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Vulnerability of terrestrial vertebrate food webs to anthropogenic threats in Europe

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Key words: trophic interactions, anthropogenic pressures, European vertebrates, agricultural intensification, direct exploitation, pollution, climate change

Running title: Threats to European vertebrate food webs

26 Abstract

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

45 Introduction

46 Biodiversity is currently declining, and there are concerns that we may be entering the
47 6th mass extinction (Ceballos et al., 2017). Ecologists have made significant progress
48 in understanding the major threats that impact different components of biodiversity:
49 land use change (*e.g.*, agricultural expansion, deforestation), direct exploitation (*e.g.*
50 hunting and trapping), pollution, climate change and IAS (invasive alien species)
51 (Joppa et al., 2016; Maxwell et al., 2016; IPBES, 2019). These human activities result
52 in species and population declines by affecting various aspects of life history (breeding,
53 nesting and feeding) and overall fitness. To gain a comprehensive understanding of
54 the scale of the impacts of multiple human-induced threats to biodiversity, a
55 macroecological perspective has recently emerged, thanks to the increasing
56 availability of datasets at large spatial and taxonomic scales (Rigal et al., 2023). Recent
57 studies have mapped the impacts of these threats on a global scale and have revealed
58 that different groups of species face distinct direct threats (Harfoot et al., 2021,
59 Newbold et al., 2020). For example, pollution was shown to be a prevalent threat for
60 amphibians worldwide, while direct exploitation is a greater threat to mammals and
61 birds (Harfoot et al., 2021). Some functional groups (carnivores, large endotherms and
62 small ectotherms) were also found to be disproportionately impacted in disturbed
63 landscapes compared with other species (Newbold et al., 2020).

64 However, previous studies primarily focused on direct threats to species and did not
65 adequately consider the cascading impacts that can arise from biotic interactions,
66 particularly trophic interactions. Species are indeed not independent of each other.
67 Species are interconnected in food webs, meaning that any human activity that
68 threatens one species or a group of similar species may indirectly affect others (Strona
69 & Bradshaw, 2018). For example, the decline or loss of prey can significantly impact a
70 predator's feeding success and survival, potentially leading to predator extinction
71 (Dobson et al., 2009). These indirect threats can be particularly strong in the case of
72 trophic specialists (a predator feeding on a specific prey), or when a threat extirpates
73 a set of species that constitute the overall resource required by one or more predators.
74 Examining trophic interactions can thus shed light on the cascading impact of threats
75 on interacting communities and ecosystem functioning (Keyes et al., 2021; Morton et
76 al., 2022). However, the overall impact of multiple threats on the intricate web of
77 interactions within ecosystems remains poorly understood. This is mainly due to i) a
78 lack of available data for interactions and ii) the fact that numerous studies focused on
79 one guild, within which trophic interactions are limited. A recent study used
80 simulations to quantify the loss of biotic interactions in seed dispersal networks
81 following habitat loss and showed that small amounts of habitat loss can cause up to
82 10% of species to lose their interaction partners (Sandor et al., 2022). But these
83 questions have yet to be addressed at a macroecological level and for large food webs.

84 In this study, we aim to bridge this knowledge gap by addressing two key questions: i)
85 Can considering species interactions improve our understanding of the impact of
86 multiple threats on biodiversity? ii) Which species, interactions, and trophic groups

87 are most vulnerable to which threats, and where? To answer these questions, we
88 analysed the vulnerability of all described European vertebrate species and their
89 trophic interactions to six major threats: agricultural intensification, direct
90 exploitation, urbanisation, climate change, pollution and invasive alien species (IAS)
91 and diseases. These six major threats each affect over 200 terrestrial vertebrates
92 species in Europe (Table S1), and are defined as follows: i) Agricultural intensification
93 involves expansion of agricultural land into previously uncultivated areas, the
94 simplification of agricultural landscapes through the removal of green linear elements
95 (e.g. hedgerows, woodland), and the widespread use of pesticides and fertilisers to
96 maximise yields. ii) Direct exploitation in the context of terrestrial vertebrates involves
97 hunting, persecution (direct killing or trapping due to perceived threats to human
98 interests), and collection for the pet trade. iii) Urbanisation encompasses the
99 expansion of housing, construction of commercial and industrial infrastructure,
100 leisure facilities, and increased human disturbance. iv) Climate change in the context
101 of European ecosystems refers to warming temperatures, changes in precipitation
102 patterns, and extreme weather events. v) Pollution refers to the introduction and
103 accumulation of harmful substances in the environment, including chemicals,
104 industrial pollutants, heavy metals, as well as the accumulation of solid waste (e.g.
105 plastics and landfill). vi) IAS and diseases refer to the biotic threats posed by
106 introduced species to vulnerable native species. We integrated data from the IUCN
107 European regional red list data on species threats, trophic interactions (Maiorano et
108 al., 2020), and geographic distributions (Maiorano et al., 2013). First, we examined
109 whether species' vulnerability to threats is related to their position in the food web,
110 including their trophic role and the number of prey and predators, to identify whether
111 certain trophic roles are more vulnerable to specific threats. Next, we quantified the
112 vulnerability of interactions, with a particular focus on bottom-up risks, as the loss or
113 decline of prey resources directly compromises the survival of predator species.
114 Finally, we mapped the vulnerability of local food webs to the six different threats
115 across Europe. By integrating network ecology with assessments of threat impacts, our
116 study contributes to a better understanding of the scale of human activity impacts on
117 biodiversity.

118 Material and methods

119 Species threats data

120 We used the European Red List of species (*European Red Lists of Species*, 2018),
121 which describes the types of threats that each species is known to be vulnerable to,
122 anywhere within their range. We extracted the threat data for all 935 terrestrial
123 vertebrate species available in the dataset. Because the data on threats to species is
124 available in the form of sentences, we searched for character strings that correspond
125 to different threats (Table S1). We define threats as human activities that have led to,
126 are currently causing, or may potentially result in the decline or loss of biodiversity
127 (Joppa et al., 2016). Building on the IUCN red list threat classification scheme, we first
128 considered 9 primary threat categories (direct exploitation, agricultural
129 intensification, invasive alien species and diseases, pollution, climate change,
130 urbanisation, aquaculture and fishing, logging and forestry, and mining and energy
131 production), and 20 subcategories (Table S1). While there is some overlap with the
132 IUCN threat classification, our threat classification diverged from the IUCN global
133 threat classification in order to be more relevant to the context of European terrestrial
134 vertebrates. We then focused on the 6 major threat categories which affected the
135 highest number of terrestrial vertebrate species in Europe (at least 200 species),
136 following Harfoot et al., 2021. Results showing threat subcategories can be found in
137 the supporting information. The six major threats were:

- 138 1) Urbanisation is associated with habitat destruction and increased disturbance
139 by humans due to visitation and higher human density (Alberti et al., 2020; Des
140 Roches et al., 2021). It includes development of housing, , of commercial
141 infrastructure, and of infrastructure for tourism and leisure.
- 142 2) Direct exploitation leads to population declines, and it refers to the intentional
143 harvesting or removal of individuals for various purposes, such as recreational
144 hunting, persecution (poisoning, trapping, or shooting a species due to
145 perceived threats to humans), or collection for the pet trade.
- 146 3) Agricultural intensification refers to the increased productivity of agricultural
147 systems and a transition from traditional farming practices to intensive
148 management practices, expansion of agricultural land, increased agrochemical
149 and pesticide use, loss of hedges and green linear elements, simplification of
150 landscapes and loss of habitat heterogeneity.
- 151 4) Pollution refers to the introduction and accumulation of contaminants into the
152 natural environment (in particular for vertebrates, in the water and in the soil),
153 leading to habitat degradation and population declines due to *e.g.* the loss of
154 food sources or direct toxicity to organisms.
- 155 5) Invasive alien species and Diseases refer to the biotic threats to vulnerable
156 native species. Invasive Alien species with documented impacts on European
157 vertebrates include the American mink, Louisiana crayfish, gray squirrel, and
158 the raccoon directly impact native vertebrates through predation and

159 competition for resources and the spread of diseases. Pathogens include fungus,
160 parasites, viruses with a documented impact on vertebrates in Europe, such as
161 chytridiomycosis, myxomatosis, malaria, influenza.
162 6) Climate change refers to any alteration in the climatic conditions that influence
163 species distributions, phenology and life history: this includes warming,
164 droughts, severe winters, extreme weather events.

165 Metaweb of trophic interactions

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

197 Species distributions

198 In addition to analysing threats at the level of the metaweb, we also analysed the
199 vulnerability of vertebrate food webs across space. The study area covered the spatial
200 extent of the European Union (EU) with the United Kingdom (EU28 +), Norway,
201 Switzerland, and the Western Balkans (Serbia, Kosovo, North Macedonia,
202 Montenegro, Albania, and Bosnia and Herzegovina). We excluded Iceland, Turkey and
203 Macaronesia to avoid border effects. We considered all species that are included in
204 both the European red list dataset and the European Tetra-EU database (Maiorano et
205 al., 2020), which includes only native species and resident and breeding birds. We
206 extracted the distributions of the species occurring in the study area from (Maiorano
207 et al., 2013). These distributions were obtained by combining the extent of occurrence
208 for each species with their habitat requirements (also known as Area of Habitat maps
209 (Lumbierres et al., 2022)). Species distributions were mapped in a regular grid of 300
210 m resolution, where cells had values of zero for unsuitable habitat, one for marginal
211 habitat (habitat where the species can be present, but does not persist in the absence
212 of primary habitat) and two for primary habitat. Here, we treated primary habitat only
213 as ‘suitable habitat’, which provides a better prediction of the actual species
214 distribution (Ficetola et al., 2015). Given that a number of vertebrate species have large
215 home ranges (e.g. 100 km²), we upscaled distribution maps to a 10 × 10 km equal-size
216 area grid (ETRS89; total of 49,818 grid cells). We considered the species potentially
217 present in a 10 × 10 km cell if the grid cell contained at least one 300 × 300m cell of
218 suitable habitat. This led to a total of 804 species included in the spatial analyses for
219 which we had spatial distributions in the study area, trophic interactions, and
220 vulnerability to threats.

221 Quantifying the vulnerability of food webs to multiple threats

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

224 First, we investigated whether a species’ vulnerability to different threats was related
225 to the trophic role of the species. To build trophic groups, we used the same
226 methodology as in (O’Connor et al., 2020): we used the stochastic blockmodel (SBM)
227 on the metaweb (R package *blockmodels*; Leger et al., 2016) to group together the
228 species that eat the same food and are eaten by similar sets of predators. The output
229 of the SBM is an aggregated graph with nodes representing trophic groups, containing
230 species that have the same probability of interacting with all other nodes in the graph
231 (O’Connor et al., 2019). We also included non-vertebrate diet categories in the
232 metaweb in order to refine trophic groups of species that feed on other species than
233 terrestrial vertebrates. Thus, two species belonging to the same trophic group have
234 similar sets of predators and food resources (including terrestrial vertebrate prey
235 species, and diet categories). Diet categories were: algae, aquatic vegetation, fishes,
236 aquatic invertebrates, aerial invertebrates, invertebrates on ground, invertebrates on

237 vegetation, fruits, flowers, nectar, bulbs, berries, leaves, bark, seeds and grains, nuts,
238 woody vegetation, other plant parts, mushrooms, mosses and lichens, cultivated
239 plants, domestic animals, garbage, detritus, dung, carrion (Maiorano et al., 2020). The
240 goodness of fit of the model is assessed with the Integrated Classification Likelihood
241 (ICL) information criterion (Figure S2). Using the SBM, we partitioned the metaweb
242 along 2 to 30 groups, and selected the optimal number of groups based on the
243 partitioning of the metaweb that maximised the ICL criterion. This partitioned the
244 metaweb into 28 trophic groups (Figure S1 and S2, Table S2). We then computed the
245 proportion of species within each group that are vulnerable to each threat.

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

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

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

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

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

267 Mapping the vulnerability of food webs to anthropogenic threats 268 across Europe

269 We combined the species distributions with the metaweb to build local food webs in
270 each grid cell. We assumed that if two species interact in the metaweb and they both
271 occur in the grid cell, then the interaction exists in the local food web. We assumed
272 that an interaction is vulnerable if it is associated with a prey and/or predator species
273 that is impacted by a threat. In other words, vulnerable interactions can be both top-
274 down (the species may stop functioning as a predator) or bottom-up (the species may

275 stop functioning as a resource). We quantified the proportion of vulnerable species,
276 and vulnerable interactions in the food web that are associated to species that are
277 vulnerable to each threat type. We first compared the proportion of vulnerable species
278 and vulnerable interactions at the level of the metaweb. Then, we quantified these
279 proportions across space: for each grid cell, we quantify the proportion of species, and
280 interactions that are vulnerable to the major threat types (Figure 4 and 5).

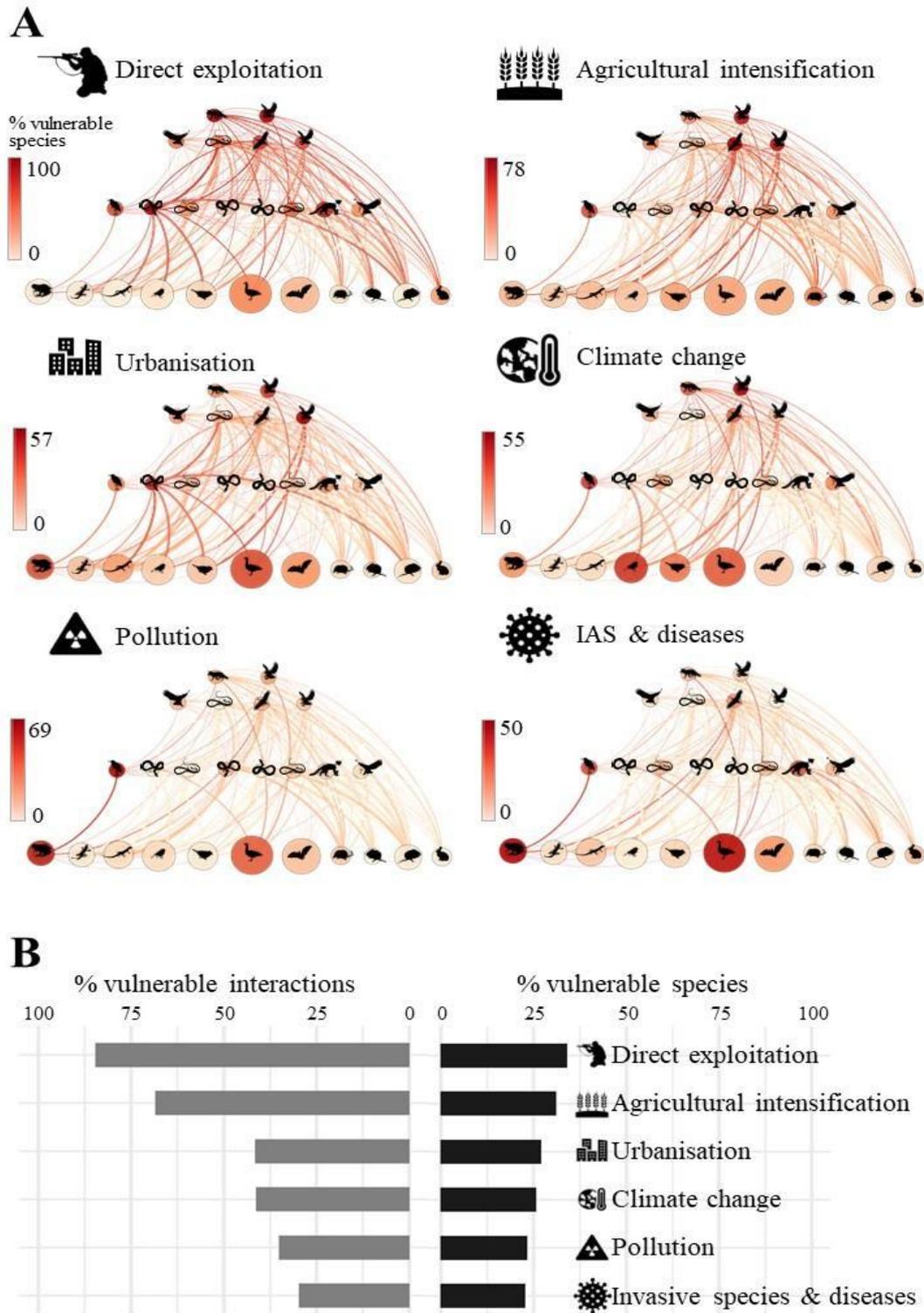
281 We then identified food web vulnerability hotspots to each major threat (Figure 6). To
282 make the metric comparable for all threat types, we first standardised (between 0 and
283 1) the number of vulnerable species to each threat type, and the number of vulnerable
284 interactions, across all grid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

291 All analyses were performed using R version 4.2.2 (R Core Team, 2022). For Figures
292 3 and 5 we used the R package *ghibli* (Henderson et al., 2022). The code and processed
293 data for the analysis are openly available in the GitHub repository maintained by the
294 authors: <https://github.com/LouiseOC/EU-foodweb-threats.git>.

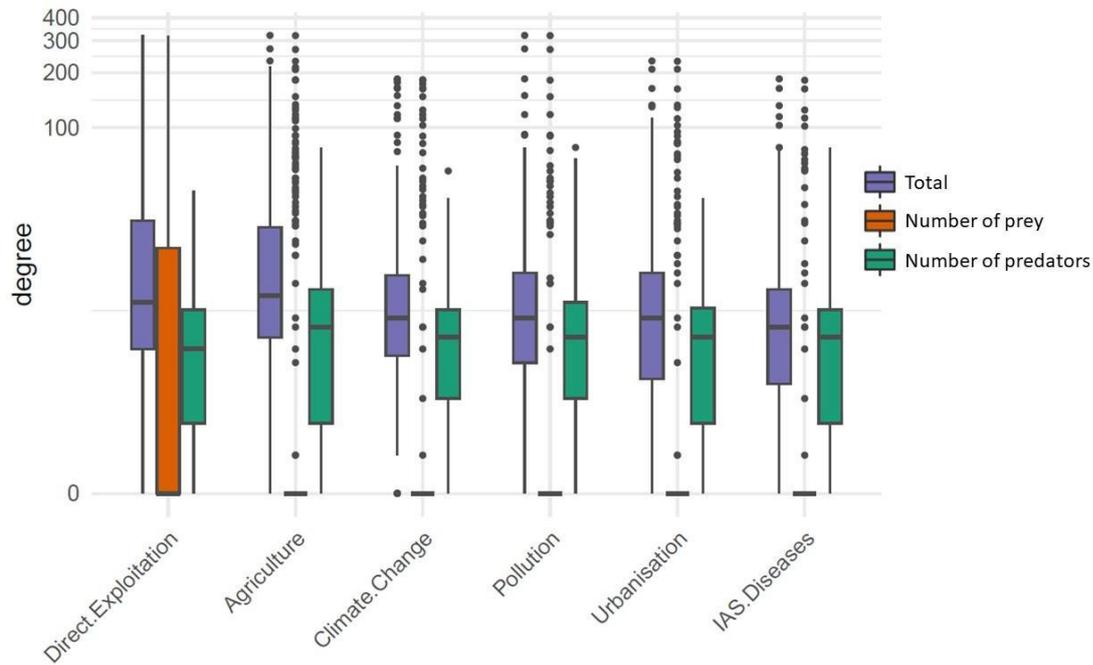
295

Results

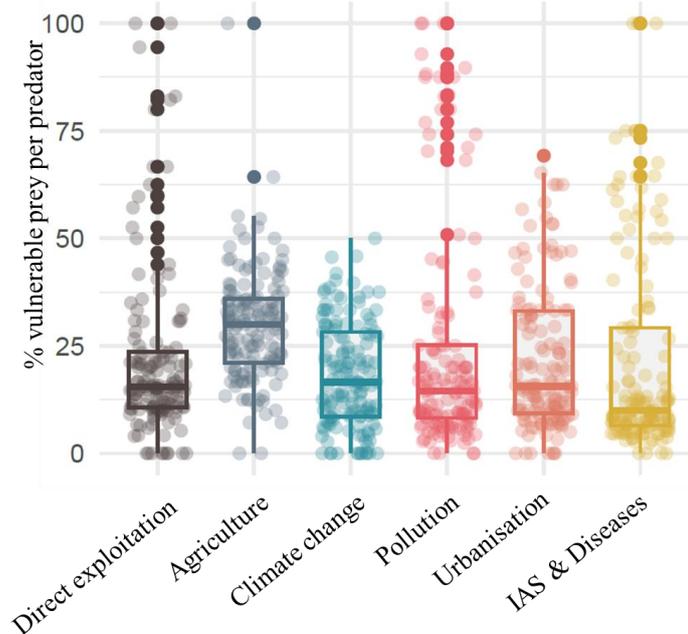
297 ***Different trophic groups face different threats.*** Direct exploitation was the
298 most impactful threat for European vertebrates, affecting 34% (387) species,
299 essentially top predators (Figure 1A) with a high number of prey (Figure 2). Species
300 vulnerable to direct exploitation were highly connected in the metaweb (they had a
301 total degree of 29 on average [95% CI: 25 to 34]), with 22 prey [95% CI: 17 to 27], and
302 7.5 predators [95% CI: 6.7 to 8.2] on average. As a result, 85% interactions in the
303 metaweb were vulnerable to direct exploitation (Figure 1B). Agricultural
304 intensification was the second most impactful threat, affecting 31% (285) species and
305 69% metaweb interactions. Importantly, species vulnerable to agricultural
306 intensification were also highly connected, with a total degree of 28 species on average
307 [95% CI: 23 to 33], including 18 prey [95% CI: 12 to 23] and 10 predators [95% CI: 8.9
308 to 11] on average. In particular, over 70% of birds of prey (groups 2, and 24) and 78%
309 of generalist predator species (group 13) were vulnerable to agricultural
310 intensification, primarily due to the use of pesticides (Figure S4); 42% of shrews and
311 moles (group 19) were also affected (Figure S1). Urbanisation was the third most
312 prevalent threat, affecting 255 species and 42% metaweb interactions, across multiple
313 trophic levels: 50% of birds of prey (groups 2 and 24), 50% of macro vipers (group 23),
314 41% of amphibians (group 1) and 41% wading birds (group 15) were found to be
315 vulnerable to urbanisation. Species vulnerable to urbanisation had a total degree of 18
316 [95% CI: 14 to 22] with 9.9 prey [95% CI: 5.9 to 14] and 7.9 predators [95% CI: 7.0 to
317 8.9] (Figure 2). Climate change was a threat for 26% (235) species and 41%
318 interactions across different trophic levels: passerines (group 11), birds of prey (group
319 24), aquatic predators (group 9). In terms of degree, species vulnerable to climate
320 change had a total degree of 19 [95% CI: 15 to 23] with 10 prey [95% CI: 6.1 to 15] and
321 8.6 predators [95% CI: 7.6 to 9.6] on average. Pollution, invasive alien species and
322 wetlands loss were major threats to all water dependent trophic groups: amphibians
323 (group 1), herbivorous water birds (group 15) and aquatic predators (group 9,
324 including the otter and predatory wading birds). Aquatic predators were also highly
325 vulnerable to direct exploitation (which affects 75% of aquatic predators) and
326 agricultural intensification (56%). Species vulnerable to pollution had a total degree of
327 19 [95% CI: 14 to 24] with 10 prey [95% CI: 4.8 to 15] and 8.8 predators [95% CI: 7.5
328 to 10]; and IAS and diseases affected species that had fewer interactions in the
329 metaweb on average compared with other threat types: species vulnerable to IAS and
330 diseases had a total degree of 15 [95% CI: 11 to 18], including 7.0 prey [95% CI: 3.5 to
331 10] and 7.9 predators [95% CI: 6.7 to 9.0] on average.



359 **Figure 1. Threats to the European vertebrate metaweb.** (A) Each network represents the
 360 metaweb, where nodes are trophic groups, and links represent feeding interactions between trophic
 361 groups. The colour intensity of the node represents the proportion of species in each group affected by
 362 the threat. Link colour is the mixed colour of the two interacting nodes. Node size represents the number
 363 of species within the group, and link width represents the number of feeding interactions between
 364 trophic groups. (B) Barplots showing the percentage of species vulnerable to each threat and the
 365 percentage of interactions in the metaweb associated with these species. Right: percentage species
 366 vulnerable to each threat type. Left: percentage of interactions in the metaweb associated with
 367 vulnerable species (both predator and prey). These results only include interactions between species
 368 that co-occur at least once in Europe.



369
 370 **Figure 2: Relationship between the degree of species and their vulnerability to each**
 371 **threat.** We consider 3 types of degree: number of prey in orange, number of predators in green and
 372 total number of neighbours (*i.e.*, total degree) in purple. The y-axis is presented on a pseudo-logarithmic
 373 scale.



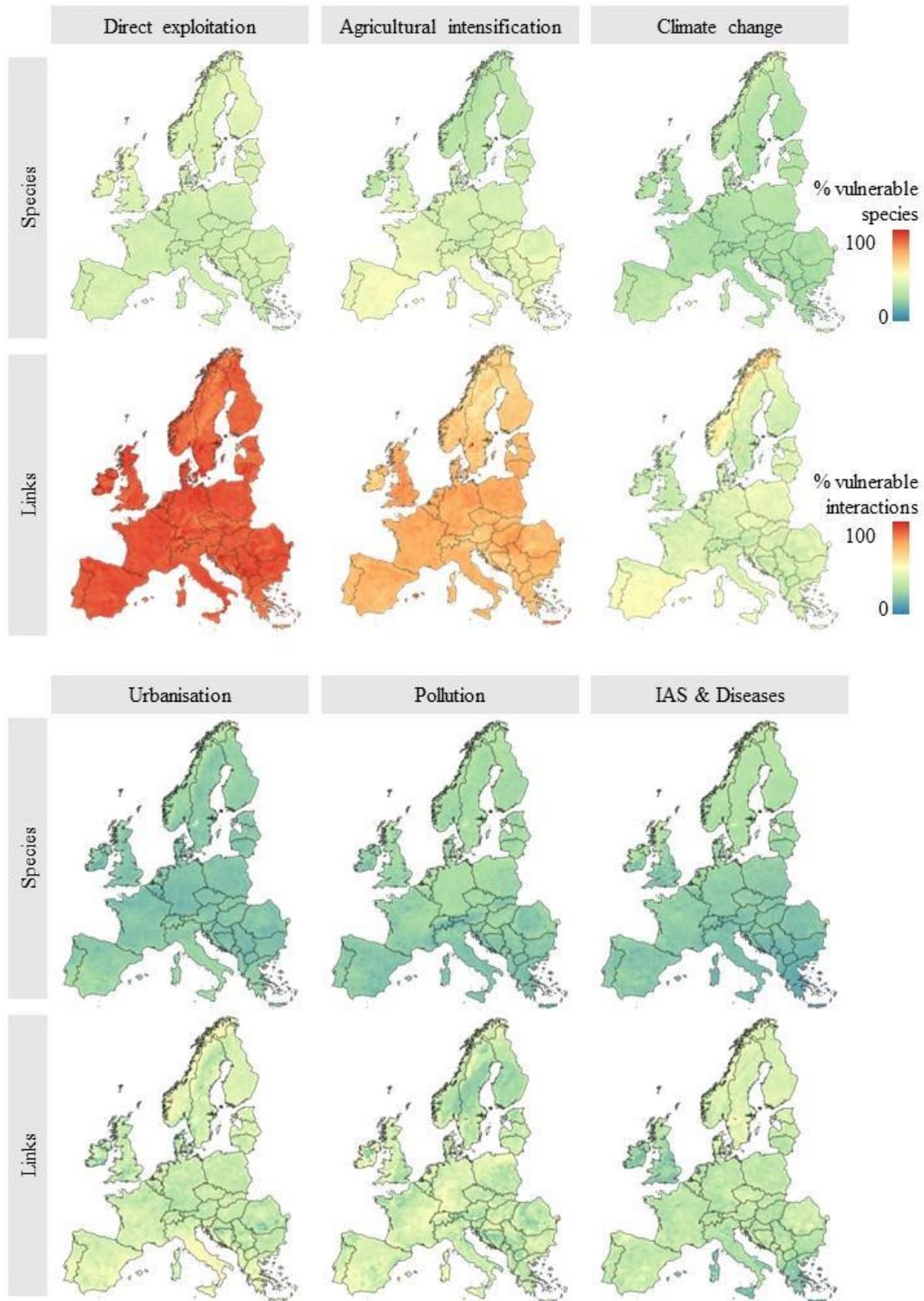
374
 375 **Figure 3: Indirect vulnerability of predators in the metaweb to each threat.** These boxplots
 376 show, for each predator, the percentage of prey species that are vulnerable to different subcategories of
 377 threat. Each dot corresponds to one predator species (*i.e.* that have at least one terrestrial vertebrate
 378 prey). The y axis shows the percentage of prey of this predator species that is affected by the threat type
 379 on the x axis.

380 **Most predators are indirectly vulnerable to agricultural intensification.**
381 When focusing on the vulnerability of prey for predators, we found that agriculture
382 was the most impactful threat for predator resources overall: on average, 33% of
383 predators' prey species are vulnerable to agricultural intensification (Figure 3) [95%
384 CI: 31 to 35%]. For example, *Lynx pardinus*, a specialist predator of the European
385 rabbit, was indirectly highly vulnerable to agricultural intensification, hunting, and
386 diseases that affect its main prey species. Climate change was another major indirect
387 threat for predators (affecting 23% prey per predator on average [95% CI: 21 to 25%])
388 (Figure 3), as well as urbanisation (affecting 27% of prey per predator [95% CI: 25 to
389 30%]), and pollution, which affected 30% of prey per predator on average [95% CI: 27
390 to 34%]. IAS and diseases affected 23% of prey per predator on average [95% CI: 20 to
391 26]. On average, 20% of prey species per predator were affected by direct exploitation
392 [95% CI: 21 to 25].

393 **Interactions are disproportionately more vulnerable than species.** In the
394 metaweb and across space, a higher number of vulnerable species inevitably leads to a
395 higher number of vulnerable interactions, but we found that some threats had a
396 disproportionate impact on interactions relative to the number of vulnerable species
397 (Figures 1B, 4 and 5). In the metaweb, we found that for instance, IAS and diseases
398 and pollution both affected 23% species and 30% metaweb interactions, while
399 pesticides affected 15% species and 53% interactions (Figure 1B and Figure S3). Direct
400 exploitation affected 34% species but these species were responsible for 85%
401 interactions in the metaweb, because these species were highly connected (Figure 2).
402 Similarly, across Europe, we found that the proportion of vulnerable interactions was
403 consistently higher than the proportion of vulnerable species in food webs (Figures 4
404 and 5). In some areas, 100% interactions in the food web were vulnerable to major
405 threats, while only a fraction of the species were vulnerable (Figure 5). The difference
406 between species vulnerability and interaction vulnerability varied with the threat type.
407 In the case of direct exploitation and agricultural intensification, the proportion of
408 threatened interactions was 85% [95% CI: 85.17 to 85.25%] and 79% [95% CI: 78.9 to
409 79.1%] on average, respectively. This was 2 to 3 times higher than the proportion of
410 threatened species, with 38% affected on average in both cases [95% CI: 38.25 to
411 38.31% for direct exploitation; and 38.4 to 38.5% for agricultural intensification]. The
412 difference between the proportion of vulnerable species and vulnerable interactions in
413 local food webs was lower for other major threats: on average across Europe, climate
414 change affected 28% species [95% CI: 27.78 to 27.84] and 39% interactions [95% CI:
415 38.8 to 38.9]; 22% species [95% CI: 22.3 to 22.4] and 35% interactions [95% CI: 35.1
416 to 35.3] were vulnerable to pollution; 21% species [95% CI: 21.3 to 21.4] and 33%
417 interactions [95% CI: 32.5 to 32.6] were vulnerable to IAS and diseases. Combining
418 the number of both vulnerable interactions and species, we highlighted hotspots of
419 food web vulnerability to major threats across Europe, *i.e.* with a high number of
420 vulnerable species and interactions (Figure 6). These were mostly located in species-
421 rich areas, but spatial patterns of vulnerability hotspots differed between threat types.
422 Hotspots of food web vulnerability to direct exploitation and agricultural

423 intensification were located in Spain (Pyrenees, Cantabria, and the Central system),
424 the southeast of France, northern Greece and the Baltic states. Hotspots of food web
425 vulnerability to pollution were concentrated in the east of France, northeast Poland,
426 and the Baltic states; while hotspots of food web vulnerability to climate change were
427 located in Spain (Pyrenees and Central system) and the southeast of France.

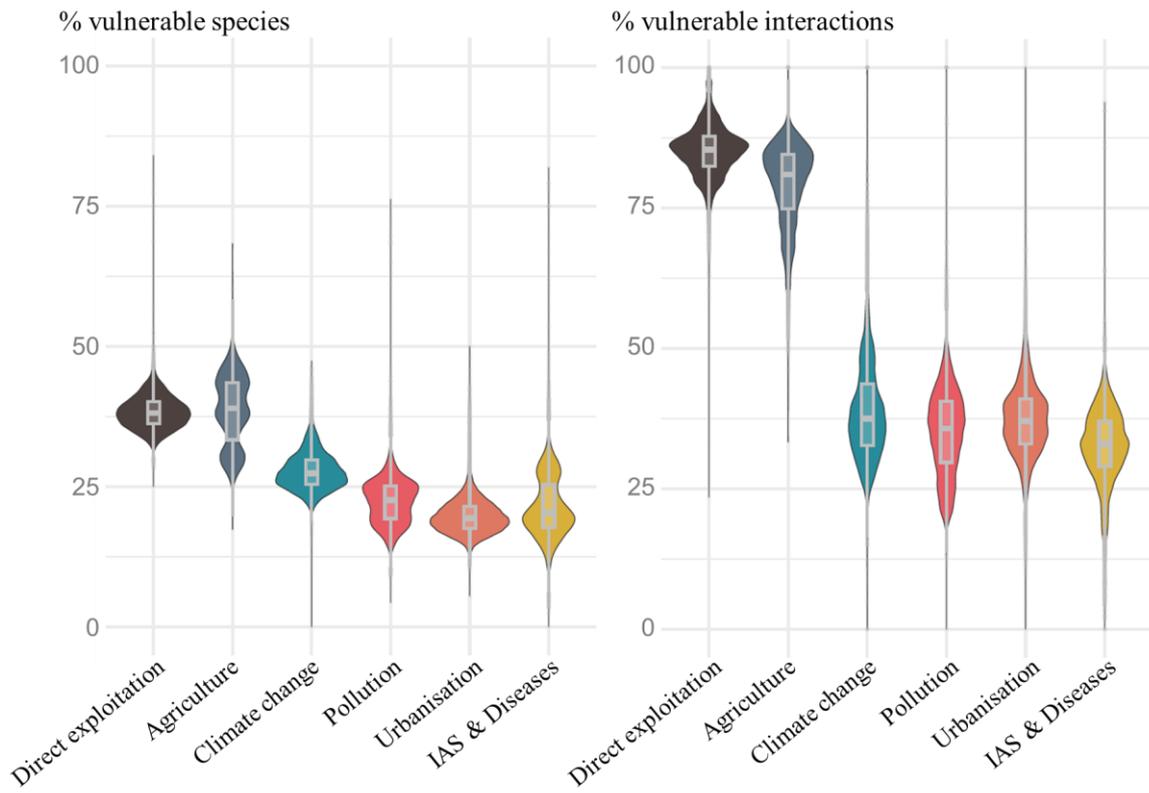
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430 **Figure 4: Vulnerability of species and interactions across Europe to the six major threats.**
 431 Top row: percentage of species in the grid cell that are vulnerable to each threat. Bottom row: percentage
 432 of interactions in the local food web that the vulnerable species are associated with. The colour gradient
 433 used is the same for all maps.

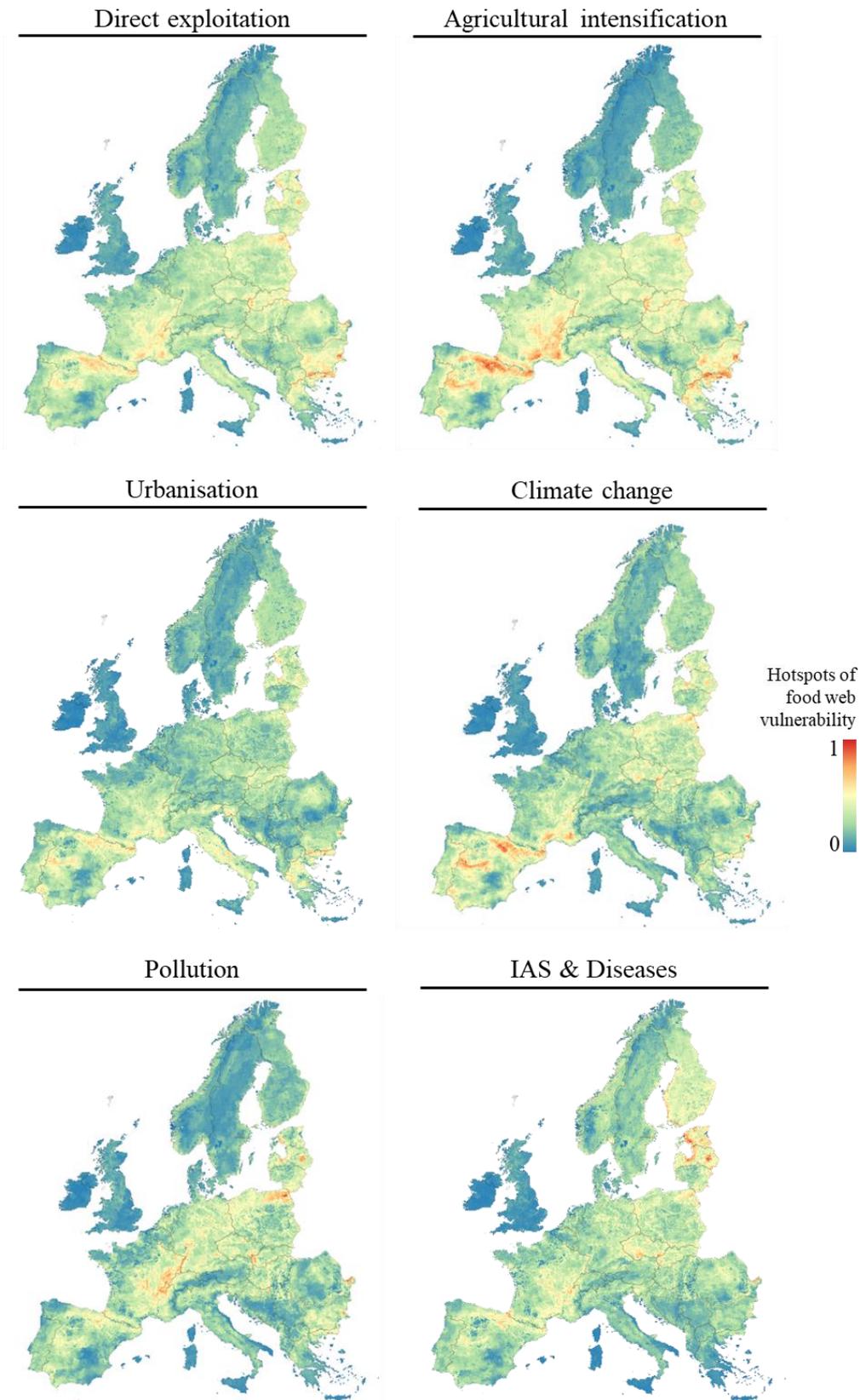
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436 **Figure 5:** Violin plots and boxplots showing the percentage of vulnerable species (left) and interactions
437 (right) to different threats across all grid cells as mapped in Figure 4.

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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 colour indicates areas with a high vulnerability of both species and interactions to each threat. Blue indicates low vulnerability values of species and interactions.

445 Discussion

446 In 1962, Rachel Carson published *Silent Spring*, describing how the impacts of
447 anthropogenic threats such as pesticides can spread in the entire food chain. Since
448 then, conservation efforts may have increased globally (Maxwell et al., 2020), but
449 remain insufficient compared to the scale and intensity of anthropogenic pressures on
450 ecosystems. Sixty years later, we are only starting to understand how different types of
451 threats are impacting interaction networks. Our study is one of the first to analyse the
452 potential impacts of anthropogenic pressures on food webs at a macroecological scale
453 (Fricke, Hsieh, et al., 2022; Botella et al., 2024). Our findings suggest that species
454 interactions can improve our understanding of the far-reaching impact of threats on
455 biodiversity. In particular, we showed that interactions tend to be disproportionately
456 more vulnerable to certain threats relative to species, in particular in the cases of direct
457 exploitation and agricultural intensification. Because both threats affect highly
458 connected species, these pressures may cause ecosystem disruption and extinction
459 cascades (Morton et al., 2022).

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

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

502 Interactions may disappear before species are lost (Valiente-Banuet et al., 2015),
503 which triggers extinction debts. Further research is needed to investigate extinction
504 debts and community dynamics following the loss or decline of interactions. In this
505 study, we did not capture temporal or spatial variability since the threat dataset lacks
506 temporal and spatial specificity (Harfoot et al., 2021). Yet, the vulnerability of species
507 to anthropogenic threats may vary spatially across their ranges, and through time.
508 Intraspecific traits variation as well as population abundance and dynamics may drive
509 this spatial and temporal variation and modify the sensitivity of populations in
510 different contexts to certain anthropogenic threats. Furthermore, interactions
511 themselves can vary across space and time, due to interaction plasticity and
512 behavioural changes, and species may adapt to the loss of interactions through
513 interaction rewiring (Kamaru et al., 2024). It is challenging to include interaction
514 plasticity with our metaweb approach, which is inherently static (Thuiller et al., 2024).
515 However, the metaweb includes information on whether interactions are obligate or
516 occasional. In the main analysis, we focused on the obligate interactions since they are
517 critical for predator survival. Yet, interaction plasticity could influence the patterns of
518 vulnerability, such as when predators switch to occasional interactions in the case of
519 food limitations. In a preliminary analysis, we investigated whether considering
520 occasional interactions in addition to obligate interactions influences the vulnerability
521 of the metaweb: we found that considering both occasional and obligate interactions
522 in the metaweb does not change the main results (Annex 2). Yet, there is evidence that
523 interaction networks with many weak interactions (*e.g.* occasional interactions) and
524 few strong links (*e.g.* obligate interactions) can contribute to buffering against
525 disturbances (Tylianakis et al., 2010). There is a need for a more spatially and
526 temporally explicit analysis to capture the variation both in species interactions and in
527 their vulnerability to threats over space and time.

528 Here, we only investigated the vulnerability of food webs to threats, and not the actual
529 impact of threats. To assess the actual impact of threats, we could mobilise spatial

530 data that reflect the risk of threat, related to land use intensification, agriculture
531 intensification, forest management, urbanisation, loss of forests, wetlands or
532 grasslands, or to pollution (Schürings et al., 2024). Combining then the spatial risk of
533 threat with the vulnerability of food webs to each threat would allow estimating threat
534 impact across Europe in a spatially explicit way. In the case of agricultural intensity,
535 this can be applied to current conditions (Dou et al., 2021), past changes (e.g. through
536 CORINE change), or future scenarios of change (Powers & Jetz, 2019). Such an
537 analysis would allow to i) identify orphaned species that lose all their interactions
538 (Sandor et al., 2022), ii) to locate areas where predators are losing vertebrate prey due
539 to the combined action of multiple threats locally, and iii) to quantify the cascading
540 impact of threats on food webs across space. There is an overwhelming scientific
541 consensus that different drivers of biodiversity loss interact synergistically (Isbell et
542 al., 2022) and one threat exacerbates the effect of another (e.g., climate and
543 agriculture) (Williams & Newbold, 2021). Food webs offer the opportunity to
544 investigate the synergistic effect between threats on a species or community: a
545 predator can lose part of its prey due to one threat, and the rest of its prey due to a
546 different threat. Quantifying the impact of multiple threats on a food web can give a
547 more realistic view of the risks posed by human activities to biodiversity (Botella et al.,
548 2024). Furthermore, our analysis focused on the vulnerability of pairwise interactions,
549 but we did not investigate the cascading impacts across trophic levels and secondary
550 extinction risks (Estes et al., 2011). To do so, we would need to include invertebrate
551 and plant species, as they form a big proportion of the diets of many terrestrial
552 vertebrates. In addition, our analysis focused on trophic interactions – but non-
553 trophic interactions (e.g. mutualism and competition) can also shape ecosystem
554 dynamics and resilience (Bascompte & Jordano, 2007; Domínguez-García & Kéfi,
555 2024). Further research is needed for developing robust metrics to measure the
556 vulnerability of interaction networks across space. In particular, one limitation of the
557 metric we used here is that vulnerability hotspots tended to occur in species-rich areas.
558 These species-rich areas are also a result of geographic (and taxonomic) sampling
559 biases due to accessibility and socio-economic factors (Hortal et al., 2015; Garcia-
560 Rosellò et al., 2023). There is thus a need to develop metrics which can quantify food
561 web vulnerability in a way that is independent from network size. Exploring deviations
562 from null models (Gaüzère et al., 2022), or using insights from graph theory
563 (Bascompte 2007), are promising avenues which could help improve estimates of food
564 web vulnerability across space. We expect that the severity of cascading extinctions
565 will result from the combination of the environmental threats faced by individual
566 species, and the susceptibility of the community itself to propagate perturbations due
567 to food web topology (Tylianakis et al., 2010). Trophic group redundancy, for example,
568 is a key driver of food web resilience, as non-threatened species can fill the functional
569 role associated with threatened species and their interactions (Sanders et al., 2018).
570 Moving forward, identifying what components of biodiversity are most at risk, and
571 where, will be critical to inform threat mitigation strategies and help locate priority
572 areas for conservation (Tulloch et al., 2015).

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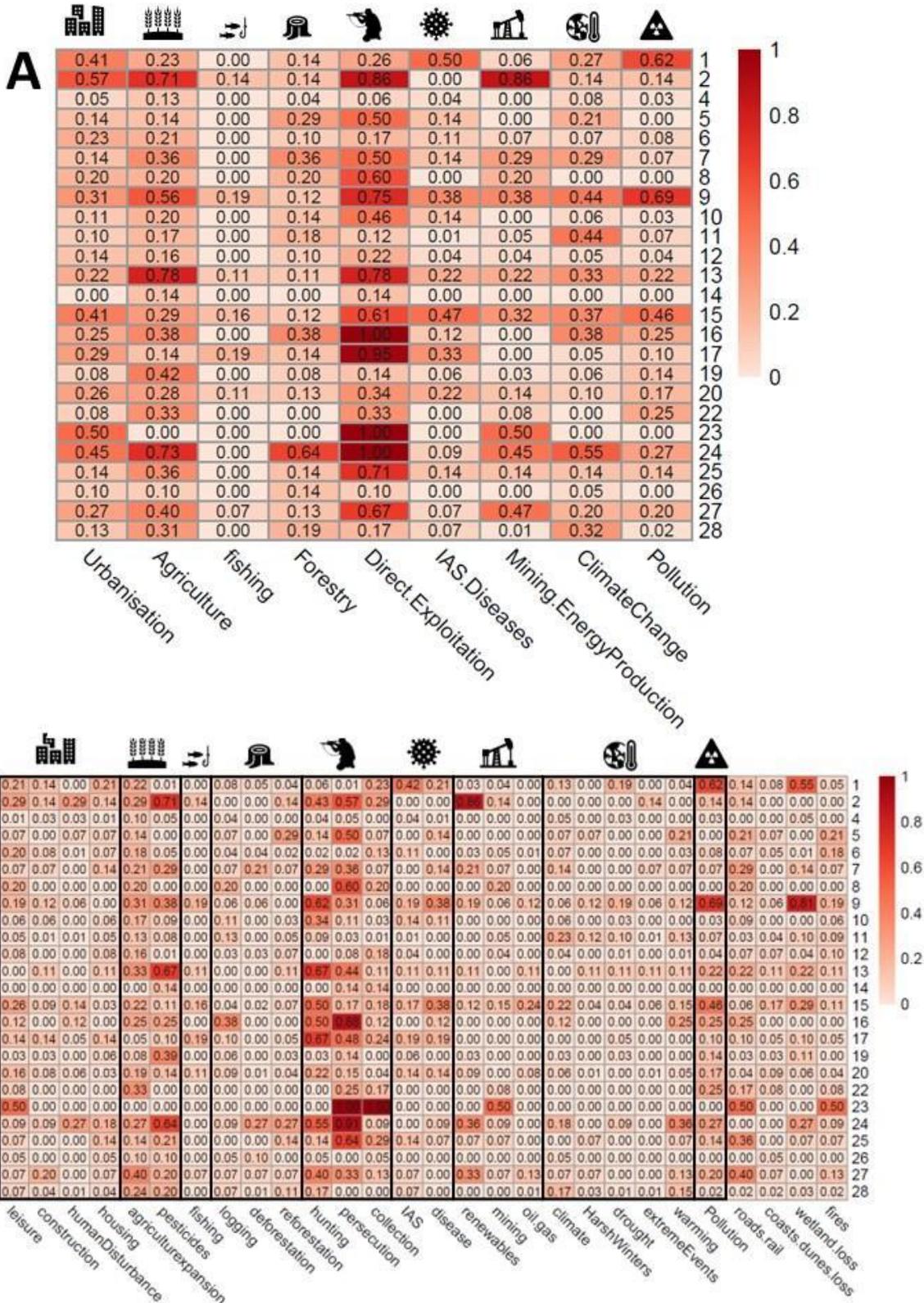
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Supporting information



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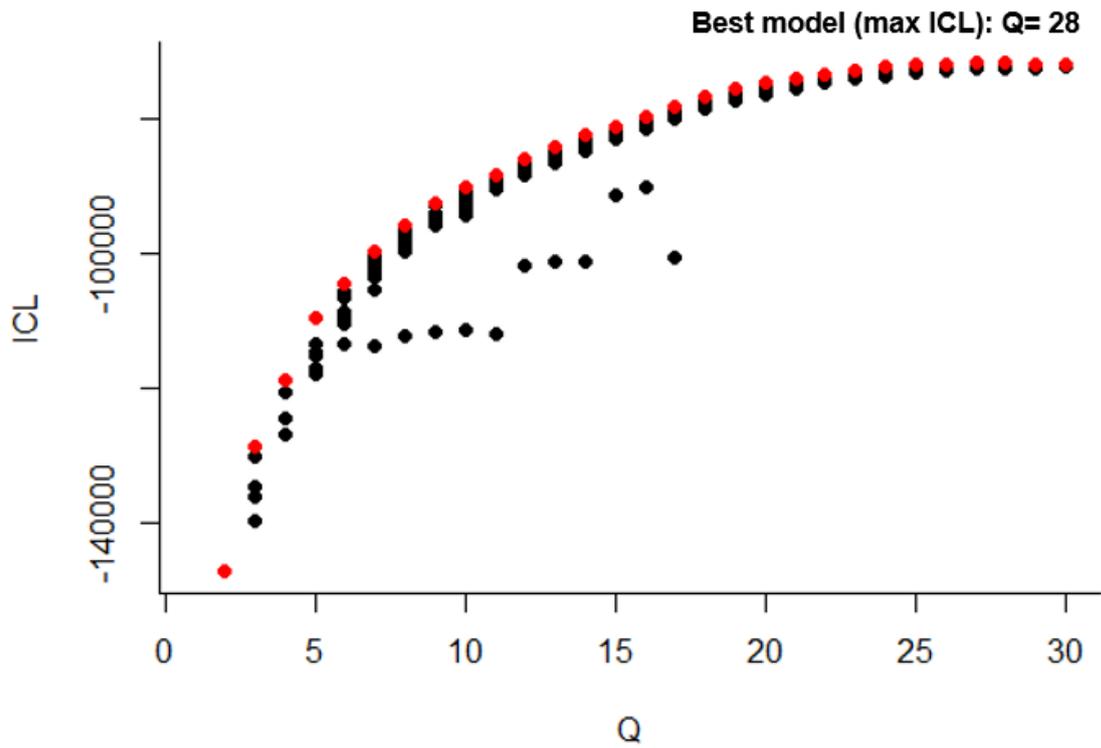
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Figure S1: Heatmap representing the proportion of vertebrate species within each trophic group (numbered from 1 to 28, in rows) that are sensitive to each main threat (A) and threat subcategory (B), according to the European red list database.

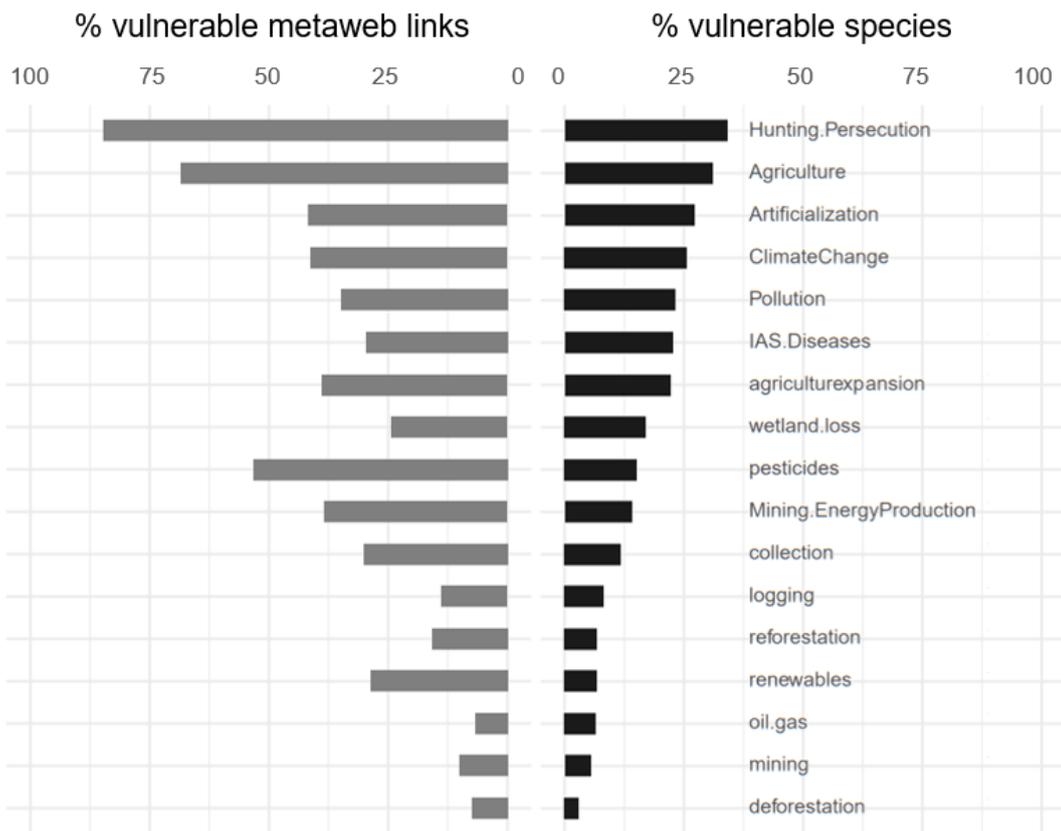
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750

751 **Figure S2:** Selecting the optimum number of trophic groups with the integrated
752 Classification Likelihood Information Criterion. We partitioned the metaweb along a
753 range of 2 to 30 classes (Q, on the x-axis) and selected the number of groups that
754 maximised the ICL criterion (y-axis).

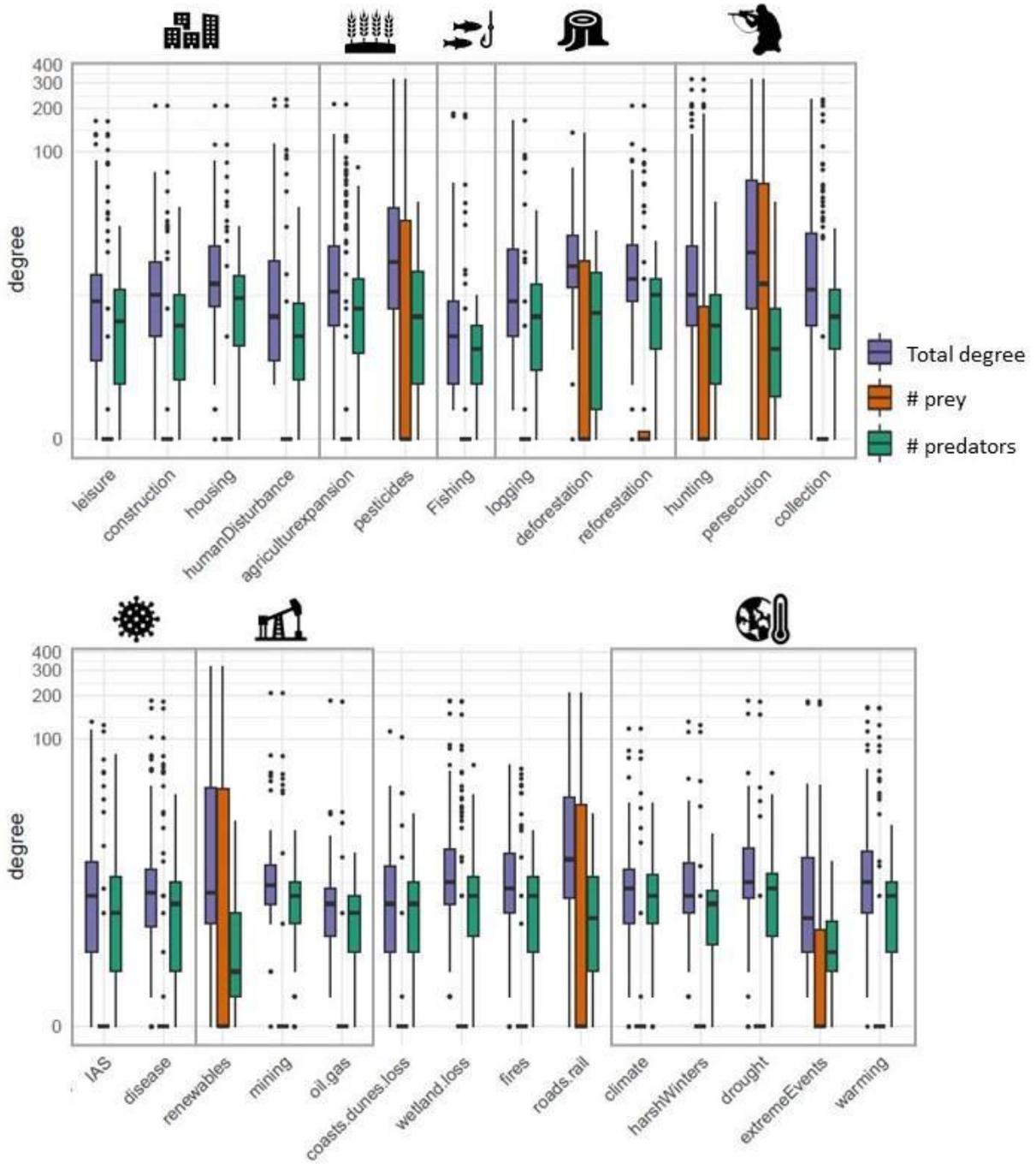
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756

757 **Figure S3:** Bar plots of the percentage of vulnerable species and vulnerable
 758 interactions in the metaweb (extended version of Figure 1B). Threat types are arranged
 759 by percentage of vulnerable species (top to bottom).

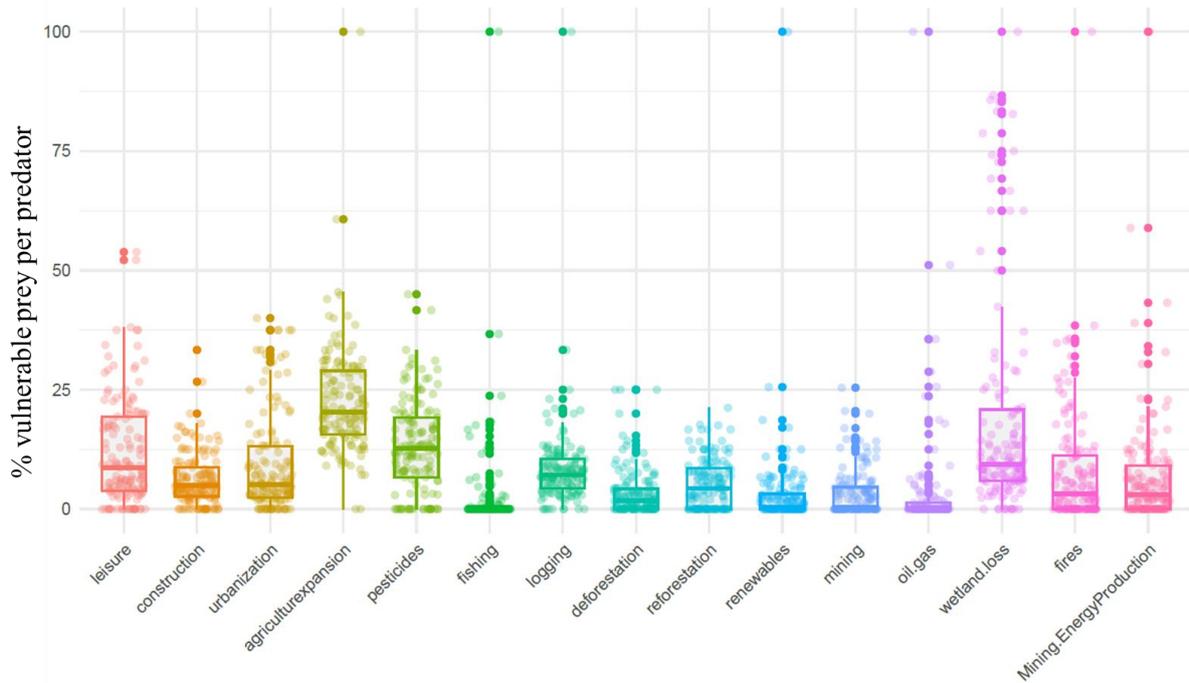
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761

762 **Figure S4:** Extended version of Figure 2 with subcategories of threats.

763



764

765 **Figure S5:** Extended version of Figure 3 with subcategories of threats, showing for
 766 each predator, the percentage of prey species that are vulnerable to different
 767 subcategories of threat (on the x-axis, and in different colours). Each dot represents a
 768 predator species. Interestingly, this figure shows that, while wetland loss was not
 769 considered among the major threats in this study due to a relatively smaller number
 770 of species impacted (Table S1), wetland loss stands out here as it tends to impact a
 771 large percentage of prey resources for many predator species.

772

773 **Table S1:** Threat classification and keywords used to create the threat classification scheme.

Threat category	Threat subcategory	Number of vulnerable species		Key words and character strings	Correspondence with IUCN threat classification scheme (2022)
Residential and commercial development (i.e. Urbanisation)	leisure, tourism	146	255	" ski ski resort skiing alpinism mountaineering tourism tourist recreati Recreation leisure golf yacht resort hotel"	1. Residential & Commercial development / 1.3 Tourism and recreation areas 6. Human intrusions and disturbance / 6.1 Recreational activities
	construction	71		"construction infrastructure development industrial development commercial development"	1. Residential & Commercial development / 1.2 Commercial & Industrial areas
	human disturbance	48		"disturbance by human human disturb disturbed by human disturbance by walk disturbance by peopl"	6. Human intrusions and disturbance
	housing and urban expansion	69		" housing urban expansion urbanization urbanisation urban develop"	1. Residential & Commercial development / 1.1 housing & urban areas
Agricultural intensification	agriculture expansion and intensification	202	285	"to agricultur livestock farming overgrazing increased cultivation abandonment of traditional agr intensive crop agricultural intensification intensive arable agriculture intensive farming agricultural development fertilisation agricultural activities intensification of farm hedge row"	2.1 Annual & perennial non-timber crops ; 2.3 Livestock farming & ranching ; 9.3 Agricultural & forestry effluents
	pesticides	140		"pesticid herbicid Pesticid biocide rodenticide"	9.3.3 Herbicides & pesticides

Fishing industry	fishing industry, aquaculture	57		"aquaculture Bycatch bycatch entanglement entangled fishing net fishing gear gillnet driftnet fishnet drown longline fish trawl fish intensification of fish fisheries overfishing"	2.4 Marine & freshwater aquaculture 5.4 Fishing & harvesting aquatic resources
Pollution	including chemical pollution in water and soils	219		"pollut chemical contamin antibiotic sewage waste water water pollution Water pollution carbamate run-off organochloride phosphate nutrient eutrophic acidification hypertrophication toxic"	9 Pollution
Energy production and mining	mining, quarries	51	136	"coal min acid rain mining gravel extract sand extract peat extract peat-extract quarries quarry mineral"	3.2 Mining & quarrying 9.2.2 Seepage from mining
	oil and gas exploration, extraction and transport	62		" oil spill petrol oil pollution gas Oil"	3.1 Oil & gas drilling 9.2.1 Oil spills
	renewables (wind farms, hydroelectricity, tidal energy plants)	66		"tidal energy wind turbine wind energy wind farm Wind farm hydroelectr"	3.3 Renewable energy
Forestry	logging	76	154	"logging sylvi wood harvesting forestry plantation"	5.3 Logging & wood harvesting 2.2 Wood & pulp plantations
	deforestation	28		"clear-cut deforest forest loss loss of forest removal of wood"	
	afforestation	60		"reforest afforest"	
Direct exploitation	hunting and exploitation	233	387	" trapping hunting hunted Hunting shoot game killing p	5.1 Hunting & collecting terrestrial animals

				oaching consumption harvest fur exploitation for food"	
	persecution	154		"persecut Persecut killed when encounter destroy egg destroy nest destruction of nest destruction of roost poison bait poisoning"	
	collection and pet trade	118		"collect pet pet trade"	
Invasive species and diseases	invasive alien species	130	212	"introduc invasi alien exotic American mink Louisiana crayfish"	8 Invasive & other problematic species, genes & diseases
	diseases and pathogens	123		" fung diseas virus viral hytridiomyco yxomatos pathogen parasites malaria influenza"	
Climate change and severe weather	including warming, droughts, severe winters, extreme weather events	235		"climate Climate climat cold winter harsh winter Harsh winter severe winter desertification drought aridity dessic de sicc decreased spring rain shorter rainy season reduced winter precipit reduced precipit reduced rain storms extremes temperature extreme extreme temperature extreme weather extreme climat Extreme weather Extreme climat Floods floods hot Hot warm Warm heat Heat temperature rise increasing temperature increased spring temperature increased summer tempera"	11 Climate change & severe weather
Other threats	loss of wetlands	158		"drainage wetland freshwater water extraction water abstraction"	7.2 Dams & water management/use 7.3 Other ecosystem modifications
	loss of coast and dune habitats	72		"coast dune"	7.3 Other ecosystem modifications

	fires	85	" fire Fire burn"	7.1.1 Increase in fire frequency/intensity
	roads and rail lines	80	"traffic accident road highway collision with cars cars vehicles heavy traffic train trains rail"	4.1 Roads & railroads

774

775

776 **Table S2:** Description of the species that typically characterise each trophic group

Trophic group ID	Composition	Size (number of species)
1	All amphibians: frogs, toads, and salamanders	78
2	Birds of prey (Montagu's harrier, five Falcon species, Arctic Skua) that feed on rodents, small birds, bird eggs, invertebrates	7
3	Diet categories: Plant parts (Berries, Bulbs, Flowers, Fruits, Leaves, Nectar, Other plant parts, Seeds, Grains, Forbs), aerial and aquatic invertebrates, fish	13
4	Rodents: mice (29 species in the <i>Muridae</i> family), voles and lemmings (48 species in the <i>Cricetidae</i> family) feeding on plants and invertebrates	77
5	Omnivorous species of birds, reptiles, and mammals that eat insects, berries, seeds (e.g. wild boar)	14
6	Lizards (<i>Lacertidae</i>)	92
7	Medium-sized birds of prey and owls: 7 species of the <i>Accipitridae</i> family (e.g. <i>Buteo buteo</i> , <i>Clanga pomarina</i>), 4 species of the <i>Strigidae</i> family, 2 species of the <i>Corvidae</i> family, and 1 skua (<i>Stercorariidae</i>)	14
8	4 <i>Dolichophis</i> species (whip Snakes) and the desert monitor	5
9	Intermediate freshwater predators feeding on fish, amphibians, aquatic invertebrates: mostly birds (wading birds (7 species of <i>Ardeidae</i> , 2 species of <i>Rallidae</i>), Smew (<i>Mergellus albellus</i>), Glossy ibis, black stork (<i>Ciconia nigra</i>)), the otter (<i>Lutra lutrea</i>), and 2 aquatic dependent snakes (<i>Natrix</i> species)	16
10	Hedgehogs, rabbits and hares, large rodents (marmots), squirrels	35

11	Passeriformes: Sylviidae, Muscicapidae, Tichodromidae, Troglodytidae, Sittidae, Regulidae, Hirundinidae, Pycnonotidae, Prunellidae, Cisticolidae, Paridae, Calcariidae, Phylloscopidae, Acrocephalidae, Aegithalidae, Bombycillidae, Certhiidae, Scotocercidae, Cinclidae, Locustellidae, Oriolidae, Panuridae, Remizidae	111
12	Predatory reptiles: 5 vipers, large lizards (8 <i>Agamidae</i> , 2 <i>Chamaeleonidae</i> , <i>Timon lepidus</i>), snake-like lizards (2 <i>Blanidae</i> , 3 <i>Anguidae</i>), 15 geckos (<i>Phyllodactylidae</i> , <i>Gekkonidae</i> , <i>Eublepharis</i>), 16 colubers (<i>Eirenis</i> genus), 17 skinks.	73
13	Intermediate, generalist predators (birds and mammals): white stork, night heron, corsac fox, Egyptian mongoose, red kite	9
14	Vipers that eats insects, lizards, small mammals	7
15	Medium and large sized omnivorous bird species. Most species in this group are semi-aquatic, including wading birds (<i>Scolopacidae</i> , <i>Rallidae</i> , <i>Podicipedidae</i> , the Flamingo), ducks (36 species of <i>Anatidae</i>), and seabirds (including seagulls, terns, auks (6 species of <i>Alcidae</i>), skua), . 40 species in this group are not semi-aquatic, but rather medium large birds living on steppe habitat: 17 species of the <i>Phasianidae</i> family, 7 species of <i>Corvidae</i> , 3 <i>Glareolidae</i> , and 3 species of <i>Otididae</i> , 9 <i>Columbidae</i> , 2 sandgrouse (<i>Pterocles</i>), and 2 woodpeckers.	160
16	Top predators feeding on mammals and birds: 2 foxes (red and arctic), the jackal (<i>Canis aureus</i>), 2 raptors (eastern imperial eagle (<i>Aquila heliaca</i>) and <i>Falco cherrug</i>), 3 large owls (including the eagle owl).	8
17	Top predators: wolverine, other mustelids (<i>Mustela</i> and <i>Martes</i> genus, the marbled polecat), wild cat, brown bear, seagulls (<i>Larus</i>), some large snakes	21
18	Diet categories: invertebrates found on ground and vegetation	2
19	Insectivorous small mammals: Shrews (28 <i>Soricidae</i> spp.) and moles (8 <i>Talpidae</i> spp.)	36
20	Peripheral species that have few predators (e.g. wolf or lynx) and/or no vertebrate prey: swifts, deer, vultures, ungulates, bats, turtles	141
21	Other diet categories: Algae, Aquatic vegetation, Mosses and Lichens, Mushrooms, Nuts, Cultivated Plants, Bark, Woody Vegetation, Carrion, Coprofagous, Detritus, Garbage.	12

22	Vipers (<i>Vipera</i>) and colubers (<i>Telescopus</i> , <i>Elaphe</i> , <i>Spalerosophis</i> , <i>Hemorrhoids</i> and <i>Hierophis</i> spp.)	12
23	2 <i>Macrovipera</i> spp.	2
24	Large birds of prey: Hawks (<i>Accipiter</i> spp.), Eagles (<i>Aquila</i> spp., <i>Clanga clanga</i> , <i>Haliaeetus albicilla</i> , <i>Hieraetus pennatus</i>), Harriers (<i>Circus</i> spp.)	11
25	Mammals, reptiles and snakes, intermediate predators	14
26	Small mouse-like rodents: <i>Gliridae</i> , <i>Dipodidae</i> , <i>Sminthidae</i> ,	21
27	Top predators: birds of prey (e.g., <i>Aquila nipalensis</i> , <i>Circaetus gallicus</i>), owls (e.g. <i>Bubo scandiacus</i> , <i>Surnia ulula</i>), wolf, lynx, large gulls (2 <i>Larus</i> spp.)	15
28	Passerines (finches, thrush, starlings) that eat invertebrates	94

777

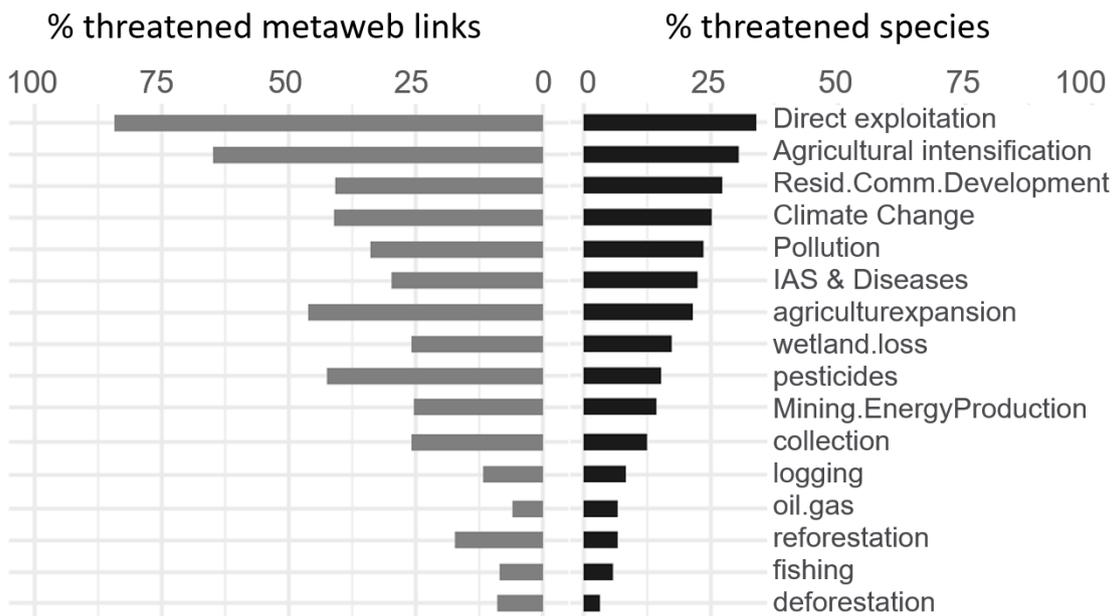
778 Annex 1: Resolving mismatches in taxonomic classification
779 between datasets

780 167 Amphibian, Reptile, Bird and Mammal species names listed in the European red
781 list dataset were not in the Tetra-EU dataset. We corrected taxonomical mismatches
782 (due to the use of synonyms) for 71 species. The remaining 96 species were either i)
783 non-native (e.g. the American bullfrog; the Canada goose; the black rat); or marine
784 mammals (e.g. pinnipeds and cetaceans); or ii) occurred outside of the European
785 continent, in Africa or Asia (e.g. *Pelophylax saharicus*; *Trogonophis wiegmanni*;
786 *Psammodromus blanci*; *Scelarcis perspicillata*; *Timon tangitanus*; *Accipiter badius*;
787 *Picus sharpei*); or iii) migratory birds that are vagrant in Europe (e.g. *Calidris bairdii*;
788 *Numenius tenuirostris*) or that winter in Europe (e.g. *Branta ruficollis*); or iv) species
789 that have only recently been recognized as a distinct species (e.g. *Larus michahellis*;
790 *Phylloscopus canariensis*; *Phylloscopus ibericus*); or v) extinct species (the great auk;
791 the Canary island oystercatcher; the aurochs; the Sardinian pika).

792 Annex 2: Including both typical and occasional interactions does
 793 not change main results

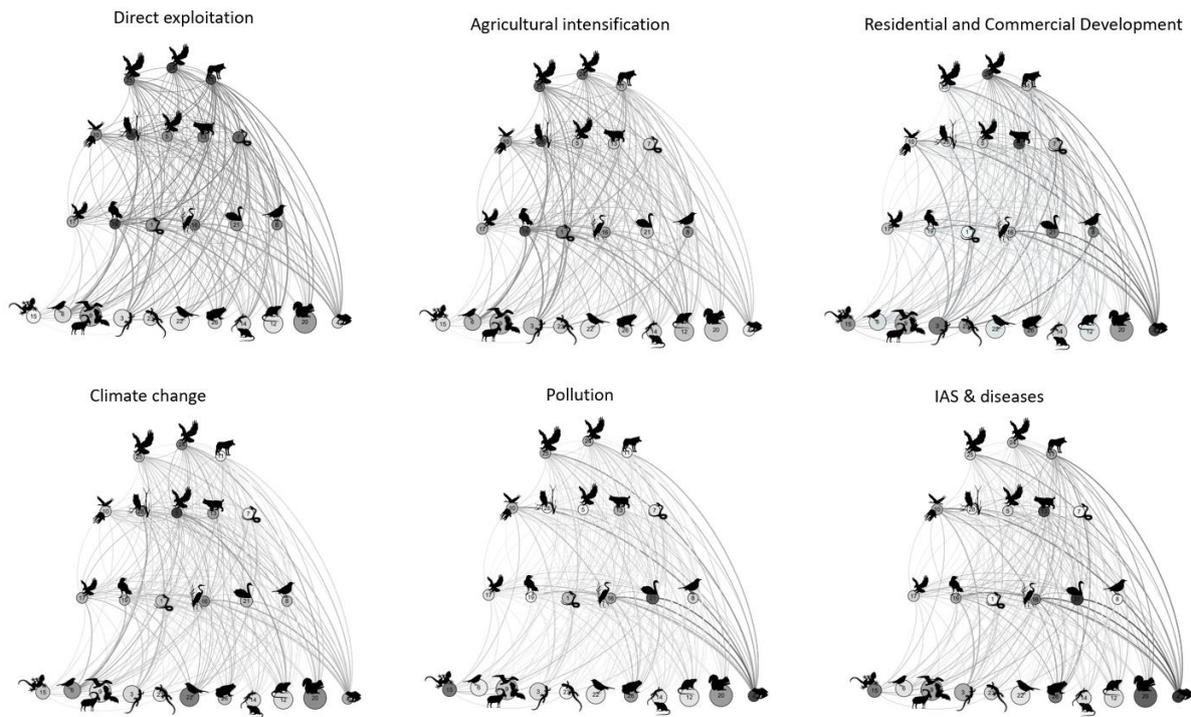
794 Predators may switch to occasional interactions, in the case of food limitations for
 795 example, which could influence the vulnerability of species and interactions. We
 796 performed a second set of analysis that considered both occasional and obligate
 797 interactions in the metaweb to test whether including both types of interactions would
 798 change the results. Figures below show that the main findings stay true when
 799 considering both obligatory and occasional interactions.

800



801

802 **Figure A2.1.** Bar plots of the percentage of vulnerable species and vulnerable
 803 interactions in the metaweb, when considering both occasional and obligatory
 804 interactions. Threat types are arranged by percentage of vulnerable species (top to
 805 bottom). In comparison with Figures 1B and S3, we see that the results in terms of
 806 vulnerable species and interactions are the same: 1) there is a symmetric relationship
 807 between the percentage of vulnerable species and the percentage of vulnerable
 808 interactions in the metaweb; and 2) for direct exploitation, and agricultural
 809 intensification (including agricultural expansion and pesticides), there is a greater
 810 difference between the percentage of vulnerable species and the percentage of
 811 vulnerable interactions than for any other threat type. Minor differences between the
 812 main analysis and this one include : i) reforestation has a greater impact on
 813 interactions in the metaweb when including occasional interactions; ii) agricultural
 814 expansion affects a greater proportion of interactions when occasional interactions are
 815 included; and iii) pesticides affect a greater percentage of interactions when occasional
 816 interactions are excluded.



818

819 **Figure A2.2:** Each network represents the metaweb (the version with both occasional
 820 and obligatory interactions), where nodes are trophic groups, and links represent
 821 feeding interactions between trophic groups. The colour intensity of the node
 822 represents the proportion of species in each group affected by the threat. Node size
 823 represents the number of species within the group, and link width represents the
 824 number of feeding interactions between trophic groups. This shows that, even when
 825 considering both occasional and obligatory interactions, trends are similar to the main
 826 analysis: 1) direct exploitation primarily affects top predators and intermediate
 827 predators; 2) agricultural intensification affects some groups of top predators as well
 828 as basal species.

829