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The Untapped Potential of Food Webs in Systematic Conservation Planning

Louise M. J. O'Connor[1,2] | Wilfried Thuiller[1] | Ulrich Brose[3,4] | Éléonore Chenevois[1] | Carla Freund[2] |
Benoit Gauzens[3,4] | Pierre Gaüzere[1] | Catherine Graham[5] | Michael Harfoot[6] | Myriam R. Hirt[3,4] |
Sébastien Lavergne[1] | Luigi Maiorano[7] | Atte Moilanen[8,9] | Peter H. Verburg[5,10] | Piero Visconti[2] | Laura J. Pollock[11]

[1]Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, LECA, Laboratoire d'Écologie Alpine, Saint-Martin-d'Heres, France | [2]Biodiversity, Ecology and Conservation Group, International Institute for Applied Systems Analysis, Laxenburg, Austria | [3]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany | [4]Institute of Biodiversity, Friedrich Schiller University Jena, Jena, Germany | [5]Swiss Federal Research Institute WSL, Birmensdorf, Switzerland | [6]UN Environment Programme World Conservation Monitoring Centre (UNEP-WCMC), Cambridge, UK | [7]Department of Biology and Biotechnologies "Charles Darwin", University of Rome "La Sapienza", Rome, Italy | [8]Finnish Natural History Museum, University of Helsinki, Helsinki, Finland | [9]Department of Geosciences and Geography, University of Helsinki, Helsinki, Finland | [10]Environmental Geography Group, Institute for Environmental Studies, Vrije Universiteit Amsterdam, Amsterdam, The Netherlands | [11]Department of Biology, McGill University, Montreal, Quebec, Canada

Correspondence: Louise M. J. O'Connor (louise.mj.oconnor@gmail.com)

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ABSTRACT

International conservation policy includes the dual aims of protecting biodiversity and nature's contributions to people (NCP). Achieving these goals requires protecting not only species and habitats but also the networks of biotic interactions that sustain them. Food webs, which represent predator-prey interactions between species, are increasingly recognised as a link between ecosystem structure, function, and resilience, which are concepts that are frequently cited in conservation policy. Yet, conservation planning and policy typically focus on individual species and habitats and overlook the interactions that support their persistence. We review the literature at the intersection of food web ecology and conservation, and highlight how food webs can inform three conservation goals: preventing species extinctions, maintaining ecosystem functions and NCP, and fostering ecosystem resilience. Food web data and metrics, such as interaction diversity, trophic diversity, connectance, or modularity, can be used to prioritize species that are key to ecosystem structure and functioning, and to guide spatial prioritization to protect functionally diverse and resilient communities. Given the growing availability of food web data, incorporating food webs in conservation planning can lead to more effective and resilient conservation outcomes that sustain biodiversity and ecosystem functions in the long term.

1 | Why Food Webs Are Relevant to Conservation

Food webs represent the feeding relationships (known as trophic interactions) between predators and their prey. Trophic interactions play a critical role in shaping biodiversity and sustaining ecosystem structure and functioning, and are recognized as an essential biodiversity variable (EBV) (Kissling et al. 2015). Global change, particularly climate change and land-use change, impacts species not only directly but also indirectly through the loss of interactions (Valiente-Banuet et al. 2015; Dirzo et al. 2014; O'Connor et al. 2024). Species responses to disturbances are likely to result in a profound reorganisation of food webs and extinction cascades, due to mismatches in interacting species ranges or phenology (Tekwa et al. 2022; Carroll et al. 2024; Quévreux et al. 2024). For example, mass die-off events of birds in the United States, primarily due to starvation, and

A. Loss of top-down control

1. Extermination of sea otters in the 20th century

2. Urchin populations are released from top-down control

3. Kelp disappear due to overgrazing by urchins

4. Benefits provided by kelp (coastal erosion control and habitat to fish species for the fishing industry) are lost

B. Loss of biotic resources

2. Iberian lynx populations decline due to prey scarcity (rabbit makes up >80% of the Iberian lynx diet)

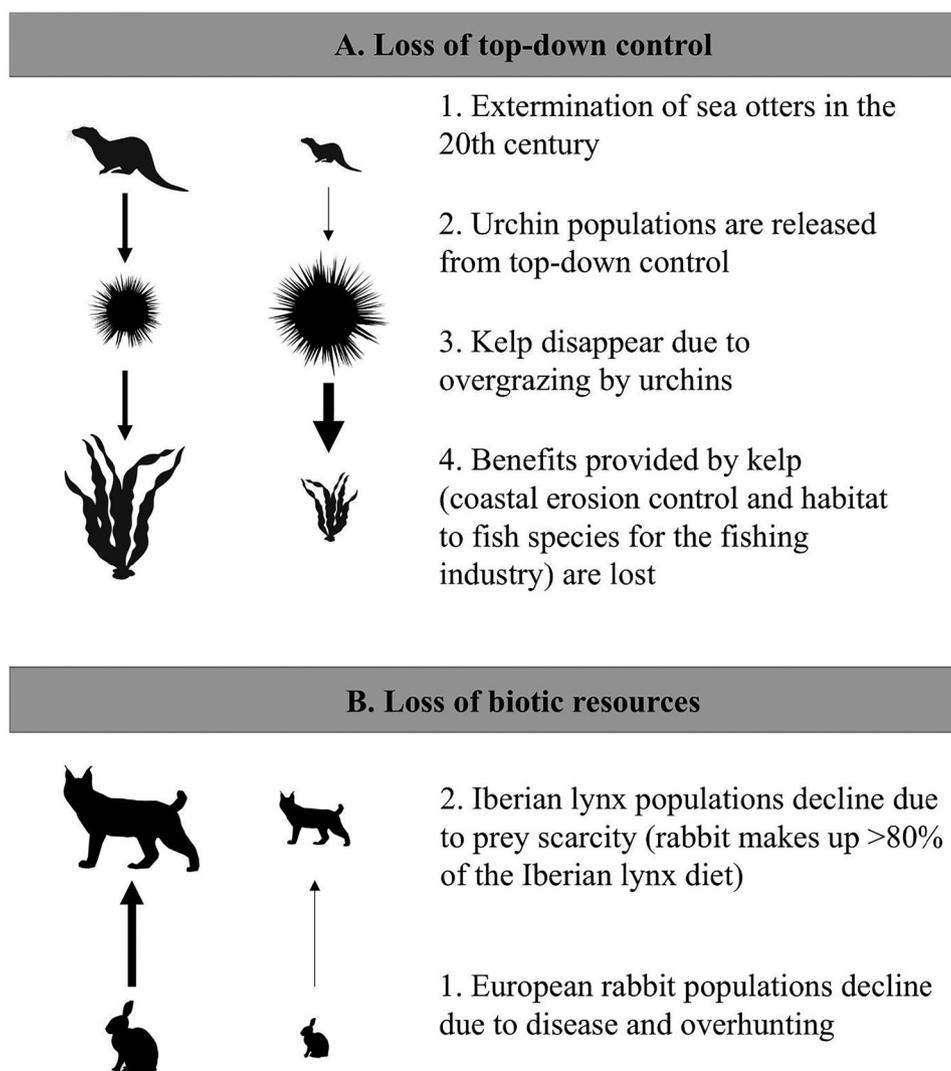1. European rabbit populations decline due to disease and overhunting

FIGURE 1 | Importance of top-down and bottom-up control for species and NCP. (A) On the one hand, predators can maintain local biodiversity by reducing competition between prey species, allowing multiple species to coexist, including rare and endangered species (Soulé et al. 2005). Top-down control can also indirectly impact species on lower trophic levels. For example, through the top-down control of urchins, sea otters help maintain kelp forests, which are important for preventing coastal erosion and also provide habitat for fish species. The extermination of sea otters in the 20th century led to the overgrazing of kelp by urchins. (B) On the other hand, prey species can sustain entire food webs through bottom-up control if many other species rely on them for food. In the case of trophic specialists, prey species are essential for the survival of their predators. For example, the Iberian lynx relies on European rabbits as their main source of food, and the overhunting of the European rabbit led to a decrease in populations of the Iberian lynx (Fordham et al. 2013).

exacerbated by extreme climate events, highlight that species need sustained biotic interactions to survive (Piatt et al. 2020; New Mexico Department of Game and Fish 2020). In the latest European Union (EU) reporting period (2013-2018), altered or lost interactions were recorded as threats for 290 habitats and 1557 populations of species. In Africa, the depletion of lions' prey due to poaching has driven lion population declines (Creel et al. 2024); in North America, the extirpation of the sea otter, a top predator, led to the collapse of marine kelp forests (Figure 1; Estes et al. 2011); and across the Arctic, diminishing sea ice is reducing polar bears' access to prey, increasing the risk of starvation (Pagano et al. 2024). Studies have suggested that secondary extinctions due to loss of biotic interactions can double the total number of extinctions compared to primary extinctions (Bascompte et al. 2019; Koh et al. 2004), often with delayed effects that result in an extinction debt in degraded communities. Some key species are disproportionately important in maintaining ecosystem stability, and their loss can severely impact the persistence of multiple species in a food web (Keyes et al. 2021; McDonald-Madden et al. 2016), with far-reaching impacts on ecosystem functioning and nature's contributions to people (NCP) (Pecl et al. 2017). Clearly, the loss of biotic interactions is a significant driver of biodiversity decline, yet interactions are rarely explicitly accounted for in the planning and management of protected area networks.

Food web information can support the implementation of international biodiversity policy frameworks that aim to preserve the structure, function, integrity, and resilience of ecosystems, such as the Kunming-Montreal Global Biodiversity Framework (KM-GBF), the EU Marine Spatial Planning Directive, the EU

Habitats Directive, the Magnuson-Stevens Fishery Conservation and Management Act, and the Ramsar Convention on the Conservation of Wetlands. The EU Habitat Directive specifically requires EU member states to conserve habitats such that "*the specific structure and functions which are necessary for [a habitat's] long-term maintenance exist*" (European Commission 1992). EU member states are also required to monitor and protect species' habitats, "*defined by specific abiotic or biotic factors,*" and including "*physical and biological requirements of the species; this includes prey, pollinators*" (European Commission 2023). In fact, trophic interactions are explicitly included as a criteria for assessing the risk of ecosystem collapse in the IUCN Red List of Ecosystems (Criterion D) (Keith et al. 2020). These criteria are also expected to be considered in the designation of Special Areas of Conservation within the EU Natura 2000 network of protected areas (European Commission 1992). The EU Biodiversity Strategy also specifically calls for ecological resilience in a trans-European nature network, in line with the United Nations Sustainable Development Goals 13, 14, and 15. Food webs can help implement these policies in a standardised and systematic way. Yet, food webs are generally overlooked in conservation planning and policy (Harvey et al. 2017; Heinen et al. 2020; McDonald-Madden et al. 2016). A likely result is that we may miss a big opportunity for the protection of biodiversity and ecosystems in the push for expanding protected areas to 30% of land and sea areas by 2030 to meet Target 3 of the KM-GBF (Godet and Devictor 2018).

Systematic conservation planning (SCP) is one of the main approaches for identifying species, habitats, or priority areas in need of protection (Jung et al. 2021; O'Connor et al. 2021). SCP optimises the spatial representation of multiple non-interacting features (e.g., species, ecosystems, or NCP) within a set of priority areas that are complementary and irreplaceable for the set of biodiversity features considered (Kukkala and Moilanen 2013). Yet, few studies have incorporated trophic information in SCP (Decker et al. 2017). One challenge has been the historical lack of data on trophic interactions, known as the Eltonian shortfall (Hortal et al. 2015), and one urgent and critical task for ecologists is to address this shortfall. Fortunately, recent methodological advances have begun to bridge this gap by providing new ways to obtain food web data at biogeographical scales (Thuiller et al. 2024). Emerging technologies such as machine learning, metabarcoding, and stable isotope analysis are rapidly expanding our ability to detect and quantify species interactions (Vacher et al. 2016; Hassan et al. 2023; Thuiller et al. 2024). Additionally, there is a growing availability of large-scale food web data, such as metawebs (Brose et al. 2019; Maiorano et al. 2020; Middleton et al. 2021), combined with novel methods that predict trophic interactions from limited data (Caron et al. 2022; Strydom et al. 2021; Hao et al. 2025). There remains a need for more field data across regions and ecosystems to parameterize and validate these models, since empirical data on trophic interactions are still scarce and unevenly distributed (with fisheries being a notable exception). Nonetheless, the rapid expansion of trophic interactions data and models now offers new opportunities to integrate food webs into SCP. However, to achieve this goal, food web data must be distilled into clear, relevant, and interpretable metrics. To date, we lack a standardized framework for integrating food webs into conservation planning, and prioritization studies have typically focused on individual species without accounting for their interactions. Here, we address these challenges and outline

ways to better integrate food webs in conservation. We first review the food web indicators that are relevant for three major conservation goals: (1) prevent species extinctions, (2) maintain ecosystem functions and NCP, and (3) foster ecosystem resilience (Table 1, Figure 2). Then, we discuss practical options for incorporating food webs in SCP.

2 | Linking Food Web Properties and Conservation Goals

Advances in food web ecology and network science have brought to light several food web metrics that are related to the diversity, functioning, and resilience of ecosystems. Food webs can be analysed and described across multiple levels: species and their interactions that are food webs' building blocks, trophic groups, and the entire network. Food web information can thus be used in different ways for different conservation objectives (Figure 2), which we describe below.

2.1 | Prevent Species Extinctions

One overarching aim of conservation is to prevent species extinctions. For example, the GBF proposes to halt species extinctions and to reduce by 10-fold the rate and risk of extinction of all species by 2050 (Convention on Biological Diversity 2022). Food webs can help identify how species persistence depends on long chains of interactions, in particular, (i) which species are most vulnerable to secondary extinctions, as well as (ii) which species are key to preventing the extinction of many others.

2.1.1 | Species Position in the Food Web Indicates Their Vulnerability

Both top-down and bottom-up effects act together to determine a species' vulnerability to direct and indirect perturbations within a food web (Curtsdotter et al. 2011). Interactions can drive species to extinction either through the decline or loss of beneficial interactions (e.g., decline of a prey) or through the increase or introduction of antagonistic interactions (e.g., competition and predation).

Top predators are thought to be particularly vulnerable because their energy supply is limited by going through long chains with imperfect assimilation, and they are affected by any disturbances that impact lower trophic levels in the food web. In addition, they typically have few offspring, occur in low densities (Brose 2011), and have been (or still are) persecuted by humans (Fricke, Hsieh, et al. 2022; O'Connor et al. 2024). Effective conservation of top predators requires both suitable and large enough habitat (Hirt et al. 2021), as well as abundant and diverse prey populations, to support them in the long term (Thompson et al. 2012).

"Trophic specialists" are species that only eat a certain type of prey. For example, the Iberian lynx, which primarily feeds on the European rabbit (Figure 1), and the European honey buzzard, which primarily eats bees and wasps, are both trophic specialists.

TABLE 1 | Integrating food web metrics into spatial conservation planning: objectives, metrics, and research gaps.

Food web component	Conservation objective	Definition and associated network metric	Applications in spatial conservation planning	Research gaps and limitations
Predators and trophic specialists	Prevent extinctions: Protect trophic specialists and top predators alongside their prey.	Top predators have a high trophic level and few or no predators (low out-degree), while trophic specialists have few prey (low in-degree). These can be identified using the R packages igraph or NetIndices.	In a prioritization, predators' distributions should include prey availability to protect predators, together with their prey.	Prey-predator mismatches under climate change need to be accounted for in biogeography andconservation planning.
Vulnerable prey species	Prevent extinctions: Protect vulnerable prey species.	Vulnerable prey species have many predators (high out-degree). These can be identified using the R packages igraph or NetIndices.	In a prioritization, vulnerable prey species can be upweighted by their out-degree and threat status. Refugia from predation can be identified by treating generalist or invasive predators as a cost.	Predators may also benefit vulnerable prey by controlling competitors. The direct and indirect effects of predator loss on prey need to be further examined.
Trophic redundancy	Enhance resilience: Prioritize trophic redundancy.	Trophic redundancy is the number of species in a trophic group, which can be identified using stochastic block models (e.g., with the R package blockmodels).	In a prioritization, trophic redundancy of different trophic groups can be used as a biodiversity feature.	Trophic redundancy should be combined with functional traits or habitat.
Ecosystem service providers and their prey	Maintain ecosystem functions: Protect service providers together with their prey.	The prey of ecosystem service providers are known as supporting species and indirectly sustain the ecosystem service (or NCP) supply.	In a prioritization, provider species distributions should include prey availability to protect both direct providers and supporting species of the ecosystem service.	Research is needed to better understand the relationship between food web structure and ecosystem service provision.
Keystone species	Prevent extinctions: Protect keystone species.	Key species that are essential to food web structure can be identified as those with a high PageRank index.	In a prioritization, key species can be upweighted by their PageRank to reflect their crucial role in sustaining many other species.	Research is needed to understand the context dependency of the keystone role, as well as a standardized metric to identify key species and interactions.
Trophic diversity, interaction diversity, distinctiveness	Maintain diversity and ecosystem functioning: Food webs that are diverse and distinct should be protected.	Trophic diversity is the number of trophic groups within a species pool. Interaction diversity is the number of species interactions, scaled by species richness. Network distinctiveness (or beta-diversity) measures how different a food web is from others.	In a prioritization, trophic diversity, interaction diversity, and network distinctiveness can be used as biodiversity features.	These metrics show promise for understanding food web structure and resilience to disturbances, but this remains to be tested.

(Continues)

TABLE 1 | (Continued)

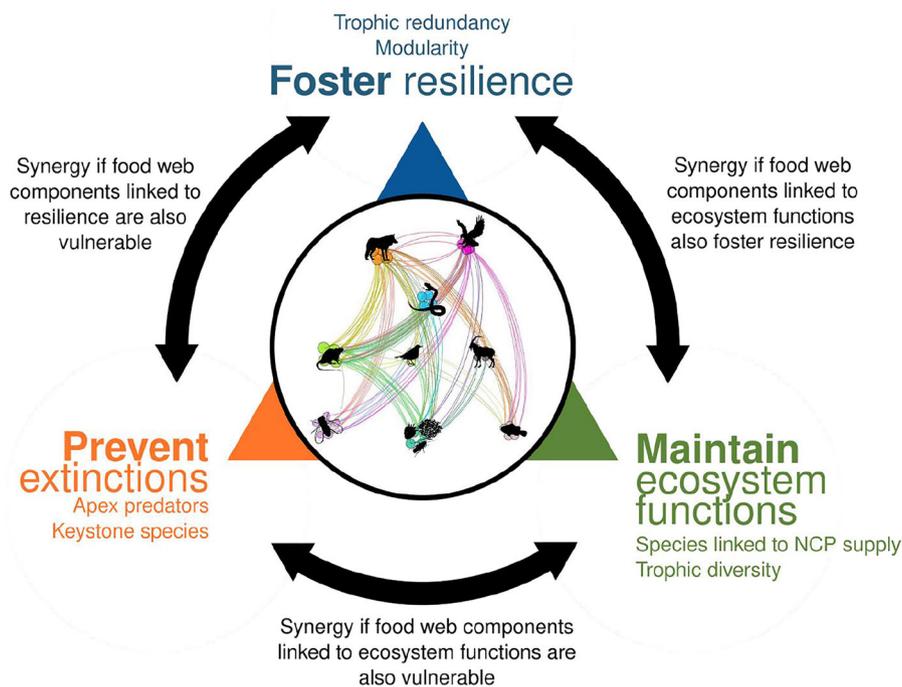| Food web component	Conservation objective	Definition and associated network metric	Applications in spatial conservation planning	Research gaps and limitations
Trophic uniqueness	Maintain ecosystem functions: Protect irreplaceable and vulnerable functions.	A species is trophically unique if it is the only member in its trophic group, meaning it has no functional equivalents in the food web (i.e., functionally irreplaceable).	In a prioritization, species with a unique trophic position should be assigned a higher weight to reflect their unique functional role.	Research is needed to develop a standardised framework to quantify trophic uniqueness, similarly to functional uniqueness.
Network motifs	Enhance resilience: Protect food webs with stabilising motifs.	Food webs with stabilising motifs should be prioritized.	In a prioritization, stabilising motifs can be used as a biodiversity feature.	Effects of motifs in larger food webs or as species disperse remain unclear.
Modularity	Enhance resilience: Protect food webs with higher modularity.	High modularity decreases the risk of secondary extinctions and can be calculated with igraph (R) or Gephi.	In a prioritization, modularity of local food webs across space can be used as a biodiversity feature.	Modularity is strongly dependent on sample size.

FIGURE 2 | The structure and function of food webs are linked to conservation goals. Food web components, including species, trophic groups, and emerging food web properties, can be used to address major conservation goals: (1) prevent species extinctions and protect rare and vulnerable biodiversity; (2) maintain ecosystem functions and NCP; and (3) foster ecosystem resilience to environmental change. "Synergy" here means that a given food web metric could simultaneously address two conservation goals. For example, functional diversity in food webs is linked to resilience to perturbation; keystone species are essential for the robustness of food webs to extinctions and the supply of NCP. Even in the absence of synergy, priorities that optimize different components may coincide across space.

Specialist predators are particularly vulnerable to the decline or loss of their prey (Cirtwill et al. 2018) and to secondary extinctions (Fordham et al. 2013; Melián and Bascompte 2002). It is crucial to protect specialist predators together with their main source of food, upon which their survival depends.

Prey species, especially those already suffering from other environmental threats, can be sensitive to predation (especially by invasive predators or mesopredators). For example, many meadow birds are endangered due to severe agricultural intensification and habitat loss, and in their rare patches of remaining

habitat, the presence of generalist mesopredators can compromise their survival. Refuges from predatory pressure can be crucial to avoid extirpation (Decker et al. 2017), especially for highly connected prey species that experience predatory pressure from multiple predators (Holt and Barfield 2009). In practice, food web data might indicate how to manage a mosaic of habitats on a local scale, in order to simultaneously protect the predator's nesting and foraging habitats, and the prey's nesting habitat that constitutes a refuge from predators (Decker et al. 2017; Rayfield et al. 2009). Further, diversionary feeding appears as a promising management option to reduce predatory pressure when vulnerable prey species are affected by vulnerable predators (Bamber et al. 2024).

Top predators, trophic specialists, and highly vulnerable prey are known to be more vulnerable to extinction than other species due to their trophic position. Network tools can quantify the direct and indirect dependency of certain species on other species in a food web, indicating their vulnerability to secondary extinctions (Kones et al. 2009). Additionally, trophically unique species tend to be sensitive to extinction cascades (Petchey et al. 2017). However, the vulnerability of species to secondary extinctions in a food web may also depend on the structure of that specific food web. To identify these vulnerable species or trophic groups, simulations of extinction scenarios can reveal which species most consistently face secondary extinctions in a food web. The effective conservation of trophically vulnerable species requires considering their interactions in addition to specific habitat requirements.

2.1.2 | Food Web Metrics Can Help Identify Key Species and Interactions

An early concept for identifying species important for community structure and stability was the keystone species. These species have a disproportionate influence on community structure via both direct and indirect effects, relative to their abundance (e.g., top predators) (Paine 1969; Power et al. 1996). Their loss triggers secondary extinction cascades that affect the entire ecosystem structure and functioning (Estes et al. 2011; Keyes et al. 2021; Hammerschlag et al. 2025; Donohue et al. 2017). The keystone species concept has intuitive and appealing implications for conservation. For example, keystone species could be added to lists of species that require legal protection (e.g., the Endangered Species Act in the United States, or the EU's Birds and Habitats Directives), and their habitat can be protected to prevent threats to these species. The role of keystone species is as critical as that of ecosystem engineers (e.g., prairie dogs, earthworms, beavers, tent-building caterpillars; Lill and Marquis 2003) and foundational species (e.g., coral reefs, kelp) in creating and maintaining habitats for other species (Díaz et al. 2018). These key species have a disproportionate role, as compared to other species, in the maintenance of community structure and thus need to be identified and protected for their essential role (Cottee-Jones and Whittaker 2012).

The structural importance of a species can be inferred from its position in the food webs. Initially focused on concepts such as the number of interactions (Tylianakis et al. 2010; Cirtwill

et al. 2018) or centrality (Jordán et al. 2007; Lai et al. 2012; Sun et al. 2020; González-del-Pliego et al. 2024), methods aiming at detecting keystone species in food webs have shifted to more integrative approaches identifying species important to preserve the energetic integrity of food webs (Allesina et al. 2009). A version of the Google Page Rank algorithm adapted to food webs appears to be a promising method to identify keystone species and quantify the structural importance of species in a food web (McDonald-Madden et al. 2016; Keyes et al. 2021). Other studies have suggested that trophic interactions, rather than species, might be the key components in communities (Harvey et al. 2017). In practice, conserving key interactions implies not only protecting both interaction partners together but also making sure the interaction can take place (e.g., spatial and phenological overlap, and abundant populations of both species).

Research is needed to compare the accuracy of different metrics to determine how well they identify key species, as well as their sensitivity to sparse interaction data. A long-standing question concerns the context dependency of the keystone role of species, but evidence suggests that trophic roles are inherent to species (Baker et al. 2015; Stouffer et al. 2012), suggesting that key species may remain critical for community structure across different contexts (Tylianakis and Morris 2017). Understanding how the structural importance of species and entire food webs change in different environments and community contexts will be a step forward on this question. In addition, an urgent and critical task for ecologists will be to continue to address the Eltonian shortfall (Hortal et al. 2015), as robust metrics for conservation ultimately depend on a reliable food web topology that must be grounded in sufficient empirical data.

2.1.3 | Implications for Conservation Planning and Policy

There is a need for policy frameworks and management practices that ensure the availability of food resources for species, protect trophic interactions, and prioritize species that are essential to food web structure. In practice, this could mean restrictions on management practices that threaten trophic interactions and deplete the resource base of food webs (e.g., mowing, pesticide use). Key species that play a vital role in sustaining entire ecosystems (such as top predators, important prey species, and keystone species) need to be systematically protected via policies such as the Birds and Habitats Directives in the EU, the Endangered Species Act in the United States, the Convention on International Trade in Endangered Species (CITES), or the Bonn Convention. These policies can provide a legal framework to maintain healthy and viable populations of species that are vital to food web functioning by mitigating threats such as hunting, trapping, and poisoning, even outside of protected areas.

In SCP algorithms, weights can be assigned to individual biodiversity features (e.g., species), reflecting their higher conservation value (Arponen et al. 2005). In the context of food webs, features could be species, trophic groups, interactions, or food-web-level properties. To prevent extinctions, higher weights could be assigned to features that are vulnerable or keystone: this includes species that are prey to a large number of species, species that

have a high PageRank, or top predators (Moreno-Mateos et al. 2020). Another option is to use trophic interactions themselves as biodiversity features, potentially weighted by their structural importance for the food web (Harvey et al. 2017). Finally, the protection of predators in areas that have many and abundant prey could be prioritized by including prey richness within the predator distributions and using this information as features in a prioritization.

2.2 | Maintain Ecosystem Functioning and NCP

Another major aim of conservation is to maintain ecosystem functions, including those that are linked to NCP (Xiao et al. 2019; O'Connor et al. 2021; Rodrigues 2025). Food web ecology helps to understand the functional role of species in a community (i.e., the Eltonian niche) and the functional structure of ecosystems (Harvey et al. 2017; Cirtwill et al. 2018; O'Connor et al. 2019). The Eltonian niche of a species in a food web could be used to prioritize species that fill irreplaceable trophic roles, maintain high ecosystem functioning, and are linked to NCPs.

2.2.1 | Trophic Uniqueness

In food webs, species with a unique trophic niche occupy a position in the food web that is shared by no other species (Lai et al. 2012). Such species typically interact with specific sets of species, as a result of unique combinations of functional traits, and can be identified based on their functional traits and trophic interactions (Gravel et al. 2016). Consequently, any ecosystem functions or biomass transfers associated with a unique trophic position would be lost if the species disappeared. For example, the bearded vulture is the only bird in Europe that is able to eat bones, and its presence benefits the decomposition of carcasses and nutrient cycling. Akin to functionally unique species (Violle et al. 2017), species that have a unique trophic position can be important contributors of functional diversity, community stability, and ecosystem functioning (O'Gorman et al. 2011). A promising research avenue will be to transpose methods from functional ecology to food web ecology to consistently quantify trophic uniqueness (Dehling and Stouffer 2018; Violle et al. 2017).

2.2.2 | Trophic Diversity

Trophic diversity is the variety of trophic niches in a food web and is a facet of functional diversity (O'Connor et al. 2019). Trophic niche diversity can also be derived from the interaction volume of a food web, based on the traits of the prey and predators of each species (this can also be used to calculate trophic uniqueness) (Dehling and Stouffer 2018; Dehling et al. 2022). Higher trophic diversity is associated with higher trophic uniqueness and functional differenciation among species, and may promote higher niche complementarity and resource partitioning. This has beens linked to increased ecosystem functioning and biodiversity (Xiao et al. 2019). Explicitly considering trophic diversity will be a step forward to enhance ecosystem functionality in the identification of conservation priorities (Rodrigues 2025).

2.2.3 | Trophic Interactions Underpin NCP

Certain NCP are directly dependent on species interactions. For example, agricultural production depends on pollinator visitation and on pest regulation by predators that feed on rodents and other agricultural pests (Civantos et al. 2012), and decomposition of organic matter is a regulating NCP that relies on necrophage species. Supporting species (i.e., the prey of NCP-providing species) are equally essential for maintaining NCP (Keyes et al. 2021). Thus, preserving species that are either directly or indirectly involved in NCP is critical for the long-term supply of these benefits. Furthermore, some species only indirectly provide NCP through trophic cascades. For example, forest regeneration is essential for carbon sequestration and depends not only on pollination and seed dispersal (by frugivores and seed hoarders) (Fricke, Ordonez, et al. 2022) but also on trophic regulation of large populations of herbivores by their predators (Estes et al. 2011) (Figure 1). Top-down control can also reduce the risk of zoonotic diseases and pandemics (Ostfeld and Holt 2004). Predators can reduce the risk of transmission by controlling the population of the vector and killing weaker individuals that have contracted the disease (IPBES 2020). To maintain NCP, it is crucial to protect and manage trophic interactions and groups of interacting species that contribute to NCP (Quévreux et al. 2024).

2.2.4 | Implications for Conservation Planning and Policy

Sectoral policies can be made more effective for both nature and people by incorporating food web metrics that are linked to ecosystem functioning. For example, the Common Agricultural Policy (CAP) in the EU or the Farm Bill in the United States could support and subsidize farming practices that restore and maintain functional food webs that support processes such as pollination, pest control, and nutrient cycling. This is in line with the UN Sustainable Development Goal 2 on sustainable food systems. Likewise, to achieve the UN Sustainable Development Goal 14 on the conservation and sustainable use of oceans and seas, fisheries policies (such as the Common Fisheries Policy in the EU or the US Magnuson-Stevens Fishery conservation and management act) network metrics could be used to help maintain functional marine food webs, through strategic fishing closures, bans on bottom trawling, and restrictions on industrial fishing.

One option to use food web information for prioritizing ecosystem functions and NCP is to assign higher weights to species that are important for sustaining ecosystem functions and NCP (e.g., pollination, seed dispersal, pest control), directly or indirectly via their interactions (Keyes et al. 2021; Dehling et al. 2022). Trophic uniqueness should also be upweighted in prioritizations to maintain the irreplaceable functions associated with these unique species (Ehrlich and Walker 1998; Loiseau et al. 2020). In addition, the spatial distribution of trophic groups and trophic diversity could be used to guide the prioritization of areas that are likely to support unique and diverse ecosystem functions and NCP. Note that there are trade-offs between the dual objectives of conserving biodiversity and NCP (O'Connor et al. 2021; Xiao et al. 2018; Xiao et al. 2019). This implies that a careful prioritization design is required to balance different conservation objectives.

2.3 | Foster Resilience to Perturbations

Ultimately, conservation aims not only to prevent species extinctions or maintain NCP but also to foster ecosystem resilience to future perturbations such as pollution, invasive species, or climate change. For example, the EU Biodiversity Strategy specifically calls for increasing ecosystem resilience in the push for protecting and restoring ecosystems. Network ecology studies have highlighted particular network properties that confer stability in food webs, many of which have been extensively reviewed (Tylianakis et al. 2010; Binzer et al. 2011; Landi et al. 2018). In this section, we provide a brief overview of how food web information can support efforts toward protecting (or restoring) ecosystems that have inherent structural properties that minimize risks of ecosystem collapse and extinctions, which is especially relevant for conservation in the context of global changes.

2.3.1 | Trophic Redundancy

"Trophic redundancy" is measured by the number of species that occupy the same trophic niche in a community. High trophic redundancy buffers the functional consequences of species losses and fosters resilience of the ecosystem (Lai et al. 2012; Sanders et al. 2018), because fluctuations in a species' presence or abundance may have no immediate consequence if that species is functionally redundant with another. High trophic redundancy reflects the resilience of a trophic position to species extinctions. In particular, the vulnerability of NCP to species extinctions depends on the trophic position and redundancy of the species (Keyes et al. 2021): NCP that are provided by species on higher trophic levels or by trophically unique species are more vulnerable to species extinctions. Note that two species with the same trophic niche in a food web may differ in other aspects of their ecology (e.g., phenology, migration, activity time), which can increase the stability of the functions associated with their trophic niche.

2.3.2 | Network Metrics Linked to Food Web Resilience

The following network metrics can help quantify the extent to which perturbations (e.g., extinctions) can spread in a network (i.e., the risk of secondary extinctions).

Connectance measures the number of interactions within a food web, relative to the number of species. Connectance has been related to food web robustness (Dunne et al. 2002) and ecosystem functioning (Montoya et al. 2003; Tylianakis et al. 2010). Higher connectance reflects that species are connected to many other species on average in the food web, which may provide a buffer to fluctuations in prey availability (Tylianakis et al. 2010). However, high connectance can also be driven by one or a few highly connected species, even if the majority of species have few connections. Another limitation is that connectance (and other metrics that summarize community structure in a single value) does not provide information on specific species, their functional importance, or their vulnerability. In addition to connectance, degree distribution can help analyze how energy flows through a food web and identify a subset of species that are network hubs and essential for food web robustness (Tylianakis et al. 2010).

"Interaction strengths" strongly influence food web structure and stability (Curtsdotter et al. 2011). Food webs with many weak interactions are more resilient to perturbations, because weak interactions can become strong if the environment changes or if a resource is lost (McCann et al. 1998; Navarrete and Berlow 2006). Evidence shows that (i) functionally unique species tend to have the weakest interactions and (ii) both unique and weakly interacting species contribute to greater stability in food webs (O'Gorman et al. 2011). Prioritizing functionally unique and weakly interacting species for conservation could enhance the resilience and stability of the ecosystem, reducing the risk of collapse and species extinctions. While measuring interaction strengths can be challenging and labor-intensive, emerging technologies such as camera trap systems (Rossa et al. 2024) and eDNA methods (Nørgaard et al. 2021) hold potential for facilitating the monitoring and quantification of trophic interactions. When observations are not possible, there are options to estimate them (Berlow et al. 2009), such as using the movement speed of predator and prey to calculate encounter rates (Pawar et al. 2012) or using a combination of local estimates of biomass, primary productivity, and feeding interactions to estimate energy fluxes (Gauzens et al. 2019).

"Motifs" are simple subgraphs (typically involving three species) within a larger food web. Motifs have been shown to be a valuable tool for examining ecological stability and to inform management strategies for threatened species and NCP (Chadès et al. 2011; Xiao et al. 2019). Common motifs in food webs include tri-trophic food chains (where species A eats species B, which in turn eats species C), omnivory (where one species A preys on two species B and C), or intraguild predation (where species A and B share a common prey C, and A preys on its competitor B). Some of these motifs, such as trophic chains and omnivory motifs, may promote food web persistence (Stouffer and Bascompte 2010). Another study has shown that motifs can be helpful for identifying keystone species in a food web, since species participating in more food web motifs are also key for food web robustness (Sun et al. 2020). To prioritize food webs with a high level of stabilizing motifs in conservation planning, stabilizing motifs could be mapped and used as a biodiversity feature alongside species distributions. Analyzing motifs may also be useful for managers by helping them determine the optimal order of intervention within a food web and efficiently prioritize resources (Chadès et al. 2011).

"Modularity" in networks measures the extent to which groups of species (modules) are more densely connected to each other than to the rest of the network—for example, due to ecological or spatial segregation between different subcommunities. For instance, food webs that contain both aquatic and terrestrial species would typically have (at least) two modules, as aquatic species are typically more connected to each other than to terrestrial species. High modularity is thought to buffer perturbations between modules (Stouffer and Bascompte 2011). Modules can additionally indicate groups of species that depend on one another and that should be conserved together as a functional assemblage (i.e., functional subnetworks). Modules are only connected through a limited number of species, which are known as connector hubs, and are crucial to the persistence of entire modules.

Connector hub species include, for example, mobile predators that connect food webs across different ecosystems through their foraging movements (McCann et al. 2005). Hub species need to be adequately protected to prevent their extinction or decline, which could have drastic consequences on the different modules the hub species connects (Moreno-Mateos et al. 2020).

2.3.3 | Fostering Resilience Across Habitat Networks

The movement of species (particularly predators) across landscapes has direct implications for food web structure and ecosystem functioning (Gonzalez et al. 2011; Hirt et al. 2018). Mobile predators can connect and stabilize multiple food webs across a landscape, and their stabilizing role is likely to be enhanced through protecting large areas that can support mobile predators (McCann et al. 2005). Spatial connectivity between habitat patches has been incorporated in prioritization algorithms (Albert et al. 2017; Lehtomäki and Moilanen 2013), while interactions are not typically considered. This is a major gap because the impact of spatial connectivity on the persistence of local populations depends on the structure and dynamics of trophic interactions (Ryser et al. 2021). Research is needed to investigate how trophic interactions can help optimize the spatial connectivity for multiple species simultaneously, while also making sure vital interactions can occur (e.g., in habitat patches where predators can forage for food [Rayfield et al. 2009]). A fascinating research avenue is to combine interaction networks with spatial habitat networks in conservation planning to protect diverse, functioning, and resilient trophic metacommunities. The challenge is to integrate species-specific (trait-based) movement capacities into food web models (Boitani et al. 2007; Guzman et al. 2019). Interestingly, both dispersal and trophic interactions have the same currency (biomass flow), a similarity that could be leveraged to use them together in conservation planning.

2.3.4 | Implications for Conservation Planning and Policy

International conservation policies such as the EU biodiversity strategy call for enhancing resilience within a trans-European nature network. Functional and resilient ecosystems emerge from food web structural complexity, which can be measured by metrics like interaction diversity, trophic diversity and redundancy, connectance, and modularity.

It is critical to simultaneously integrate multiple food web metrics that are linked to ecosystem resilience (Tylianakis et al. 2010) (Figure 3). In practice, one could, for example, combine metaweb data and species distributions to map food webs across a region of interest, in order to derive spatial estimates of multiple food web metrics (Thuiller et al. 2024). This includes stabilizing motifs, network hubs, connectance, trophic diversity, trophic redundancy, or trophic modularity (Braga et al. 2019; Botella et al. 2024; Gaüzère et al. 2023). These spatial layers can then be used as biodiversity features in SCP to prioritize the conservation of resilient ecosystems that are likely to remain valuable for biodiversity in the face of global change, or to highlight areas that require restoration to increase resilience (Table 1).

3 | Linking Food Web Ecology With SCP

SCP can integrate many components of biodiversity (e.g., evolutionary distinctiveness, functional diversity, and habitat connectivity), but species interactions are typically not considered (Rayfield et al. 2009). Below, we highlight ways forward to integrate food web information into SCP.

3.1 | Using Food Webs to Weight Individual Features

Weights in prioritization can be used to reflect the relative importance of different features. Higher weights could be assigned to features that are identified as essential for the diversity, functioning, or resilience of food webs, such as keystone species or interactions. Similarly, the size of trophic groups (their species richness) indicates the trophic uniqueness or redundancy of species and can be used for upweighting trophic groups that are represented by fewer species. However, because SCP algorithms are designed to optimize benefits for each feature (e.g., species) individually across a reserve, the use of weights alone may not be sufficient for protecting interacting species in the same location. Therefore, merely adding weights to individual species may not always be sufficient to achieve the desired outcome of protecting functional and diverse food webs.

3.2 | Using Food Web Components as Biodiversity Features

The outcome of a prioritization is largely shaped by the biodiversity features used as spatial input layers in the prioritization (Figure 3) (Lehtomäki and Moilanen 2013). The following conservation units derived from species interactions data and species distributions can be used to identify key areas for species and for food web diversity, functioning, and resilience:

i. Prioritizing predator–prey interactions. Focusing on the interactions themselves could protect vital areas where predators co-occur and interact with their prey, and where food webs are densely connected. Distributions of interactions can be reconstructed through the combination of species distributions and their known trophic interactions (Braga et al. 2019) and can then be used directly as features within the prioritization (Figure 4). Keystone interactions can be identified and weighted according to their structural importance for the food web (Harvey et al. 2017). However, using interactions at the species level will risk skewing the prioritization to interactions involving rare species and could instead be aggregated for trophic groups. For instance, a nocturnal insectivorous bat needs to co-occur with nocturnal flying insects, rather than with a specific species.

ii. Species requirements in habitats and prey. Species distributions included as features should include not only habitat suitability but also the availability and diversity of prey, in order to prioritize areas that can sustain the species (and any NCP it provides) in the long term (Figures 4 and 5). This would enhance the long-term persistence of top
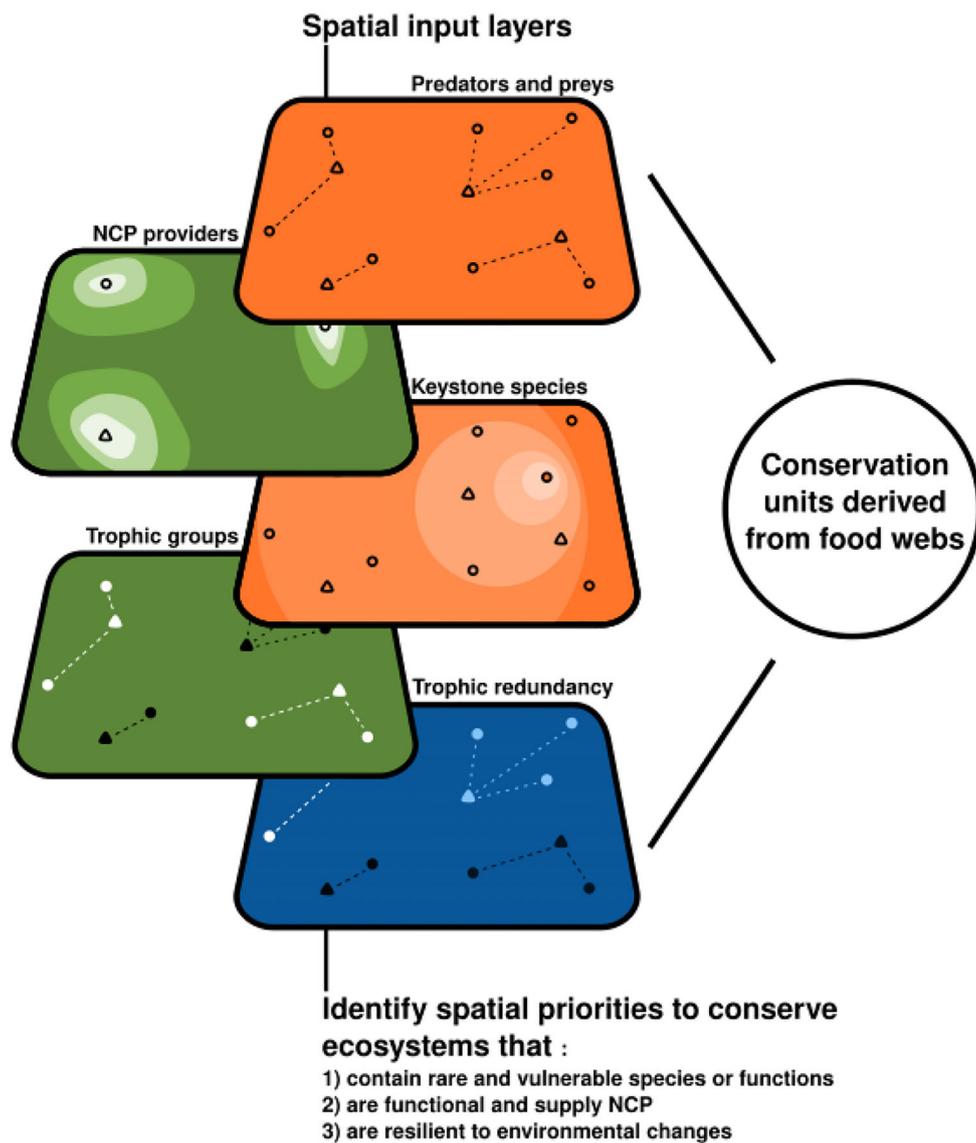
Spatial input layers

FIGURE 3 | Framework to integrate food web components into spatial conservation prioritization. Spatial input layers are colored by conservation goal: prevent extinctions in orange, maintain ecosystem functioning and NCP in green, and foster ecosystem resilience in blue.

predators, threatened species, keystone species, and species that provide NCP. In practice, distributions accounting for both habitat suitability and prey availability can be built by combining the distributions of species with their known trophic interactions (Maiorano et al. 2020; Braga et al. 2019) and used as features in the prioritization. This approach could also help identify locations with low abundance of prey where other types of actions may be required to increase food resources locally for the species of interest (e.g., prey reintroduction, or agricultural set-aside) (Decker et al. 2017). As an example, the map in Figure 5 evaluates the implications of including interactions within spatial conservation prioritization. Mostly, the two approaches lead to the same sites being selected as top priorities for protected area expansion. However, we found that 10.6% of those top priorities do not overlap (Figure 5). These small differences are likely beneficial for the long-term persistence of predators in those areas, since these are areas with both suitable habitat and a diversity of available prey.

iii. Prioritizing trophic groups. Using trophic groups as biodiversity features would prioritize ecosystems with high trophic diversity and with high trophic redundancy (more resilient) and rare trophic groups (functionally irreplaceable) (Figure 4). Once they have been identified in the food web (Gauzens et al. 2015), trophic group distributions can be constructed by aggregating the distributions of species that compose each trophic group (O'Connor et al. 2019).

3.3 | Using Insights From Food Web Biogeography to Identify Irreplaceable Areas

Recent advances in network ecology have made it possible to quantify the compositional turnover (i.e., the complementarity) between different food webs and their distinctiveness. Food web distinctiveness can be measured through network beta-diversity (Poisot et al. 2012) at the level of species or trophic groups (Ohlmann et al. 2019). Distinct food webs, measured by
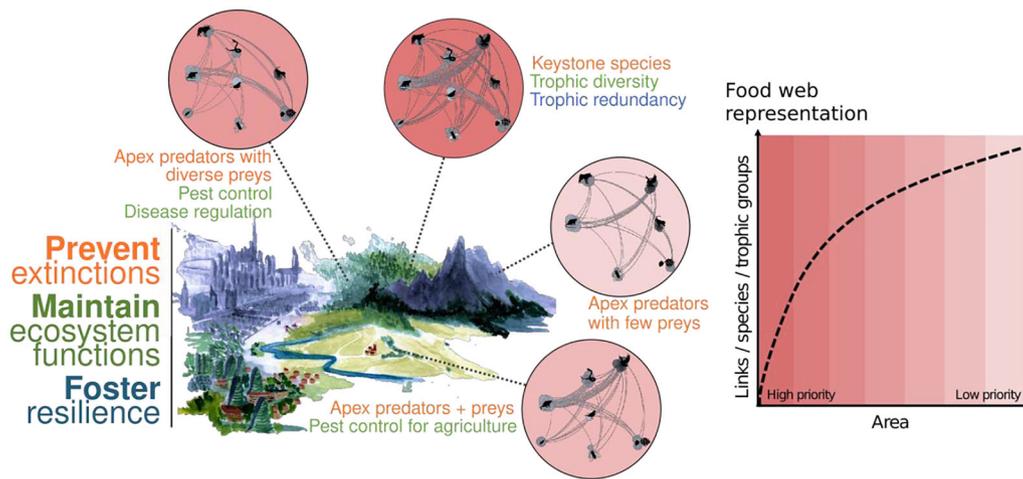
FIGURE 4 | Using food webs to rank priority areas. For example, to improve the conservation of species, priority areas should optimize the protection of species of conservation interest (threatened species, species that provide NCP, and keystone species) together with diverse prey. To maintain ecosystem functioning and resilience, priority areas should maximize trophic diversity, interaction diversity, and trophic redundancy (functional resilience), and prioritize distinct food webs. Performance curves (on the right) help quantify the biodiversity features contained within a set of areas, ranked from high to low priority.
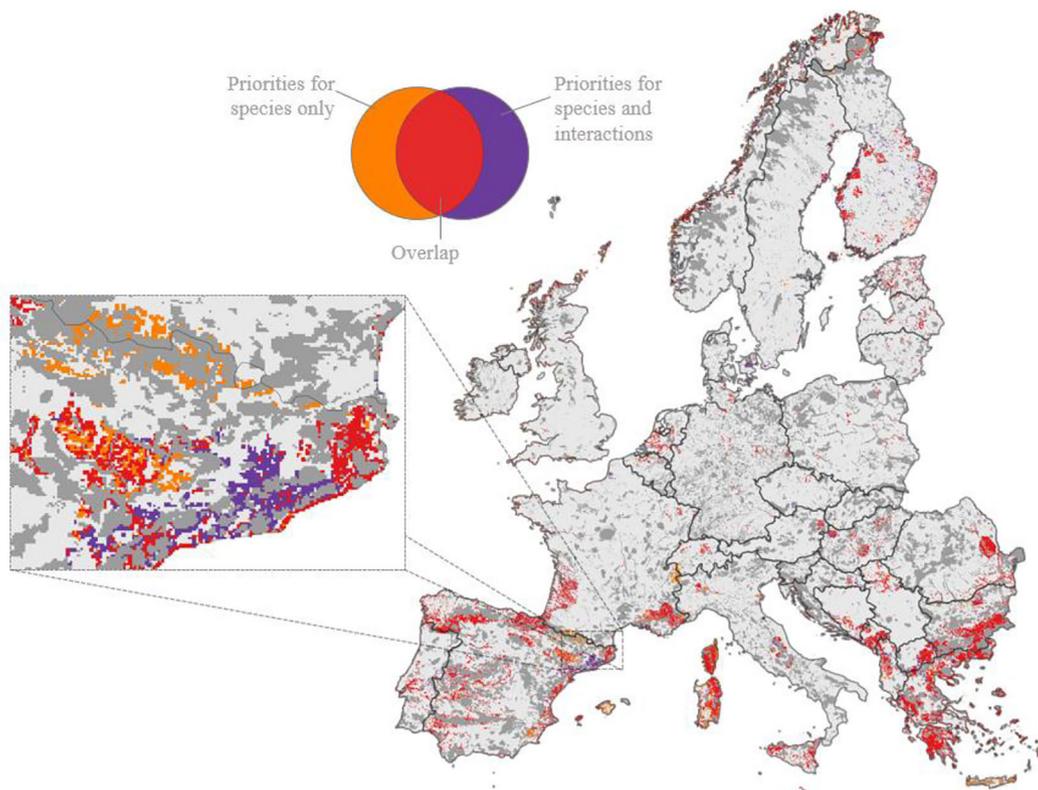
FIGURE 5 | Including food web information shifts top priorities for protected area expansion. Using Zonation with European vertebrate species distributions and their trophic interactions (Maiorano et al. 2013; Maiorano et al. 2020), we ran two prioritizations that expanded on existing protected areas for reaching the target of 30% of protected area coverage in Europe: the first prioritization ignored interactions and only considered species habitat suitable range as features; in the second prioritization including interactions, we used the diversity of available prey within the distribution of predators as an input biodiversity feature. On the map, colored areas show the top priorities resulting from two variant prioritizations that expanded on existing protected areas (in gray on the map) at 1 km² resolution. Orange areas on the map represent the resulting top priorities of a typical approach for spatial prioritization that uses single-species distributions as features, considering the suitable habitat for species, but ignoring their interactions (as in O'Connor et al. 2021). Purple areas on the map are the outcome of the prioritization that incorporated the need for predators to coexist with their prey, where features consisted of a combination of suitable habitats and prey richness within predator distributions. The red areas show the overlap between the two prioritizations.

high network beta-diversity, contain assemblages of species and interactions that are not nested in others: they are unique and irreplaceable at a regional level. Furthermore, distinct food webs are thought to be less degraded (Tylianakis and Morris 2017) and less prone to invasions, and to contribute to the robustness of trophic metacommunities (Santos et al. 2021).

The approaches outlined above relate to different conservation strategies, and they likely represent very different prioritization outcomes. A key decision is whether to target specific predator–prey pairs or whether to use information derived from the entire food web, and it will depend on the conservation goal (Figure 2). A similar dichotomy has been addressed in species-versus community-based prioritization (Leathwick et al. 2010). Likewise, prioritizing evolutionarily distinct species (which protects the global tree of life) is not the same as prioritizing local assemblages that have high phylogenetic diversity (Pollock et al. 2017). A metric to measure conservation gains for food webs could correspond to the marginal gain in food web diversity, functioning, and resilience by protecting additional species or restoring habitat. Once suitable metrics are determined, then SCP algorithms (e.g., Zonation, Marxan, prioritizr) could be used or adapted, but establishing how the metric relates to conservation targets will be critically important (Pollock et al. 2020) (Figure 4). Going forward, another task will be to investigate how these strategies perform, compared with traditional approaches that ignore species interactions, in terms of species representation (particularly for endemic species), ecosystem functioning, and long-term species viability (Figure 5). This exercise will help identify which food web components provide better insights than simpler species-based metrics—this is crucial information, given that food web data are often more challenging to measure. Understanding when these complex metrics offer significant advantages will be key to prioritizing conservation efforts more effectively and allocating resources where they will provide the greatest benefits for biodiversity and ecosystem functioning.

4 | Concluding Remarks

Species interactions are fundamental components of functioning ecosystems, yet they remain virtually unused in conservation planning. In this review, we identify a clear set of food web metrics that are linked to major conservation goals and how they can be used in spatial conservation prioritization. Food webs can be used to (1) identify *species* of conservation concern and (2) identify key *areas* with functional, diverse, and resilient communities. Methods and data now allow for spatial planners seeking to prioritize areas for conservation and restoration to explicitly account for food web information, starting with species trophic interactions and ensuring that interaction partners are protected together (Figure 5). We show how insights from food web ecology and network science have the potential to guide more effective and robust conservation decisions in the long term and can complement other biodiversity data (e.g., population densities, generation times, body mass, genetic diversity) (Pollock et al. 2020). This is essential given the uncertain and dynamic nature of trophic interactions: interactions vary through seasons and species' life stages. Using metawebs (Thuiller et al. 2024), probabilistic food web models (Li et al. 2023), or multiple integrated networks that reflect the full set of possible interactions

(Peterson et al. 2021) may be a solution to account for uncertainty. In providing many (realistic) possibilities, these approaches allow for more detailed management and conservation alternatives to potentially be tested with simulations.

To date, many conservation policies and management actions remain narrowly focused on listed species and habitats, without acknowledging the complex interactions that sustain them. Species require suitable biotic interactions to persist, and food webs support species and NCP (Keyes et al. 2021). There is a need for conservation planners, policy makers, and managers to transition from a single-species perspective to a systems perspective that preserves interaction networks and ecosystem processes (Harvey et al. 2017). Our work can serve as a guide for how to use interaction data in conservation planning applications. Research is now needed to explore how conservation priorities change with and without considering food web interactions (Figure 5), which metrics are essential to measure and monitor, and their sensitivity to sampling effort (Figure 4), and, crucially, which species and areas are essential for maintaining resilient and irreplaceable ecosystems through conservation, management, or restoration actions, for example, by reintroducing missing trophic groups (Araujo and Alagador 2024). Beyond advancing research, this work could also inform the adaptation of policy plans to improve conservation outcomes and guide the creation of new biodiversity policies, especially in regions of high conservation value where such policy instruments remain scarce (Shen et al. 2023; Mouillot et al. 2024).

Local initiatives have demonstrated the potential for using insights from food webs in conservation, including: Cambodian farmers setting aside a portion of their croplands to grow food for endangered red cranes (Pinto-Rodrigues 2021); the protection of the European rabbit to enable the recovery of the Iberian lynx (LIFE LynxConnect 2025); or the establishment of feeding stations for vultures in Mediterranean countries (LIFE With Vultures 2025). Thanks to legal frameworks such as the Endangered Species Act and the EU Birds and Habitats directives, the legal protection of predator species such as the wolf and the sea otter has facilitated their natural recolonization of habitats, allowing them to resume their ecological role and to restore diverse food webs. However, the recent deregulation of the wolf's protection status in the EU Habitats Directive marks a concerning setback. Even though many top predators are included in international legislation, they are not necessarily protected within networks that can sustain them in the long term (e.g., with sufficient prey). These actions and policies must now be scaled up in a systematic way to protect biodiversity and NCP. Importantly, perturbations such as those caused by global change or invasive species can impact communities, which is visible in the interaction structure (not single pairwise interactions), the biomass distributions (e.g., top-heavy food webs), and consistent changes in food web metrics that indicate instability. In this sense, food web metrics are indicators or early-warning signals. Research is thus needed to better understand the consequences of disturbances, such as climate change or invasive alien species, in the context of food webs, for example, by exploring the relationship between food web metrics (such as connectance and trophic redundancy) and secondary extinctions from a disturbance such as invasion success (O'Connor et al. 2024). A network perspective on communities is essential to achieve community resilience, protect

keystone species, and maintain the fluxes of energy and matter that sustain our natural world.

Data Availability Statement

Data used in the production of Figure 5 will be made available upon request.

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