Ecology Letters

WILEY

ECOLOGY LETTERS

LETTER OPEN ACCESS

Food Web Similarity Increases With Productivity Similarity at a Continental Scale

Ann E. Finneran[1] | César A. Uribe[2,3] | Kai M. Hung[4] | Chia Hsieh[5,6,7] | Matthew A. Wuensch[5,6] | Matthew A. McCary[1] | Lydia Beaudrot[5,6]

[1]Department of Biosciences and Program in Ecology & Evolutionary Biology, Rice University, Houston, Texas, USA | [2]Department of Electrical and Computer Engineering, Rice University, Houston, Texas, USA | [3]Ken Kennedy Institute, Rice University, Houston, Texas, USA | [4]Institute of Data, Systems, and Society, Massachusetts Institute of Technology, Cambridge, Massachusetts, USA | [5]Ecology, Evolution & Behavior Program, Michigan State University, East Lansing, Michigan, USA | [6]Department of Integrative Biology, Michigan State University, East Lansing, Michigan, USA | [7]W.K. Kellogg Biological Station, Michigan State University, Hickory Corners, Michigan, USA

Correspondence: Ann E. Finneran (af58@rice.edu)

Received: 7 July 2025 | **Revised:** 3 February 2026 | **Accepted:** 19 February 2026

Editor: Paulo Guimaraes

Keywords: Africa | ecological networks | food webs | fragmentation | mammals | metaweb | primary productivity

ABSTRACT

Primary productivity and trophic interactions are fundamentally linked. However, it remains largely unknown how food web structure varies along primary productivity gradients at continental scales or how the influence of primary productivity on food webs varies within regions. Furthermore, anthropogenic pressure threatens the integrity of food webs globally with potentially predictable food web disassembly. Here, we test how plant productivity and anthropogenic fragmentation predict the pairwise similarity of food web networks within and among regions for 127 protected areas spanning deserts to rainforests. We measured food web structural equivalence independent of species identities and accounted for inherent scaling of food web structure with richness and connectance. Food webs were significantly more similar at sites with similar plant productivity at the continental scale and within woodland savannas, and in tropical rainforests with similar anthropogenic fragmentation. These empirical results inform how food web structure mediates biodiversity and ecosystem function.

1 | Introduction

Most understanding of food web ecology has been derived from single-site studies or microcosm experiments, which inhibits generalisations across scales and hampers predictions of how global change will impact trophic networks and ecosystem functioning (Baiser et al. 2019). Excitingly, the study of food web networks at biogeographic scales has become possible due to the extensive compilation of species interaction data and methodological improvements, creating the possibility for improved understanding of ecological systems (Windsor et al. 2023). Because ecological and evolutionary constraints may shape networks differently in different environments, food web structure likely varies along environmental gradients (Pellissier et al. 2018). For example, multiple aspects of food web structure vary with climate and species richness throughout Europe (Braga et al. 2019). Temperature and precipitation influence the distribution of biomes and their plant productivity (Whittaker 1970), and plant productivity is positively associated with consumer species richness at macroecological scales (Jetz et al. 2009). Although food web structure is known to scale with species richness (Dunne et al. 2008; Riede et al. 2010), direct tests of how plant productivity influences food web structure—independent of species richness—remain scarce.

Primary productivity and trophic interactions are fundamentally linked through the energy flow from basal resources through consumers (Elton 1927). In both natural and experimental systems, primary productivity is strongly associated with aspects of food web structure such as the proportion of basal species (Vermaat et al. 2009) and food chain length (Post 2002; Ward and McCann 2017; Young et al. 2013). Inefficient energy transfer between trophic levels restricts the energy available in a system, inherently impacting species interactions and food chain length (Baiser et al. 2019; Hutchinson 1959; Pimm 1982; Post 2002). Although longer food chains can intensify trophic cascades that suppress primary productivity (Loreau 2010), complex interactions such as omnivory may dampen these effects (Polis and Strong 1996). Omnivory tends to become more common with increasing productivity, with predators feeding across multiple trophic levels in response to competition and changing prey availability (Baiser et al. 2019). These differences in interactions may drive convergence in food web structure across highly productive systems.

In addition to classic bottom-up expectations, differences in consumer species can have variable top-down effects on productivity (Schneider et al. 2016; Wojdak 2005). Theoretical models have identified mechanisms through which trophic interactions can reduce plant productivity (Thébault and Loreau 2003), as well as mechanisms by which multi-trophic interactions among consumers can enhance plant productivity through synergistic feedbacks in resource complementarity (Albert et al. 2022; Amyntas et al. 2023; Wang and Brose 2018). Specifically, resource complementarity among multi-trophic consumers can contribute to higher producer complementarity resulting in higher plant species richness and primary productivity (Albert et al. 2022). Nevertheless, how the structure of food web networks changes along gradients of primary productivity across large spatial scales remains poorly understood. Therefore, empirical tests of the relationship between primary productivity and food web structure within and among regions spanning gradients of productivity are needed (Baiser et al. 2019). Given that food webs play a critical role in the maintenance of biodiversity and ecosystem functioning (Estes et al. 2011; Rooney and McCann 2012), identifying the fundamental relationship between plant productivity and food web structure at large scales has never been more urgent.

Importantly, habitat fragmentation can disrupt productivity-biodiversity relationships (Terborgh et al. 2001). Hence, to identify relationships between plant productivity and food web structure, it is important to account for the potential mediating influence of fragmentation. Habitat loss and fragmentation intensify local-scale changes in abundance, species richness, and community compositional turnover (Daskalova et al. 2020), resulting in decreased local and regional diversity (Gonçalves-Souza et al. 2025). Top predators are particularly vulnerable to extinction in fragmented landscapes (Pires et al. 2023; Ripple et al. 2014), and theoretical modelling predicts the loss of large-bodied predators from food webs before smaller species (Ryser et al. 2019). Despite longstanding expectations that habitat fragmentation from anthropogenic land use change affects food web structure (Hagen et al. 2012), little research has explicitly linked spatial variation in food web structure to fragmentation (O'Connor et al. 2024). Furthermore, as anthropogenic land use change continues to fragment natural habitats globally (Haddad et al. 2015), and protected areas face increasing human pressures (Jones et al. 2018), including forest loss and degradation (Geldmann et al. 2019), quantifying how food web structure varies across fragmentation gradients is critical for predicting the ecological impacts of future land use change.

Here, we test the extent to which primary productivity and anthropogenic fragmentation predict the similarity of food webs at the continental scale and within regions spanning desert habitats to tropical rainforests. Because food webs spanning large spatial scales lack shared species, we use a novel measure that is independent of species identities to quantify food web similarity based on the shape of networks (i.e., predator–prey links) and the functional similarity of species within them (Hung et al. 2026). We hypothesize that if primary productivity is an important determinant of food web structure at the continental scale (H1), then communities in locations with more similar primary productivity will have more similar food webs. If anthropogenic fragmentation results in predictable community disassembly, then communities facing similar levels of anthropogenic fragmentation will have more similar food webs (H2). If basal resource availability primarily determines food web structure, we predict that similarity in primary productivity will more strongly predict food web similarity in regions with lower primary productivity (H3). Alternatively, if resource complementarity among multi-trophic consumers enhances primary productivity (H4) (Albert et al. 2022), then more similar levels of primary productivity will more strongly predict food web similarity in regions with higher productivity (Figure 1).

2 | Methods

2.1 | Study System

Mammals are an excellent focal group for testing associations between primary productivity, fragmentation and food web structure due to their extensive data availability, extinction risk and diverse ecological roles. More studies have been published describing predator–prey interactions in mammals than in other taxa (Guimarães 2020). Globally, mammals face unprecedented extinction risk as a consequence of human impacts (Cardillo et al. 2023). Furthermore, large mammals have diverse and important impacts on community structure and ecosystem functions (Lacher et al. 2019). For example, top-down regulation by large carnivores affects disease, wildfire, carbon sequestration, invasive species and biogeochemical cycles (Estes et al. 2011).

Around the world, Africa harbours a greater proportion of extant megafauna than any other continent (Barnosky et al. 2004; Faurby and Svenning 2015) and spans a broad latitudinal range that encompasses diverse biomes (Burkart 2023; Olson et al. 2001). These attributes make African mammal communities ideal for comparing food webs across large-scale gradients in primary productivity. We used published mammal species composition data (Rowan et al. 2020) from 127 sites within African protected areas (Figures 2 and 3). These data comprise the most comprehensive mammal community composition data spanning a large spatial extent that have been compiled using standardised screening and verification protocols to minimise impacts from variation in sampling effort and species detectability (see Rowan et al. 2020 supplement). We chose data from protected areas due to the importance of protected areas

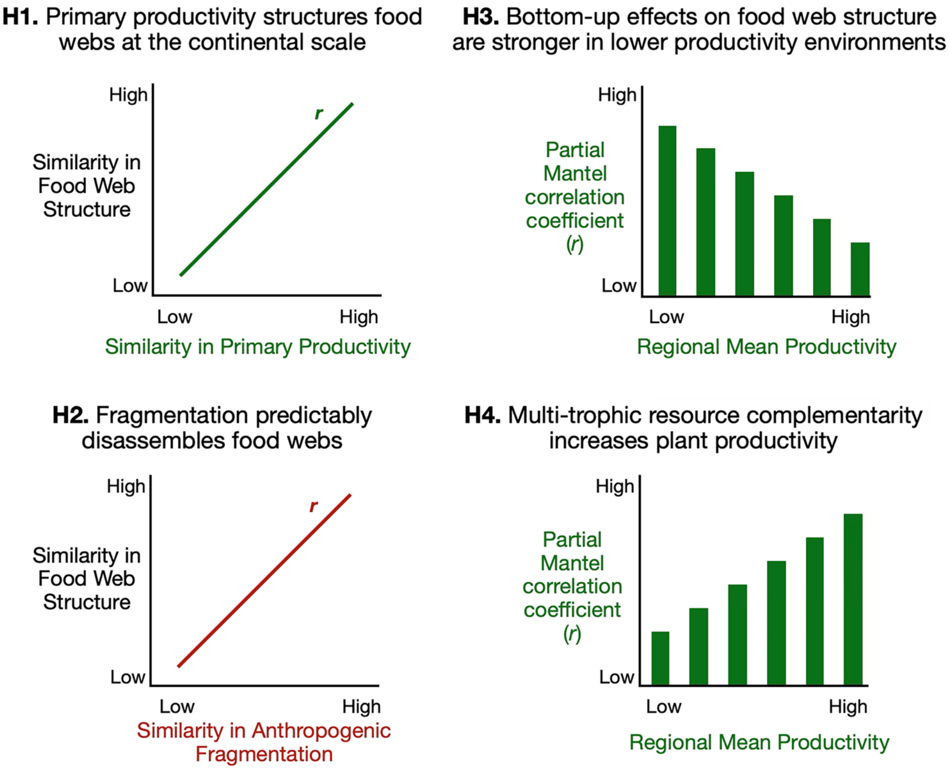

FIGURE 1 | Conceptual figure of hypotheses. We tested hypotheses H1 and H2 at the continental scale. We then tested hypotheses H2, H3 and H4 within regions defined by broadly similar habitat.

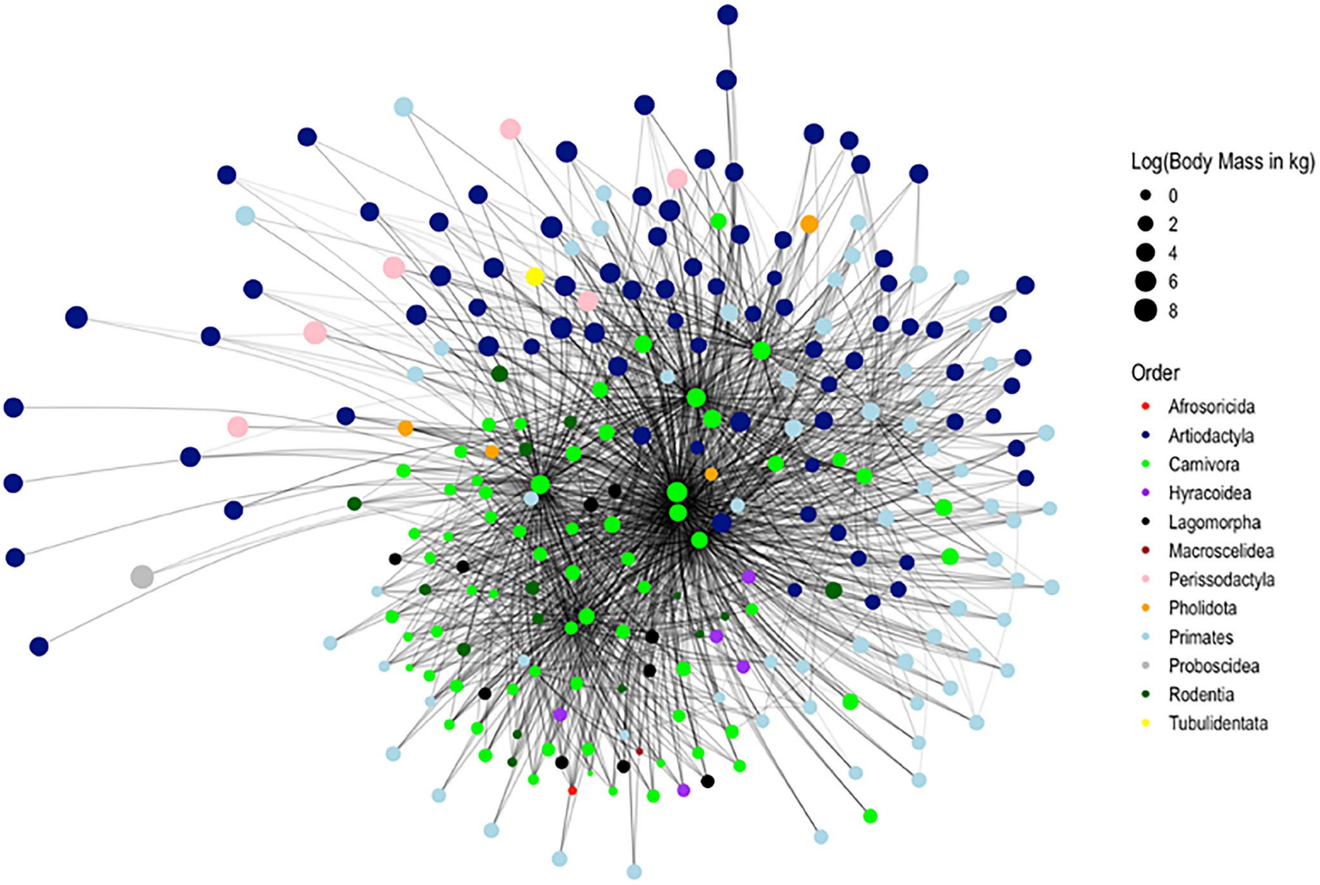

FIGURE 2 | Metaweb of predator–prey interactions among 258 African mammal species. Links include documented interactions between species as well as likely interactions based on known consumption of the prey genus or prey with similar body mass. Food webs for each African site (Figure 3) were subsampled from the metaweb using site-specific species occurrence data.

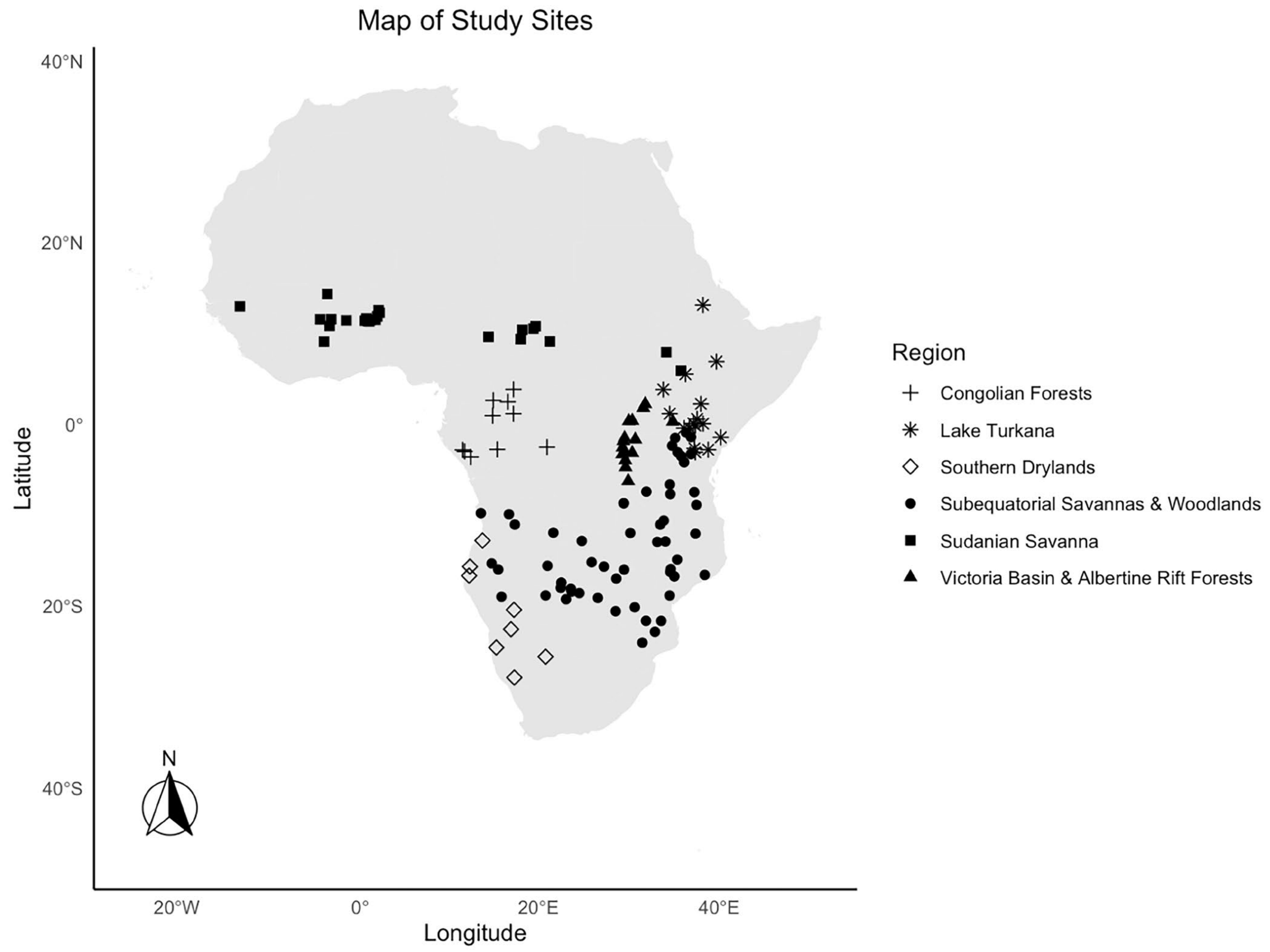

FIGURE 3 | Map of African mammal communities ($n=127$). Each of the six biogeographic regions is represented by a symbol that corresponds to the region names: Congolian Forests (CONGO, $n=10$), Victoria Basin & Albertine Rift Forests (VBAR, $n=15$), Lake Turkana (LAKET, $n=16$), Southern Drylands (DRY, $n=8$), Subequatorial Savannas & Woodlands (SVN, $n=54$) and Sudanian Savannas (SDSVN, $n=24$).

for conservation goals. Restricting analyses to protected areas facilitates clearer cross-site comparisons, as these sites operate under shared conservation objectives that render them comparable units. The mammal community data included non-volant species weighing ≥500 g, encompassing 258 species across 12 orders and 33 families.

2.2 | Food Web Construction

Limited data availability on the occurrence, strength, or frequency of realised local interactions precludes their use at large spatial scales. We used the metaweb approach to construct predator–prey interactions for the mammal community species composition data because it provides an alternative for constructing food webs in the absence of realised local interaction data. The metaweb represents a comprehensive interaction matrix that includes all species from all sites and their interactions (Pascual and Dunne 2006; Thuiller et al. 2024). Site-specific food webs are then subsampled from the metaweb for the species that occur at a site. This approach allows all local food webs to be created in the same manner and reduces issues arising from aggregating networks from different sources (Brimacombe et al. 2023), which is particularly important for quantifying differences among food webs due to environmental conditions (Pascual and Dunne 2006). Because the metaweb approach assumes that an interaction between two species occurs wherever the two species co-occur, it does not allow for spatial or temporal variation in interactions. It therefore describes the potential for interactions between species, which does not assume any impact on demography and cannot be used to model temporal dynamics (Thuiller et al. 2024). Nevertheless, at large spatial scales, metacommunity processes likely influence food web structure more than local dynamical selective processes (Saravia et al. 2022). Furthermore, investigating ecological networks at large spatial scales provides the opportunity to examine variation in ecosystem functioning (Windsor et al. 2023) and can provide frameworks for further theoretical work and empirical research at the local scale (Adhurya and Park 2025).

We combined predator–prey interactions from the *Mammals of Africa* (Kingdon et al. 2013) with published global predator–prey interaction data (Fricke et al. 2022) (Figure 2). Fully quantifying species interactions is challenging because species may be rare, interactions may be rare, or both (Fründ et al. 2016). Previous theoretical modelling of food web structure has demonstrated

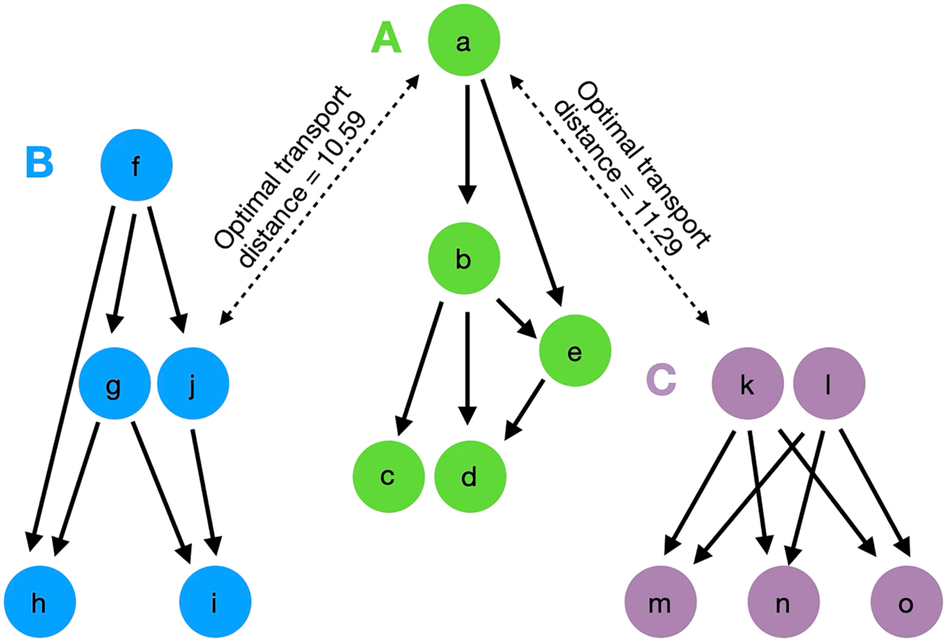

FIGURE 4 | Conceptual figure illustrating the use of optimal transport distances to compare food webs using toy networks. Food webs A, B and C each have five unique species, indicated by distinct letters (a–o). Each web has six predator–prey interaction links. Optimal transport distances measure the distance between two networks by identifying functionally equivalent species between networks using the predator–prey links within each network (Hung et al. 2026). The optimal transport distance between food webs A and B is smaller (10.59) than the optimal transport distance between food webs A and C (11.29), indicating a more similar network structure between food webs A and B than between A and C. Note that in A species b consumes species e, whereas in B species g does not consume species j. Additionally, in B, species f consumes species h whereas in A, species a does not consume species c. Food web C has fewer trophic levels than A or B. In food web C, species k and species l each consume species m, n and o.

that defining predator consumption as a continuous sequence of prey based on body size generates realistic food web structure (Stouffer et al. 2006, 2011; Williams and Martinez 2000). In terrestrial mammals, maximisation of energy gain likely constrains the body size of prey that predators consume (Carbone et al. 2007); both minimum and maximum prey body size increase with terrestrial carnivore body size (Tucker and Rogers 2014). Furthermore, predator and prey body sizes are used widely to predict food web structure (Brose et al. 2019; Gravel et al. 2013). We therefore supplemented previously documented predator–prey interactions with additional possible predator–prey interactions based on taxonomy and body size (Beaudrot et al. 2024) and constructed a binary (0/1) metaweb. Specifically, we classified a potential 'interaction' as occurring (i.e., '1') for each species pair in the metaweb when (1) the species had been documented as prey of the predator (337 links), (2) the species' genus but not the species itself had been documented as prey of the predator (407 links) and (3) the body size of the species was within the body mass range of the predator's documented prey (i.e., its body mass was between the minimum and maximum body mass of the documented prey species) (887 links) (Appendix S1). If none of these three criteria were met, we classified the prey species as not eaten by the predator species (i.e., '0').

2.3 | Similarity Among Sites in Food Web Structure

A common approach for comparing differences among multiple ecological communities is to measure differences between each pair of communities using a pairwise dissimilarity index. Numerous pairwise dissimilarity indices have been developed and applied to study differences among communities in taxonomic, functional and phylogenetic diversity (Graham and Fine 2008; Lengyel and Botta-Dukát 2023; Tuomisto 2010). The few existing ecological network dissimilarity methods are not suitable for comparing communities that lack shared species (Pellissier et al. 2018; Poisot 2022; Poisot et al. 2012), limiting the spatial extent of ecological network comparisons (Pellissier et al. 2018). To overcome these limitations, we harness recent methodological developments that use optimal transport distances (Peyré and Cuturi 2019; Villani 2009) for measuring dissimilarity in food web networks (Hung et al. 2026). By capturing the structure of entire food webs without requiring species identities, optimal transport distances preserve ecological information that is lost in traditional food web metrics and are well-suited for comparing the dissimilarity of ecological networks sharing few or no species (Hung et al. 2026).

Optimal transport distances identify functionally equivalent species between networks. Numerical optimization tools simultaneously provide as output a distance measure and a 'transport plan' for an 'optimal' matching between species pairs across each pair of networks. The 'optimal' transport plan best preserves the pairwise relationship between species across webs and therefore best preserves the functional role of species among food webs. Consequently, a shorter optimal transport distance between two food webs indicates greater structural similarity between their networks (Figure 4) (Hung et al. 2026).

To quantify pairwise differences among site-specific mammal food webs while accounting for species' dietary traits (e.g., consumption of invertebrates, plants, etc.), we used a network dissimilarity measure from optimal transport theory, specifically, a fused Gromov-Wasserstein distance (fGW) that improves the functional mapping between species pairs across networks by incorporating trait data (Hung et al. 2026). For each species, we included categorical diet data for consumption of vertebrates (0/1), invertebrates (0/1), mammals (including small mammals not in the food web; 0/1) and plants (0/1). We applied a Gower distance to the functional trait information. We then weighted network topology and functional trait distances equally within the fGW by setting the alpha hyper-parameter to 0.5 following an evaluation of the effect of alpha on fGW distances that demonstrated similar outputs for moderate values of alpha (Hung et al. 2026). We used the NetworkX (Hagberg et al. 2008) and POT (Flamary et al. 2021) packages in Python to create edge lists and calculated fused Gromov-Wasserstein distances between the most connected component of each pair of food webs.

Importantly, we log-transformed the food web distances prior to statistical analysis to remove the effect of species richness and connectance (Appendix S2). Only changes to network structure (i.e., nodes or links) or the functional similarity measure (e.g., Gower distance) affect fGW distances. Because optimal transport distances are not dependent on a particular unit of measurement and there is no direct ecological interpretation of the exact value of the distance, the log-transformation does not affect ecological interpretation. At last, we multiplied the distances by negative one to continue analysis with a similarity measure.

2.4 | Similarity Among Sites in Primary Productivity and Anthropogenic Fragmentation

We quantified similarity among sites in primary productivity, anthropogenic fragmentation and geographic proximity using distance-based pairwise measures. Primary productivity and land cover data were extracted using Google Earth Engine (GEE) (Gorelick et al. 2017) at a 500 m resolution for a 10 km buffer around the published geographic coordinates for each site. The use of a 10 km buffer was informed by a recent sensitivity analysis (Semper-Pascual et al. 2022), which evaluated the effects of landscape-scale fragmentation on mammal occupancy patterns and identified this distance as a key threshold for detecting mammal responses.

We quantified primary productivity using the Enhanced Vegetation Index (EVI), which more accurately captures productivity dynamics in densely vegetated regions—particularly tropical forests—compared to the Normalised Difference Vegetation Index (NDVI) (Vermote et al. 2016). For each site, we calculated the mean EVI from 1 January 2001 to 1 January 2020 (MODIS/061/MOD13A1) as a measure of long-term average productivity level. Because the mammal community composition data were collected at different times among sites (Rowan et al. 2020), we aggregated the primary productivity and fragmentation data to a coarser temporal scale. Variability in these data are presented in Appendix S3. We then measured primary productivity dissimilarity as pairwise Euclidean distances between sites for mean EVI. To convert values to a measure of similarity, we multiplied the Euclidian distances by negative one.

Due to natural differences in landscape composition and habitat mosaics among biomes, application of the same fragmentation metrics across biomes is challenging (Jacobson et al. 2019). To ensure consistency in the fragmentation measure among biomes, we defined fragmentation based on anthropogenic land use, which does not account for effects of fragmentation on food web structure from other forms of habitat fragmentation such as logging or fires. We quantified anthropogenic fragmentation similarity among sites using a binary classification for land cover data from MODIS/006/MCD12Q1 LC_Type1 (Friedl and Sulla-Menashe 2022) and calculated the mode for the land cover classification over the same time period as EVI. We designated built-up areas and cropland land cover as 'anthropogenic' land cover and other land cover types (excluding water) as 'other'. We then used the R package 'landscape metrics' to calculate an aggregation index (bounded by (0,1)) for the binary 'anthropogenic-other land use' classification using class level to measure anthropogenic patch configuration (Hesselbarth et al. 2019). Lower values indicate lower aggregation (i.e., more extensive fragmentation) whereas higher values indicate higher aggregation (i.e., lower fragmentation) (He et al. 2000; Neel et al. 2004). We converted to anthropogenic fragmentation similarity by multiplying the Euclidean pairwise distances of this index by negative one.

To quantify geographic proximity, we calculated the distance (in km) between each pair of sites based on their geographic coordinates using the functions 'st_as_sf' and 'st_distance' in the sf package (Pebesma and Bivand 2023), and multiplied the distances by negative one to create a measure of proximity. We scaled predictor variables before analysis and examined collinearity between primary productivity and anthropogenic fragmentation with Pearson's correlations.

2.5 | Statistical Analysis

We modelled food web similarity among sites as a function of primary productivity similarity and fragmentation similarity measured from remotely sensed data while accounting for underlying spatial structure using geographic proximity among sites. To test H1 and H2 at the continental scale, we analysed all food webs simultaneously. To test H2, H3 and H4 at the regional scale, we analysed food webs within biogeographic regions defined from One Earth classifications (Burkart 2023). Specifically, we used the realm and sub-realm designations to group sites with similar habitats within the same realm or sub-realm, resulting in 6 regions (Figure 3).

To test the relative importance of primary productivity and anthropogenic fragmentation, we conducted partial-Mantel tests, which are suited for the analysis of similarity matrices (Smouse et al. 1986). The partial Mantel test measures the correlation between the residuals of two similarity matrices (e.g., food web similarity and primary productivity similarity) after the linear regression of each on additional similarity matrices (e.g., anthropogenic fragmentation similarity, geographic proximity). Therefore, this approach allowed us to investigate the influence of each predictor variable on food web similarity after accounting for the other predictors. Geographic proximity simultaneously quantified the spatial structure of food web, primary productivity and fragmentation similarity. Primary productivity similarity

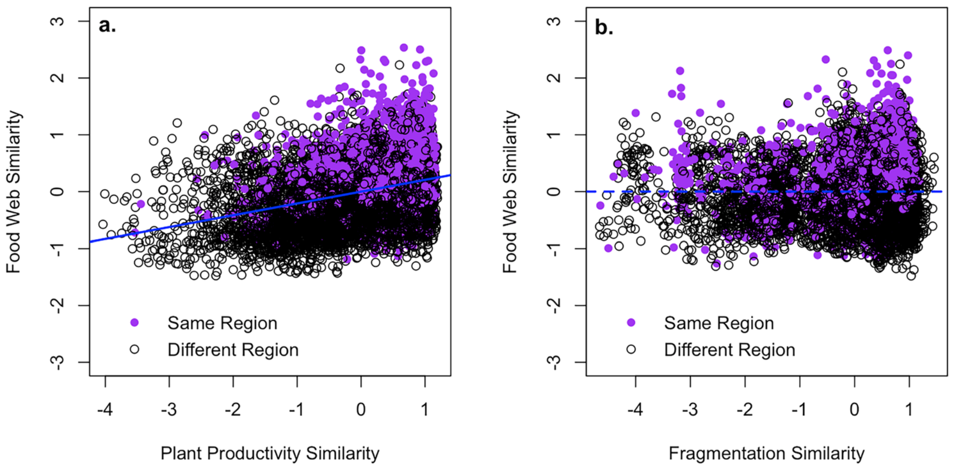

FIGURE 5 | Partial Mantel results for all African sites. Added variable plots of the partial relationship between (a) food web similarity and primary productivity similarity (i.e., residuals from having accounted for anthropogenic fragmentation similarity and geographic proximity) and (b) food web similarity and anthropogenic fragmentation similarity (i.e., residuals from having accounted for primary productivity similarity and geographic proximity). Each point represents the similarity between two sites. The blue lines show the partial Mantel correlations (*r*). The solid line indicates a significant relationship (a), and the dashed line indicates a non-significant relationship (b). Pair-wise comparisons of sites from the same region are shown with filled purple circles. Pairwise comparisons of sites from different regions are shown with open black circles.

quantified non-spatially structured primary productivity similarity, and fragmentation similarity quantified non-spatially structured fragmentation similarity. The partial Mantel correlation coefficients (*r*) provide the strength and directionality of the relationship between food web similarity and each predictor variable. Larger absolute *r* indicates a stronger relationship. We tested the relative roles of primary productivity and fragmentation on food web similarity at two spatial scales while controlling for the effects of geographic proximity: (1) all African sites and (2) sites within each biogeographic region. Specifically, we used the 'mantel' function from the ecodist package (Goslee and Urban 2007) with the Pearson method and 10,000 permutations. We also used the 'MRM' function from this package to calculate R^2 values. We report significance for results based on $\alpha = 0.05$. Analyses were conducted in R (v4.3.2; R Core Team 2023).

3 | Results

Throughout Africa, mammal food webs were significantly more similar at sites with more similar levels of primary productivity (partial Mantel test: $r = 0.32$, $p < 0.001$, $N = 127$ sites, $R^2 = 0.12$; Figure 5) independent of species richness (Appendix S2) and geographic proximity (Appendix S4). Among regions, mean productivity varied, yet the range in primary productivity overlapped (Figure 6a). In the Subequatorial Savannas & Woodlands region, mammal food webs were also significantly more similar at sites with more similar primary productivity ($r = 0.13$, $p = 0.039$, $R^2 = 0.04$; Figure 6b). Full partial Mantel test results can be found in Appendix S4.

In the tropical forests of the Congolian Forest region, food webs were significantly more similar where anthropogenic fragmentation was more similar ($r = 0.41$, $p = 0.009$, $R^2 = 0.43$, Figure 6b). Importantly, sites had little anthropogenic fragmentation overall (min = 0.16% of the 10 km buffer, 1st quartile = 0.18%, median = 0.25%, 3rd quartile = 1.56%, max = 13.2%, Appendix S5). Primary productivity and the anthropogenic fragmentation index values for all African sites were weakly correlated ($r = 0.05$). Correlations within each region are reported in Appendix S6.

4 | Discussion

We compared the network-level (i.e., global) structure of food webs in response to environmental and anthropogenic conditions by quantifying food web similarity from the structure of predator–prey interactions for the first time. Our goal was to identify the importance of primary productivity and anthropogenic landscape fragmentation for understanding food web similarity at macroecological scales. In support of the hypothesis that primary productivity is an important macroecological determinant of food web structure (H1), African mammal food webs at the continental scale were significantly more similar at sites where primary productivity levels were similar. Importantly, this relationship was independent of species richness and geographic proximity. In support of the hypothesis that anthropogenic fragmentation predictably disassembles food web structure (H2), we found that African mammal food webs within the tropical rainforests of the Congolian region were significantly more similar at sites where anthropogenic fragmentation levels were more similar. The extent to which similarity in plant productivity predicted similarity in food web structure varied among regions. We did not find support for the hypothesis that bottom-up effects primarily determine food web structure (H3) or the hypothesis that resource complementarity among multi-trophic consumers enhances primary productivity (H4). Instead, we found that similarity in plant productivity most strongly predicted food web similarity in regions with intermediate productivity.

4.1 | Primary Productivity

Despite the links between primary productivity and trophic interactions, the correlation between primary productivity similarity

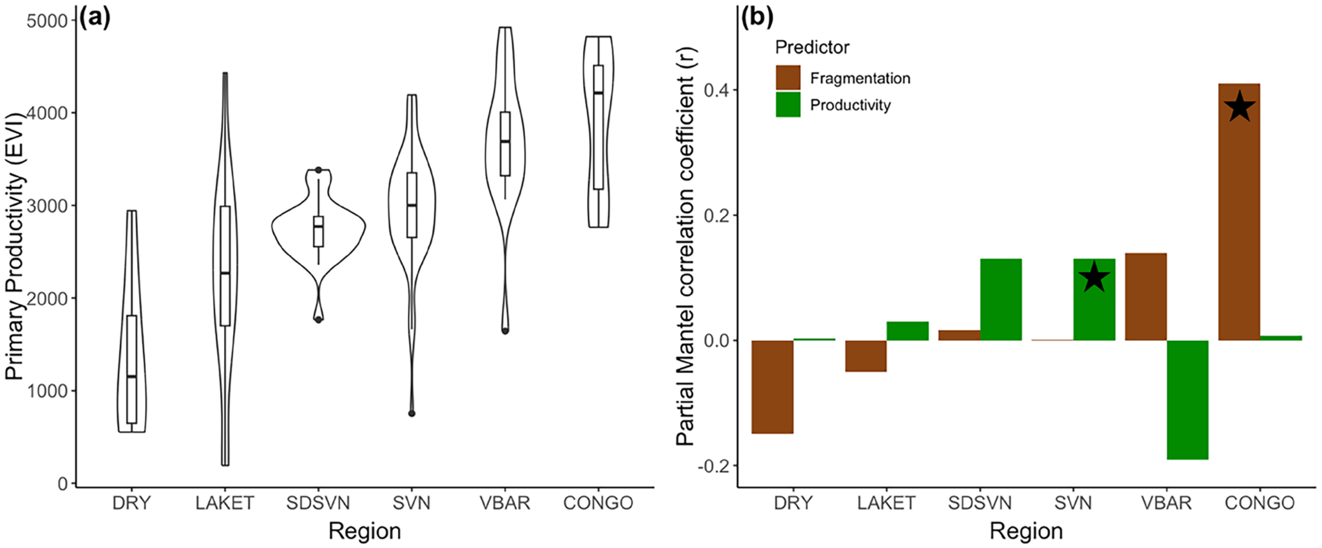

FIGURE 6 | Regional variation in plant productivity and partial Mantel results. (a) Primary productivity (EVI) within regions, sorted by increasing mean productivity. (b) Barplots of the partial Mantel correlation coefficients (*r*) illustrate the relative effects of primary productivity and anthropogenic landscape fragmentation on food web similarity within and among African regions while controlling for spatial autocorrelation. Regions correspond with Figure 3: Southern Drylands (DRY), Lake Turkana (LAKET), Sudanian Savanna (SDSVN), Subequatorial Savannas and Woodlands (SVN) and Victoria Basin & Albertine Rift Forests (VBAR), Congolian Forests (CONGO). Significance denoted with *$p < 0.05$.

and overall food web structure has not previously been measured at the continental scale. We found that similarity in primary productivity significantly predicted African mammal food web similarity. Notably, our analysis circumvented previous analytical limitations because we compared food webs constructed from a single approach (Brimacombe et al. 2023) and accounted for the inherent scale dependency of food web metrics with species richness and connectance (Dunne et al. 2008; Pascual and Dunne 2006; Riede et al. 2010; Vermaat et al. 2009). Consequently, our results quantified the strength of the association solely between similarity in primary productivity and predator–prey interaction structure while accounting for spatial autocorrelation. Furthermore, the observed association was independent of species identities, indicating that it was not influenced by taxonomic or phylogenetic similarities among mammal communities. Although previous approaches have measured the structural equivalence of components within food webs (e.g., motifs) (Cirtwill et al. 2018), our approach quantified structural equivalence of entire food webs (Hung et al. 2026). We therefore provided an empirical test of the relationship between food web similarity and plant productivity that can inform the study of biodiversity and ecosystem function mediated by food web structure.

Within regions, the extent to which primary productivity predicted food similarity varied. In contrast with our expectations, primary productivity most strongly predicted food web similarity in regions with intermediate productivity, and significantly so in the Subequatorial Savannas & Woodlands region. Differences in the strength of the association among regions may be due to geographical variation in the role of top-down consumer control on vegetation. For example, a meta-analysis of experimental studies found that top-down control varied geographically and based on ecosystem type (Marino et al. 2018). Differences in primary productivity among African regions may alter constraints on mammal food web structure that influence geographical variation in top-down control.

4.2 | Fragmentation

Evidence of large-scale human impacts on food webs has begun to emerge. For example, at the global scale, the nestedness of scavenger food web networks declines as the human footprint increases (Sebastián-González et al. 2020). At the continental scale, land use intensity has negatively affected components of European tetrapod food webs such as proportions of basal species and apex predators (Botella et al. 2024). And within Amazonian forests, terrestrial food web complexity decays with habitat loss (Pires et al. 2023).

In our results, anthropogenic fragmentation emerged as a significant predictor exclusively for tropical rainforest mammal food webs. This occurred despite the Congolian Forest region having less fragmentation than most regions, and despite the demonstrated effectiveness of tropical forest protected areas in limiting fragmentation (Zou et al. 2025). Specifically, mammal food webs within the Congolian Forest region were significantly more similar where anthropogenic fragmentation was more similar. Because the food web similarity measure maps functionally equivalent species between networks, this result indicates that two food webs facing similar fragmentation consist of species with more similar functional roles than two food webs facing different degrees of fragmentation. The measure is sensitive to both species loss and the loss of interactions. As such, anthropogenic fragmentation may predictably disassemble mammal food webs (H2) within tropical forest protected areas by affecting not only species composition but also the functional roles associated with lost interactions. These potential impacts of fragmentation on mammal food web structure are consistent with growing evidence for widespread anthropogenic impacts on mammal communities within tropical forest protected areas (Gorczynski et al. 2021, 2022; Greco et al. 2025; Semper-Pascual et al. 2022).

While differences in fragmentation may not have affected African mammal food webs outside of the Congolian Forest region, the absence of other evidence may be due to measurements of anthropogenic fragmentation or food web similarity. For example, the anthropogenic fragmentation index measured from agricultural and built-up land use may not have sufficiently captured habitat fragmentation in all regions. Despite large increases in human pressure on Afrotropical protected areas over the past several decades, particularly from agricultural expansion (Geldmann et al. 2019), anthropogenic fragmentation was low overall. Anthropogenic fragmentation did not capture other aspects of human pressure that likely impact mammal food webs such as poaching intensity (Brodie et al. 2021). In addition, due to limits in data availability, food webs were defined using species presence rather than abundance. Hence, the impacts of anthropogenic fragmentation on abundance declines, which precede local extinctions, were not measurable. Although sites within the Victoria Basin Albertine Rift Forests are embedded within one of the most densely populated regions of Africa (Central Intelligence Agency 2022), most other sites were located outside of human density hotspots. Extensive species losses may not have occurred. Nevertheless, empirical evidence has demonstrated extinction debt for both species and species interactions in fragmented landscapes (Haddad et al. 2015; Kuussaari et al. 2009; Santos et al. 2025). Time-lagged extinction debt may impact African mammal food webs within protected areas in the years to come.

4.3 | Additional Factors

Beyond primary productivity and anthropogenic fragmentation, additional contemporary and historical factors have likely influenced the structure of African mammal food webs. Species losses from other human impacts may have affected mammal food web similarity (Tuyisingize et al. 2025). Climatic conditions since the Last Glacial Maximum 22,000 years ago shaped the functional and phylogenetic structure of contemporary African mammal communities variably among taxa and trophic levels (Rowan et al. 2016), illustrating legacies of historical climate on contemporary communities that have likely influenced food web structure. Over the past 125,000 years, extinctions and range contractions of African mammal species that decreased food web complexity varied spatially (Fricke et al. 2022). Furthermore, evolutionary history over geologic time has influenced community composition and, therefore, likely influenced food web structure. Integrated assessments of the macroecological and macroevolutionary processes that have shaped contemporary food webs are needed.

Our study provides a new perspective on the macroecology of trophic interactions centered on predator–prey interactions among mammals. Like almost all multi-trophic studies, ours relies on a subset of interactions among organisms (Seibold et al. 2018). Further research would benefit from the incorporation of more taxa, site-specific species interactions, and temporal variability in species interactions, which are inherently difficult data to collect over large spatial scales (Thuiller et al. 2024). Despite the protocols used to curate the mammal composition data (Rowan et al. 2020), variation in sampling effort or species detectability may have affected the food webs. The most likely consequence would be the absence of rare or elusive species from local webs or potentially the meta-web itself. Because communities with higher richness have more rare species, species-rich communities would be more likely to have undetected species. Simulated species removal demonstrated that the fGW is less impacted by species removal from communities with higher richness than lower richness, which would reduce the effects of species missing from species-rich communities (Hung et al. 2026). Although our study did not assess ecological dynamics, the use of mean productivity and fragmentation values over 20 years could have obscured ecologically relevant dynamics from shifts in plant productivity or land use. Finally, our results may have been affected by difficulties in measuring how primary productivity translates to resources in different environments (Lu et al. 2025; Mendoza and Araújo 2019). For example, net primary productivity estimated from remotely sensed data only partially captures seed productivity from trees, and this discrepancy increases with temperature globally. As a consequence, primary productivity most poorly predicts tropical forest seed production (Journé et al. 2022), yet tropical forests support the highest frugivorous mammal species richness (Losada et al. 2024). Thus, food web structure may be more strongly associated with seed productivity in tropical forests than other environments.

5 | Conclusions

We have demonstrated for the first time that primary productivity similarity predicts food web similarity at the continental scale, and the relationship between productivity similarity and food web similarity varies geographically. Furthermore, we documented a significant link between food web similarity and anthropogenic fragmentation in tropical rainforests that is consistent with fragmentation predictably disassembling mammal food webs. Africa is projected to have the highest human population growth worldwide in the coming decades (United Nations Department of Economic and Social Affairs, Population Division 2024). The species richness of mammal communities within tropical forest protected areas decreases by 1% with each increase of 16 people per km^2 (Greco et al. 2025), suggesting widespread species losses of protected mammals will occur with ongoing human population growth. Furthermore, extensive land use change is expected to accompany Africa's rapid human population growth. Global projections of terrestrial vertebrate food web change in face of land use change are stark (Hao et al. 2025). Our results are consistent with the interpretation that fragmentation may already impact mammal food web structure within tropical forest protected areas and suggest that the integration of network analysis into conservation assessments may benefit decision-making (Dansereau et al. 2025). The diverse and important functional roles that mammals perform (Lacher et al. 2019) are critical to the conservation of biodiversity and ecosystem functioning.

Author Contributions

A.E.F. study design, analysis, data gathering and manuscript writing. C.A.U. Study design, analysis, funding and advising. K.M.H. study design and analysis. C.H. study design and analysis. M.A.W. study design and analysis. M.A.M. analysis and advising. L.B. conceptualization, study design, funding, writing and advising.

Acknowledgements

The authors thank Ava Johnson, Zachary Katz, María José Guerrero, Yifan Xu and Mallory Tucker for assisting in food web data collection and organisation (A.J. and M.T.), code for analysis (Z.K., M.J.G. and Y.X.) and troubleshooting (M.J.G. and Y.X.). This project was funded by NSF DEB 2213568 and NSF CCF 2443064.

Data Availability Statement

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.zkh1893nh.

References

Adhurya, S., and Y.-S. Park. 2025. "Metaweb Approaches for Understanding Complex Ecological Interactions: A Review." *Ecological Informatics* 91: 103367.

Albert, G., B. Gauzens, M. Loreau, S. Wang, and U. Brose. 2022. "The Hidden Role of Multi-Trophic Interactions in Driving Diversity–Productivity Relationships." *Ecology Letters* 25: 405–415.

Amyntas, A., E. Berti, B. Gauzens, et al. 2023. "Niche Complementarity Among Plants and Animals Can Alter the Biodiversity–Ecosystem Functioning Relationship." *Functional Ecology* 37: 2652–2665.

Baiser, B., D. Gravel, A. R. Cirtwill, et al. 2019. "Ecogeographical Rules and the Macroecology of Food Webs." *Global Ecology and Biogeography* 28: 1204–1218.

Barnosky, A. D., C. J. Bell, S. D. Emslie, et al. 2004. "Exceptional Record of Mid-Pleistocene Vertebrates Helps Differentiate Climatic From Anthropogenic Ecosystem Perturbations." *Proceedings of the National Academy of Sciences of the United States of America* 101: 9297–9302.

Beaudrot, L., M. A. Acevedo, D. Gorczynski, and N. C. Harris. 2024. "Geographic Differences in Body Size Distributions Underlie Food Web Connectance of Tropical Forest Mammals." *Scientific Reports* 14: 6965.

Botella, C., P. Gaüzère, L. O'Connor, et al. 2024. "Land-Use Intensity Influences European Tetrapod Food Webs." *Global Change Biology* 30: e17167.

Braga, J., L. J. Pollock, C. Barros, et al. 2019. "Spatial Analyses of Multi-Trophic Terrestrial Vertebrate Assemblages in Europe." *Global Ecology and Biogeography* 28: 1636–1648.

Brimacombe, C., K. Bodner, M. Michalska-Smith, T. Poisot, and M.-J. Fortin. 2023. "Shortcomings of Reusing Species Interaction Networks Created by Different Sets of Researchers." *PLoS Biology* 21: e3002068.

Brodie, J. F., S. Williams, and B. Garner. 2021. "The Decline of Mammal Functional and Evolutionary Diversity Worldwide." *Proceedings of the National Academy of Sciences of the United States of America* 118: e1921849118.

Brose, U., P. Archambault, A. D. Barnes, et al. 2019. "Predator Traits Determine Food-Web Architecture Across Ecosystems." *Nature Ecology & Evolution* 3: 919–927.

Burkart, K. 2023. "One Earth Bioregions Framework."

Carbone, C., A. Teacher, and J. M. Rowcliffe. 2007. "The Costs of Carnivory." *PLoS Biology* 5: e22.

Cardillo, M., A. Skeels, and R. Dinnage. 2023. "Priorities for Conserving the World's Terrestrial Mammals Based on Over-the-Horizon Extinction Risk." *Current Biology* 33: 1381–1388.e6.

Central Intelligence Agency. 2022. "Africa: Population Density."

Cirtwill, A. R., G. V. Dalla Riva, M. P. Gaiarsa, et al. 2018. "A Review of Species Role Concepts in Food Webs." *Food Webs* 16: e00093.

Dansereau, G., J. Braga, G. F. Ficetola, et al. 2025. "Overcoming the Disconnect Between Species Interaction Networks and Biodiversity Conservation." *Trends in Ecology & Evolution* 40: 840–851.

Daskalova, G. N., I. H. Myers-Smith, A. D. Bjorkman, et al. 2020. "Landscape-Scale Forest Loss as a Catalyst of Population and Biodiversity Change." *Science* 368: 1341–1347.

Dunne, J. A., R. J. Williams, N. D. Martinez, R. A. Wood, and D. H. Erwin. 2008. "Compilation and Network Analyses of Cambrian Food Webs." *PLoS Biology* 6: e102.

Elton, C. S. 1927. *Animal Ecology*. Macmillan.

Estes, J. A., J. Terborgh, J. S. Brashares, et al. 2011. "Trophic Downgrading of Planet Earth." *Science* 333: 301–306.

Faurby, S., and J.-C. Svenning. 2015. "Historic and Prehistoric Human-Driven Extinctions Have Reshaped Global Mammal Diversity Patterns." *Diversity and Distributions* 21: 1155–1166.

Flamary, R., N. Courty, A. Gramfort, et al. 2021. "POT: Python Optimal Transport." *Journal of Machine Learning Research* 22: 1–8.

Fricke, E. C., C. Hsieh, O. Middleton, et al. 2022. "Collapse of Terrestrial Mammal Food Webs Since the Late Pleistocene." *Science* 377: 1008–1011.

Friedl, M., and D. Sulla-Menashe. 2022. "MODIS/Terra+ Aqua Land Cover Type Yearly L3 Global 500m SIN Grid V061."

Fründ, J., K. S. McCann, and N. M. Williams. 2016. "Sampling Bias Is a Challenge for Quantifying Specialization and Network Structure: Lessons From a Quantitative Niche Model." *Oikos* 125: 502–513.

Geldmann, J., A. Manica, N. D. Burgess, L. Coad, and A. Balmford. 2019. "A Global-Level Assessment of the Effectiveness of Protected Areas at Resisting Anthropogenic Pressures." *Proceedings of the National Academy of Sciences* 116: 23209–23215.

Gonçalves-Souza, T., J. M. Chase, N. M. Haddad, et al. 2025. "Species Turnover Does Not Rescue Biodiversity in Fragmented Landscapes." *Nature* 640: 702–706.

Gorczynski, D., C. Hsieh, J. Ahumada, et al. 2022. "Human Density Modulates Spatial Associations Among Tropical Forest Terrestrial Mammal Species." *Global Change Biology* 28: 7205–7216.

Gorczynski, D., C. Hsieh, J. T. Luciano, et al. 2021. "Tropical Mammal Functional Diversity Increases With Productivity but Decreases With Anthropogenic Disturbance." *Proceedings of the Royal Society B: Biological Sciences* 288: 20202098.

Gorelick, N., M. Hancher, M. Dixon, S. Ilyushchenko, D. Thau, and R. Moore. 2017. "Google Earth Engine: Planetary-Scale Geospatial Analysis for Everyone." *Remote Sensing of Environment* 202: 18–27.

Goslee, S. C., and D. L. Urban. 2007. "The Ecodist Package for Dissimilarity-Based Analysis of Ecological Data." *Journal of Statistical Software* 22: 1–19.

Graham, C. H., and P. V. A. Fine. 2008. "Phylogenetic Beta Diversity: Linking Ecological and Evolutionary Processes Across Space in Time." *Ecology Letters* 11: 1265–1277.

Gravel, D., T. Poisot, C. Albouy, L. Velez, and D. Mouillot. 2013. "Inferring Food Web Structure From Predator–Prey Body Size Relationships." *Methods in Ecology and Evolution* 4: 1083–1090.

Greco, I., L. Beaudrot, C. Sutherland, et al. 2025. "Landscape-Level Human Disturbance Results in Loss and Contraction of Mammalian Populations in Tropical Forests." *PLoS Biology* 23: e3002976.

Guimarães, P. R. 2020. "The Structure of Ecological Networks Across Levels of Organization." *Annual Review of Ecology, Evolution, and Systematics* 51: 433–460.

Haddad, N. M., L. A. Brudvig, J. Clobert, et al. 2015. "Habitat Fragmentation and Its Lasting Impact on Earth's Ecosystems." *Science Advances* 1: e1500052.

Hagberg, A. A., D. A. Schult, and P. J. Swart. 2008. “Exploring Network Structure, Dynamics, and Function Using NetworkX.” In *Proceedings of the 7th Python in Science Conference*, edited by G. Varoquaux, T. Vaught, and J. Millman, 11–15. Los Alamos National Laboratory (LANL).

Hagen, M., W. D. Kissling, C. Rasmussen, et al. 2012. “2—Biodiversity, Species Interactions and Ecological Networks in a Fragmented World.” In *Advances in Ecological Research, Global Change in Multispecies Systems Part 1*, edited by U. Jacob and G. Woodward, 89–210. Academic Press.

Hao, X., M. Holyoak, Z. Zhang, and C. Yan. 2025. “Global Projection of Terrestrial Vertebrate Food Webs Under Future Climate and Land-Use Changes.” *Global Change Biology* 31: e70061.

He, H. S., B. E. DeZonia, and D. J. Mladenoff. 2000. “An Aggregation Index (AI) to Quantify Spatial Patterns of Landscapes.” *Landscape Ecology* 15: 591–601.

Hesselbarth, M. H. K., M. Sciaini, K. A. With, K. Wiegand, and J. Nowosad. 2019. “Landscapemetrics: An Open-Source R Tool to Calculate Landscape Metrics.” *Ecography* 42: 1648–1657.

Hung, K. M., L. Beaudrot, A. E. Finneran, A. G. Zalles, and C. A. Uribe. 2026. “Quantifying Functionally Equivalent Species and Ecological Network Dissimilarity With Optimal Transport Distances.” *Methods in Ecology and Evolution* 17, no. 2: 301–321. https://doi.org/10.1111/2041-210x.70130.

Hutchinson, G. E. 1959. “Homage to Santa Rosalia or Why Are There So Many Kinds of Animals?” *American Naturalist* 93: 145–159.

Jacobson, A. P., J. Riggio, A. M. Tait, and J. E. M. Baillie. 2019. “Global Areas of Low Human Impact (‘Low Impact Areas’) and Fragmentation of the Natural World.” *Scientific Reports* 9: 14179.

Jetz, W., H. Kreft, G. Ceballos, and J. Mutke. 2009. “Global Associations Between Terrestrial Producer and Vertebrate Consumer Diversity.” *Proceedings of the Royal Society B* 276: 269–278.

Jones, K. R., O. Venter, R. A. Fuller, et al. 2018. “One-Third of Global Protected Land Is Under Intense Human Pressure.” *Science* 360: 788–791.

Journé, V., R. Andrus, M. Aravena, et al. 2022. “Globally, Tree Fecundity Exceeds Productivity Gradients.” *Ecology Letters* 25: 1471–1482.

Kingdon, J., D. Happold, T. Butynski, M. Hoffmann, M. Happold, and J. Kalina. 2013. *Mammals of Africa*. Bloomsbury Publishing.

Kuussaari, M., R. Bommarco, R. K. Heikkinen, et al. 2009. “Extinction Debt: A Challenge for Biodiversity Conservation.” *Trends in Ecology & Evolution* 24: 564–571.

Lacher, T. E., Jr., A. D. Davidson, T. H. Fleming, et al. 2019. “The Functional Roles of Mammals in Ecosystems.” *Journal of Mammalogy* 100: 942–964.

Lengyel, A., and Z. Botta-Dukát. 2023. “A Guide to Between-Community Functional Dissimilarity Measures.” *Ecography* 2023: e06718.

Loreau, M. 2010. “Linking Biodiversity and Ecosystems: Towards a Unifying Ecological Theory.” *Philosophical Transactions of the Royal Society B* 365: 49–60.

Losada, M., M. Suárez-Couselo, and M. Sobral. 2024. “Geographic Distribution of Mammal Diets.” *Web Ecology* 24: 71–79.

Lu, X., C. Chung, Y. Malhi, and C. Huang. 2025. “Global Patterns in the Allocation of Forest Net Primary Production.” *Journal of Biogeography* 52: jbi.15094.

Marino, N. D. A. C., G. Q. Romero, and V. F. Farjalla. 2018. “Geographical and Experimental Contexts Modulate the Effect of Warming on Top-Down Control: A Meta-Analysis.” *Ecology Letters* 21: 455–466.

Mendoza, M., and M. B. Araújo. 2019. “Climate Shapes Mammal Community Trophic Structures and Humans Simplify Them.” *Nature Communications* 10: 5197.

Neel, M. C., K. McGarigal, and S. A. Cushman. 2004. “Behavior of Class-Level Landscape Metrics Across Gradients of Class Aggregation and Area.” *Landscape Ecology* 19: 435–455.

O'Connor, L. M. J., F. Cosentino, M. B. J. Harfoot, et al. 2024. “Vulnerability of Terrestrial Vertebrate Food Webs to Anthropogenic Threats in Europe.” *Global Change Biology* 30: e17253.

Olson, D. M., E. Dinerstein, E. D. Wikramanayake, et al. 2001. “Terrestrial Ecoregions of the World: A New Map of Life on Earth: A New Global Map of Terrestrial Ecoregions Provides an Innovative Tool for Conserving Biodiversity.” *Bioscience* 51: 933–938.

Pascual, M., and J. Dunne. 2006. *Ecological Networks: Linking Structure to Dynamics in Food Webs*. Oxford University Press.

Pebesma, E., and R. Bivand. 2023. *Spatial Data Science: With Applications in R*. Chapman and Hall/CRC.

Pellissier, L., C. Albouy, J. Bascompte, et al. 2018. “Comparing Species Interaction Networks Along Environmental Gradients.” *Biological Reviews* 93: 785–800.

Peyré, G., and M. Cuturi. 2019. “Computational Optimal Transport: With Applications to Data Science.” *Foundations and Trends in Machine Learning* 11: 355–607.

Pimm, S. L. 1982. “Food Webs.” In *Food Webs*, edited by S. L. Pimm, 1–11. Springer Netherlands.

Pires, M. M., M. Benchimol, L. R. Cruz, and C. A. Peres. 2023. “Terrestrial Food Web Complexity in Amazonian Forests Decays With Habitat Loss.” *Current Biology* 33: 389–396.e3.

Poisot, T. 2022. “Dissimilarity of Species Interaction Networks: Quantifying the Effect of Turnover and Rewiring.” *Peer Community Journal* 2: e35.

Poisot, T., E. Canard, D. Mouillot, N. Mouquet, and D. Gravel. 2012. “The Dissimilarity of Species Interaction Networks.” *Ecology Letters* 15: 1353–1361.

Polis, G. A., and D. R. Strong. 1996. “Food Web Complexity and Community Dynamics.” *American Naturalist* 147: 813–846.

Post, D. M. 2002. “The Long and Short of Food-Chain Length.” *Trends in Ecology & Evolution* 17: 269–277.

R Core Team. 2023. *R: A Language and Environment for Statistical Computing (Manual)*. R Foundation for Statistical Computing.

Riede, J. O., B. C. Rall, C. Banasek-Richter, et al. 2010. “Scaling of Food-Web Properties With Diversity and Complexity Across Ecosystems.” In *Advances in Ecological Research*, 139–170. Elsevier.

Ripple, W. J., J. A. Estes, R. L. Beschta, et al. 2014. “Status and Ecological Effects of the World's Largest Carnivores.” *Science* 343: 1241484.

Rooney, N., and K. S. McCann. 2012. “Integrating Food Web Diversity, Structure and Stability.” *Trends in Ecology & Evolution* 27: 40–46.

Rowan, J., L. Beaudrot, J. Franklin, et al. 2020. “Geographically Divergent Evolutionary and Ecological Legacies Shape Mammal Biodiversity in the Global Tropics and Subtropics.” *Proceedings of the National Academy of Sciences* 117: 1559–1565.

Rowan, J., J. M. Kamilar, L. Beaudrot, and K. E. Reed. 2016. “Strong Influence of Palaeoclimate on the Structure of Modern African Mammal Communities.” *Proceedings of the Royal Society B* 283: 20161207.

Ryser, R., J. Häussler, M. Stark, U. Brose, B. C. Rall, and C. Guill. 2019. “The Biggest Losers: Habitat Isolation Deconstructs Complex Food Webs From Top to Bottom.” *Proceedings of the Royal Society B: Biological Sciences* 286: 20191177.

Santos, M., D. P. Vázquez, and J. Resasco. 2025. "Extinction Debt of Species and Ecological Interactions in a Fragmented Landscape." *Proceedings of the Royal Society B* 292: 20251640.

Saravia, L. A., T. I. Marina, N. P. Kristensen, M. De Troch, and F. R. Momo. 2022. "Ecological Network Assembly: How the Regional Metaweb Influences Local Food Webs." *Journal of Animal Ecology* 91: 630–642.

Schneider, F. D., U. Brose, B. C. Rall, and C. Guill. 2016. "Animal Diversity and Ecosystem Functioning in Dynamic Food Webs." *Nature Communications* 7: 12718.

Sebastián-González, E., Z. Morales-Reyes, F. Botella, et al. 2020. "Network Structure of Vertebrate Scavenger Assemblages at the Global Scale: Drivers and Ecosystem Functioning Implications." *Ecography* 43: 1143–1155.

Seibold, S., M. W. Cadotte, J. S. MacIvor, S. Thorn, and J. Müller. 2018. "The Necessity of Multitrophic Approaches in Community Ecology." *Trends in Ecology & Evolution* 33: 754–764.

Semper-Pascual, A., R. Bischof, C. Milleret, et al. 2022. "Occupancy Winners in Tropical Protected Forests: A Pantropical Analysis." *Proceedings of the Royal Society B: Biological Sciences* 289: 20220457.

Smouse, P. E., J. C. Long, and R. R. Sokal. 1986. "Multiple Regression and Correlation Extensions of the Mantel Test of Matrix Correspondence." *Systematic Zoology* 35: 627–632.

Stouffer, D. B., J. Camacho, and L. A. N. Amaral. 2006. "A Robust Measure of Food Web Intervality." *Proceedings of the National Academy of Sciences of the United States of America* 103: 19015–19020.

Stouffer, D. B., E. L. Rezende, and L. A. N. Amaral. 2011. "The Role of Body Mass in Diet Contiguity and Food-Web Structure: Body Mass and Food-Web Structure." *Journal of Animal Ecology* 80: 632–639.

Terborgh, J., L. Lopez, P. Nuñez, et al. 2001. "Ecological Meltdown in Predator-Free Forest Fragments." *Science* 294: 1923–1926.

Thébault, E., and M. Loreau. 2003. "Food-Web Constraints on Biodiversity–Ecosystem Functioning Relationships." *Proceedings of the National Academy of Sciences of the United States of America* 100: 14949–14954.

Thuiller, W., I. Calderón-Sanou, L. Chalmandrier, et al. 2024. "Navigating the Integration of Biotic Interactions in Biogeography." *Journal of Biogeography* 51: 550–559.

Tucker, M. A., and T. L. Rogers. 2014. "Examining the Prey Mass of Terrestrial and Aquatic Carnivorous Mammals: Minimum, Maximum and Range." *PLoS One* 9: e106402.

Tuomisto, H. 2010. "A Diversity of Beta Diversities: Straightening Up a Concept Gone Awry. Part 2. Quantifying Beta Diversity and Related Phenomena." *Ecography* 33: 23–45.

Tuyisingize, D., L. Kulik, D. Assou, et al. 2025. "Complex Variation in Afrotropical Mammal Communities With Human Impact." *Ecology and Evolution* 15: e71331.

United Nations Department of Economic and Social Affairs, Population Division. 2024. "World Population Prospects 2024: Summary of Results."

Vermaat, J. E., J. A. Dunne, and A. J. Gilbert. 2009. "Major Dimensions in Food-Web Structure Properties." *Ecology* 90: 278–282.

Vermote, E., C. Justice, M. Claverie, and B. Franch. 2016. "Preliminary Analysis of the Performance of the Landsat 8/OLI Land Surface Reflectance Product." *Remote Sensing of Environment* 185: 46–56.

Villani, C. 2009. *Optimal Transport: Old and New*. Springer.

Wang, S., and U. Brose. 2018. "Biodiversity and Ecosystem Functioning in Food Webs: The Vertical Diversity Hypothesis." *Ecology Letters* 21: 9–20.

Ward, C. L., and K. S. McCann. 2017. "A Mechanistic Theory for Aquatic Food Chain Length." *Nature Communications* 8: 2028.

Whittaker, R. H. 1970. *Communities and Ecosystems*. Macmillan.

Williams, R. J., and N. D. Martinez. 2000. "Simple Rules Yield Complex Food Webs." *Nature* 404: 180–183.

Windsor, F. M., J. Van Den Hoogen, T. W. Crowther, and D. M. Evans. 2023. "Using Ecological Networks to Answer Questions in Global Biogeography and Ecology." *Journal of Biogeography* 50: 57–69.

Wojdak, J. M. 2005. "Relative Strength of Top-Down, Bottom-Up, and Consumer Species Richness Effects on Pond Ecosystems." *Ecological Monographs* 75: 489–504.

Young, H. S., D. J. McCauley, R. B. Dunbar, M. S. Hutson, A. M. Ter-Kuile, and R. Dirzo. 2013. "The Roles of Productivity and Ecosystem Size in Determining Food Chain Length in Tropical Terrestrial Ecosystems." *Ecology* 94: 692–701.

Zou, Y., T. W. Crowther, G. R. Smith, et al. 2025. "Fragmentation Increased in Over Half of Global Forests From 2000 to 2020." *Science* 389: 1151–1156.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Summary of documented and likely predator–prey interactions for the metaweb based on genus and body mass, (A) overall metaweb links belonging to each definition. (B) Metaweb link information by Order of the Prey. (C) Metaweb link information by Order of the Predator. **Appendix S2:** Log transformation of fused Gromov-Wasserstein distances (fGW). **Appendix S3:** Standard deviations (SD) and mean of primary productivity and fragmentation over time. **Appendix S4:** Partial-Mantel test results for the fused Gromov-Wasserstein distance. **Appendix S5:** Anthropogenic landscape fragmentation within and among biogeographic regions, sorted by increasing mean value. **Appendix S6:** Pearson correlations between the two predictor variables in each region.