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Vulnerability of terrestrial vertebrate food webs to anthropogenic threats in Europe

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Abstract

Vertebrate species worldwide are currently facing significant declines in many populations. Although we have gained substantial knowledge about the direct threats that affect individual species, these threats only represent a fraction of the broader vertebrate threat profile, which is also shaped by species interactions. For example, threats faced by prey species can jeopardize the survival of their predators due to food resource scarcity. Yet, indirect threats arising from species interactions have received limited investigation thus far. In this study, we investigate the indirect consequences of anthropogenic threats on biodiversity in the context of European vertebrate food webs. We integrated data on trophic interactions among over 800 terrestrial vertebrates, along with their associated human-induced threats. We quantified and mapped the vulnerability of various components of the food web, including species, interactions, and trophic groups to six major threats: pollution, agricultural intensification, climate change, direct exploitation, urbanization, and invasive alien species and diseases. Direct exploitation and agricultural intensification were two major threats for terrestrial vertebrate food webs: affecting 34% and 31% of species, respectively, they threaten 85% and 69% of interactions in Europe. By integrating network ecology with threat impact assessments, our study contributes to a better understanding of the magnitude of anthropogenic impacts on biodiversity.

KEYWORDS

agricultural intensification, anthropogenic threats, climate change, direct exploitation, European vertebrates, pollution, trophic interactions

1 | INTRODUCTION

Biodiversity is currently declining, and there are concerns that we may be entering the sixth mass extinction (Ceballos et al., 2017). Ecologists have made significant progress in understanding the major threats that impact different components of biodiversity: land use change (e.g., agricultural expansion, deforestation), direct exploitation (e.g., hunting and trapping), pollution, climate change, and invasive alien species (IAS) (IPBES, 2019; Joppa et al., 2016; Maxwell et al., 2016). These human activities result in species and population declines by affecting various aspects of life history (breeding, nesting, and feeding) and overall fitness. To gain a comprehensive understanding of the scale of the impacts of multiple human-induced threats to biodiversity, a macroecological perspective has recently emerged, thanks to the increasing availability of datasets at large spatial and taxonomic scales (Rigal et al., 2023). Recent studies have mapped the impacts of these threats on a global scale and have revealed that different groups of species face distinct direct threats (Harfoot et al., 2021; Newbold et al., 2020). For example, pollution was shown to be a prevalent threat for amphibians worldwide, while direct exploitation is a greater threat to mammals and birds (Harfoot et al., 2021). Some functional groups (carnivores, large endotherms, and small ectotherms) were also found to be disproportionately impacted in disturbed landscapes compared with other species (Newbold et al., 2020).

However, previous studies primarily focused on direct threats to species and did not adequately consider the cascading impacts that can arise from biotic interactions, particularly trophic interactions. Species are indeed not independent of each other. Species are interconnected in food webs, meaning that any human activity that threatens one species or a group of similar species may indirectly affect others (Strona & Bradshaw, 2018). For example, the decline or loss of prey can significantly impact a predator's feeding success and survival, potentially leading to predator extinction (Dobson et al., 2009). These indirect threats can be particularly strong in the case of trophic specialists (a predator feeding on a specific prey), or when a threat extirpates a set of species that constitute the overall resource required by one or more predators. Examining trophic interactions can thus shed light on the cascading impact of threats on interacting communities and ecosystem functioning (Keyes et al., 2021; Morton et al., 2022). However, the overall impact of multiple threats on the intricate web of interactions within ecosystems remains poorly understood. This is mainly due to (i) a lack of available data on trophic interactions, especially at large spatial and taxonomic scales, and (ii) the fact that numerous studies have focused on one guild, within which trophic interactions are limited. A recent study used simulations to quantify the loss of biotic interactions in seed dispersal networks following habitat loss and showed that small amounts of habitat loss can cause up to 10% of species to lose their interaction partners (Sandor et al., 2022). But this has yet to be addressed at a macroecological level and for large food webs.

In this study, we aim to bridge this knowledge gap by addressing two key questions: (i) Can considering species interactions improve our understanding of the impact of multiple threats on biodiversity? (ii) Which species, interactions, and trophic groups are most vulnerable to which threats, and where? To answer these questions, we analyzed the vulnerability of all described European vertebrate species and their trophic interactions to six major threats: agricultural intensification, direct exploitation, urbanization, climate change, pollution, and IAS and diseases. These six major threats each affect over 200 terrestrial vertebrate species in Europe (Table S1) and are defined as follows: (i) Agricultural intensification involves the expansion of agricultural land into previously uncultivated areas, the simplification of agricultural landscapes through the removal of green linear elements (e.g., hedgerows, woodland), and the widespread use of pesticides and fertilizers to maximize yields. (ii) Direct exploitation in the context of terrestrial vertebrates involves hunting, persecution (direct killing or trapping due to perceived threats to human interests), and collection for the pet trade. (iii) Urbanization encompasses the expansion of housing, construction of commercial and industrial infrastructure, leisure facilities, and increased human disturbance. (iv) Climate change refers to warming temperatures, changes in precipitation patterns, and extreme weather events. (v) Pollution refers to the introduction and accumulation of harmful substances in the environment, including chemicals, industrial pollutants, heavy metals, as well as the accumulation of solid waste (e.g., plastics and landfill). (vi) IAS and diseases refer to the biotic threats posed by introduced species to native species. We integrated data from the IUCN European regional red list data on species threats (EEA, 2018), trophic interactions (Maiorano et al., 2020), and geographic distributions (Maiorano et al., 2013). First, we examined whether species' vulnerability to threats is related to their position in the food web, including their trophic role and their number of prey and predators, to analyze whether certain trophic roles are more vulnerable to specific threats. Next, we quantified the vulnerability of interactions, with a particular focus on bottom-up risks, as the loss or decline of prey resources directly compromises the survival of predator species. Finally, we mapped the vulnerability of local food webs to the six different threats across Europe. By integrating network ecology with threat impacts, our study contributes to a better understanding of the scale of the impacts of human activities on biodiversity.

2 | MATERIALS AND METHODS

2.1 | Species threats data

We used the European Red List of species (EEA, 2018), which describes the types of threats that each species is known to be vulnerable to, anywhere within their range. We extracted the threat data for all 935 terrestrial vertebrate species available in the dataset. Because the data on threats to species are available in the form of sentences, we searched for character strings that correspond to different threats (Table S1). We define threats as human activities that have led to, are currently causing, or may potentially result in the decline or loss of biodiversity (Joppa et al., 2016). Building on the IUCN red list threat classification scheme (2022), we first considered nine primary threat categories (direct exploitation, agricultural intensification, IAS and diseases, pollution, climate change, urbanization, aquaculture and fishing, logging and forestry, and mining and energy production), and 20 subcategories (Table S1). While there is some overlap with the IUCN threat classification, our threat classification diverged from the IUCN global threat classification in order to be more relevant to the context of European terrestrial vertebrates. We then focused on the six major threat categories which affected the highest number of terrestrial vertebrate species in Europe (at least 200 species), following Harfoot et al. (2021). Results showing threat subcategories can be found in the Supporting Information

(Figures S1, S3 and S4). The six categories hereafter referred to as major threats were:

1. Urbanization, which is associated with habitat destruction and increased disturbance by humans due to visitation and higher human density (Alberti et al., 2020; Des Roches et al., 2021). It includes development of housing, of commercial infrastructure, and of infrastructure for tourism and leisure.
2. Direct exploitation, which leads to population declines, and it refers to the intentional harvesting or removal of individuals for various purposes, such as recreational hunting, persecution (poisoning, trapping, or shooting a species due to perceived threats to humans), or collection for the pet trade.
3. Agricultural intensification, which refers to the increased productivity of agricultural systems and a transition from traditional farming practices to intensive management practices, expansion of agricultural land, increased agrochemical and pesticide use, loss of hedges and green linear elements, simplification of landscapes and loss of habitat heterogeneity.
4. Pollution, which refers to the introduction and accumulation of contaminants into the natural environment (in particular for vertebrates, in the water and in the soil), leading to habitat degradation and population declines due to, for example, the loss of food sources or direct toxicity to organisms.
5. IAS and diseases, which refer to the biotic threats to vulnerable native species. IAS with documented impacts on European vertebrates include the American mink, Louisiana crayfish, gray squirrel, and the raccoon, which directly impact native vertebrates through predation and competition for resources and the spread of diseases. Pathogens include fungus, parasites, viruses with a documented impact on vertebrates in Europe, such as chytridiomycosis, myxomatosis, malaria, and influenza.
6. Climate change, which refers to any alteration in the climatic conditions that influence species distributions, phenology, and life history: This includes warming, droughts, severe winters, extreme weather events.

2.2 | Metaweb of trophic interactions

We used an updated version of the Tetra-EU metaweb of the trophic interactions between all vertebrate species in Europe (Maiorano et al., 2020), which includes species that occur in the entire European subcontinent plus Turkey. This version distinguishes obligate interactions (i.e., typical food resources for the predator species), from occasional feeding interactions (which do not sustain the predator). Here, we chose to consider only the obligate feeding interactions on the adult life stage of the prey species, since these are necessary for the survival of the predator, and represent significant pathways of energy flow. Although occasional interactions may act as a buffer for predators in case of typical prey declining due to anthropogenic pressures (or other drivers), from the perspective of assessing threat impacts, we believed obligate interactions are more informative, because the loss of obligate interactions directly compromises the survival of the predator. Therefore, we assumed that occasional interactions are unlikely to play a role in the propagation of threats in the food web. Furthermore, the metaweb includes potential interactions between pairs of species that do not necessarily co-occur: these potential interactions would take place due to trait matching between the potential prey–predator pair, for example, if their ranges would overlap in changing conditions (Maiorano et al., 2020). For example, the wolverine only occurs in the north of Europe, but would potentially be able to feed on any species of rabbit or vole living in the south of Europe, if they co-occurred. Because we are only interested in interactions that currently exist, we used species distributions (see below) to remove the interactions between species that never co-occur across Europe given their spatial distributions from Maiorano et al. (2013). In practice, we built a co-occurrence matrix based on species distributions, and then multiplied the co-occurrence matrix with the metaweb adjacency matrix to remove the interactions between species that did not co-occur. We corrected taxonomical mismatches between the metaweb data and the threats data (see Annex S1 in the Supporting Information), and also removed the species that are disconnected from the metaweb (i.e., that are neither a predator nor a prey in the metaweb). The resulting metaweb contained 1084 species and 12,226 interactions. The metaweb dataset and the threat dataset had a total of 884 species in common, for which we could analyze the vulnerability of species and interactions at the metaweb level (Figures 1–3).

2.3 | Species distributions

In addition to analyzing threats at the level of the metaweb, we also analyzed the vulnerability of vertebrate food webs across space. The study area covered the spatial extent of the European Union (EU) with the United Kingdom (EU28+), Norway, Switzerland, and the Western Balkans (Serbia, Kosovo, North Macedonia, Montenegro, Albania, and Bosnia and Herzegovina). We excluded Iceland, Turkey, and Macaronesia to avoid border effects. We considered all species that are included in both the European red list dataset and the European Tetra-EU database (Maiorano et al., 2020), which includes only native species and resident and breeding birds. We extracted the distributions of the species occurring in the study area from Maiorano et al. (2013). These distributions were obtained by combining the extent of occurrence for each species with their habitat requirements (also known as area of habitat maps; Lumbierres et al., 2022). Species distributions were mapped in a regular grid of 300 m resolution, where cells had values of zero for unsuitable habitat, one for marginal habitat (habitat where the species can be present, but does not persist in the absence of primary habitat) and two for primary habitat. Here, we treated primary habitat only as "suitable habitat," which provides a better prediction of the actual species distribution (Ficetola et al., 2015). Given that a number of vertebrate species have large home ranges (e.g., 100 km^2), we upscaled distribution maps to a 10 × 10 km equal-size area grid (ETRS89; total of 49,818 grid cells). We considered the species potentially present in a 10 × 10 km cell if the grid cell contained at least one 300 × 300 m cell of suitable habitat. This led to a total of 804 species included in the spatial analyses for which we had spatial distributions in the study area, trophic interactions and vulnerability to threats.

2.4 | Quantifying the vulnerability of food webs to multiple threats

We quantified the main threats faced by species and their interactions, as well as particular trophic groups.

First, we investigated whether a species' vulnerability to different threats was related to the trophic role of the species. To build trophic groups, we used the same methodology as in O'Connor et al. (2020): we used the stochastic block model (SBM) on the metaweb (R package *blockmodels*; Leger, 2016) to group together the species that eat the same food and are eaten by similar sets of predators. The output of the SBM is an aggregated graph with nodes representing trophic groups, containing species that have the same probability of interacting with all other nodes in the graph (O'Connor et al., 2019). We also included non-vertebrate diet categories in the metaweb in order to refine trophic groups of species that feed on other species than terrestrial vertebrates. Thus, two species belonging to the same trophic group have similar sets of predators and food resources (including terrestrial vertebrate prey species and diet categories). Diet categories were algae, aquatic vegetation, fishes, aquatic invertebrates, aerial invertebrates, invertebrates on ground, invertebrates on vegetation, fruits, flowers, nectar, bulbs, berries, leaves, bark, seeds and grains, nuts, woody vegetation, other plant parts, mushrooms, mosses and lichens, cultivated plants, domestic animals, garbage, detritus, dung, carrion (Maiorano et al., 2020). The goodness of fit of the model is assessed with the Integrated Classification Likelihood (ICL) information criterion (Figure S2). Using the SBM, we partitioned the metaweb along 2–30 groups and selected the optimal number of groups based on the partitioning of the metaweb that maximized the ICL criterion. This partitioned the metaweb into 28 trophic groups (Figures S1 and S2; Table S2). We then computed the proportion of species within each group that are vulnerable to each threat.

In addition, we computed the degree (number of prey, number of predators, and sum of prey and predators [i.e., number of neighbors in the graph]) of each species using the R package *igraph* (Csardi & Nepusz, 2006). This allowed us to investigate whether highly connected species are vulnerable to certain threats, which would have a potential higher impact on the rest of the food web (Figure 2; Figure S3).

Second, we quantified the indirect threats to predator species as the number of species' prey that are affected by each threat. To do so, we performed a matrix multiplication between:

- the threats matrix, of dimensions 6 × 804, where element (*i*, *j*) is equal to 1 if species *j* is threatened by threat *i*, and
- the adjacency matrix representing the food web, of dimensions 804 × 804, where element (*i*, *j*) is equal to 1 if species *i* is eaten by species *j*

This matrix multiplication results in a matrix of dimensions 6 × 804, where each element (*i*, *j*) is equal to the number of prey species of predator *j* that are affected by threat *i*. Then, we divided each value by the total number of prey species of the predator, to get a proportion of vulnerable prey for each predator for each threat (Figure 3).

In this matrix multiplication, we assumed that predators are indirectly vulnerable to threats that affect their prey. We only quantified the threats associated with species that are neighbors in the food web, rather than cascading threats across multiple trophic levels.

2.5 | Mapping the vulnerability of food webs to anthropogenic threats across Europe

We combined the species distributions with the metaweb to build local food webs in each grid cell. We assumed that if two species interact in the metaweb and they both occur in the grid cell, then the interaction exists in the local food web. We assumed that an interaction is vulnerable if it is associated with a prey and/or predator species that is impacted by a threat. In other words, vulnerable interactions can be both top-down (the species may stop functioning as a predator) or bottom-up (the species may stop functioning as a resource). We quantified the proportion of vulnerable species, and vulnerable interactions in the food web that are associated with species that are vulnerable to each threat type. We first compared the proportion of vulnerable species and vulnerable interactions at the level of the metaweb. Then, we quantified these proportions across space: For each grid cell, we quantify the proportion of species, and interactions that are vulnerable to the major threat types (Figures 4 and 5).

We then identified food web vulnerability hotspots to each major threat (Figure 6). To make the metric comparable for all threat types, we first standardized (between 0 and 1) the number of vulnerable species to each threat type, and the number of vulnerable interactions, across all grid cells in Europe. Then, we multiplied these two values for each threat type, so that hotspots of food web vulnerability are areas with many vulnerable species and many vulnerable interactions. Consequently, areas with either few vulnerable interactions, or few species, cannot be food web vulnerability hotspots. This metric expresses a first estimate of the relative magnitude of the impact of each threat on vertebrate assemblages across Europe, taking into account not only species but also their interactions.

All analyses were performed using R version 4.2.2 (R Core Team, 2022). For Figures 3 and 5, we used the R package *ghibli* (Henderson, 2022). The code and data processed for the analysis are openly available in the GitHub repository maintained by the authors: https://github.com/LouiseOC/EU-foodweb-threats.git.

3 | RESULTS

3.1 | Different trophic groups face different threats

Direct exploitation was the most impactful threat for European vertebrates, affecting 34% (387) species, essentially top predators (Figure 1a) with a high number of prey (Figure 2). Species vulnerable to direct exploitation were highly connected in the metaweb (they had a total degree of 29 on average [95% CI: 25–34]), with 22 prey [95% CI: 17–27], and 7.5 predators [95% CI: 6.7–8.2] on average. As a result, 85% interactions in the metaweb were vulnerable to direct exploitation (Figure 1b). Agricultural intensification was the second most impactful threat, affecting 31% (285) species and 69% metaweb interactions. Importantly, species vulnerable to agricultural intensification were also highly connected, with a total degree of 28 species on average [95% CI: 23–33], including 18 prey [95% CI: 12–23] and 10 predators [95% CI: 8.9–11] on average. In particular, over 70% of birds of prey (groups 2 and 24) and 78% of generalist predator species (group 13) were vulnerable to agricultural intensification, primarily due to the use of pesticides (Figure S4); 42% of shrews and moles (group 19) were also affected (Figure S1). Urbanization was the third most prevalent threat, affecting 255 species and 42% metaweb interactions, across multiple trophic levels: 50% of birds of prey (groups 2 and 24), 50% of macro vipers (group 23), 41% of amphibians (group 1), and 41% wading birds (group 15) were found to be vulnerable to urbanization. Species vulnerable to urbanization had a total degree of 18 [95% CI: 14–22] with 9.9 prey [95% CI: 5.9–14] and 7.9 predators [95% CI: 7.0–8.9] (Figure 2). Climate change was a threat for 26% (235) species and 41% interactions across different trophic levels: passerines (group 11), birds of prey (group 24), aquatic predators (group 9). In terms of degree, species vulnerable to climate change had a total degree of 19 [95% CI: 15–23] with 10 prey [95% CI: 6.1–15] and 8.6 predators [95% CI: 7.6–9.6] on average. Pollution, IAS, and wetlands loss were major threats to all water-dependent trophic groups: amphibians (group 1), herbivorous water birds (group 15), and aquatic predators (group 9, including the otter and predatory wading birds). Aquatic predators were also highly vulnerable to direct exploitation (which affects 75% of aquatic predators) and agricultural intensification (56%). Species vulnerable to pollution had a total degree of 19 [95% CI: 14–24] with 10 prey [95% CI: 4.8–15] and 8.8 predators [95% CI: 7.5–10]; and IAS and diseases affected species that had fewer interactions in the metaweb on average compared with other threat types: species vulnerable to IAS and diseases had a total degree of 15 [95% CI: 11–18], including 7.0 prey [95% CI: 3.5–10] and 7.9 predators [95% CI: 6.7–9.0] on average.

3.2 | Most predators are indirectly vulnerable to agricultural intensification

When focusing on the vulnerability of prey for predators, we found that agriculture was the most impactful threat for predator resources overall: on average, 33% of predators' prey species are vulnerable to agricultural intensification (Figure 3) [95% CI: 31–35]. For example, *Lynx pardinus*, a specialist predator of the European rabbit, was indirectly highly vulnerable to agricultural intensification, hunting, and diseases that affect its main prey species. Climate change was another major indirect threat for predators (affecting 23% prey per predator on average [95% CI: 21–25]) (Figure 3), as well as urbanization (affecting 27% of prey per predator [95% CI: 25–30]), and pollution, which affected 30% of prey per predator on average [95% CI: 27–34]. IAS and diseases affected 23% of prey per predator on average [95% CI: 20–26]. On average, 20% of prey species per predator were affected by direct exploitation [95% CI: 21–25].

3.3 | Interactions are disproportionately more vulnerable than species

In the metaweb and across space, a higher number of vulnerable species inevitably leads to a higher number of vulnerable interactions, but we found that some threats had a disproportionate impact on interactions relative to the number of vulnerable species (Figures 1b, 4 and 5). In the metaweb, we found that for instance, IAS and diseases and pollution both affected 23% species and 30% metaweb interactions, while pesticides affected 15% species and 53% interactions (Figure 1b; Figure S3). Direct exploitation affected 34% species, but these species were responsible for 85% interactions in the metaweb, because these species were highly connected (Figure 2). Similarly, across Europe, we found that the proportion of vulnerable interactions was consistently higher than the proportion of vulnerable species in food webs (Figures 4 and 5). In some areas, 100% interactions in the food web were vulnerable to major threats, while only a fraction of the species were vulnerable (Figure 5). The difference between species vulnerability and interaction vulnerability varied with the threat type. In the case of direct exploitation and agricultural intensification, the proportion of threatened interactions was 85% [95% CI: 85.17–85.25] and 79% [95% CI: 78.9–79.1] on average, respectively. This was two to three times higher than the proportion of threatened species, with 38% affected on average in both cases [95% CI: 38.25–38.31 for direct exploitation; and 38.4–38.5 for agricultural intensification]. The difference between the proportion of vulnerable species and vulnerable interactions in local food webs was lower for other major threats: on average across Europe, climate change affected 28% species [95% CI: 27.78–27.84] and 39%

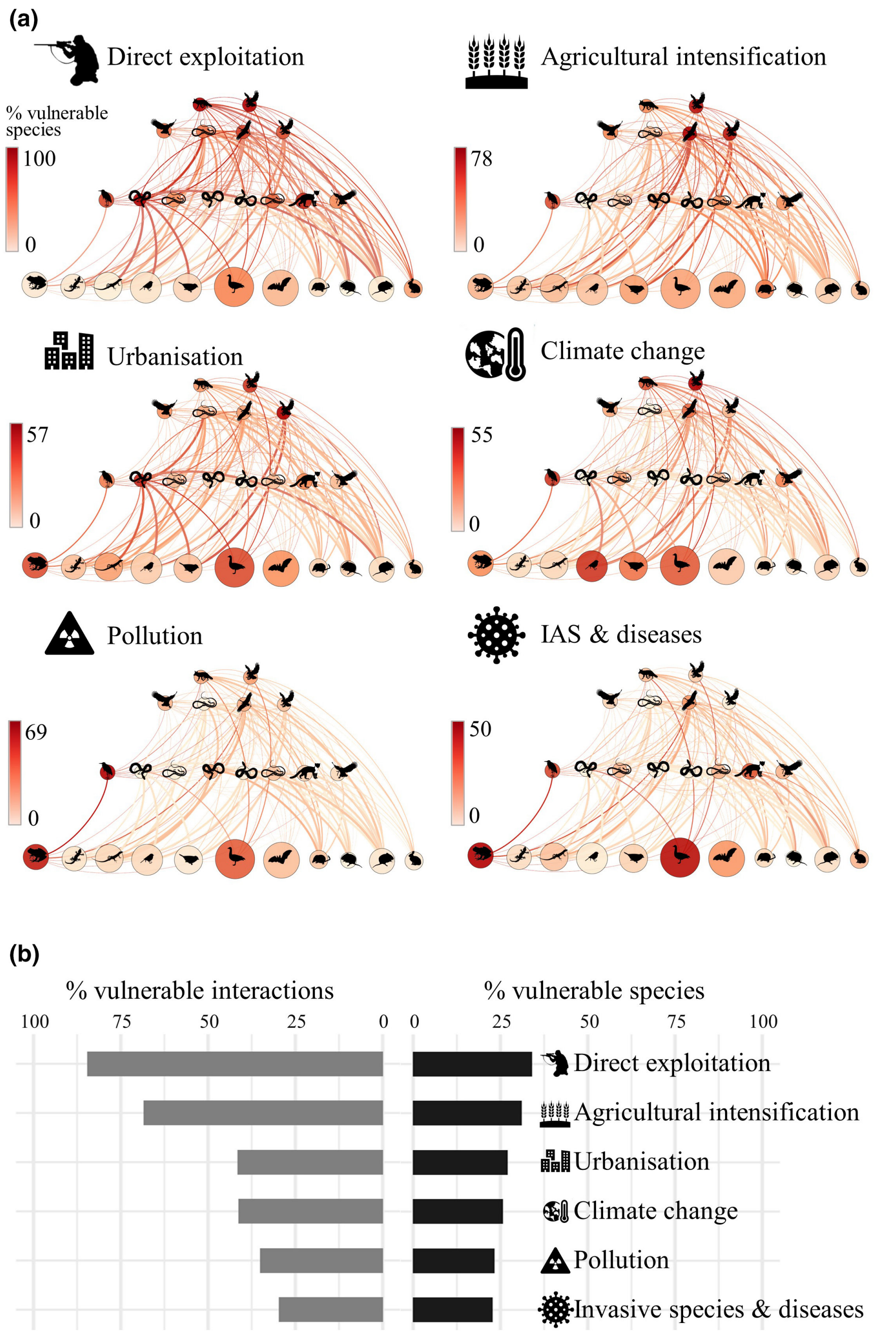

FIGURE 1 Threats to the European vertebrate metaweb. (a) Each network represents the metaweb, where nodes are trophic groups, and links represent feeding interactions between trophic groups. The color intensity of the node represents the proportion of species in each group affected by the threat. Link color is the mixed color of the two interacting nodes. Node size represents the number of species within the group, and link width represents the number of feeding interactions between trophic groups. (b) Barplots showing the percentage of species vulnerable to each threat and the percentage of interactions in the metaweb associated with these species. Right: percentage species vulnerable to each threat type. Left: percentage of interactions in the metaweb associated with vulnerable species (both predator and prey). These results only include interactions between species that co-occur at least once in Europe. IAS, invasive alien species.

interactions [95% CI: 38.8–38.9]; 22% species [95% CI: 22.3–22.4] and 35% interactions [95% CI: 35.1–35.3] were vulnerable to pollution; 21% species [95% CI: 21.3–21.4] and 33% interactions [95% CI: 32.5–32.6] were vulnerable to IAS and diseases. Combining the number of both vulnerable interactions and species, we highlighted hotspots of food web vulnerability to major threats across Europe, that is, with a high number of vulnerable species and interactions (Figure 6). These were mostly located in species-rich areas, but spatial patterns of vulnerability hotspots differed between threat types. Hotspots of food web vulnerability to direct exploitation and agricultural intensification were located in Spain (Pyrenees, Cantabria, and the Central system), the southeast of France, northern Greece, and the Baltic states. Hotspots of food web vulnerability to pollution were concentrated in the east of France, northeast Poland, and the Baltic states; while hotspots of food web vulnerability to climate change were located in Spain (Pyrenees and Central system) and the southeast of France.

4 | DISCUSSION

In 1962, Rachel Carson published *Silent Spring*, describing how the impacts of anthropogenic threats such as pesticides can spread in the entire food chain (Carson, 2000). Since then, conservation efforts have increased globally (Maxwell et al., 2020), but remain insufficient compared to the scale and intensity of anthropogenic

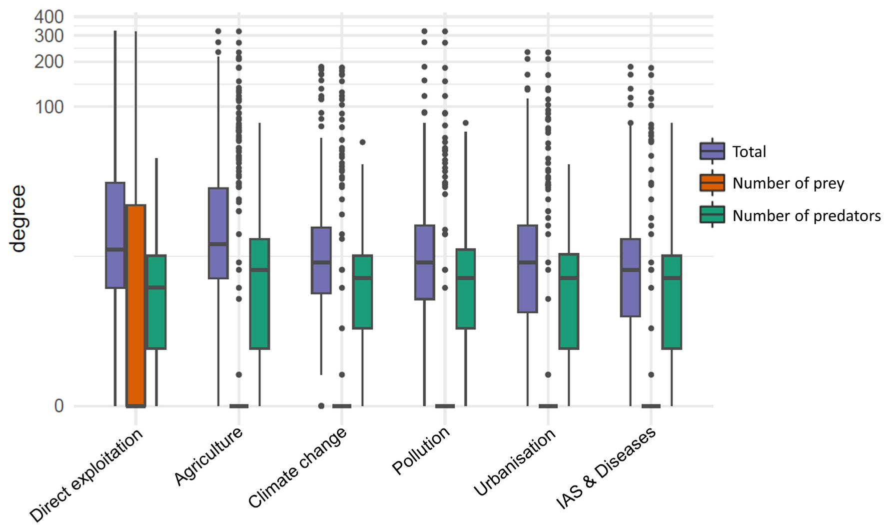

FIGURE 2 Relationship between the degree of species and their vulnerability to each threat. We consider three types of degree: number of prey in orange, number of predators in green and total number of neighbors (i.e., total degree) in purple. The *y*-axis is presented on a pseudo-logarithmic scale. IAS, invasive alien species.

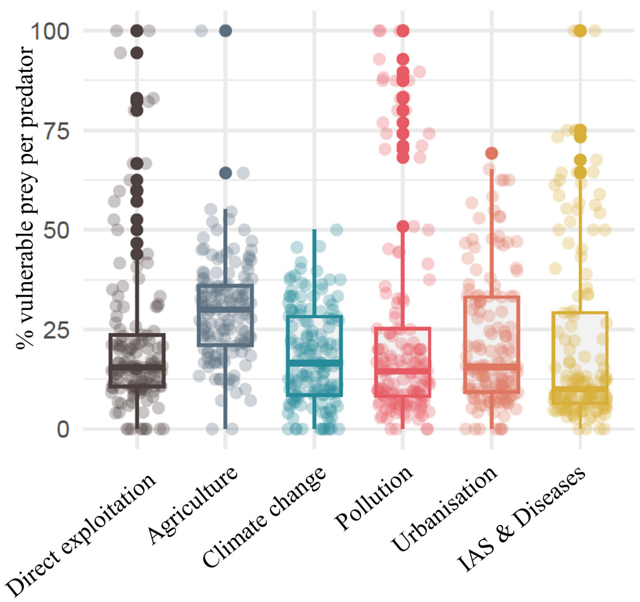

FIGURE 3 Indirect vulnerability of predators in the metaweb to each threat. These boxplots show, for each predator, the percentage of prey species that are vulnerable to different subcategories of threat. Each dot corresponds to one predator species (i.e., that have at least one terrestrial vertebrate prey). The *y*-axis shows the percentage of prey of this predator species that is affected by the threat type on the *x*-axis. IAS, invasive alien species.

pressures on ecosystems. Sixty years after *Silent Spring*, we are only beginning to understand how different types of threats are impacting interaction networks at large spatial and taxonomic scales. Our study is one of the first to analyze the potential impacts of anthropogenic pressures on food webs at a macroecological scale (Botella et al., 2024; Fricke, Hsieh, et al., 2022). Our findings suggest that species interactions can improve our understanding of the far-reaching impact of threats on biodiversity. In particular, we showed that interactions tend to be disproportionately more vulnerable to certain threats relative to species, in particular in the cases of direct exploitation and agricultural intensification. Because both threats affect highly connected species, these pressures may cause ecosystem disruption and extinction cascades (Morton et al., 2022).

The impact of direct exploitation on terrestrial vertebrates is unsurprising given the numerous species that have been hunted to extinction in the past (Dirzo et al., 2014; Fricke, Hsieh, et al., 2022). Our results highlight the need for a strict regulation of the direct exploitation of species (and particularly of top predators) in Europe in order to avoid large-scale disruptions of food webs (Estes et al., 2011). The scale of the impact of agricultural intensification on species and their interactions is also deeply worrying (Rigal et al., 2023). It is well established that agricultural intensification has a negative impact on many species through multiple processes: The use of pesticides and nitrates leads to a decline of biodiversity, particularly of invertebrates (Hallmann et al., 2017; Seibold et al., 2019). In Europe, over 300,000 tonnes of pesticides are used annually, and this trend is on the rise (European Commission, 2023), despite the documented negative impacts on biodiversity and on human health. Other impacts of agricultural intensification include excessive nutrient input leading to the eutrophication of ecosystems; direct disturbance and mortality of species such as ground-nesting birds and small mammals; the loss of habitats as well as hedges and green linear elements that form essential habitats for many species and their prey; expansion of agricultural land, simplification of agricultural landscapes, and loss of habitat heterogeneity (Stanton et al., 2018). Our study goes a step further by describing the staggering impact of direct exploitation and agricultural intensification on terrestrial vertebrate food webs across Europe (Figures 1 and 5). In particular, we found that agricultural intensification poses a significant threat to essential feeding resources for predator species. This is consistent with recent findings that suggest that food webs complexity and functional diversity decrease in highly intensive landscapes (Botella et al., 2024; Etard et al., 2022). The loss of interactions and food web complexity in intensive agricultural landscapes is concerning as terrestrial vertebrates and their interactions underpin essential ecosystem services, such as pest control (Civantos et al., 2012).

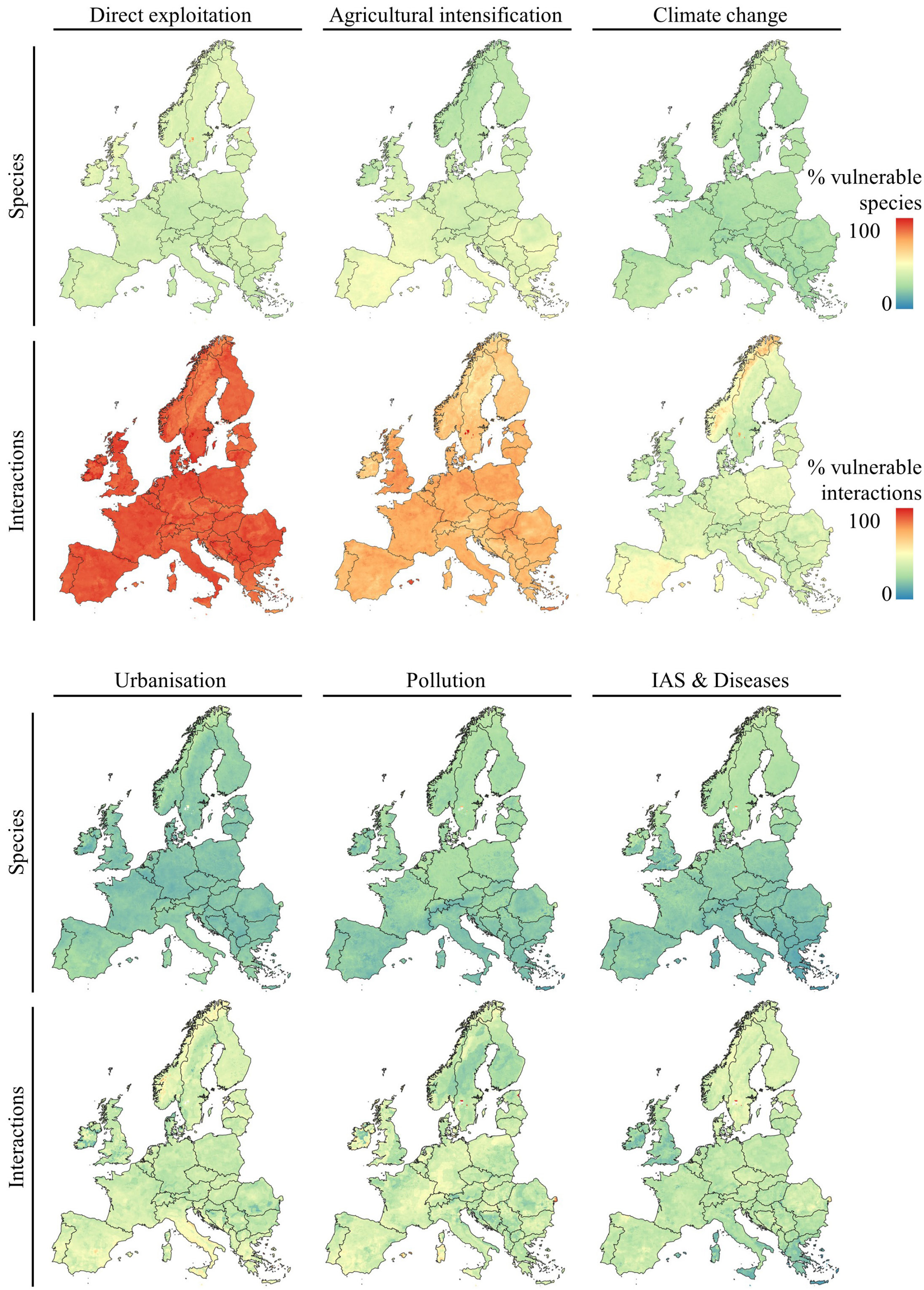

FIGURE 4 Maps of the vulnerability of species and interactions across Europe to the six major threats. Top row: Percentage of species in the grid cell that are vulnerable to each threat. Bottom row: percentage of interactions in the local food web that the vulnerable species are associated with. The color gradient used is the same for all maps. Map lines delineate study areas and do not necessarily depict accepted national boundaries. IAS, invasive alien species.

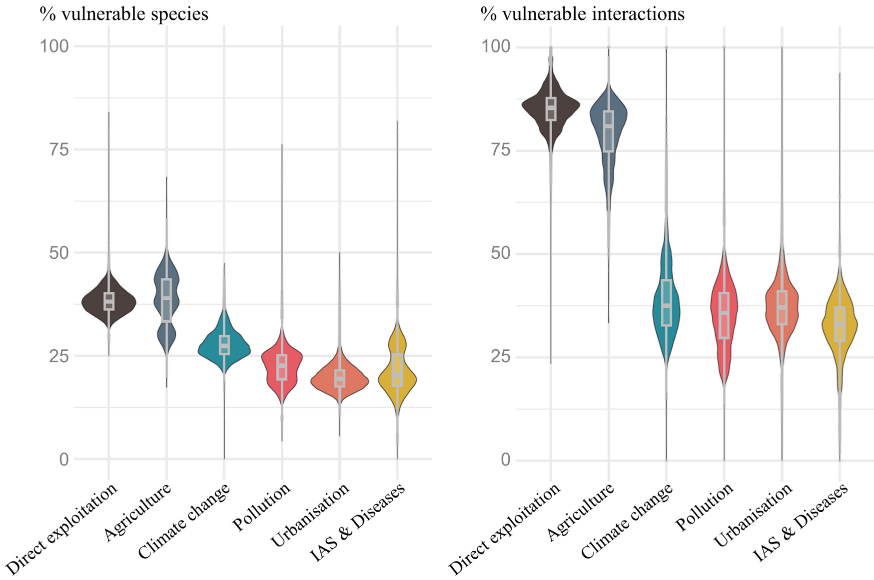

FIGURE 5 Vulnerability of species (left) and interactions (right) to different threats across all grid cells as mapped in Figure 4, shown as violin plots and boxplots. IAS, invasive alien species.

The disruption of food webs in highly intensive agricultural landscapes may result in the loss of natural processes that regulate pest populations, further amplifying pest outbreaks and the reliance on pesticide use. In particular, we found that agricultural intensification affects highly connected prey and previous studies have found that highly connected prey species are critical for the robustness of food webs, and indirectly support many ecosystem services (Keyes et al., 2021). Therefore, there is a pressing need to preserve biodiversity in agricultural systems (Ortiz et al., 2021), by de-intensifying agricultural practices, decreasing pesticide use, and re-establishing habitat heterogeneity within agricultural landscapes. While IAS and diseases and pollution impact relatively less species and interactions overall among terrestrial vertebrates, they affect over half of water-dependent species and trophic groups, meaning that freshwater and wetland food webs are at serious risk of disruption (Figure S5) (Dudgeon et al., 2006; Haase et al., 2023). Incorporating biotic interactions has the potential to improve our understanding of the scale of impacts of anthropogenic threats on biodiversity and nature's contributions to people (Fricke, Ordonez, et al., 2022) and to better inform policymaking on threat mitigation.

Interactions may disappear before species are lost (Valiente-Banuet et al., 2015), which triggers extinction debts. Further research is needed to investigate extinction debts and community dynamics following the loss or decline of interactions. In this study, we did not capture temporal or spatial variability since the threat dataset lacks temporal and spatial specificity (Harfoot et al., 2021). Yet, the vulnerability of species to anthropogenic threats may vary spatially across their ranges, and through time. Intraspecific traits variation as well as population abundance and dynamics may drive this spatial and temporal variation and modify the sensitivity of populations in different contexts to certain anthropogenic threats. Furthermore, interactions themselves can vary across space and time, due to interaction plasticity and behavioral changes, and species may adapt to the loss of interactions through interaction rewiring (Kamaru et al., 2024). It is challenging to include interaction plasticity with our metaweb approach, which is inherently static (Thuiller et al., 2023). However, the metaweb includes information on whether interactions are obligate (i.e., typical) or occasional. In the main analysis, we focused on the obligate interactions since they are typical interactions and critical for predator survival. Yet, interaction plasticity could influence the patterns of vulnerability, such as when predators switch to occasional interactions in the case of food limitations. In a preliminary analysis, we investigated whether considering occasional interactions in addition to obligate interactions influences the vulnerability of the metaweb: We found that considering both occasional and obligate interactions in the metaweb does not change the main results (see Annex S2 in the Supporting Information). Yet, there is evidence that interaction networks with many weak interactions (e.g., occasional interactions) and few strong links (e.g., obligate interactions) can contribute to buffering against disturbances (Tylianakis et al., 2010). There is a need for a more spatially and temporally explicit analysis to capture the variation both in species interactions and in their vulnerability to threats over space and time.

Here, we only investigated the vulnerability of food webs to threats, and not the actual impact of threats. To quantify the actual impact of threats, we could mobilize spatial data that reflect the risk of threat, related to land use intensification, agriculture intensification, forest management, urbanization, loss of forests, wetlands or grasslands, or to pollution (Schürings et al., 2024). Combining then the spatial risk of threat with the vulnerability of food webs to each threat would allow estimating threat impact across Europe in a spatially explicit way. In the case of agricultural intensity, this can be applied to current conditions (Dou et al., 2021), past changes (e.g., through CORINE change), or future scenarios of change (Powers & Jetz, 2019). Such an analysis would allow us (i) to identify orphaned species that lose all their interactions (Sandor et al., 2022), (ii) to locate areas where predators are losing vertebrate prey due to the

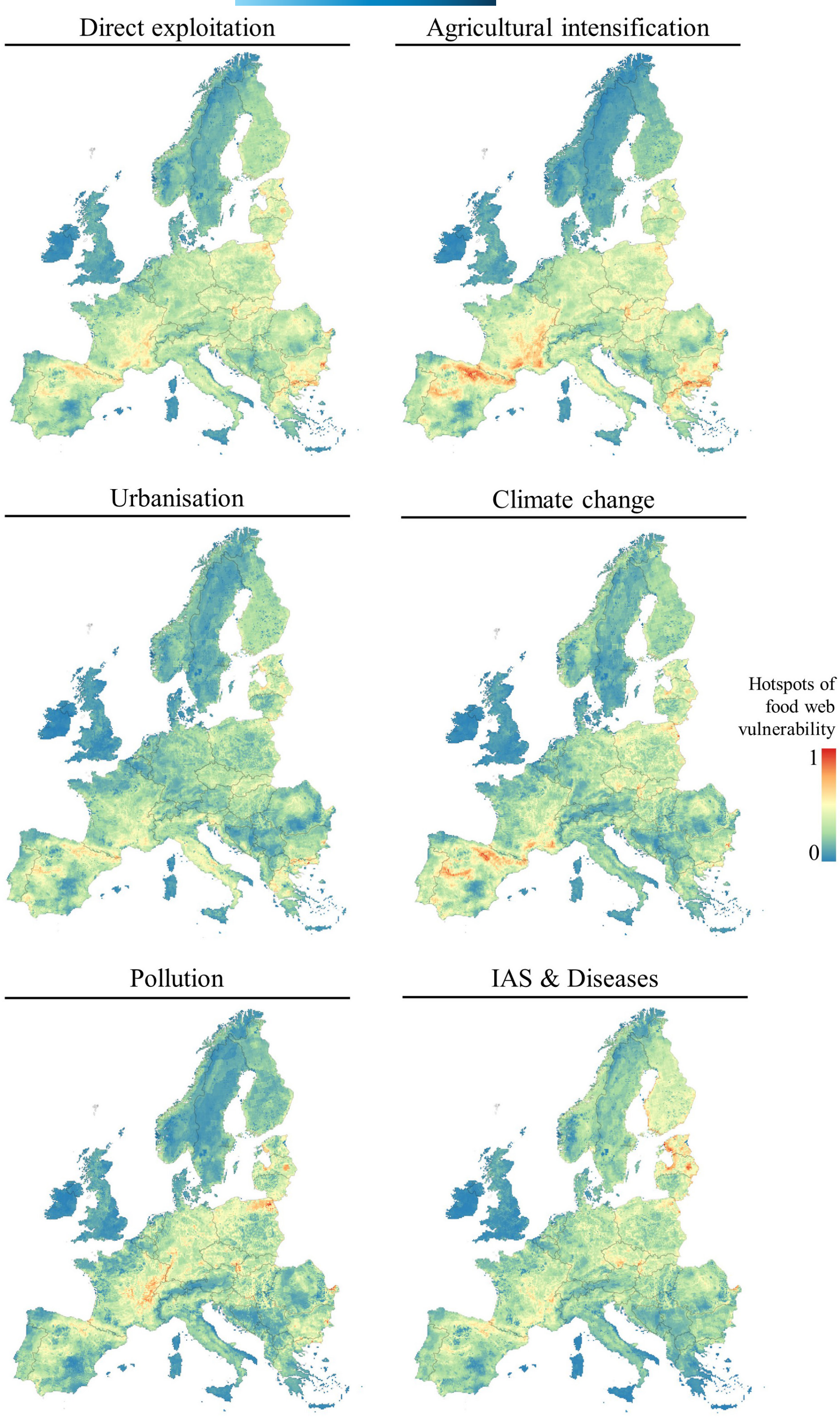

FIGURE 6 Hotspots of food web vulnerability to six major threats. The value in each cell is the multiplication of the number of vulnerable species (scaled between 0 and 1) and the number of vulnerable interactions (scaled between 0 and 1) in each grid cell, for each threat. Red color indicates areas with a high vulnerability of both species and interactions to each threat. Blue indicates low vulnerability values of species and interactions. Map lines delineate study areas and do not necessarily depict accepted national boundaries. IAS, invasive alien species.

combined action of multiple threats locally, and (iii) to quantify the cascading impact of threats on food webs across space. There is an overwhelming scientific consensus that different drivers of biodiversity loss interact synergistically (Isbell et al., 2022) and one threat exacerbates the effect of another (e.g., climate and agriculture) (Williams & Newbold, 2021). Food webs offer the opportunity to investigate the synergistic effect between threats on a species or community: A predator can lose part of its prey due to one threat, and the rest of its prey due to a different threat. Quantifying the impact of multiple threats on a food web can give a more realistic view of the risks posed by human activities to biodiversity (Botella et al., 2024). Furthermore, our analysis focused on the vulnerability of pairwise interactions, but we did not investigate the cascading impacts across trophic levels and secondary extinction risks (Estes et al., 2011). To do so, we would need to include invertebrate and plant species, as they form a big proportion of the diets of many terrestrial vertebrates. In addition, our analysis focused on trophic interactions—but non-trophic interactions (e.g., mutualism and competition) can also shape ecosystem dynamics and resilience (Bascompte & Jordano, 2007; Domínguez-García & Kéfi, 2024). Further research is needed for developing robust metrics to measure the vulnerability of interaction networks across space. In particular, one limitation of the metric we used here is that vulnerability hotspots tended to occur in species-rich areas. These species-rich areas are also a result of geographic (and taxonomic) sampling biases due to accessibility and socio-economic factors (García-Roselló et al., 2023; Hortal et al., 2015). There is thus a need to develop metrics which can quantify food web vulnerability in a way that is independent from network size. Exploring deviations from null models (Gaüzère et al., 2022), or using insights from graph theory (Bascompte, 2007), are promising avenues which could help improve estimates of food web vulnerability across space. We expect that the severity of cascading extinctions will result from the combination of the environmental threats faced by individual species, and the susceptibility of the community itself to propagate perturbations due to food web topology (Tylianakis et al., 2010). Trophic group redundancy, for example, is a key driver of food web resilience, as non-threatened species can fill the functional role associated with threatened species and their interactions (Sanders et al., 2018). Moving forward, identifying what components of biodiversity are most at risk, and where, will be critical to inform threat mitigation strategies and help identify priority areas for conservation (Tulloch et al., 2015).

AUTHOR CONTRIBUTIONS

Louise M. J. O'Connor: Conceptualization; data curation; formal analysis; investigation; methodology; visualization; writing – original draft. **Francesca Cosentino:** Data curation; resources; writing – review and editing. **Michael B. J. Harfoot:** Conceptualization; writing – review and editing. **Luigi Maiorano:** Data curation; resources; writing – review and editing. **Chiara Mancino:** Data curation; resources. **Laura J. Pollock:** Conceptualization; supervision; visualization; writing – review and editing. **Wilfried Thuiller:** Conceptualization; funding acquisition; project administration; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest regarding the publication of this article.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Zenodo repository at http://doi.org/10.5281/zenodo.10679902.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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