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# The Serengeti food web: empirical quantification and analysis of topological changes under increasing human impact

**Sara N. de Visser*, Bernd P. Freymann and Han Olff**

*Community and Conservation Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands*

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## Summary

**1.** To address effects of land use and human overexploitation on wildlife populations, it is essential to better understand how human activities have changed species composition, diversity and functioning. Theoretical studies modelled how network properties change under human-induced, non-random species loss. However, we lack data on realistic species-loss sequences in threatened, real-world food webs to parameterize these models.

**2.** Here, we present a first size-structured topological food web of one of the most pristine terrestrial ecosystems in the world, the Serengeti ecosystem (Tanzania). The food web consists of 95 grouped nodes and includes both invertebrates and vertebrates ranging from body masses between $10^{-7}$ and $10^{4}$ kg.

**3.** We study the topological changes in this food web that result from the simulated IUCN-based species-loss sequence representing current species vulnerability to human disturbances in and around this savanna ecosystem. We then compare this realistic extinction scenario with other extinction sequences based on body size and connectance and perform an analysis of robustness of this savanna food web.

**4.** We demonstrate that real-world species loss in this case starts with the biggest (mega) herbivores and top predators, causing higher predator–prey mass ratios. However, unlike theoretically modelled linear species deletion sequences, this causes poor-connected species to be lost first, while more highly connected species become lost as human impact progresses. This food web shows high robustness to decreasing body size and increasing connectance deletion sequences compared with a high sensitivity to the decreasing connectance deletion scenario.

**5.** Furthermore, based on the current knowledge of the Serengeti ecosystem, we discuss how the focus on food web topology alone, disregarding nontrophic interactions, may lead to an underestimation of human impacts on wildlife communities, with the number of trophic links affected by a factor of two.

**6.** This study underlines the importance of integrative efforts between the development of food web theory and basic field work approaches in the quantification of the structure of interaction networks to sustain natural ecosystems in a changing world.

**Key-words:** anthropogenic impact, extinction order, IUCN Red List, robustness, Serengeti National Park

## Introduction

Food webs represent complex patterns of feeding links among species within an ecosystem. Discovering what determines food web structure is a major and long-term goal in ecology (Pimm 1982; Petchey *et al.* 2008a), both from a fundamental and applied perspective. As humans increasingly dominate the structure and functioning of the world's communities and ecosystems (Vitousek *et al.* 1997), we urgently need the quantification of the structures of the last remaining near-pristine food webs as points of reference. This will help in understanding and predicting the effects and magnitudes of human activities on biodiversity.

The loss of some species in food webs often induces cascades of secondary extinctions that are difficult to predict (Hairston, Smith & Slobodkin 1960) and causes impairment

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*Correspondence author. E-mail: sndevisser@hotmail.com of ecosystem function (Duffy *et al.* 2007; Reiss *et al.* 2009). Higher extinction risks are more often found among large-sized species and/or species at high trophic levels (Cardillo *et al.* 2005). This observation provides a predictable sequence of species loss under increased human pressure and is used in theoretical studies that investigate the consequences of primary species loss on secondary extinctions (e.g. Borrvall, Ebenman & Jonsson 2000; Ebenman, Law & Borrvall 2004; Petchey *et al.* 2004; Borrvall & Ebenman 2006).

Other species removal protocols have instead been based on the trophic connectance of a species (e.g. Solé & Montoya 2001; Dunne, Williams & Martinez 2002a). Connectance describes how well species are trophically linked to others in a network (i.e. the proportion of possible trophic interactions that are realized in a network, Gardner & Ashby 1970). Connectance has been argued to correlate with the robustness ($R$) of food webs to perturbations. This metric is defined as the minimum fraction of primary species deletions that cause ≥50% of all species in a web to go extinct through both primary removals and secondary extinctions (Dunne, Williams & Martinez 2002b). Furthermore, the frequency distribution of the number of links per species (i.e. the link distribution) reveals the degree of hierarchy in network structure (e.g. with random or scale-free networks as extreme cases) and has been viewed as an indicator of how sensitive a food web is to the loss of poor vs. highly connected nodes and to random versus selective node loss (e.g. Solé & Montoya 2001). With potentially some exceptions, the loss of species with a large number of trophic links to other species is expected to cause the largest number of secondary extinctions (Ebenman & Jonsson 2005). However, the assumption that the trophic connectedness of a species (i.e. generalists vs. specialists) predicts the order of extinction has so far not been verified with empirical data from real-world networks (Gilbert 2009). Recently, Raffaelli (2004), Srinivasan *et al.* (2007) and Naeem (2008) pointed out the urgent need for ecologically realistic extinction sequences and community assemblies to improve the understanding of biodiversity loss on ecosystems. Additionally, it seems unlikely that food web topology alone correctly informs us about the diversity consequences of species loss. Certainly, the question how trophic interactions structure food webs has received by far the most empirical and theoretical attention (Cohen 1978; Polis & Winemiller 1996). However, spatial interactions (Sinclair 2003), modification of abiotic environmental conditions (ecosystem engineering) (*sensu* Jones, Lawton & Shachak 1994) and mutualistic interactions (Joppa *et al.* 2009) may all play a significant role in the cascading effects following primary species loss, thus affecting the robustness of ecological communities. The effects of these nontrophic and indirect interactions are, however, rarely integrated with food web theory (Ings *et al.* 2009; Olff *et al.* 2009), partly because species-rich interaction webs in the field that quantify both trophic and nontrophic interactions are rare.

In this study, we newly describe the food web topology of the well-studied, savanna ecosystem of Serengeti National Park, Tanzania, at an intermediate level of taxonomic aggregation. This captures the topology-based trophic interaction web of the more common terrestrial plant, invertebrate and vertebrate species. We then explore the unique situation of Serengeti as a natural experimental manipulation of real-world species loss. Serengeti and surrounding conservation areas provide a spatial gradient of different degrees of nature protection that mirrors the temporal increase of human impact on African savanna food webs through the centuries and reflects what is currently taking place outside the boundaries of the major East-African protected areas. We analyse the effects of a realistic species extinction sequence, based on the risk assessment per species by the *Red List of Threatened Species* of the World Conservation Union (IUCN 2009), on topological properties. We then compare the results of the realistic extinction scenario with the analysis of robustness using common species deletion sequences based on connectance and body size applied to the same food web. We also preliminarily explore the effects of species loss on biodiversity beyond food webs by considering nontrophic interactions. The outcome of this study is of importance for both fundamental and applied food web theory and for the validation and understanding of the effects of realistic species extinction scenarios on food webs.

## Materials and methods

### STUDY AREA

Serengeti National Park (SNP) is located in the north of Tanzania, bordering Kenya as part of the larger Serengeti-Mara ecosystem (1°15′-3°30′S, 34°-36°E), that covers in total some 25 000 km$^2$. The Serengeti ecosystem is a semi-arid savanna, with an average annual rainfall gradient ranging from 600 to 1000 mm/year and an elevation gradient ranging from 1100 to 1800 m a.s.l. (Sinclair 1979). Mainly because of strict tourism regulations and local management involvement (Polasky *et al.* 2008), the inner centre has, except for some burning management by early hunters and pastoralists, remained mostly unchanged and undisturbed for thousands of years (Sinclair 1979; Sinclair *et al.* 2007). The park and differently protected surrounding reserves mirror the changing life style of people over time and their impact on wildlife (Olff & Hopcraft 2008): hunters (game reserves), pastoralists (Ngorongoro Conservation Area) and agriculturalists (non-protected areas) (Fig. 1). The Serengeti is one of the most intensively studied savanna ecosystems (Sinclair *et al.* 2007), with work focused on trophic interactions between plants and the larger and charismatic mammal species, but also of small rodents (e.g. Magige & Senzota 2006), small predators (e.g. Waser 1980), birds (e.g. Sinclair, Mduma & Arcese 2002), dung beetles (Foster 1993) and other arthropods (Freymann *et al.* 2007; De Visser, Freymann & Schnyder 2008). This enabled us to construct the first and rather complete descriptive food web topology of a natural savanna ecosystem.

### DEFINING THE SAVANNA FOOD WEB

Previous studies on the Serengeti food web mixed taxonomic resolution among compartments (species vs. aggregated species groups), simplified the web to its essentials (mainly large mammals) and excluded invertebrates and consequently also insectivores (McNaughton 1992; Dobson 2008; Holt *et al.* 2008). The trophic groups that were distinguished for the current food web compilation

**Fig. 1.** Serengeti National Park (dark) and surrounding conservation areas (grey), game reserves (light grey) and human-populated areas (white), Tanzania.

are listed in the Supporting Information (see Appendix S1). The invertebrates encompassed 23 common-occurring taxa of arthropods (identified at the level of order or family) found by field surveys across SNP (de Visser, unpubl. data), three additional higher-defined groups of Arthropoda and two higher defined groups of Mollusca. All observed and recorded mammal species for this area were included; a total of 146 species. The most commonly occurring reptiles encompassed 44 species while the amphibians were represented by 18 species. For the highly diverse birds (about 606 species, A.R.E. Sinclair pers. comm.), we selected the common-occurring resident species (113 species) and left out rare, non-breeding and migratory species. Species restricted to aquatic habitats were left out of this description (surveys of aquatic invertebrates and fishes were not available), except for some common prey-groups among fishes (Perciformes) and aquatic invertebrates (Arthropoda, Decapoda). Full annual diet breadth of each species was compiled from literature (see Appendix S2), but explicitly mentioned 'unusual' diet items were excluded. As trophic links were based on literature reviews, we cannot provide sampling effort curves. However, in a survey on the source literature, the highly connected nodes (number of consumer links) did not necessarily belong to the best-studied species (Ings *et al.* 2009), but in fact belonged correctly to the generalists and omnivorous species (see Appendix S2). By using the full annual diet breadths, we inherently corrected for seasonal diet shifts and allowed diet switching. Feeding links of predator and prey were defined for the adult life stages. Average adult body mass was compiled from published literature (vertebrates and molluscs) and own measurements (arthropods, de Visser, unpubl. data). All included animals summed up to a total of 321 species and 29 orders. The aggregation into trophic species was based on similarity in diet and predators (Cohen 1978) and a higher-order taxonomical classification. In addition, we split highly size-structured trophic species into multiple nodes according to body size (small, medium and large sized). This aggregation resulted in 88 trophic species (15 invertebrate and 73 vertebrate nodes); of which seven belonged to the human-introduced group (humans, dogs, cats, cattle, goat, sheep, chicken and duck). We will further refer to these aggregated groups as food web nodes. For each node, we averaged the body masses and counted the number of total trophic links to other nodes. With this approach, the taxonomical bias towards vertebrates is considerably reduced compared with previous food web compilations of Serengeti. The resource and vegetation level was grouped into seven general functional types, mainly restricted by the limited knowledge on detailed diets of herbivorous invertebrates. We distinguished decaying plant and animal matter, plant juices, fruits and nectar, grains and seeds, grasses and herbs, trees and shrubs, and human-introduced cultivated crops. The resulting food web thus consisted of 95 nodes. For this food web topology, we did not take into account host–pathogen and parasitic interactions, as these are not classical predator–prey interactions. Furthermore, we excluded scavenger feeding links on taxonomically unresolved carcasses from analysis, which excluded one node completely, i.e. two vulture species (*Gyps* spp., node 62). This resulted in 86 nodes in the pristine food web and eight additional human-introduced nodes.

### STRUCTURAL FOOD WEB PROPERTIES AND SPECIES DELETION SEQUENCE

A topological food web can be depicted as a consumer-resource matrix of S number of species, with consumers as columns and resources as rows, both ordered by increasing body mass (Cohen 1978; Petchey *et al.* 2008a). Interactions in the upper-right triangle above the diagonal therefore indicate consumers feeding on resources smaller than themselves, a pattern often found in empirical food webs ('upper-triangularity', Warren & Lawton 1987; Cohen *et al.* 1993; Petchey *et al.* 2008a). Because we used trophic species, the diagonal line indicates cannibalism and/or intraguild predation. The size of the matrix ($S \cdot S = S^2$) equals the number of possible links, with L the number of links actually realized in our web.

We simulated human-induced species loss by cumulatively removing nodes that consisted of a threatened species (in case of single-species nodes) or with a certain proportion of threatened species (in case of multi-species nodes), based on the latest *Red List of Threatened Species* of the World Conservation Union (IUCN 2009). Three classes were recognized: (critically) endangered, vulnerable and near threatened. The IUCN criteria for threatened species integrate several kinds of extinction risks because of human influences (habitat loss, over-exploitation and introduced species) and document the observed decline in abundance of the species. In multi-species nodes, the highest IUCN category present determined its rank in the species deletion sequence. We removed nodes from the system when 20% or more of its members were listed threatened (this excluded two species-rich nodes). In this food web, this procedure equalled a deletion sequence based on the average of the risk categories per node. Importantly, although we allowed for prey-switching, nodes were deleted when several of the main prey items were extinct. Even if trophic links with smaller-sized species were still present, these were judged (based on literature) inadequate to sustain a population of the consumer species. To investigate the connectance among the removed nodes, we tested for differences in the average number of trophic links of the nodes per IUCN category using a Kruskal–Wallis test. The cumulative species deletion sequence produced a temporal sequence of

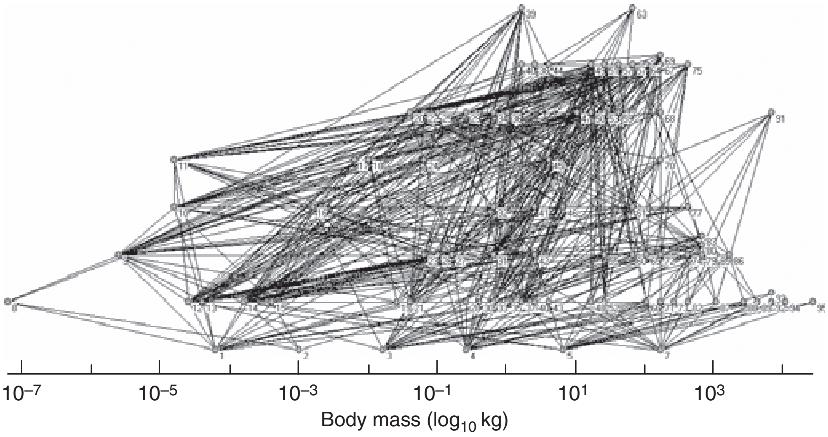

**Fig. 2.** Graphic representation of the pristine food web topology of Serengeti National Park, Tanzania, on a $\log_{10}$ body mass scale. Invertebrates, mammals, birds, reptiles and amphibians are included. Nodes represent taxonomical aggregated groups of trophic species, the total number of nodes presented in this web is 86. Lines indicate diet links. Rows indicate trophic positions, e.g. omnivores feeding both on plants and animals are placed intermediate with herbivores and (higher level) carnivores. Nodes ranging from left to right increase in body size, $10^{-7}$–$10^{3}$ kg. Labels numbered 1–7 are resources (ordered not necessarily by kg), numbers 8–95 are consumers. Exact labels and data sources are explained in Appendix S1 and S2 in the Supporting Information. The network was drawn with the Pajek freeware available at http://vlado.fmf.uni-lj.si/pub/networks/pajek.

five different stages of the savanna food web impairment for the Serengeti, reflecting the consequences of increased human activities in this system: (i) pristine state (P), (ii) endangered and higher species lost (EN), (iii) vulnerable and higher species lost (VU), (iv) near threatened and higher species lost (NT) and (v) the non-protected areas described as an impoverished food web with human-introduced species (humans, crops and livestock) (HU). We created food web matrices for each of the different scenarios to visualize the size-selective removal of nodes [cumulative species removal (Fig. 3a–d) and introduction (Fig. 3e)].

We examined the consequences of the IUCN-predicted species loss on the following food web topological properties: number of nodes in the food web (S), number of realized feeding links (L), linkage density (L/S), directed connectance (C) (fraction of all possible trophic links including cannibalism that are realized, L/S$^2$), percentage of nodes without a predator (T), percentages of omnivory (O) and cannibalism/intraguild predation (K) (fraction of nodes that feed at multiple levels or its own node, respectively), average adult body mass (kg) across all nodes (M), predator–prey ratio (PPR, ratio of predator nodes over prey nodes present in the web) and predator–prey mass ratio (PPMR, ratio of predator mass over average prey mass). In addition, we examined the effect of human-caused species loss on the link distribution frequencies. Calculating the deviation from symmetry (skewness) of the observed link distributions and testing for the fit of real to Poisson distributions is indicative for a deviation from a random link distribution and indicates the sensitivity of a network to selective node loss (Montoya & Solé 2003).

We compared the findings of the IUCN-simulation with three theoretical extinction scenarios that delete nodes with decreasing body size (starting with the larger-bodied nodes), increasing connectance and decreasing connectance (starting with the least-connected and highest-connected nodes, respectively). Using these extinction scenarios, we tested the robustness of this Serengeti food web structure as measured by the fraction of primary extinctions needed to cause a loss of ≥50% of the nodes (primary and secondary extinctions) in the food web, $R_{50}$ (Dunne, Williams & Martinez 2002b; Staniczenko *et al.* 2010). We also provide values for $R_n$, showing the fraction of primary species loss needed to cause a loss of 10%, 20%, 30% and 40% (*n*) of all species. This enabled us to compare the analysis with the realistic IUCN-based scenario that contains limited species loss.

Furthermore, we reviewed for all taxa in this food web their known functional role in ecosystem processes through nontrophic interactions and their associated impacted species from the literature. This included habitat modification, ecosystem engineering, keystone roles in nutrient cycling processes, bioturbation or important roles in seed dispersal and disease control by removing carcasses. Similar to the IUCN-based species deletion sequence, we included a node into the high-impact group when 20% or more of its members were of likely functional importance to the system. Out of the 86 nodes in the pristine food web (P), 15 nodes were thus grouped to contain the following species with documented nontrophic effects on the savanna ecosystem: *Aepyceros melampus* (impala), *Connochaetes taurinus* (wildebeest), *Crocodylus niloticus* (Nile crocodile), *Giraffa camelopardalis* (giraffe), *Hippopotamus amphibious* (hippopotamus), *Loxodonta africana* (African elephant), *Madoqua kirkii* (dikdik), *Orycteropus afer* (aardvark), *Potamochoerus porcus* (bushpig), *Raphicerus campestris* (steenbuck), *Sylvicapra grimmia* (common duiker), termites (*Macrotermes* sp., *Odontotermes* sp.), vultures (*Gyps* sp., *Torgos tracheliotus*), small rodents (*Mastomys* sp., *Rattus rattus*), ants (Formicidae) and dung beetles (Scarabaeidae) (see Appendix S3). Using the software package STATISTICA v.7 software (2004), we tested with a Mann–Whitney U-test the potential differences in the mean number of trophic links between the high-impact and no-impact group. Based on preliminary data, we computed within the IUCN-based extinction scenario the number of trophic links additionally affected (not necessarily lost) through nontrophic interactions of the functionally important species with the associated species (see Appendix S3).

## Results

### SPECIES LOSS AND TROPHIC INTERACTIONS

We compiled a pristine Serengeti food web that includes vertebrates as well as invertebrates, containing 86 food web

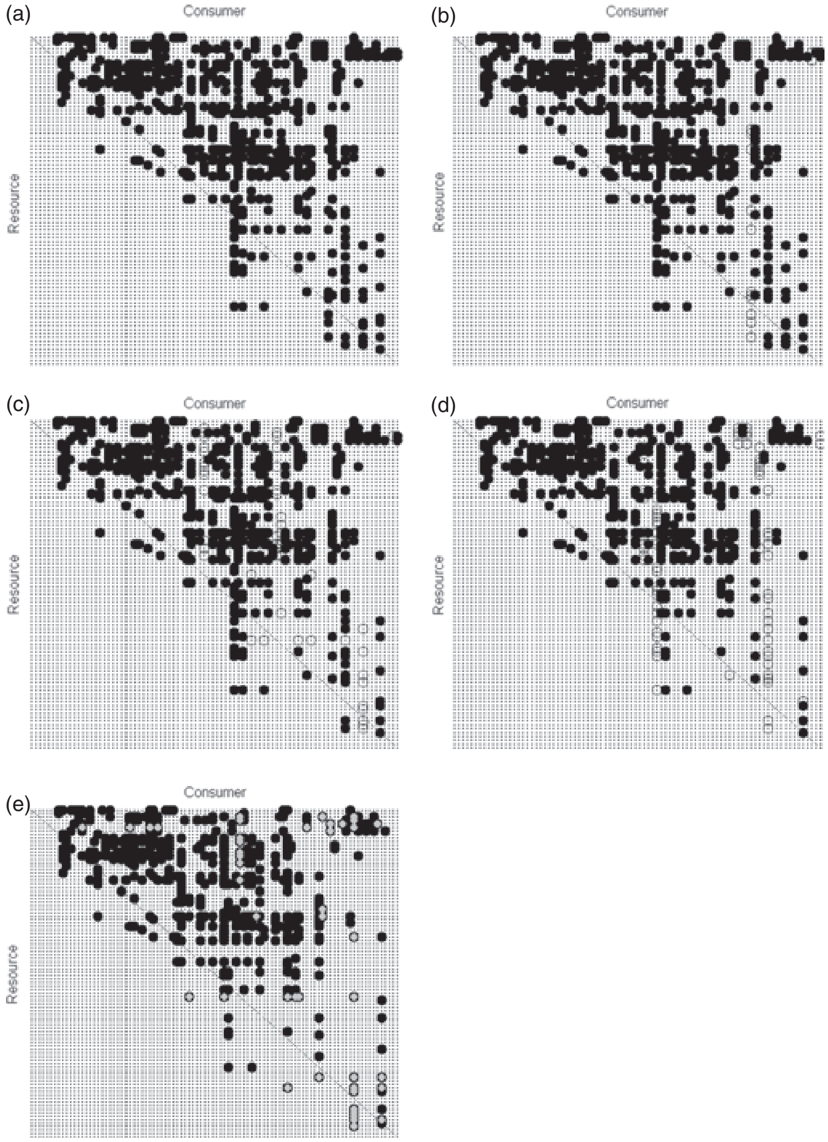

**Fig. 3.** Food web structures illustrated in consumer-resource matrices show effects of human impact progressing through time estimated by the categories of the *Red List of Threatened Species* (IUCN 2009). Each matrix shows cumulative node loss: a) pristine state without human influence (P), b) endangered and higher species lost (EN), c) vulnerable and higher species lost (VU), d) near threatened and higher species lost (NT), and e) near-threatened stage with introduced humans and livestock (HU). Columns represent consumers, rows represent resources. Body size increases from left to right and top to bottom. Black dots indicate the consumer in that column feeds upon the resource in that row. Open circles represent feeding links lost compared to the previous matrix. Grey dots indicate links of introduced groups. The dashed diagonal line represents the position that cannibalistic⁄intraguild-predation links would occupy.

nodes, consisting of six basal nodes (primary producer level), 16 top predaceous nodes and 64 intermediate nodes (Fig. 2). This food web displayed a typical trophic hierarchy, with predators tending to be larger than their prey, resulting in a food web matrix that is upper triangular (Fig. 3a). In some cases, predators were found to eat prey larger than themselves; i.e. in social hunting species among the mammals like lion and arthropods in general. We found an overall predator–prey ratio of 0·83, which was related to the high percentage of omnivores (feeding on plant and animal matter) (58·1%). Predator–prey mass ratio ($\log_{10}$) was high, caused by the many insectivores that feed on small-sized prey (5·55). Furthermore, we found substantial cannibalistic⁄intraguild-predation links (12·8%) mainly among the arthropod feeding guilds. Our web had in total 547 realized links, resulting in a directed connectance of 0·074 (Table 2).

The IUCN-based species extinction sequence resulted in an expected but accelerated decline of diversity (first two (EN), then five (VU), then seven (NT) nodes lost) (Table 1). More importantly, this removal was selective against large body-sizes and (large) predators, indicated by a decreasing PPR and increasing PPMR (Table 2). At the near-threatened stage (NT), the percentage of nodes without a predator suddenly increased, as several prey species found themselves – without their predators – at the top of the food chain. The proportion of omnivores and cannibals in the food web remained relatively constant, as these groups occurred mainly in the smaller-sized and yet untouched part of the food web (Table 2). Human impact caused an accelerating decrease in linkage density that levelled off as human-introduced species populated the impoverished food web. The link distributions of the different stages of the Serengeti food web were highly right-skewed and clearly different from an expected Poisson distribution (Table 3). As human impact progressed, we found this skewness to become less negative and the coefficient of variation of the link density increased, irrespective of the introduced diversity at the human stage (HU) (Table 3). In addition, connectance increased with decreased species diversity from the pristine (P) to the near-threatened (NT) stage, although not constantly. The patterns

**Table 1.** Threatened species (IUCN Red List 2009) occurring in the pristine Serengeti food web, their appointed node and number of total trophic links (L). Critically endangered (CE), endangered (EN), vulnerable (VU) and near threatened (NT)

| Status | Species | Common name | Node | L |
|---|---|---|---|---|
| CE[*] | *Diceros bicornis* | Black rhinoceros | 93 | 2 |
| EN[*] | *Lycaon pictus* | African wild dog | 74 | 11 |
| VU | *Acinonyx jubatus* | Cheetah[†] | 74 | 11 |
| | *Hippopotamus amphibious* | Hippopotamus | 94 | 1 |
| | *Panthera leo* | Lion | 86 | 9 |
| | *Torgos tracheliotus* | Lappet-faced vulture | 63 | 7 |
| | *Malacochersus tornieri* | Pancake tortoise | 61 | 15 |
| | *Balearica regulorum* | Grey-crowned crane | 42 | 15 |
| NT | *Loxodonta africana* | African elephant | 95 | 2 |
| | *Panthera pardus* | Leopard | 80 | 20 |
| | *Hyaena hyaena* | Striped hyena | 77 | 7 |
| | *Gazella thomsoni* | Thomson's gazelle | 73 | 7 |
| | *Tragelaphus imberbis* | Lesser kudu | 71 | 8 |
| | *Terathopius ecaudatus* | Bateleur | 49 | 23 |
| | *Polemaetus bellicosus* | Martial eagle | 49 | 23 |
| | *Phoenicopterus minor* | Lesser flamingo | 46 | 13 |
| NT[‡] | *Hipposideros gigas* | Giant leaf-nosed bat | 23 | 2 |
| | *Otomops martiensseni* | Large-eared free-tailed bat | 23 | 2 |
| | *Gyps rueppellii* | Rueppell's vulture | 62 | – |
| | *Gyps africanus* | African white-backed vulture | 62 | – |
| | *Agapornis fischeri* | Fischer's lovebird | 33 | 19 |

[*] CE and EN were grouped together for analysis as EN and higher endangered.

[†] Cheetah is stated as vulnerable (VU) in the IUCN (2009) but for purposes of this study aggregated with the African wild dog (Endangered, EN).

[‡] The following five (NT) listed species were excluded from analysis.

**Table 2.** Structural properties of the Serengeti food web at different stages under increased human impact: pristine (P), endangered and higher (EN), vulnerable and higher (VU), near threatened and higher species lost (NT), human (HU) state. Structural properties include S (number of nodes that have been classified for this food web based on higher taxonomy, diet and body size), L (number of realized links), L/S (linkage density), C ($L/S^2$) (connectance or proportion of possible trophic links that are realized in a network), T (nodes without predator, %), O (nodes feeding at multiple trophic levels (omnivory), %), K (nodes feeding on themselves (cannibalism/intraguild predation), %), M (average body mass (kg)), PPR (predator–prey ratio, number of predator nodes over prey nodes), PPMR ($\log_{10}$ predator–prey mass ratio, mass of predator nodes over average mass of prey nodes).

| Food web | S | L | L/S | C ($L/S^2$) | T | O | K | M | PPR | PPMR |
|---|---|---|---|---|---|---|---|---|---|---|
| P | 86 | 547 | 6·36 | 0·074 | 18·6 | 58·1 | 12·7 | 0·51 | 0·83 | 5·55 |
| EN | 84 | 534 | 6·36 | 0·076 | 17·9 | 58·3 | 13·1 | 0·44 | 0·81 | 5·56 |
| VU | 79 | 488 | 6·18 | 0·078 | 17·7 | 58·2 | 13·9 | 0·34 | 0·79 | 5·59 |
| NT | 72 | 415 | 5·76 | 0·080 | 26·4 | 58·3 | 15·3 | 0·21 | 0·77 | 5·63 |
| HU | 80 | 457 | 5·71 | 0·071 | 23·8 | 57·5 | 13·8 | 0·34 | 0·81 | 5·59 |

in link density and the increase in connectance in this food web indicated that increased human impact generally led to the loss of poorly connected species. The levelling off in the increase of connectance with species loss was caused by the (non-significant) increase in the average number of trophic links per threatened node from 6·5 ± 6·4 SD, $n = 2$ (EN), 9·4 ± 5·9 SD, $n = 5$ (VU), to 11·4 ± 7·6 SD, $n = 7$ (NT) ($P = 0·78$). This implies that more well-connected species were lost as human impact progressed. At the final stage (HU), the predator–prey ratio and the percentage of nodes at the top of the food chain increased, whereas PPMR decreased slightly, caused by human-introduced larger-sized predaceous and omnivorous species (eight nodes). However, this introduction lowered the connectance of the system significantly, meaning that these introduced species contained few feeding links to the existing wildlife (Table 2). With a primary loss of 16·3%, this realistic species removal scenario resulted in no secondary extinctions.

The Serengeti food web seemed highly robust to deletion of nodes according to the removal of large to small body-sized nodes, as well as of poor to highly connected nodes, with a slight increase in secondary extinctions as the number of primary species losses progressed (Table 4). Both yielded $R_{50}$ values of 0·465 and 0·442, respectively. The observed absence of secondary extinctions in the IUCN-removal sequence was reflected in the initial phases of both the body size-based and increasing connectance-based removal sequence ($R_{10}$ and $R_{20}$). In contrast, the food web seemed

**Table 3.** Measures concerning link distribution frequencies of the Serengeti food web at different stages under increased human impact: pristine (P), endangered and higher (EN), vulnerable and higher (VU), near threatened and higher species lost (NT), human (HU) state. S indicates the number of nodes. CV, the coefficient of variation of the link density. Skewness measures the deviation of distribution from symmetry (for a normal distribution it equals 0). $\chi^2$ is the value for the fit of real to Poisson distributions (which equals a random link distribution), with * indicating significant differences, $P < 0{\cdot}001$.

| Food web | S | CV | Skewness | $\chi^2$ |
|---|---|---|---|---|
| P | 86 | 0·6365 | −3·9914 | 1107·26* |
| EN | 84 | 0·6381 | −3·9663 | 2441·14* |
| VU | 79 | 0·6396 | −3·9447 | 1366·68* |
| NT | 72 | 0·6565 | −3·6596 | 8215·60* |
| HU | 80 | 0·6856 | −3·1977 | 8279·85* |

**Table 4.** Robustness of the Serengeti food web, measured by the fraction of primary species loss needed ($R_n$) to cause a loss of *n* % of all species (primary and secondary extinctions) under different extinction scenarios based upon body size and connectance.

| | Robustness ($R_n$) | | |
|---|---|---|---|
| Percentage total species loss (*n*) | Large body-size scenario | Low Connectance scenario | High Connectance scenario |
| 10 | 0·093 | 0·105 | 0·047 |
| 20 | 0·186 | 0·209 | 0·093 |
| 30 | 0·267 | 0·279 | 0·116 |
| 40 | 0·372 | 0·360 | 0·151 |
| 50 | 0·465 | 0·442 | 0·221 |

highly sensitive to deletion of highly to poor-connected nodes. Secondary extinctions occurred almost immediately and increased steeply, resulting in a considerable lower robustness ($R_{50}$) of 0·221 (Table 4).

### SPECIES LOSS AND NONTROPHIC INTERACTIONS

Of the 86 nodes in the pristine food web, 15 were classified as having high functional (nontrophic) impact. However, these nodes showed no difference ($P = 0{\cdot}17$) in the mean connectedness compared with other nodes without such impact (11·5 ± 11·4 SD, $n = 15$ for high impact, and 13·0 ± 7·3 SD, $n = 71$ for no known impact). This indicates that functionally important keystones are not necessarily important trophic key interactors in this food web. A preliminary analysis that incorporated known nontrophic links during the IUCN-deletion sequence resulted in a doubling of the number of trophic links ($n = 264$) being negatively affected or potentially lost compared to the number of links lost under the trophic scenario. Owing to limited information and standardisation of the quantitative impacts of each individual nontrophic interaction, we cannot state whether these lead to secondary extinctions. If we assume this to be true, an increase of 17·4% lost nodes would be expected on top of the trophically defined extinctions ($n = 29$ vs. $n = 14$ out of 86).

## Discussion

We presented here the first version of a complex and taxonomically rich, size-structured food web topology of one of the world's most pristine terrestrial ecosystems. This food web consists of 15 nodes formed by invertebrates (aggregates of 28 higher-order taxa), 73 nodes by vertebrates (aggregates of 321 species and one order) and seven nodes representing the resource and vegetation level (Fig. 2). This includes all species currently and commonly observed in Serengeti. We explored the simulated responses of this near-pristine savanna food web to various extinction scenarios, most importantly including one based upon real-world and human-induced threats.

### HUMAN IMPACT ON TOPOLOGICAL PROPERTIES

The connectance value of 0·074 (Table 2) falls within the range documented for other food webs (Dunne, Williams & Martinez 2002a). As indicated by the skewed link distributions, this food web would be more susceptible to selective rather than random species loss (Table 3). Our simulations of realistic species loss based on the IUCN rank categories indicate that human impact on the Serengeti food web caused selective loss of the larger species, predators and poorly-connected species. However and more importantly, we show that this realistic species loss did not follow the simple rules commonly used in theoretical models (e.g. according to connectance or trophic level of species). Instead, we found that humans affect several topological properties in a nonlinear and less predictable way. In agreement with other studies (e.g. Montoya *et al.* 2009), we found that in this near-pristine food web, poor-connected nodes were more vulnerable to disturbances and were the first lost under human impact. The species deletion sequence based on increased connectance showed nevertheless a high robustness to this type of extinction (Table 4). However, the variation in connectedness of the nodes in the realistic IUCN-deletion sequence (EN, VU, NT) was high, and as human impact progressed, we soon also found threatened species grouped within the higher-connected nodes. Here, the food web showed high sensitivity to an extinction scenario based on decreased connectance (Table 4). However, this topological analysis of structural robustness may underestimate the effects caused by the loss of poor-connected nodes. It is generally assumed that poor-connected species (i.e. specialists) have strong interaction strengths while species with many links tend to have weak connections (Montoya & Solé 2003; Wootton & Emmerson 2005). The patterning of interaction strengths is an important factor in the stability of food webs (De Ruiter, Neutel & Moore 1995). In fact, food web studies that incorporated dynamic analyses have shown how small changes in population densities of poor-connected species resulted, through direct and indirect interactions, in the largest effects on the remaining species within the food web (Pimm 1991; Montoya *et al.* 2009).

Interestingly, although diversity (number of nodes) at the human-dominated stage (HU) roughly equalled that of the vulnerable stage (VU), none of the topological properties remained similar, except PPMR. Most striking were the smaller linkage density and lower connectance and the higher number of nodes positioned at the top of the food chain as well as the higher predator–prey ratio at the human stage (Table 2). These changes were caused by human-introduced predator species (including themselves) and protection of livestock that would otherwise be heavily predated upon. Human-introduced species, however, re-established PPMR by introducing smaller predator–prey size differences. According to recent theory, increases in predator–prey mass ratios have large effects on community dynamics, as they scale positively with interaction strengths that in turn tend to destabilize community dynamics (May 1972; Emmerson, Montoya & Woodward 1995; Berlow *et al.* 2009). We therefore conclude that human impact decreases diversity in a size-biased way that may destabilize the food web. Although human-introduced species enrich the food web, these new species showed low connectance to the prevalent wildlife and may not replace the functional roles of the species they displace.

### TOPOLOGICAL ANALYSIS AND REALISTIC EXTINCTION SCENARIO

Certain aggregation procedures were necessary. We currently lack full taxonomic resolution as well as specific diet data for the invertebrate taxa to create a full species-resolved food web, while the larger vertebrates, especially the predators, would allow resolution to species level. However, unequal aggregation criteria would give a highly skewed and mammal-focused food web producing unrealistic conclusions. We therefore aggregated taxa on the generally known basis of diet and body size. This aggregation may in itself also involve some inaccuracy (e.g. a highly aggregated vegetation level and still a skewed pattern towards vertebrates when we consider actual species diversity). However, it enabled us to explore for the first time the many vertebrate–invertebrate feeding interactions in this savanna web and to address human impact consequences on diversity, connectance and link distribution of the entire food web. Furthermore, as data on quantified interaction strengths are not yet available for this system, and population estimates of the smaller-bodied and lesser known species scarce, we were restricted to a topological approach for the quantification of the food web (presence/absence of links) instead of an approach based on population densities and interaction strengths (e.g. the per capita effects of predators and prey on each others population growth rate) (De Ruiter, Neutel & Moore 1995; Neutel, Heesterbeek & De Ruiter 2002). Although our chosen intermediate level of aggregation and annual maximum diet for each node depicts a less spatial and temporal dynamic food web, its major advantage is that species loss-induced, adaptive diet shifts are inherently taken into account. Such diet shifts are generally not accounted for in topological food web approaches resolved to the species level, where extinction of the unique prey of a predator would directly predict the consumer's extinction.

The classification by the IUCN Red List (2009) incorporates the effects of most human impacts, but also includes a bias towards vertebrates in our simulation as invertebrate species have often not been evaluated. However, it may seem justified to assume that the common invertebrate groups incorporated in this food web are the least prone to extinction, because of much higher population sizes. The IUCN-removal sequence caused no secondary extinctions in our species-loss simulation based on topological criteria only. Secondary extinctions would have occurred when a primary extinction creates an unfeasible community (when a consumer is without its prey) (Petchey *et al.* 2008b), or in our case, when a consumer is without its main items of prey. However, as we used the full diet breadth (except for unusual prey items) for a consumer to allow potential prey switching, the chance for such an extinction event was rather small and the number of secondary extinctions may be underestimated. On the other hand, in the real world, diets are dynamic and may shift towards similar prey when the primary prey goes extinct. This may prevent those secondary extinctions, which our approach thus accounted for. Supporting this point, more complex and diverse communities with high levels of omnivory and/or high connectance seem more resistant to species loss than simple communities (Eklöf & Ebenman 2006; Dunne & Williams 2009). Also, we found a similar lack of secondary extinctions during the initial phases of species removal based upon large body size and poor connectance. Importantly, our methods did not exclude the potential of secondary extinctions to occur. The removal sequence with decreased connectance showed immediate and increasing secondary extinctions, similar to the findings from other food web studies using a topological analysis (Solé & Montoya 2001; Dunne, Williams & Martinez 2002b) or dynamic analysis (Eklöf & Ebenman 2006).

### NONTROPHIC INTERACTIONS

Most studies performed so far on food webs and extinction sequences have largely ignored the role of nontrophic interactions or were restricted to local subsets of interactions (Berlow *et al.* 2004). We investigated in a preliminary analysis the effects of incorporating interactions through ecosystem engineering and habitat modification on secondary extinctions in a nearly complete terrestrial food web. Among nodes that were predicted to be lost according to the IUCN scenario (Table 1), five nodes contained species that play important roles in the structure and functioning of the system through nontrophic interactions (i.e. Hippopotamus, Lappet-faced vulture, African elephant, Impala, Steenbuck and Kirk's dikdik; Table 1). The loss of some of these nodes may affect other non-threatened but functionally important species. Considering nontrophic interactions into the IUCN-based extinction sequence showed a doubling of the number of trophic links being affected and potentially lost. This 'non-trophic' cascade may cause in worst-case scenario an additional loss of 15 nodes. Therefore, the consequences of the loss of functionally important species for biodiversity may be larger than predicted by their trophic role in the system. Moreover, we showed in this savanna community that indeed functional keystones are not the same as topological keystones, as we found no difference and large variation in connectance between nodes with high functional impact and other nodes.

We elaborate on this point with three case-studies from Serengeti. Small and abundant omnivorous mammals, such as *Ichneumia albicauda* (white-tailed mongoose) (Waser 1980), had many trophic links (25 according to our aggregation), but do not seem to have major impacts on the ecosystem beyond their trophic interactions. Termites (Insecta, Isoptera) also had many trophic links (19 according to our aggregation). In the Serengeti, they act as important macrodetritivores (Freymann *et al.* 2008; Freymann, De Visser & Olff 2010), provide through their mound structures habitat to other arthropods (De Visser, Freymann & Schnyder 2008) and have in general as ecosystem engineers major impacts on savanna ecosystem processes (Bignell & Eggleton 2000). The highly abundant wildebeests play a key role in the spatial interactions of the Serengeti by their annual migration (Sinclair 2003), but instead had few trophic links (six according to our aggregation). These three case-studies illustrate the potential magnitude of indirect interaction effects mediated through ecosystem processes and habitat modification being unrelated to trophic interaction effects.

### INTEGRATIVE NETWORKS

The focus on trophic interactions in the food web community clearly results in minimum estimates of community responses and potential secondary extinctions to species loss. The implementation of nontrophic interactions into a full interaction web model, including direct and indirect species interactions, has shown the importance of nontrophic interactions in particular on ecosystem properties, such as biomass and production (Goudard & Loreau 2008). Recent studies that incorporated species interactions beyond predation or intraspecific competition, such as direct interspecific competition (Eklöf & Ebenman 2006) or indirect pathways with which species are connected via linkages with intermediate species (Montoya *et al.* 2009), showed large effects on secondary extinctions. We addressed here interactions via habitat modification, ecosystem engineering or facilitation that incorporate the functional role of a species in the system. However, this kind of interactions, as we pointed out in this study, does not necessarily have to cause extinctions when absent. In fact, whereas some species may be negatively affected, others may benefit from the loss of this interaction type. Little is known about how to classify, organize and quantify these other ecological networks and their mutual interplay with trophic networks (Olff *et al.* 2009). Recently, topological analyses have been complemented with dynamical analyses that incorporate interaction strengths and direction with which multiple species interactions effects may be estimated (Yodzis 2000; Eklöf & Ebenman 2006; Berlow *et al.* 2009; Montoya *et al.* 2009). However, in attempts to incorporate nontrophic interactions by integrating food web patterns and dynamics using interaction strengths, several issues became apparent regarding the definition of interaction strength and the lack of integration between theory and field (Berlow *et al.* 2004). Yet, when accurate field data are available, a comparative approach of predicted (trophic only) and observed effects revealed both the sign and magnitude of nontrophic interaction effects (Berlow *et al.* 2009; Montoya *et al.* 2009). The existence of natural experiments, spatial or temporal gradients of disturbances, will prove invaluable here. Progress in this field therefore requires integrative efforts between the development of food web theory and basic field work approaches in the quantification of the structure of interaction networks.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** Details of food web nodes.

**Appendix S2.** Data sources of diets, body masses and sampling effort bias.

**Appendix S3.** Data sources of functional impacts of species.

**Appendix S4.** Consumer-resource links.