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Servicescape of the Greater Serengeti-Mara Ecosystem: Visualizing the linkages between land use, biodiversity and the delivery of wildlife-related ecosystem services

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ABSTRACT

Understanding how anthropogenic activities and management actions influence the delivery of ecosystem services is complicated by the interrelated nature of diverse factors. We present a Bayesian Belief Network to highlight the likely consequences of a set of interventions on four wildlife-related ecosystem (dis)services and for supporting biodiversity and human welfare in the Greater Serengeti-Mara Ecosystem. According to the model, core protected areas are important for biodiversity and safari tourism provision. In adjacent game reserves safari tourism opportunities may be hampered by trophy and bushmeat hunting causing fear in wildlife. Most multiple-use areas strike a good balance between the costs and benefits derived from wildlife. Loliondo, however, requires drastic changes in management to either maximize green value creation or sustainable welfare. Although further globalization is expected to render highest levels of welfare, this will be at the expense of biodiversity and related ecosystem services. An online version of the model is available (https://africanbioservices.shinyapps.io/servicescape) to interactively explore five future scenarios with alternative management strategies, and visualization of the resultant consequences thereof. Identifying areas of conflicts and potential trade-offs between ecosystem (dis)services are crucial to find pathways to nature-based tourism strategies that simultaneously maintain biodiversity and promote the socioeconomic viability of local communities.

1. Introduction

The Greater Serengeti-Mara Ecosystem (GSME) is world famous for its biodiversity as well as home to a rapidly increasing human population adjacent to the GSME protected areas (Estes et al., 2012; Ogutu et al., 2011). These rural communities are considered to have a significant problem regarding poverty and unemployment. Low skills and rapid population growth are the main factors contributing to increase pressure on natural resources, not in the least close to areas with some sort of conservation status (Estes et al., 2012; McCabe et al., 2010). At the same time, the local communities depend on what the land provides them and have few alternatives (Homewood et al., 2012; McCabe et al., 2010). These communities are therefore directly dependent on services provided by the ecosystem including grazing lands for their livestock and fertile soils for agriculture (Estes et al., 2012; McCabe et al., 2010). Land-use practices vary across the GSME and pose different threats to ecosystem functioning and thereby the provisioning of ecosystem services (ES) in the longer term (Dobson, 2009; Msoffe et al., 2011; Ogutu et al., 2016). The provisioning of ES are crucially dependent on biodiversity (Cardinale et al., 2012). However, it is also be aware of potential trade-offs between supporting biodiversity and ecosystem services. Wildlife may not only provide ES but also ecosystem disservices (Lele et al., 2013). While wildlife provides opportunities for nature-based tourism and trophy hunting, the same wildlife may also cause conflicts with human activities (Shemwetta and Kideghesho, 2000). For local communities in the GSME, large mammals may be both a positive and negative resource. While large herbivores provide communities with bushmeat or trophy hunting incomes, for example, the same animals may destroy crops or transmit diseases to livestock (Craft, 2015). Both herbivores and carnivores provide an important service to local communities for nature-based tourism. Carnivores, however, being attractive to the economically important tourist and trophy hunting industries, are at the same time responsible for the depredation of culturally and economically important livestock (Ogutu et al., 2005; Ripple et al., 2014; Røskaft et al., 2003).

Nature-based tourism involves activities such as wildlife safaris,

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trophy hunting as well as local cultural experiences such as visiting Maasai bomas (Homewood et al., 2012), thus observing animals and the natural and cultural landscapes, having limited negative environmental impacts. The tourism industry accounted for 9.7% of Kenya's and 9.0% of Tanzania's GDP in 2017 and is expected to increase the coming years ahead (WTTC, 2018a,b). The Ngorongoro Conservation Area, for example, received approximately US$ 70 million in 2016 from entrance fees alone (Slootweg, 2017). Nature-based tourism therefore has the potential to contribute to the preservation of the region's wildlife populations and their habitats whilst creating socioeconomic benefits for the local people through employment opportunities and/or through leasing of village lands for tourism activities (Charnley, 2005; Msoffe et al., 2011). In contrast to the loss of natural habitat to agriculture or overstocking of livestock, tourism therefore represents an attractive and more sustainable form of land-use. Still, this necessitates that local rural communities benefit from tourist-based activities. A transition to tourism would, however, need to be culturally appropriate and weigh-up the costs and benefits that such ventures may generate for a specific area. Thus, it is crucial to establish a nature-based tourism pattern that simultaneously maintains biodiversity and supports socioeconomic viable local communities (Baldus and Cauldwell 2004; Caro and Davenport, 2016; Naughton-Treves et al., 2005).

Livestock is a central and socio-economically important component of many local communities' lives. Especially the Maasai people, inhabiting the north-eastern parts of the GSME, depend on a pastoral lifestyle with cattle, sheep and goats (Homewood et al., 2012). West of the GSME, other tribes (e.g. Sukuma, Kurya, Ikoma) employ agropastoral or agricultural livelihood strategies. Carnivore populations living within the semi-protected areas adjacent to the Serengeti National Park and Maasai Mara National Reserve prey on livestock, creating animosity between protected area managers and livestock owners (Holmern et al., 2007; Kolowski and Holekamp, 2006). This leads to the killing of carnivores as either a preventative or retaliatory response to livestock depredation (Ikanda and Packer, 2008). Villages closer to protected area boundaries are frequently more likely to incur livestock losses (Holmern et al., 2007; Kolowski and Holekamp, 2006; Ogutu et al., 2005). The financial losses can equate to a substantial portion of annual income and tolerance to carnivores is usually low (Holmern et al., 2007; Mfunda and Røskaft, 2010). Tourism may therefore provide an alternative land-use option in certain mixed land-use areas. For most forms of nature-based tourism, however, wildlife populations need to be habituated to vehicles and present in moderate to high densities to meet tourist expectations (Grünewald et al., 2016; Okello et al., 2008). In this way, legal trophy hunting and illegal bushmeat hunting may well threaten the viability of tourism operations.

Illegal bushmeat hunting is conducted to supply households with protein and individual economic gain. These activities are largely conducted by young men with few livestock and no alternative forms of income (Hariohay et al., 2019; Loibooki et al., 2002). The availability of and preference for targeted species varies between different parts of the ecosystem and between tribes (Ndibalema and Songorwa, 2007). The most common form of hunting and trapping involves use of wire snares (Holmern et al., 2002). This indiscriminate form of trapping results in several non-target species, including large carnivores, being caught in the traps. Trophy hunting is generally better regulated than illegal hunting and offtake is largely limited to specified quotas. However, quotas are rarely based on sound wildlife population census data and may consequently have detrimental effects (Packer, 2015). Although trophy hunting secures large amounts of foreign income, local people normally enjoy few benefits (Lindsey et al., 2007b). In addition to lowering the densities of local wildlife populations, trophy hunting and nature-based tourism are not compatible, since hunted wildlife populations fear people and the vehicles that tourists use to view them (Hariohay et al., 2018).

Any changes to wildlife and its consequences for ecosystem functioning, is expected to affect the delivery of ecosystem services (Daw et al., 2016; Dobson, 2009). The vital benefits derived by society are thus threatened by rapidly increasing human populations and the associated changes in land use (Msoffe et al., 2011; Ogutu et al., 2011; Reid et al., 2016). Mitigating long-term impacts requires informed and timely decision-making. Land-use planning, with the specific intention to maintain ecosystem integrity, is a complex and challenging task. At the landscape level, the main challenge is to determine how to optimise the allocation and management of diverse land-use alternatives while simultaneously considering the interests of different stakeholders (de Groot et al., 2010; Nuno et al., 2014). Assessing the impacts of current and potential future land-use activities are therefore important for ensuring the sustainable provision of ecosystem services (Egoh et al., 2012).

The objective of this paper is to explore the interlinkages between land cover/land use, (mammalian) wildlife and ecosystem service provision in the Greater Serengeti-Mara Ecosystem using a Bayesian Belief Network (BBN) framework. This exploration further aims to spatially assess the ecosystem service trade-offs between nature-based tourism, legal trophy hunting, illegal bushmeat hunting and livestock depredation, as well as biodiversity and human welfare.

2. Material and methods

2.1. Study area

The Greater Serengeti-Mara Ecosystem (GSME, Fig. 1) encompasses over 30,000 km^2 of wildlife-dominated land in northern Tanzania and southwestern Kenya. The GSME includes Serengeti National Park (NP), Ngorongoro Conservation Area (CA), Loliondo Game Controlled Area (GCA), Maswa, Ikorongo and Grumeti Game Reserves (GR) and in Kenya the Maasai Mara National Reserve (NR) and adjacent Conservancies. Serengeti NP and Maasai Mara NR are important protected areas internationally renowned for conservation and nature-based safari tourism (Bedelian, 2014; Sekar et al., 2014). The GSME hosts the

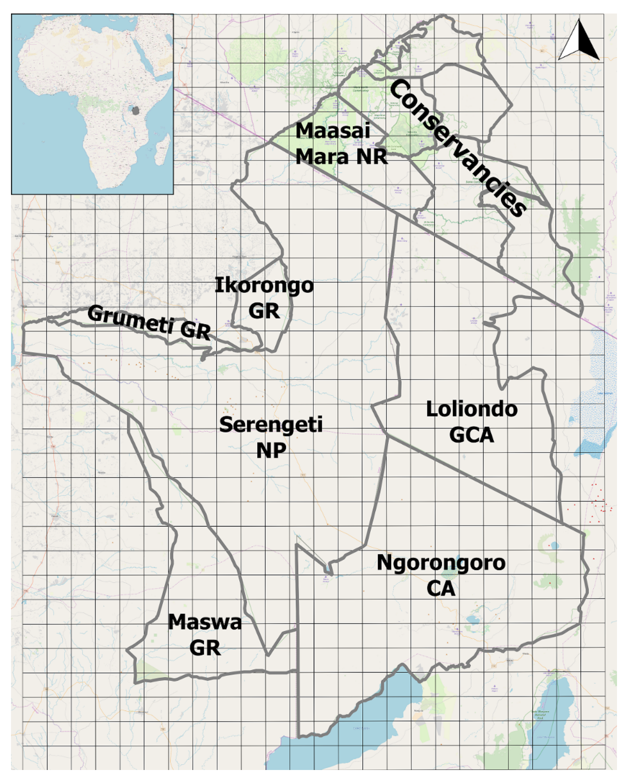


Fig. 1. Location of the study area at the Greater Serengeti-Mara Ecosystem, including the boundaries of the different management areas. The 10 × 10 km grid is superimposed on the map (scale 1:1,250,000).

largest mammal migration in the world consisting of wildebeests, zebras and gazelles. The semi-protected areas surrounding these, consist of landscapes with mixed land-use practices. Whereas in Loliondo GCA and the Conservancies, Maasai livestock husbandry intermixed with small-scale subsistence farming are of major importance, the other reserves are important areas for trophy hunting and conservation. Unprotected areas surrounding the GSME consist mainly of subsistence farming and livestock husbandry. The landscape of the GSME is characterized by vast savannah plains with grassland and open woodlands. The region is bordered in the east-southeast by the mountain ranges of the East African Rift and the Ngorongoro crater, westwards by Lake Victoria and northwards by the Mau Forest in Kenya.

2.2. Methodology

To explore the linkages between land cover/land use, wildlife and the delivery of ecosystem services, we built a Bayesian Belief Network (BBN). A BBN provides an integrated modelling framework to structure specific scientific problems and explore future scenarios (Landuyt et al., 2013; McCann et al., 2006; Smith et al., 2018). By explicitly addressing interactions between variables and uncertainty, BBNs provide a mechanism for graphically and probabilistically modelling the causal effects of specific management actions on wildlife or environmental states (McCann et al., 2006; Oliver and Smith, 1990; Smith et al., 2018). BBNs assume that the system under study can be described through a directed acyclic graph (i.e. no feedback loops), where each variable is conditionally independent of its non-descendants given its parent variables (i.e. local Markov property). Such models incorporate the logical or causal effects between specified ecological factors that influence the likelihood of certain states arising. A BBN links various nodes – representing e.g. land cover, a species' presence or ecosystem service delivery – using Conditional Probability Tables (CPT) or equations. BBN can, as a semi-quantitative modelling approach, be based on any combination of quantitative (in our case the input maps of the parent nodes) and qualitative (in our case the derived of the child nodes) input that enables combining ecological models with expert knowledge to model and spatially map ES (Landuyt et al., 2013; Landuyt et al., 2015; McCann et al., 2006; Smith et al., 2018). Advantages of using BBNs are their ability to model complex socio-ecological systems, to address uncertainty, to explore management strategies, and to spatially visualize management consequences facilitating communication to non-experts. While frequentist models may be equally good to assess aleatory uncertainty (i.e. variability or stochasticity), BBNs are also able to address epistemic uncertainty (i.e. lack of information or knowledge) through posterior distribution of probabilities (i.e. 'degrees of belief') based on prior information of each state (McCann et al., 2006). The BBN was built in the software program Netica (version 5.22, Norsys Software Corp.). We focused on four ecosystem services and disservices: (legal) trophy hunting, safari tourism, (illegal) bushmeat hunting and livestock depredation. In addition, biodiversity and human welfare available to local communities was assessed. Although these two nodes may not fully cover all aspects of welfare (e.g. education, income) and biodiversity (species other than large mammals, such as birds or insects), they do provide an indication of their respective distribution in the GSME. Welfare was here defined as peoples' average accessibility to markets (as defined by the road density and distance to settlements, and human population), anthropogenic land-use and per capita livestock density (cf. Moro et al., 2013; Nielsen et al., 2014). The four (dis)services were linked to large mammalian wildlife species deemed important for these services, and the land cover/land use conditions they are dependent on (Table 1). The expected probability of presence of each of these species was evaluated by linking these to their expected habitat preferences and management-related influences. Human-related information (e.g. livestock presence, welfare) was evaluated in a similar manner. The influence of the linkages on each node's state was quantified using conditional probability tables. Aggregated intermediate and final ES nodes were calculated using equations to obtain CPT values (Tables 1, 2). The model structure, linkages and CPT values were derived by reviewing the peer-reviewed literature concerning how different ES were affected by wildlife (Supplementary Information Table S1). Because often multiple studies were used to identify relevant linkages and their expected relative importance, CPT-values were interpreted based on the general conclusions from these studies rather than directly trying to integrate modelled estimates across studies. Unless the literature clearly indicated differential relative importance of the linkages, we employed equal weights in the equations. We built the BBN using a probabilistic approach assessing the probability of presence for each of the nodes included in the BBN (Fig. 2). Several of the wildlife nodes were spatially validated using independent data sources available to us. Independent point data (Table S5, Fig. S1) was superimposed on the visualized BBN wildlife maps (10×10 km resolution). Statistics (mean probability (+S.D.), % in cells $P > 0.5$) for each of the covered grid cells were calculated as a measure for goodness-of-fit.

To assess how ES provision, as well as welfare and biodiversity, varied across the landscape, we thereafter imported the BBN into the statistical program R (version 3.2.2; R Core Team, 2015) using the RNetica library (version 5.04; Almond, 2015) to run it iteratively over a 10×10 km resolution grid covering the entire GSME. We chose this scale because that would allow us to model the relative distribution of ES delivery across the landscape and compare management areas, while providing a realistic scale for the modelled social-ecological processes as derived from the available literature. For each grid cell, we gathered existing spatially-explicit background data on management (Table S3) and land cover (Table S2) as a basis to estimate the consequent expected probability of presence of wildlife species, human-related information, and ultimate ecosystem (dis)service provision as well as welfare and biodiversity. All land cover data (Table S2, excluding the management regions) was normalized using Fuzzy Logic to transform 10×10 km grid cell data into a [0,1] range using a sigmoid function with the 5% and 95% inflection points defined as the 5% and 95% quantile of the actual data. This was done to reduce overly strong influence of extreme values on the model. The human-related information and ecosystem (dis)services were assessed using specific equations (Table 2). All ultimate expected values were normalized using a linear stretch to render values within a [0,1] range. In this way each final node's expected relative distribution can be compared at the same scale. Note that the resultant outcomes allow for a relative comparison of where more or less of each ES can be delivered across the landscape, not how much in absolute terms. We took this approach because the actual use of ES (e.g. number of animals poached, number of livestock killed, number of reported trophies per quota) could not be rigorously estimated due to lack of knowledge and available information. We therefore deemed it better to evaluate the relative delivery of ES in order to evaluate the spatially-explicit overlap of ES in the landscape. For each unique pair of ecosystem services, we calculated the mean degree of spatial overlap (defined as their product) per management area and estimated their pixel-by-pixel correlation using Pearson's product-moment tests.

Finally, the model was used to assess and contrast five hypothetical scenarios for development: Business As Usual (basic model), Downward Spiral (limited management and enforcement), Green Haven (maximizing green value creation), Globalization (change towards maximizing welfare), and Local Communities (balancing welfare with green value creation) (Fig. 3). These scenarios were grounded on published concerns for potential development of the GSME (Caro and Davenport, 2016; Estes et al., 2012; Homewood et al., 2001; Veldhuis et al., 2019). The scenarios were meant to depict contrasting –and therefore extreme– strategies to alternative futures using four area-specific adjustments to the management-related input nodes (land-use allowed, hunting allowed, law enforcement and social system [i.e. as pertaining to livelihood strategy: pastoral versus agricultural]). The settings were set by ourselves with the purpose to best contrast the scenarios (see

Table 1
Overview of the nodes included in the Bayesian Belief Network for wildlife-related ecosystem (dis)services for the Greater Serengeti-Mara Ecosystem.

Human-related nodes	Land cover nodes	Wildlife nodes		Management-related nodes	ES nodes
Human population[1]	Land use	Lion	[predator] Diet preference[3]	Land use allowed[1,2]	Trophy hunting[3]
Social system[1,2]	Distance to PA edge[1]	Leopard	Predators[3]	Hunting allowed[1,2]	Bushmeat hunting[3]
Lodges and camps[1]	Road network[1]	Hyena	Game species[3]	Law enforcement[1,2]	Safari tourism[3]
Cattle[4]	Settlements[1]	Wild dog[4]	Big five[3]		[livestock] Depredation[3]
Shoats (sheep & goats)[4]	Water sources[1]	Giraffe	Migratory[3]		
Welfare[3]	Woody cover[1]	Impala[4]	[other] Wildlife[3]		
	Productivity[1]	Gazelles	Biodiversity[3]		
	Topography[1]	Wildebeest[4]			
		Zebra[4]			
		Rhinoceros			
		Elephant[4]			
		Buffalo[4]			
		Hippopotamus			

[1] Input nodes without any dependent parent nodes.
[2] Management-related input nodes which were used to adjust the different development scenarios.
[3] Calculated aggregation nodes using equations instead of Conditional Probability Tables.
[4] Nodes that were validated using independent spatially explicit data (S.I.).

Table 2
Equations used to assess the expected node values for the intermediate and ultimate nodes in the Bayesian Belief Network for wildlife-related ecosystem (dis)services in the Greater Serengeti-Mara Ecosystem.

Node	Equation
[predator] Diet preference[1]	(((Cattle + Shoats)/2) + (1 − ((Impala + Gazelles + Wildebeest + Zebra + Buffalo)/5)))/2
Predators	(Wild_Dog + Hyena + Leopard + Lion)/4 * Law_Enforcement
Game species[2]	(0.05 * Giraffe + 0.15 * Impala + 0.1 * Gazelles + 0.5 * Wildebeest + 0.15 * Zebra + 0.05 * Hippopotamus)
Wildlife	(Hyena + Wild_Dog + ((Impala + Gazelles + Hippopotamus + Giraffe) * (1−0.5 * Bushmeat_Hunting)))/6
Migratory	((Zebra + Wildebeest) * (1–0.5 * Bushmeat_Hunting))/2
Big five	(((Lion + Leopard + Elephant + Buffalo) * (1 − Trophy_Hunting)) + Rhinoceros)/5
Biodiversity[3]	(Wildlife + Big_Five + Migratory)/3
Welfare	(((1 − Human_Population) + (Settlements + Road_Network)/2) + Land_Use + ((0.85 * Cattle + 0.15 * Shoats) * (1 − Depredation)))/4
Trophy hunting[4]	((0.11 * Elephant + 0.21 * Lion + 0.42 * Buffalo + 0.21 * Leopard + 0.05 * Game_Species) + Edge_PA)/2 * Hunting_Allowed
Bushmeat hunting	(((1 − Welfare) * max(Edge_PA, Land_Use_Allowed)) + ((1 − Law_Enforcement) * (0.1 * Buffalo + 0.9 * Game_Species)))/2
Safari tourism[5]	(((Lodges_Camps + Road_Network)/2) + (0.40 * Big_Five + 0.35 * Migratory + 0.25 * Wildlife))/2
[livestock] Depredation	(((1 − Diet_Preference) + Predators + Water_Sources + (1 − Woody_Cover) + Settlements + (Edge_PA * Land_Use_Allowed))/6) * Land_Use_Allowed

[1] Diet preference represents an intermediate node indicating the relative preference of predators for respectively livestock or wildlife for their diet.
[2] Relative bushmeat hunting preferences were derived from (Bitanyi et al., 2012; Holmern et al., 2006; Lindsey et al., 2006; Mwakatobe et al., 2012; Ndibalema and Songorwa, 2008).
[3] Equal weights for all wildlife species (groups) were used as to convey the distribution of biodiversity in the landscape, irrespective of safari tourism (see also footnote [5]).
[4] Relative trophy hunting preferences were derived from (Baldus and Cauldwell, 2004; Di Minin et al., 2016; Lindsey et al., 2006).
[5] Relative tourist preferences for the three wildlife categories were derived from (Kaltenborn et al., 2006; Lindsey et al., 2007a; Maciejewski and Kerley, 2014).

Supplementary Information for which settings were used per scenario). The scenarios did, however, not consider any adjustments to the biophysical input data such as the spatial arrangement of infrastructure (roads, settlements, lodges and camps). In other words, the scenarios superimpose another form of management on the current biophysical area and investigate its consequences on wildlife-related ES. We tested whether there was a significant change in all unique pairs of ES, as well as biodiversity and human welfare, from the Business As Usual scenario to any of the future development scenarios using Student's *t*-tests with the difference as response variable and expected mean of zero. The outcomes of each of these scenarios are also visualized on a web-based interface specifically designed for this purpose: https://africanbioservices.shinyapps.io/servicescape. This interface was built using the shiny library (Chang et al., 2018). The interface allows the mapping, and renders area-specific boxplots, of areas of overlap (square-root of the product of two final nodes' output maps) for a chosen development scenario or the relative change in overlap between two scenarios. Also, the level of overlap between biodiversity and human welfare is visualized.

3. Results

3.1. Model structure

The six final nodes (four (dis)services, welfare and biodiversity) was overall most affected by the Land_Use node (7.4%, range: 0.5–15.3; Table S4). Management-related nodes (especially Land_Use_Allowed (6.3%, range: 0.9–18.5) and Hunting_Allowed (5.3%, range: 0.0–21.3)) and wildlife-related nodes (especially [other] Wildlife (6.0%, range: 0.4–20.5), [predator] Diet_Preference (5.4%, range: 0.0–12.8) and Mmigratory_Species (5.3%, range: 0.0–15.6)) had a stronger effect on the outcomes than did human-related nodes or landcover-related nodes (cf. Table 1). The species with most influence on the outcome of the predicted presence of these four (dis)services were Cattle and Shoats (both 2.7%), Lions (2.5%) and Hyenas (2.3%). These contributions, however varied by (dis)service.

The sensitivity of the outcome for each ecosystem (dis)service, as well as welfare and biodiversity, relative to the findings of other outcomes of the six final nodes was limited (Table 3). Relatively,

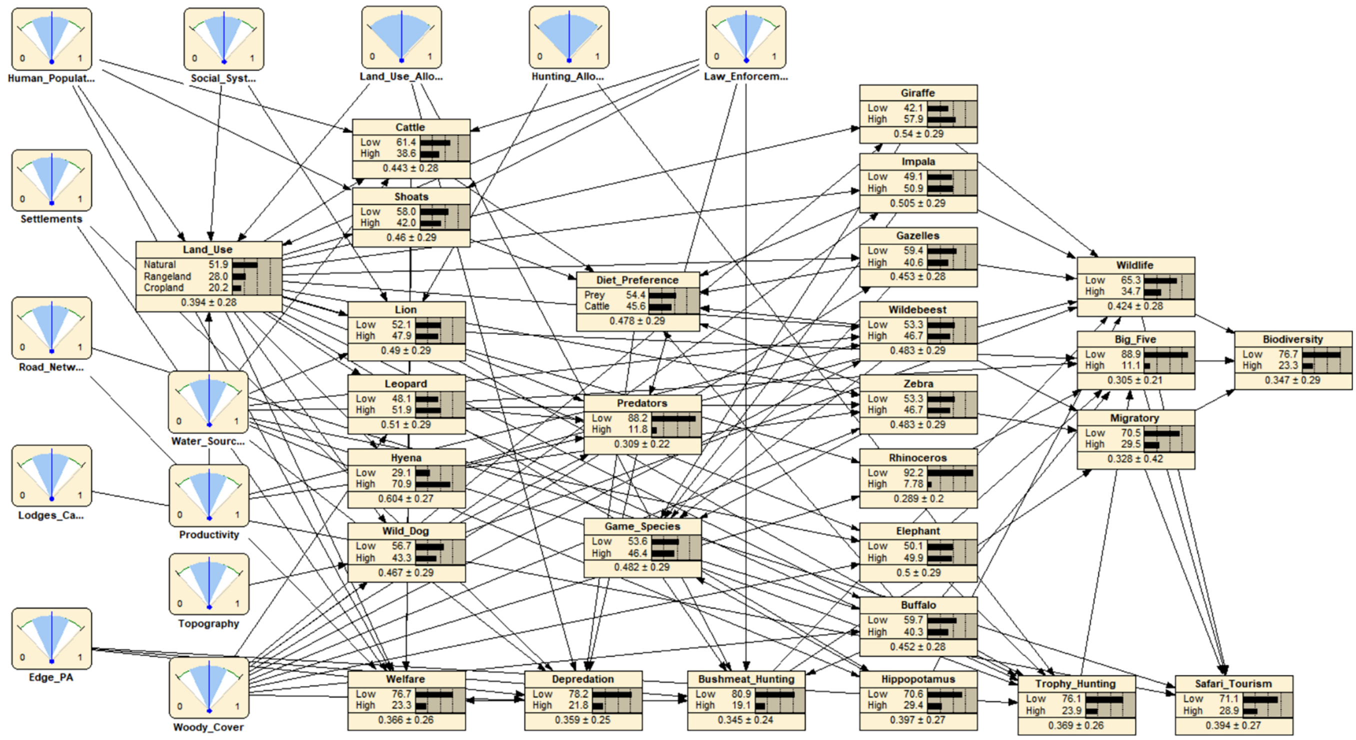


Fig. 2. Bayesian Belief Network for wildlife-related ecosystem (dis)services in the Greater Serengeti-Mara Ecosystem. More details on each node's linkages can be found in the Supplementary Information, Table S1.

biodiversity had a stronger influence on the presence of the four (dis) services than did welfare (respectively 3.2%, range: 0.04–9.30; and 1.2%, range: 0.07–3.86%). These two nodes did not influence each other much (1.5%). The (dis)services did not affect each other much either (0.5%, range: 0.01–0.93). Not surprisingly, the presence of safari tourism was strongest influenced (9.30%) by the findings at the biodiversity node. Bushmeat hunting was affected by welfare by 3.86%. These two effects were reciprocal with 8.83% for biodiversity and 4.05% for welfare, respectively.

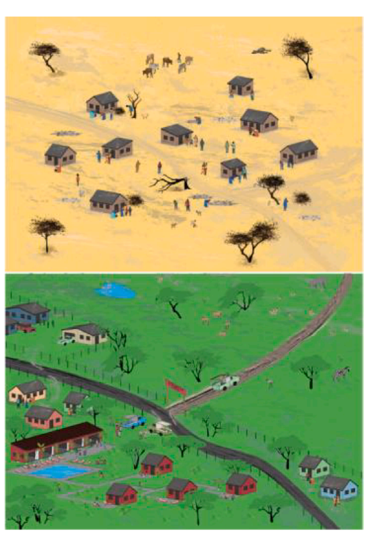
Validated species nodes indicated a good spatial predictability of species presence based on independent spatial data on area use (Table S5, Fig. S1). Although the mean predicted presence of used cells varied from species to species, the general overlap was good. For instance, while the mean predicted presence for wild dogs was below 0.5 there was generally a good spatial overlap between used areas and areas of high predicted presence. More information is given in the Supplementary Information.

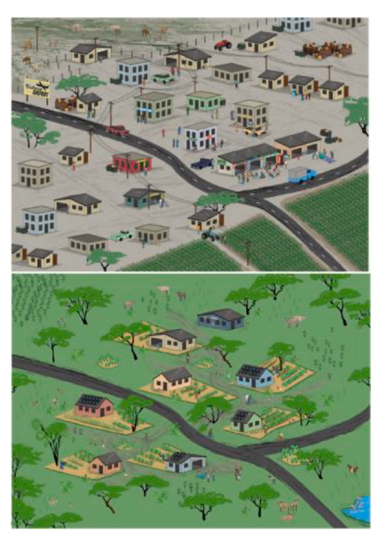
3.2. Model predictions

The BBN visualizes the relative probability (and therefore value distribution) of ecosystem (dis)services delivery across the landscape and clearly shows spatial patterns in the delivery of the four wildlife-related (dis)services, and supporting biodiversity and human welfare in the GSME (Figs. 4 and 5, Table S6). The model outcomes seem to fit well with the overall management aims for each of the different management areas. Trophy hunting was only assessed within the regions where trophy hunting is allowed: Loliondo GCA, Grumeti, Ikorongo and

Downward Spiral
In this scenario, lack of governance structures leads to eroded agricultural and pastoral production and lack of tourism income, in turn causing reduced welfare of communities and pressure on the environment through increased illegal activities.

Green Haven
In this scenario, top-down conservation-driven governance ensures the services and livelihood of few communities obtaining revenues from ecotourism, and strict preservation of wildlife and their habitats.





Globalization
In this scenario, national governance structure provides good infrastructure and service provision for communities, who through intensification of land-use have good access to markets and trade at the cost of natural and cultural heritage.

Local communities
In this scenario, local governance of communities enables stable and self-sustainable livelihoods through agropastoral sustenance opportunities from natural resource use, while conserving natural and cultural heritage.

Fig. 3. Visualization of the four development scenarios (excluding Business As Usual) for the Greater Serengeti-Mara Ecosystem (illustrated by: Roar Lerche Studio).

Table 3
Sensitivity analysis of the Bayesian Belief Network for wildlife-related ecosystem (dis)services in the Greater Serengeti-Mara Ecosystem. The values indicate to which extent the variability of the predicted distribution of each final node is influenced by a single finding at each of the other nodes as measured by the percentual variance reduction (%) relative to the full variance of the node (shaded diagonal).

Comparison node	Welfare	Biodiversity	Safari tourism	Trophy hunting	Bushmeat hunting	Livestock depredation
Welfare	0.066	1.50	0.07	0.61	3.86	0.41
Biodiversity	1.51	0.064	9.30	0.04	1.44	2.17
Safari tourism	0.07	8.83	0.072	0.02	0.82	0.88
Trophy hunting	0.60	0.04	0.02	0.066	0.28	0.01
Bushmeat hunting	4.05	1.50	0.89	0.30	0.059	0.67
Livestock depredation	0.42	2.18	0.93	0.01	0.64	0.063

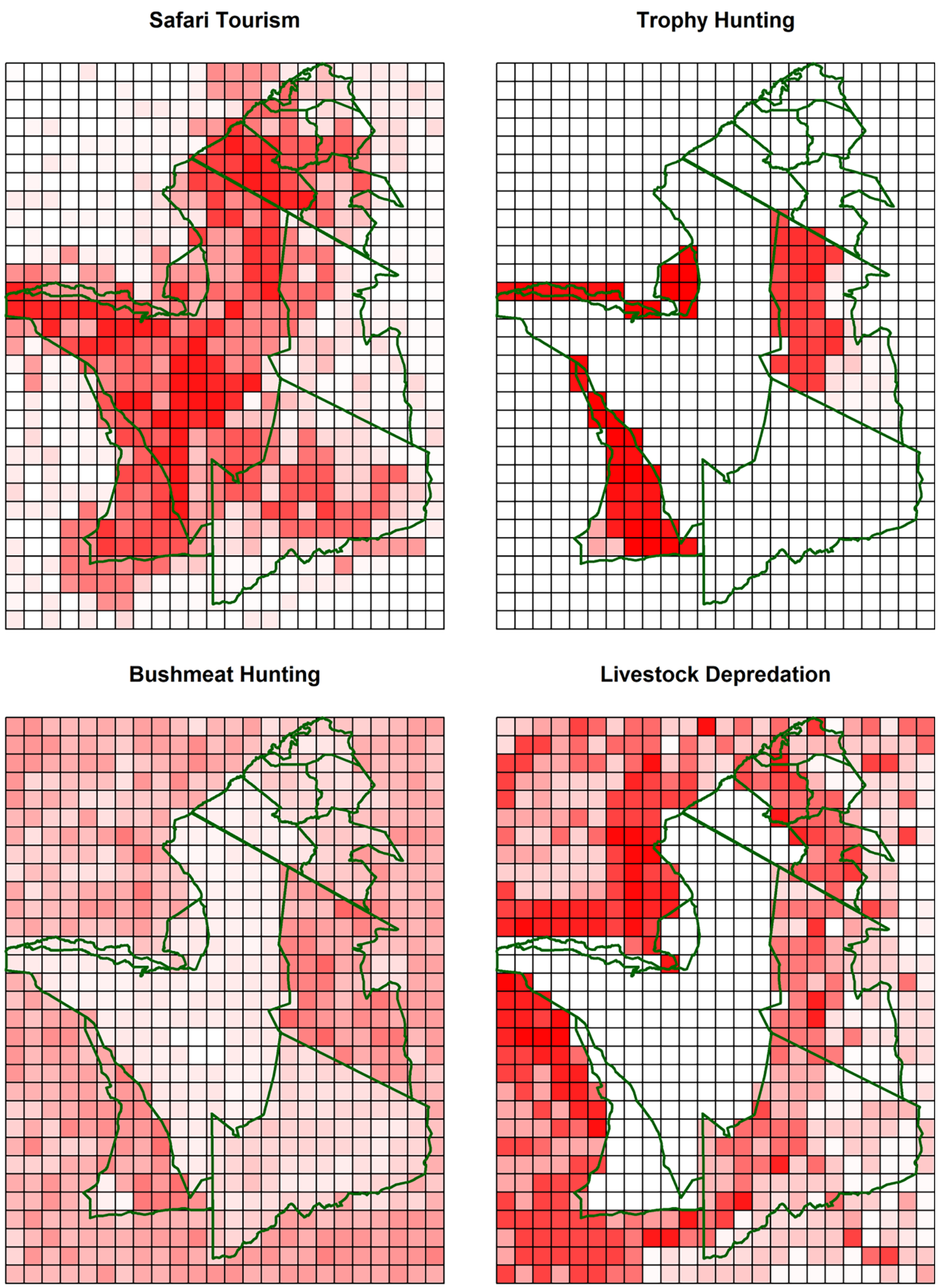


Fig. 4. Expected level of delivery of four wildlife-related ecosystem (dis)services in the Greater Serengeti-Mara Ecosystem, as derived from a Bayesian Belief Network for the Business As Usual scenario. Darker colours indicate higher levels.

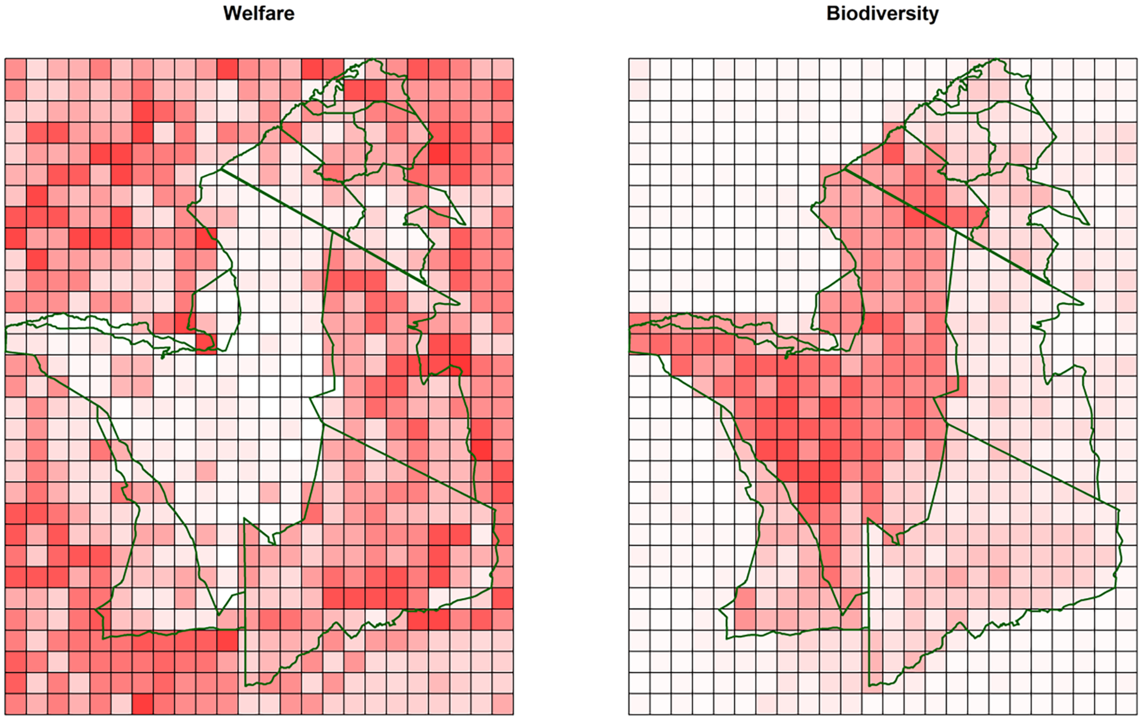


Fig. 5. Relative indicators for household welfare and biodiversity in the Greater Serengeti-Mara Ecosystem, as derived from a Bayesian Belief Network for the Business As Usual scenario. Darker colours indicate higher levels.

Maswa GR. This was not further specified into actual hunting blocks and related quotas. The model indicated a strong link with the distance to edge of the protected areas (Fig. 4). Bushmeat hunting was estimated at lower probabilities in the BBN relative to the other ecosystem (dis) services. Bushmeat hunting increased nearby existing infrastructure outside management regions where land use is not allowed. As expected, safari tourism scored highest in the Maasai Mara NR and Serengeti NP, followed by Ngorongoro CA, Maswa GR and the Conservancies. Loliondo GCA was believed to have lower values for safari tourism. However, cultural-inspired tourism (e.g. visiting local Maasai villages) was not assessed in this model. Livestock depredation presence was believed to be highest in the unprotected regions, followed by Loliondo GCA, Ngorongoro CA and the Conservancies. There was a strong link to existing infrastructure in the evaluated level of livestock depredation conflict. The Kenyan Conservancies did not score high on any of the four ecosystem (dis)services, however, safari tourism came closest in providing benefits. This may of course also be due to limitations in the actual model. Biodiversity was highest in the Serengeti NP and Maasai Mara NR, and with medium values for the managed areas (Fig. 5). To the contrary, welfare was higher outside of the two before-mentioned strictly protected areas.

In the different management areas, ecosystem (dis)services overlapped to differing degrees causing potential for co-benefits, trade-offs and conflicts. Safari tourism and trophy hunting, in the areas where this was allowed, overlapped significantly in Loliondo GCA ($r = 0.583$; P (overlap) = 0.117), but not in the game reserves even though the combined probabilities were higher in the game reserves (P (overlap) = 0.438–0.542; Table 4). While safari tourism and bushmeat hunting in Maasai Mara NR overlapped ($r = 0.724$), there was a significant separation in unprotected areas ($r = -0.246$) and Ngorongoro CA ($r = -0.422$). However, the combined probabilities were highest in Maswa GR (P(overlap) equals 0.237 versus 0.059 in Maasai Mara NR). In all multiple-use areas there was a significant overlap between safari tourism and livestock depredation (Unprotected: $r = 0.293$; Ngorongoro CA: $r = 0.274$; Loliondo GCA: $r = 0.536$; Conservancies: $r = 0.502$). This effect was strongest in the conservancies as measured by the combined probabilities (P(overlap) equals respectively 0.052, 0.096 and 0.083 versus 0.189 for the conservancies). There was spatial overlap between trophy and bushmeat hunting in Maswa GR ($r = 0.824$; P(overlap) = 0.362) and spatial separation in Grumeti GR ($r = -0.868$), but no effect in Loliondo GCA and Ikorongo GR. In Loliondo GCA there was, however, spatial overlap in trophy hunting and livestock depredation ($r = 0.676$; P(overlap) = 0.198). Bushmeat hunting and livestock depredation overlapped both in the unprotected areas ($r = 0.194$; P(overlap) = 0.137) and the conservancies ($r = 0.388$; P(overlap) = 0.083). Although the combined probabilities generally were low (Table 4), welfare and biodiversity overlapped in the unprotected areas ($r = 0.402$), Ngorongoro CA ($r = 0.285$), Loliondo GCA ($r = 0.367$) and Maswa GR ($r = 0.472$).

The BBN can also be used to evaluate different development scenarios, based on the current biophysical and socioeconomic landscape. By adjusting different management settings (land-use and hunting allowed, law enforcement, social system; see Table S3), the expected outcome can be visualized and compared to the current situation. Here, the purpose is not so much as to visualize alternative 'truths' but rather to contrast various extreme pathways. The development scenarios (Fig. 6) indicated that Green Haven was the only scenario where the safari tourism increased relative to Business As Usual (for the GSME by 3.0%, Table 5) due to an increase in biodiversity (for the GSME by 4.5%). In the other scenarios, reduced safari tourism opportunities foremost affected the game reserves (Fig. 6). Trophy hunting opportunities improved for all but the Green Haven scenario; mostly for Globalization (for the GSME by 15.4%). This effect was mainly caused by allowing trophy hunting in additional areas (Fig. 6). Bushmeat hunting was predicted to be reduced in Green Haven and Local communities (for the GSME by 7.9% and 1.3%, respectively), but increased in the Downward Spiral scenario (for GSME by 0.9%). Welfare was predicted to increase in all scenarios but for Green Haven congruent with the predicted changes to livestock depredation, and then especially in the game reserves (Table 5, Fig. 6).

Table 4
Predicted level of spatial overlap, or separation, between pairs of ecosystem (dis)services and between social (welfare) and natural (biodiversity) capital within the management areas of the Greater Serengeti-Mara Ecosystem for the Business As Usual scenario. P(overlap) indicates the mean and 95% C.I. (calculated using a logit transformation) for the product of probabilities per management area. The statistics (correlation and 95% C.I.) indicate the results from a Pearson's product-moment correlation test.

Area	Safari tourism Trophy hunting	Safari tourism Bushmeat hunting	Safari tourism Depredation	Trophy hunting Bushmeat hunting	Trophy hunting Depredation	Bushmeat hunting Depredation	Welfare Biodiversity
Unprotected		P(overlap) = 0.023 [0.022, 0.025] $r = -0.246$ [-0.339 to -0.148] $t = 4.888$, $P < 0.001$	P(overlap) = 0.052 [0.050, 0.054] $r = 0.293$ [0.197–0.383] $t = 5.902$, $P < 0.001$			P(overlap) = 0.137 [0.134, 0.141] $r = 0.194$ [0.095–0.290] $t = 3.818$, $P < 0.001$	P(overlap) = 0.017 [0.016, 0.018] $r = 0.402$ [0.314–0.484] $t = 8.468$, $P < 0.001$
Serengeti NP		P(overlap) = 0.043 [0.039, 0.046] $r = -0.042$ [-0.216 to 0.134] $t = 0.470$, $P = 0.639$					P(overlap) = 0.033 [0.030, 0.036] $r = 0.123$ [-0.053 to 0.291] $t = 1.378$, $P = 0.171$
Ngorongoro CA		P(overlap) = 0.039 [0.035, 0.043] $r = -0.422$ [-0.581 to -0.231] $t = 4.285$, $P < 0.001$	P(overlap) = 0.096 [0.090, 0.102] $r = 0.274$ [0.067–0.458] $t = 2.624$, $P = 0.010$			P(overlap) = 0.043 [0.039, 0.048] $r = 0.157$ [-0.056 to 0.356] $t = 1.462$, $P = 0.147$	P(overlap) = 0.058 [0.053, 0.063] $r = 0.285$ [0.079–0.468] $t = 2.744$, $P = 0.007$
Loliondo GCA	P(overlap) = 0.117 [0.109, 0.126] $r = 0.583$ [0.376–0.735] $t = 5.225$, $P < 0.001$	P(overlap) = 0.068 [0.062, 0.075] $r = -0.191$ [-0.435 to 0.078] $t = 1.419$, $P = 0.162$	P(overlap) = 0.083 [0.076, 0.090] $r = 0.536$ [0.316–0.702] $t = 4.623$, $P < 0.001$	P(overlap) = 0.186 [0.176, 0.197] $r = 0.162$ [-0.108 to 0.409] $t = 1.192$, $P = 0.239$	P(overlap) = 0.198 [0.187, 0.208] $r = 0.676$ [0.500–0.798] $t = 6.676$, $P < 0.001$	P(overlap) = 0.136 [0.127, 0.145] $r = 0.122$ [-0.148 to 0.376] $t = 0.898$, $P = 0.373$	P(overlap) = 0.038 [0.033, 0.043] $r = 0.367$ [0.113–0.577] $t = 2.876$, $P = 0.006$
Maswa GR	P(overlap) = 0.542 [0.524, 0.560] $r = -0.191$ [-0.521 to 0.189] $t = 1.009$, $P = 0.322$	P(overlap) = 0.237 [0.222, 0.253] $r = 0.056$ [-0.317 to 0.414] $t = 0.291$, $P = 0.773$		P(overlap) = 0.362 [0.345, 0.380] $r = 0.824$ [0.655–0.914] $t = 7.551$, $P < 0.001$			P(overlap) = 0.052 [0.045, 0.061] $r = 0.472$ [0.128–0.715] $t = 2.785$, $P = 0.010$
Ikorongo GR	P(overlap) = 0.438 [0.399, 0.478] $r = 0.400$ [-0.610 to 0.915] $t = 0.872$, $P = 0.433$	P(overlap) = 0.037 [0.024, 0.055] $r = 0.024$ [-0.803 to 0.820] $t = 0.048$, $P = 0.964$		P(overlap) = 0.078 [0.059, 0.103] $r = 0.194$ [-0.733 to 0.869] $t = 0.396$, $P = 0.712$			P(overlap) = 0.027 [0.016, 0.043] $r = 0.414$ [-0.599 to 0.917] $t = 0.908$, $P = 0.415$
Grumeti GR	P(overlap) = 0.531 [0.498, 0.564] $r = 0.188$ [-0.544 to 0.757] $t = 0.506$, $P = 0.629$	P(overlap) = 0.046 [0.034, 0.061] $r = -0.318$ [-0.811 to 0.439] $t = 0.886$, $P = 0.405$		P(overlap) = 0.074 [0.059, 0.094] $r = -0.868$ [-0.972 to -0.480] $t = 4.618$, $P = 0.002$			P(overlap) = 0.022 [0.014, 0.034] $r = -0.016$ [-0.673 to 0.655] $t = 0.042$, $P = 0.967$
Maasai Mara NR		P(overlap) = 0.059 [0.049, 0.072] $r = 0.724$ [0.356–0.898] $t = 3.929$, $P = 0.002$					P(overlap) = 0.061 [0.050, 0.073] $r = -0.210$ [-0.639 to 0.318] $t = 0.806$, $P = 0.434$
Conservancies		P(overlap) = 0.059 [0.052, 0.066] $r = -0.115$ [-0.401 to 0.192] $t = 0.739$, $P = 0.464$	P(overlap) = 0.198 [0.186, 0.210] $r = 0.502$ [0.238 to 0.697] $t = 3.718$, $P = 0.001$			P(overlap) = 0.083 [0.075, 0.091] $r = 0.388$ [0.099–0.616] $t = 2.695$, $P = 0.010$	P(overlap) = 0.040 [0.034, 0.046] $r = 0.109$ [-0.198 to 0.396] $t = 0.702$, $P = 0.486$

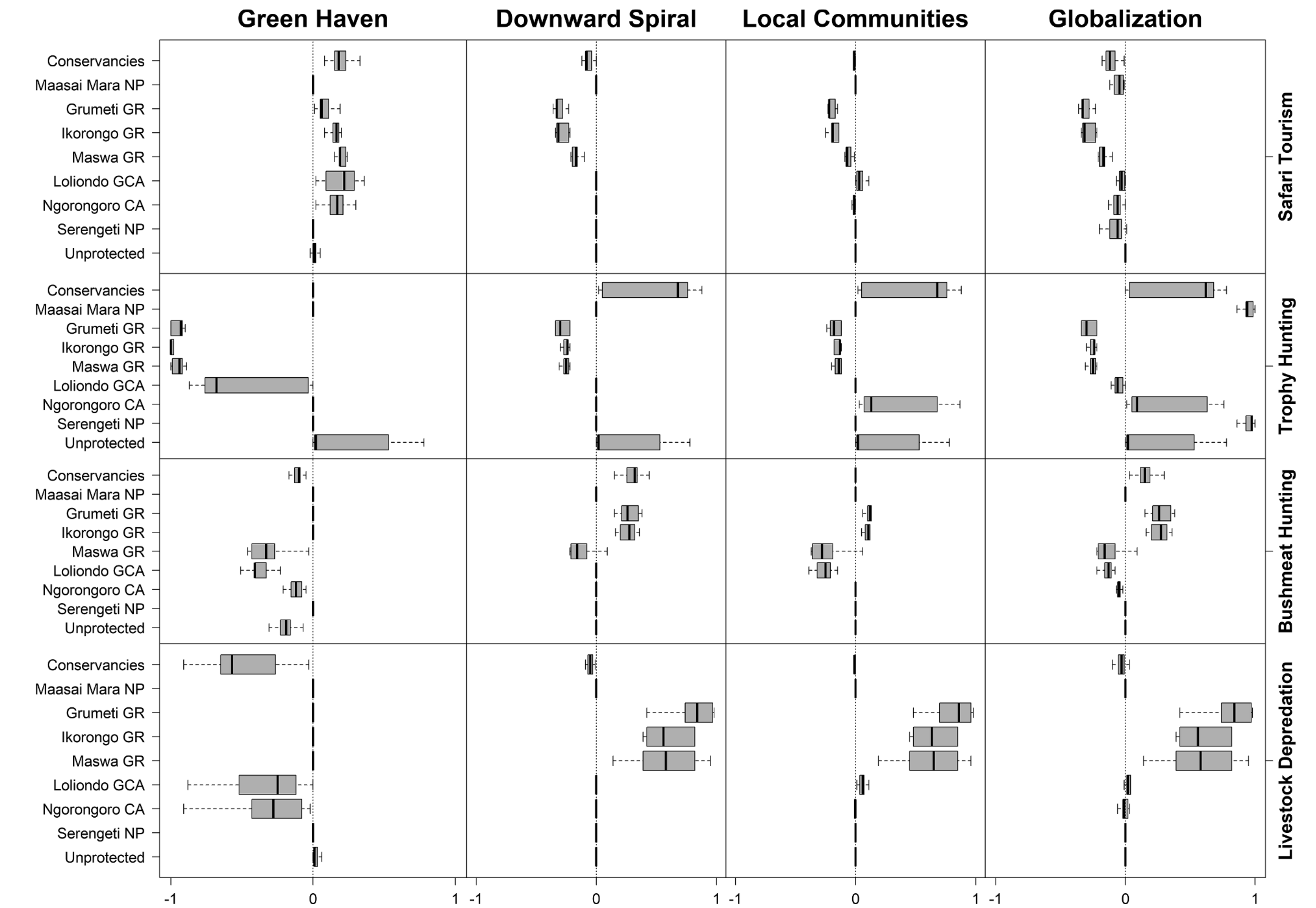


Fig. 6. Changes in the expected ecosystem (dis)services delivery in the different management areas within the Greater Serengeti-Mara Ecosystem for the development scenarios relative to Business As Usual.

4. Discussion

Contrary to other spatially-explicit predictive models providing in-depth insight into single components (e.g. species distribution modelling, land-cover mapping), a BBN model provides an integrated understanding into the linkages between components within a social-ecological system (McCann et al., 2006; Oliver and Smith, 1990; Smith et al., 2018). BBN models have proved to be particularly suitable for use in cases with limited data available together with significant reservations, i.e. factors that can affect decision-making extensively (Landuyt et al., 2013; McCann et al., 2006; Smith et al., 2018). Thereby, the developed BNN for wildlife-related ecosystem services can be used to predict what type of ecosystem services that can be delivered where given the existing or expected circumstances. Identifying areas of conflicts and potential trade-offs between ecosystem (dis)services are crucial to find pathways to nature-based tourism strategies that simultaneously maintains biodiversity and supports socioeconomic viable local communities (Baldus and Cauldwell, 2004; Caro and Davenport, 2016; Naughton-Treves et al., 2005; Nuno et al., 2014).

The Bayesian Belief Network was aimed at elucidating the linkages

Table 5
Changes in the probability of ES delivery, as well as social (welfare) and natural (biodiversity) capital, of different development scenarios relative to Business As Usual for the Greater Serengeti-Mara Ecosystem.

Scenario	Safari_Tourism	Trophy_Hunting	Bushmeat_Hunting	Depredation	Welfare	Biodiversity
Green Haven	0.030 [0.027–0.033] $t = 17.677$, $P < 0.001$	0.000 [−0.013 to 0.012] $t = 0.048$, $P = 0.962$	−0.079 [–0.083 to −0.074] $t = 36.586$, $P < 0.001$	−0.038 [−0.045 to −0.031] $t = 10.566$, $P < 0.001$	−0.036 [−0.040 to −0.031] $t = 15.401$, $P < 0.001$	0.045 [0.040–0.050] $t = 18.177$, $P < 0.001$
Downward Spiral	−0.009 [−0.011 to −0.007] $t = 8.667$, $P < 0.001$	0.050 [0.041–0.059] $t = 10.844$, $P < 0.001$	0.009 [0.006–0.012] $t = 5.679$, $P < 0.001$	0.018 [0.012–0.024] $t = 5.849$, $P < 0.001$	0.011 [0.008–0.015] $t = 6.455$, $P < 0.001$	−0.010 [−0.013 to −0.008] $t = 8.724$, $P < 0.001$
Local Communities	−0.003 [−0.005 to −0.002] $t = 5.414$, $P < 0.001$	0.075 [0.065–0.085] $t = 14.708$, $P < 0.001$	−0.013 [−0.017 to −0.010] $t = 8.225$, $P < 0.001$	0.022 [0.016–0.028] $t = 7.017$, $P < 0.001$	0.005 [0.003–0.007] $t = 5.156$, $P < 0.001$	−0.005 [−0.006 to −0.003] $t = 5.48$, $P < 0.001$
Globalization	−0.022 [−0.024 to −0.020] $t = 18.030$, $P < 0.001$	0.154 [0.139–0.168] $t = 20.674$, $P < 0.001$	−0.003 [−0.005 to 0.000] $t = 1.868$, $P = 0.062$	0.019 [0.013–0.025] $t = 6.175$, $P < 0.001$	0.031 [0.027–0.035] $t = 14.584$, $P < 0.001$	−0.028 [−0.031 to −0.025] $t = 19.388$, $P < 0.001$

between wildlife and four ecosystem (dis)services central to the GSME. As it tried to capture the most important aspects of the ecosystem, not all intricate components and/or species may have been included. Also, the species nodes were based on coarse and limited input variables, thus not capturing all fine-scale responses of those species to their environment. We were also able to validate only eight of the model's nodes for which we had independent datasets available. To clarify this limitation, we visualized the model outcomes on a coarse 10x10 km resolution, as not to assume we can model these linkages at a finer scale. The purpose of the model is therefore also not to provide full insight into ecosystem dynamics, but rather provide an integrated framework to structure the ecosystem as pertaining to the four ecosystem (dis)services and exploring future scenarios (Landuyt et al., 2013; McCann et al., 2006; Smith et al., 2018). Instead, BBN provides a mechanism for modelling the likelihood of specific management strategies on the potential outcomes of these (dis)services (McCann et al., 2006; Oliver and Smith, 1990; Smith et al., 2018). Due to limited available knowledge, we were forced to use equal weights for some of the nodes (see Table S1); these should be seen as a first best guess. Further finetuning of the model's CPTs, combined with more extensive validation, may help identify trade-offs or win–win situations set within the stakeholders' reality. Different management regimes for the areas were represented by four simple factors (land-use allowed, hunting allowed, law enforcement, and social system), thus potentially over- or underrepresenting the actual complexity of management practices, not in the least regarding cross-boundary effects. An attempt was made to alleviate such limitations by including the distance to the protected area boundaries (Serengeti NP and Maasai Mara NR) in the model. The model has been constructed based on the current state of the international literature and therefore represents an expert-based model. Not all of this information, however, originated from the GSME and local variability in certain factors may decrease levels of confidence of the predicted outcomes. To this end, the extent to which this model represents the beliefs of local inhabitants or managers of the protected areas, would be an interesting further development of this model. Such user-defined input would contribute to the refinement of the expert-based BBN.

As expected, the well-protected Serengeti NP and Maasai Mara NR deliver the highest values for safari tourism. In the Ngorongoro CA and Kenyan Conservancies extensive levels of land use are allowed. In these areas values for safari tourism are, however, offset against increased risk of livestock depredation and bushmeat hunting. Local communities therefore need to balance potential revenues of biodiversity from safari tourism with the negative implications of biodiversity for livestock depredation and the negative consequences of bushmeat hunting on biodiversity (Blackburn et al., 2016; Catherine et al., 2015; Ogutu et al., 2005). This, however, requires local communities to be able to benefit from the tourism revenues in a fair and just manner (Charnley, 2005; Lamprey and Reid, 2004; Msoffe et al., 2011; Slootweg, 2017). All three game reserves surrounding the Serengeti NP (Maswa, Grumeti and Ikorongo) deliver values for both safari tourism and trophy hunting, however, as buffer areas to the NP they also have increased levels of bushmeat hunting. Increased hunting pressure on wildlife may hamper safari tourism opportunities as species become more fearful of humans (Hariohay et al., 2018). Game reserves, as buffer zones to the national park, law enforcement against poaching and illegal grazing incursions will be important (Knapp, 2012; Mwakaje et al., 2013). Given their location as buffer between the national park and unprotected areas, the game reserves are expected to be most sensitive to relative changes in the delivery of ecosystem services for the different development scenarios (Fig. 6). East of the GSME, the Loliondo GCA has according to the model relatively high values for livestock depredation and bushmeat hunting due to high livestock densities and low biodiversity. Until recently, trophy hunting and safari tourism were still possible towards the national park boundary, within an allocated strip excluding pastoralism (Bartels, 2016). Due to high levels of conflict between the pastoral Maasai and the hunting companies and government (Slootweg, 2018; Tanzania Natural Resource Forum, 2011) the hunting company's license was recently revoked (November–December 2017). This potential for conflict is also clearly exemplified in the model through the high level of overlap between trophy hunting and livestock depredation (P (overlap) = 0.198; r = 0.676). When comparing the different development scenarios, Loliondo GCA may benefit most from the Green Haven (maximizing green value creation) or Local Communities (maximizing sustainable welfare) scenarios in the future (Fig. 6; Slootweg, 2018). This will, however, require radical policy changes and local investments to overcome the current conflictual situation (Burgoyne and Mearns, 2016; Msoffe et al., 2011; Mwakaje et al., 2013; Slootweg, 2018). In the unprotected areas surrounding the GSME only the negative ecosystem (dis)services prevail, with heightened levels of bushmeat hunting and livestock depredation. Livestock depredation levels were predicted to be highest in the unprotected areas, especially closer to the protected area boundaries where both predators (inhabiting the protected areas) and livestock co-occur (Holmern et al., 2007; Kolowski and Holekamp, 2006). To the contrary, livestock depredation risk was more variable in areas with both livestock and predator populations, such as the Kenyan Conservancies, Ngorongoro CA and Loliondo GCA (cf., Ogutu et al., 2005). Similarly, Ngorongoro CA and the Conservancies appear to be low risk for bushmeat hunting and still have a relatively high level of welfare (cf. Figs. 4 and 5), due to these being protected areas with restricted land use. There, and in Ngorongoro CA, Loliondo GCA and in the Conservancies, welfare was relatively high without losing benefits derived from ecosystem services. Thus, it seems that the management strategies for these areas have proven to be successful in maintaining a balance although concerns remain (Blackburn et al., 2016; Catherine et al., 2015; Ogutu et al., 2016). Welfare was expected to increase most in the Globalization scenario at the expense of biodiversity and related ecosystem services. In the web-interface of the model, more elaborate comparisons can be made explicit to enhance understanding on the interactions between ecosystem (dis)services for all development scenarios.

This Bayesian Belief Network for wildlife-related ecosystem (dis) services in the GSME may further provide a tool to pose new hypotheses for further study for researchers in the GSME. Based on the BBN expected values, research can address questions as to what ecological processes affect wildlife most (by adjusting input data/settings), which linkages are most influential, and what other potential ecological processes or components may improve the predictive power of the model (McCann et al., 2006). The spatially-explicit BBN – including the web interface – may also be helpful in communicating with nonexperts about making natural resource management decisions, and supports adaptive management approaches by updating the model to evaluate management decisions (McCann et al., 2006). The GSME, with its variety of protected area types and associated land uses, provides an ideal case study. Not only do we expect that future management and land use will impact ecosystem service provisioning, but we already see the effects thereof. By simply moving a short distance outside of Serengeti NP's boundaries, biodiversity and ecosystem functionality differ considerably, thereby affecting ecosystem services. The local-scale land-use variability is thus useful in that it allows us to assess whether predicted outcomes do in fact match that which is already evident today.

The model serves as tool to understand the likely consequences of different management and human-influence scenarios. The value of model is by no means restricted to the GSME; it is relatively straightforward to develop similar models for protected area systems elsewhere in Africa or the world. Many areas share similar challenges related to increasing human and livestock populations and land cover changes in close proximity to protected areas. Such BBN models may be useful to highlight particularly challenging scenarios and thereby aid managers in making timeous and focused management decisions. This is especially important given the limited resources available to managing wildlife populations and the ecosystems they depend on.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoser.2019.101025.

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