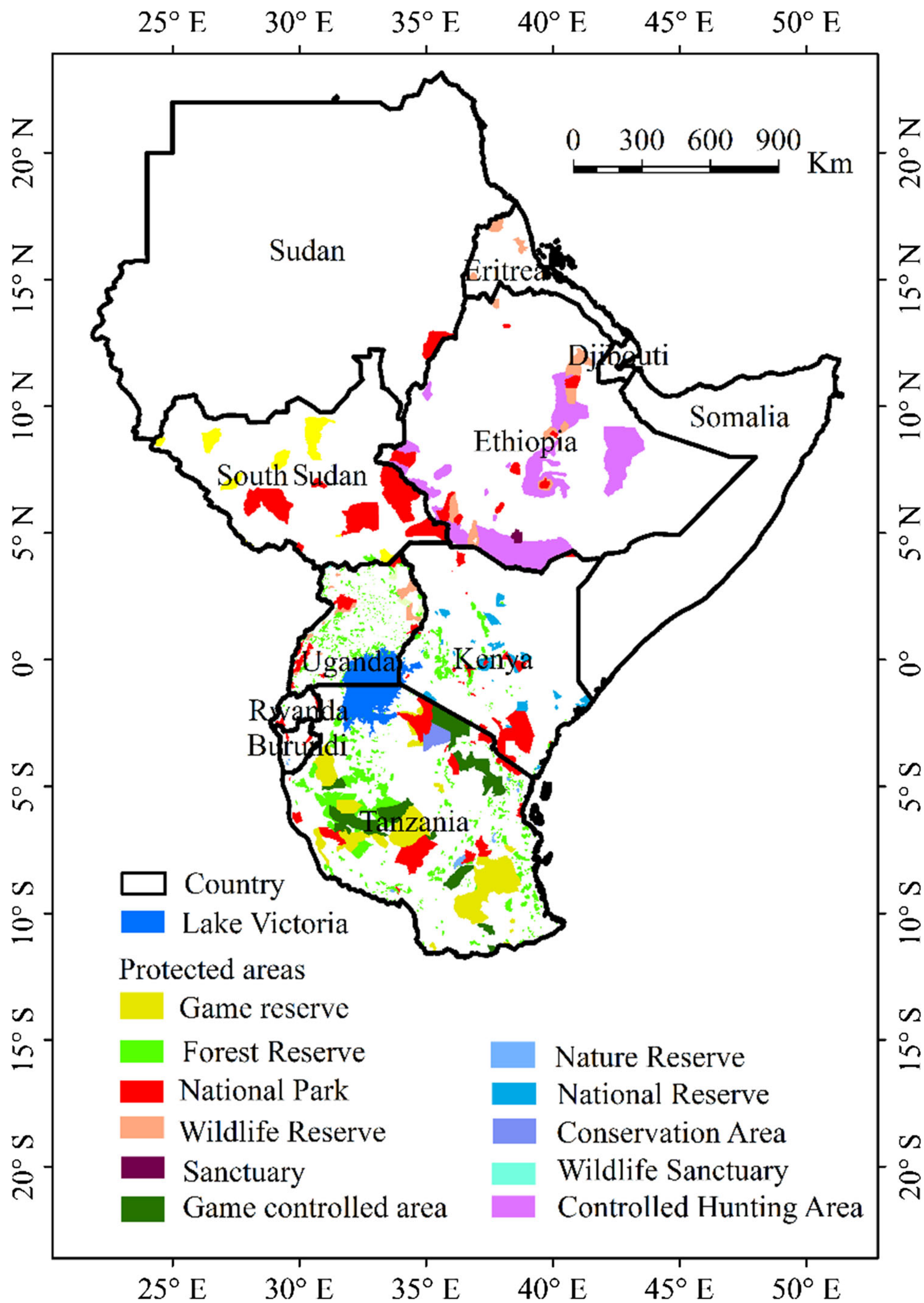

Fig. 1 The study area and main protected areas in East Africa

Biodiversity assessment

In this study, we used species richness as a surrogate for biodiversity and assessed the extent to which the current PAs network captures species richness (Costanza et al. 2007; Bai et al. 2011). For mammals and amphibians, we used range maps from the International Union for the Conservation of Nature (IUCN). For birds, we used range maps from the Birdlife International (Jenkins et al. 2013). For plants, we used published plant species richness data for 867 terrestrial ecoregions (Kier et al. 2005). We did not include invertebrates, even though they likely represent at least 95% of all species, they are undocumented largely (Myers et al. 2000). Similarly, we also normalized the value for each taxon separately to a scale that ranges from 0 to 100 using the minimum–maximum normalization method and defined a priority area for biodiversity conservation as the top 20% of the cumulative area (Qiu and Turner 2013; Xu et al. 2017b) (Fig. S2).

Hotspots analysis

Hotspots are commonly defined as areas that contain the upper range of multiple ES or species richness (Schröter and Remme 2016), which can be identified by overlaying and summing maps of the upper 20th percentile (directly from the cumulative frequency distributions (CFDs)) of each ES and species taxon (Fig. S2) (Egoh et al. 2009; Bai et al. 2011). In this study, ES hotspots were defined as locations containing at least four ES in the upper 20th percentile, which represented a majority that allowed multiple upper range services to be supplied with at least two regulating services (Qiu and Turner 2013). Similarly, species richness hotspots were defined as locations containing four species taxa in the upper 20th percentile.

Correlation and factor analyses

Spatial interactions among multiple species richness and ES were analysed based on 10 000 non-zero points sampled randomly across the study area, which ensured the robustness of our results. To identify trade-offs or synergies among them, we performed Pearson's correlation analyses to measure correlations among each pair of variables. We then used factor analysis, a powerful statistical method that searches for the fewest number of independent latent variables (factors) that account for the structure of a set of observable variables. The number of factors was determined by a Scree test and the interpretability of factors derived, and we extracted the first three orthogonal factors (with varimax rotation). All correlation and factor analyses were performed using R 3.4.0.

Representation analyses

First, we extracted all PAs covering at least 5 km^2 from the World Database of Protected Areas, and excluded from our analyses all marine PAs and all areas designated only by international conventions (i.e., not gazetted nationally). By the end of 2015, there were 926 PAs in 9 of the 11 countries in East Africa (Fig. 1) (*SI Text*). To determine whether the conservation priorities of species richness or ES captured within the PAs network in East Africa was greater than by chance alone, we performed a representation analysis (Lu et al. 2017; Xu et al. 2017b). Specifically, if the priority areas (the upper 20th percentile) of species richness or ES supply within the PAs relative to the total priority areas was above the PAs coverage of study areas, the PAs network was deemed to represent biodiversity or ES well. Otherwise, the PAs network was deemed to represent biodiversity or ES poorly.

RESULTS

Distributions of biodiversity and ecosystem services in East Africa

The areas in which the greatest richness of different terrestrial vertebrate taxa (amphibians, mammals, and birds) are distributed is similar. The shrub, grassland, and forests in the southern and south-western parts of East Africa (Tanzania, western Kenya, Rwanda and Uganda) held the greatest number of amphibian and mammal species (Fig. 2, Fig. S1). Bird species' richness also was high in Ethiopia's mountainous areas. Further, the geographic distributions of vertebrate were aggregated spatially (Moran's $I > 0.88$, $p < 0.001$) (Table S3). However, the distribution pattern of plants was disparate from those of vertebrates, except in forest, shrub, herbaceous cover, and riparian areas in the southern and south-western areas. The eastern and north-eastern part of East Africa also included many plant species. Overall, our analysis revealed the important conservation areas with relatively high species richness for each taxon (Fig. 2).

The provision of individual ES varied substantially across the study area (all Moran's $I > 0.3$, $p < 0.001$). Generally, the areas that provided high carbon storage and water yield were similar and were distributed primarily in forests, shrubs, and riparian areas in the southern, south-western and central areas (Ethiopia) of East Africa. For soil retention, the important source areas were distributed primarily in high altitude areas with trees and shrubs in the central (Ethiopia, Eritrea) and the south-eastern corner of the study area (Fig. 2, Fig. S1). However, the principal production areas for crops and livestock were located in cultivated and managed areas, shrub, and grassland mosaics in southern Sudan, western Ethiopia, and the surroundings of Lake Victoria, which differ somewhat from regulating services. For CFDs of each species taxon and ES, see Fig. S2.

Spatial concordance between biodiversity and ecosystem services in East Africa

Areas of different ES with high service value often were not spatially concordant (Fig. 3). ES hotspots occupied only 4.1% of the study area and were dispersed largely around Lake Victoria and in Ethiopia's high mountain areas. Nearly 69% of the study areas generated high values of only one or no ES, and these locations primarily were bare areas, artificial surfaces, croplands, and areas with

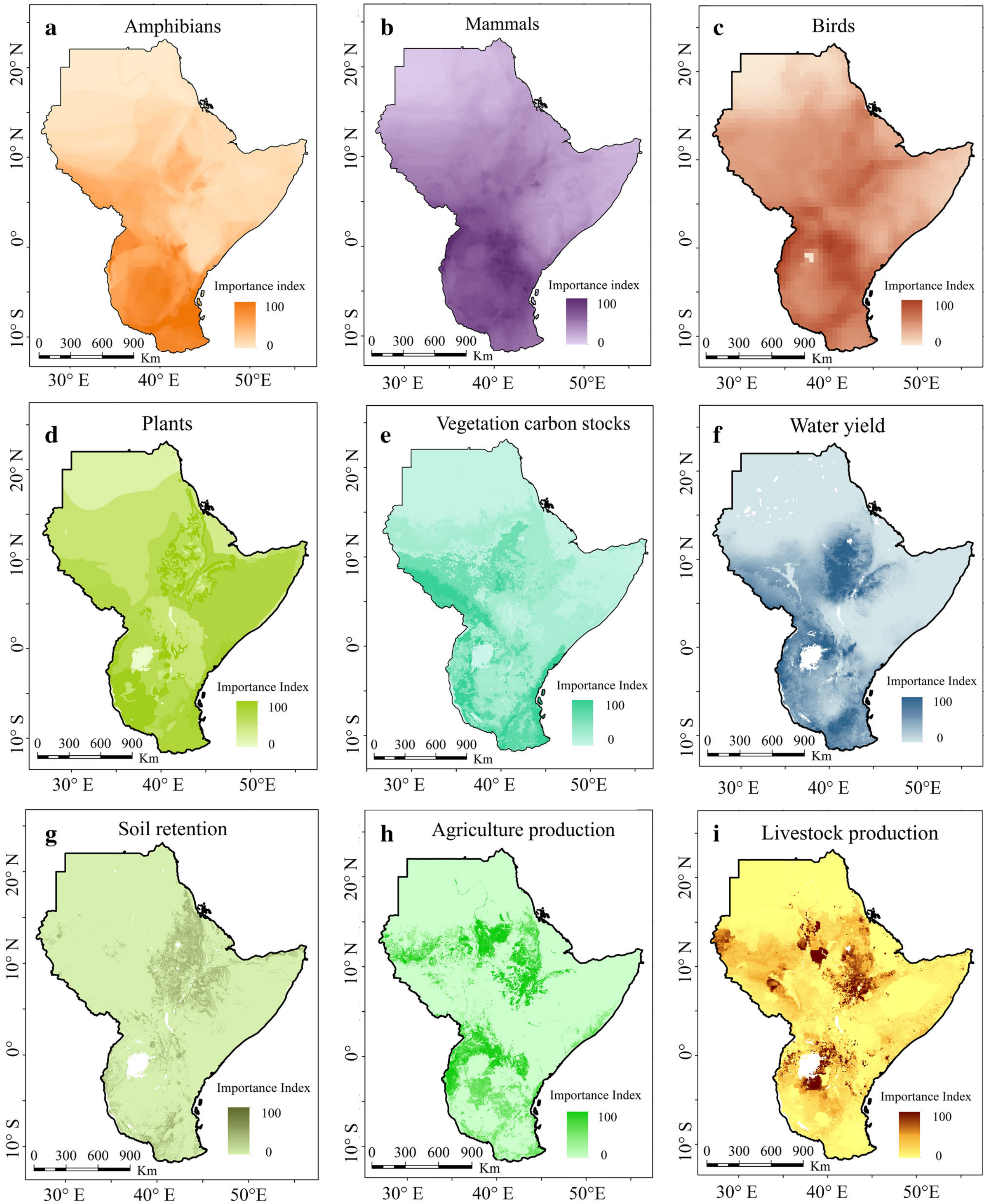

Fig. 2 The importance level of biodiversity conservation and ecosystem service supply in East Africa. **a–d** Results of species richness for amphibians, mammals, birds, and plants, respectively. **e–i** Results for carbon storage, water yield, soil retention, crop production, and livestock production, respectively. Scale 0–100 shows the importance level of each species taxon and service

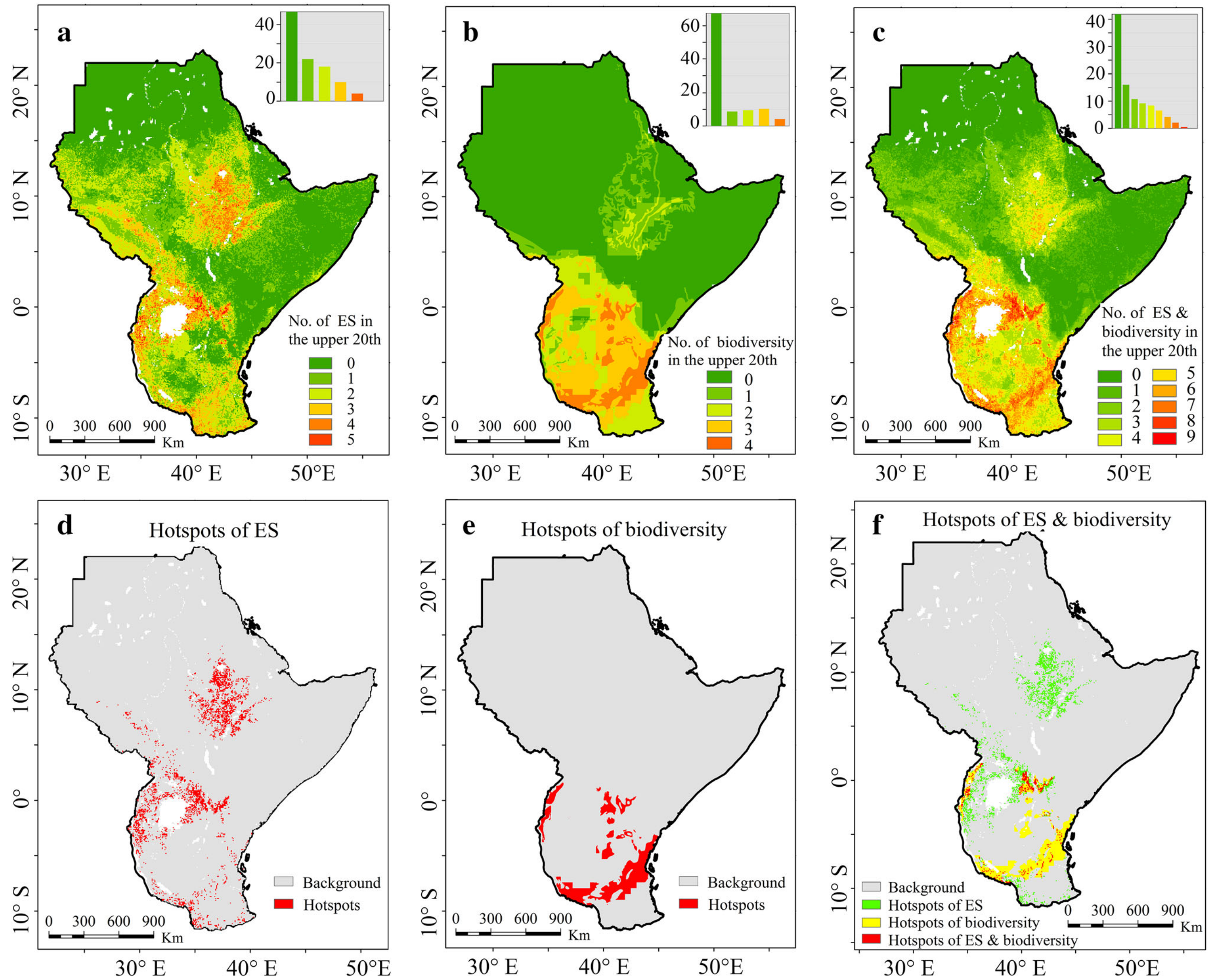

Fig. 3 Maps of hotspots for multiple services and biodiversity variables. **a** number of services in the upper 20th percentile, **b** number of species richness in the upper 20th percentile, **c** number of services and species richness in the upper 20th percentile, **d** ES hotspots where four or more services were in the upper 20th percentile, **e** hotspots of species richness where all species taxa were in the upper 20th percentile, and **f** spatial concordance between services and biodiversity hotspots

sparse vegetation. The biodiversity hotspots covered 4.0% of the study area and were distributed primarily around Lake Victoria and in Tanzania in PAs with trees, herbs, and shrubs. We found that the hotspots of ES and species richness do not always match well—as only 14.4% of the areas overlapped (Fig. 3f).

All pairwise correlations between water yield and other variables were significantly positive ($p < 0.05$), and generally, priority areas of water yield highly overlapped with those of other variables, indicating that water yield is related closely to species richness and other services supplies (Table S4). However, there was little relation between soil retention and other variables, perhaps because many factors (e.g., rainfall erosivity factor, soil erodibility factor, topographic factor) determine soil retention and uncertainty exists in data sources and factor estimates (Van der Knijff et al. 2000). In addition, we found synergy between carbon and water, both of which showed strong correlations and high overlaps with species richness (Table 1, Table S4). Thus, conservation priorities that target biodiversity could conserve optimal levels of carbon stocks and water yield.

Factor analysis identified three distinct groups of biodiversity and ES variables that could be managed and conserved separately (Table 2). The first factor ("vertebrate synergy") identified a strong positive relation among three vertebrate species taxa (mammals, amphibians, birds). The second factor ("vegetation and water synergy") identified a positive relation among two regulating services (carbon storage and water yield) and plant richness. The third factor

Table 1 Pearson correlation coefficients among multiple services and biodiversity variables (bold refers to $p < 0.05$)

	Amphibian	Mammal	Bird	Plant	Crop	Livestock	Soil retention	Water yield	Carbon storage
Amphibian	**1.00**								
Mammal	**0.87**	**1.00**							
Bird	**0.73**	**0.91**	**1.00**						
Plant	**0.58**	**0.55**	**0.57**	**1.00**					
Crop	**0.26**	**0.31**	**0.39**	**0.18**	**1.00**				
Livestock	**0.11**	**0.17**	**0.24**	**0.11**	**0.31**	**1.00**			
Soil retention	− 0.01	0.03	0.10	0.10	0.03	0.04	**1.00**		
Water yield	**0.64**	**0.68**	**0.69**	**0.51**	**0.37**	**0.19**	**0.11**	**1.00**	
Carbon storage	**0.53**	**0.42**	**0.33**	**0.38**	0.03	0.02	− 0.01	**0.45**	**1.00**

Table 2 Loading of variable estimates on each of three orthogonal axes derived from factor analysis (with varimax rotation) on the basis of 10 000 random points

Services and biodiversity	Factor 1: vertebrate synergy	Factor 2: vegetation and water synergy	Factor 3: crop and livestock synergy
Amphibian	**0.69**	0.56	0.13
Mammal	**0.96**	0.31	0.17
Bird	**0.79**	0.28	0.41
Plant	0.42	**0.46**	0.18
Crop	0.2	0.02	**0.61**
Livestock	0.09	− 0.01	**0.43**
Soil retention	0.01	0.03	0.12
Water yield	0.46	**0.52**	0.41
Carbon storage	0.22	**0.67**	− 0.03

Bold refers to that variables contained in each factor

("crop and livestock synergy") identified a positive relation between two provisioning services (crop and livestock production). Soil retention remained independent (three factor loadings < 0.20).

Representation of biodiversity and ecosystem services in protected areas

The results showed that the PAs network in East Africa encompasses 26.43% and 26.37, 20.62 and 22.29% of the priority areas for amphibians, mammals, birds, and plants, respectively. Thus, we can infer that the PAs network performs reasonably well for biodiversity as the coverage percentages of vertebrate species and plants were all above the PAs network's 10.96% coverage of the study area. Similarly, the PAs network encompasses more than 16.23% of priority areas for three regulating services, but only 6.17% and 5.22% for crop and livestock production, respectively (Fig. 4a). The same pattern is true for the percentage within strict PAs (strictly protected IUCN categories I–IV) (Rodrigues et al. 2004; Jenkins et al. 2013). The percentage of priority areas for species richness and regulating services (provisioning services) that are within strict PAs is greater (less) than an average of 4.75% (Fig. 4b). These findings indicate that East Africa's current PAs network represent biodiversity and regulating services well, and provisioning services poorly.

It is worth noting that PAs managed strictly are more effective than all PAs for three vertebrate groups' species diversity and two regulating services (Fig. S3), indicating that management policy (e.g. strict PAs with guard forces and law sanctions) may affect the levels of species protection and services provision. We also compared different types of PAs' representation of species richness and ES in Tanzania, where PAs occupy a large proportion of the country (nearly 29%) (Wei et al. 2018a). The results showed that the representation of PAs overall varied with management policies, and the representation of the same type of PAs for different species richness and services is also diverse depending on the conservation objectives of PAs (Fig. S4).

At the national scale, the representation of different species richness and ES in the PAs network exhibited high spatial heterogeneity. The PAs' representativeness with respect to conservation priority areas overall was highest in the southern countries of East Africa (Tanzania, Uganda, Rwanda, Kenya, and Burundi), where PAs exhibited good representation for species diversity and regulating services (Fig. 5). In Ethiopia, large areas have high species richness and are important service source areas as well, but the representation of PAs is relatively low. This indicates that large gaps exist in Ethiopia and need more attention in future conservation planning and actions, as it will be necessary to realistically expand the PAs network to mitigate biodiversity loss and sustain services key to human wellbeing. In contrast, most parts of Sudan and Eritrea are bare areas, where all species richness and provisioning services are lowest.

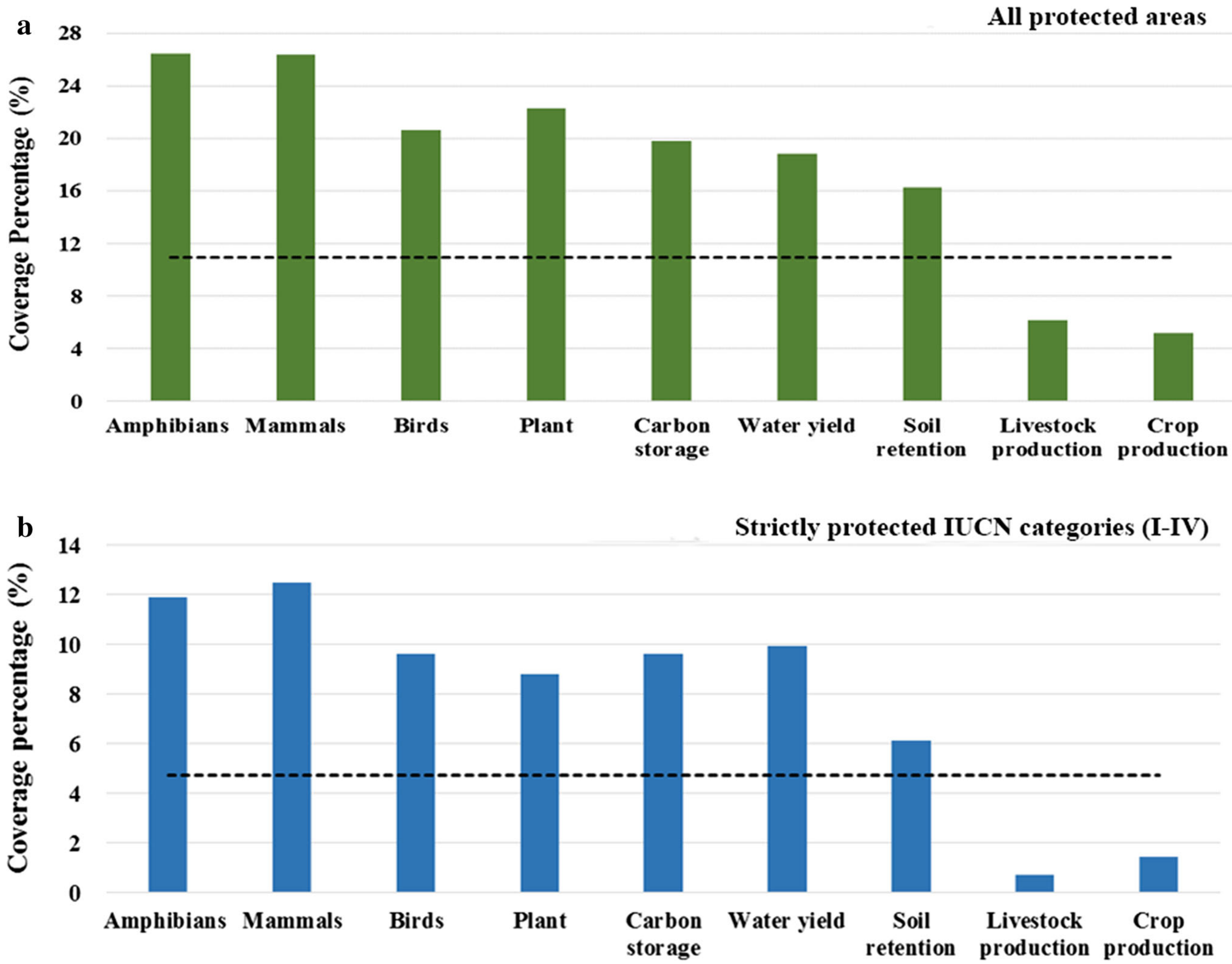

Fig. 4 Representation of biodiversity and ecosystem services in current PAs network. Comparison of conservation priority areas for species richness and ecosystem services within all PAs (**a**), and **b** the strict PAs (strictly protected IUCN categories I–IV) in East Africa

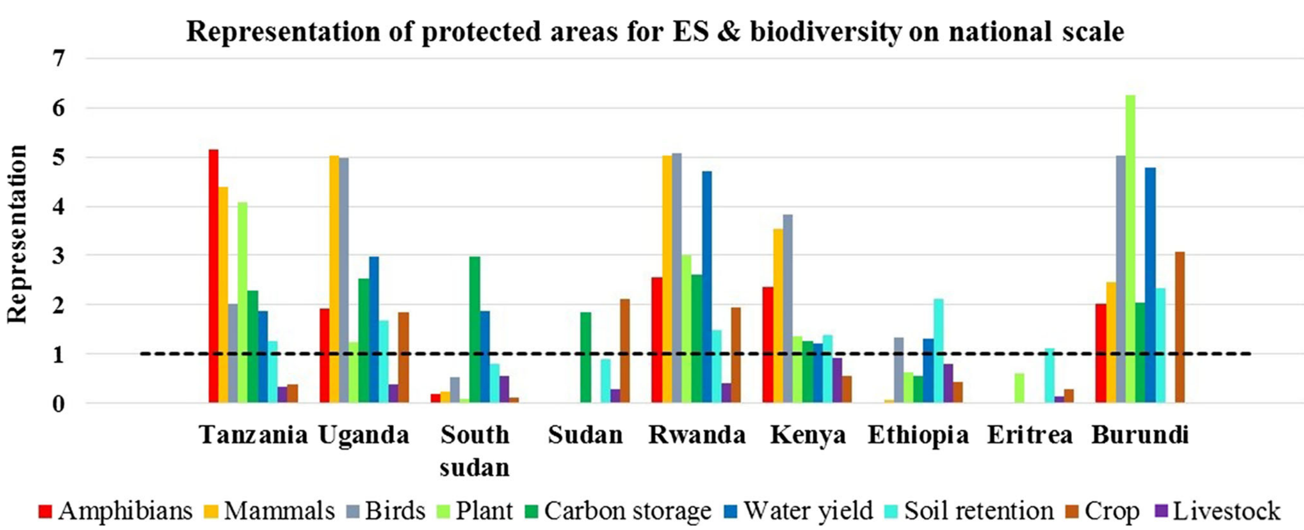

Fig. 5 Effectiveness of protected areas for each species taxon and service at the national scale

DISCUSSION

Protecting biodiversity has the potential to deliver regulating services

In our study, we found that the current PAs network in East Africa represents species richness (both vertebrate and plant species) and regulating services well, but underrepresents provisioning services (Fig. 4). These results are consistent with those Egoh et al. (2007) reported—biodiversity likely contributes more to regulating and cultural services, and less to provisioning services. Biodiversity plays a key role in all levels of the ES hierarchy: as a regulator of underpinning ecosystem processes, such as sustain ecosystems' resilience and stability (Sandifer et al. 2015), and as a final ES or a good that has a range of values, such as aesthetic, recreational, economic, and existence (Mace et al. 2012; Cimon-Morin et al. 2013). Indeed, virtually any decision about the way an ecosystem is managed will involve trade-offs among services. Interventions in PAs such as site protection, habitat management and incentive mechanisms influence land management, which in turn determines changes in service delivery or biodiversity in a particular site (Eastwood et al. 2016). Our results support the notion that actions taken to conserve biodiversity also will protect certain ES (Egoh et al. 2009; Castro et al. 2015; Eastwood et al. 2016), which could in turn build political and financial support for biodiversity conservation in East Africa (Harrison et al. 2014; Dee et al. 2017). However, some studies have presented contrasting results and found that PAs underrepresent source areas of ES (Naidoo et al. 2008; Xu et al. 2017b). Scale (Naidoo et al. 2008), the ES selected (Eastwood et al. 2016), and human intervention (Egoh et al. 2007) may affect the relation (trade-offs or synergies) observed among biodiversity conservation actions and ES delivery. For example, win–win ecoregions for biodiversity and carbon storage can contain both win–win and trade-off locations that emerge on a finer scale (Naidoo et al. 2008). An ambitious interdisciplinary research effort is perhaps needed to move beyond these preliminary and illustrative analyses to fully evaluate the spatial concordance between biodiversity and ES.

Implications for biodiversity and ecosystem co-management

Hotspots (approximately 4%) may be disproportionally important and represent conservation priorities, as the loss or degradation of these areas could cause multiple services or species richness to decrease. Correspondingly, more species or ES conceivably might be protected with smaller land areas, assuming these hotspot areas are selected optimally. In our study, we observed that the hotspots of ES and species richness did not match well, in that 14.4% of the areas overlapped (Fig. 3f). Further, although there are six categories in the IUCN PA system, none of the PA types target securing ES (Xu et al. 2017a). Thus, we suggest that, in addition to PAs for biodiversity conservation, a new PAs category particularly for ES supply is needed in East Africa, within which such human activities as grazing, harvesting, and gathering on a sustainable basis are permitted if they do not interfere with key services (Dudley 2008; Xu et al. 2017b). Thus, multiple conservation goals can be achieved in protecting and co-managing biodiversity and ES (Mace et al. 2012).

In addition, we suggest that regions identified as conservation priorities that are represented poorly in the current PAs network require more attention in future conservation actions. For example, in Ethiopia, we recommend expanding the PAs system to cover more high-priority areas for biodiversity conservation and ES provision. Indeed, uniform conservation strategies based on protecting a percentage of each country or biome are less effective because they are blind to the fact that biodiversity and ES are not distributed uniformly (Fig. 2).

Further, different management regimes alter the levels of species protection and service provision (Fig. S3). Generally, PAs managed strictly (e.g., nature reserve) benefit from complete management practices and strengthened legal powers that demonstrate good representation of species richness and regulating services, although those strict measures restricted local people's access to provisioning services, such as grazing and harvesting (Fig. S4). In contrast, PAs such as game-controlled areas (commonly gazetted as multi-resource use area) are devoid of on-site patrols, which leads often to the overuse of natural resources and the underrepresentation of regulating services (Fig. S4). Thus, further study on the way PAs balance nature conservation and local livelihoods is required. Nevertheless, the long-term protection of biodiversity and ES remains a major challenge in East Africa, where there is an urgent need for a clear PAs planning framework to maximize the efficiency and representation of conservation targets. The continual engagement model (Reid et al. 2016), which provides continual feedbacks among researchers, policymakers, and communities, and the citizen science movement (Steger and Butt 2015) in which citizens are encouraged to participate in science, may promote future conservation and natural resources management.

Limitations

While the information presented here improves our understanding of the relation between biodiversity conservation actions and ES delivery, our study is nevertheless constrained by the availability and accuracy of spatial datasets. Choosing simplified proxy-models to match data availability may lead us to ignore the important biotic processes that determine services supply (Lavorel et al. 2017). There also is uncertainty from spatial data source, level of process understanding, parameterization and model selection in assessing species richness and ES at a large spatial scale, and quantifying and eliminating these uncertainties remain the main challenges by far (Martínez-Harms and Balvanera 2012; Schulp et al. 2014; Lavorel et al. 2017; Wang et al. 2018). Further, our study focused largely on the spatial distribution of species richness and ES, not their temporal changes, and thus deviations caused by time lags among datasets could be neglected (Manhaes et al. 2016; Xu et al. 2017b).

Due to the lack of detailed information and methodological constraints, species richness—a common indicator used as a surrogate for biodiversity, cannot fully represent biodiversity's components and attributes. Thus, we recommend that better surrogates should be developed or that perhaps direct measures of biodiversity should be used. Then, our study assessed a limited number of services. For example, we did not include cultural services here because it is difficult to quantify their biophysical value accurately (Plieninger et al. 2013). Actually, many biodiversity components have cultural value, such as appreciation of wildlife and scenic places, and spiritual and recreational values (Mace et al. 2012). Studies have shown that, in general, PAs provide higher levels of cultural services (e.g. aesthetics, tourism/recreation, education) than do non-PAs (Eastwood et al. 2016). Accordingly, further efforts should be made to define, assess and value cultural services, and strengthen the associations among biodiversity, cultural services and human well-being (Hernandez-Morcillo et al. 2013). Further, depending on the method applied, the relative importance of endemic species and their degree of threat in biodiversity and ES hotspots should be considered in future (Myers et al. 2000). In addition, as ES social demand was not completely accordant with the biophysical supply in spatial distribution, further studies should consider the human need for services and the mismatch between ES supply and demand (Wei et al. 2018b).

Despite these limitations, our findings have wide-ranging policy implications, as they identified the conservation priorities of species richness and ES and illustrated biodiversity and ES representation in the current PAs network in East Africa. These results can be used to optimize conservation strategies for both biodiversity and multiple ES in East Africa.

CONCLUSION

Our study was an interdisciplinary assessment that analysed spatial relation between biodiversity and ES conservation priorities and provided a snapshot of how well the current PAs network encompasses biodiversity and ES in East Africa. The results showed that PAs represent species richness (both vertebrate and plant species) and regulating services well, but underrepresent provisioning services, as the priority areas within PAs was greater than the average for species richness and regulating services, but lower than the average for provisioning services. Moreover, strong spatial correlations existed between species richness and regulating services. Thus, we believe that biodiversity conservation has the potential to deliver certain ES, which could in turn build political and financial support for biodiversity conservation. This broadened focus on protecting ES better aligns the interests of people and biodiversity conservation (Armsworth et al. 2007; Turner and Daily 2008).

In summary, these results have significant policy implications and can be used to allocate conservation resources, manage ecosystems and guide practical decision-making. We recommend regions identified as conservation priorities that are represented poorly in the current PAs network require more attention in future conservation actions. Our systematic method also makes use of data that are available readily, and therefore, is applicable to evaluating the level of the PAs system devoted to biodiversity and ES in other locations.

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