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Land-use intensity influences European tetrapod food webs

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Abstract

Land use intensification favours particular trophic groups which can induce architectural changes in food webs. These changes can impact ecosystem functions, services, stability and resilience. However, the imprint of land management intensity on food-web architecture has rarely been characterized across large spatial extent and various land uses. We investigated the influence of land management intensity on six facets of food-web architecture, namely apex and basal species proportions, connectance, omnivory, trophic chain lengths and compartmentalization, for 67,051 European terrestrial vertebrate communities. We also assessed the dependency of this influence of intensification on land use and climate. In addition to more commonly considered climatic factors, the architecture of food webs was notably influenced by land use and management intensity. Intensification tended to strongly lower the proportion of apex predators consistently across contexts. In general, intensification also tended to lower proportions of basal species, favoured mesopredators, decreased food webs compartmentalization whereas it increased their connectance. However, the response of food webs to intensification was different for some contexts. Intensification sharply decreased connectance in Mediterranean and Alpine settlements, and it increased basal tetrapod proportions and compartmentalization in Mediterranean forest and Atlantic croplands. Besides, intensive urbanization especially favoured longer trophic chains and lower omnivory. By favouring mesopredators in most contexts, intensification could undermine basal tetrapods, the cascading effects of which need to be assessed. Our results support the importance of protecting top predators where possible and raise questions about the long-term stability of food webs in the face of human-induced pressures.

KEYWORDS
anthropization, biotic homogenization, crowdsourcing, food webs, intensification, land use, tetrapods, trophic networks

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[†]Deceased before publication (17/06/2023).

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1 | INTRODUCTION

Land use intensification and change have been identified as the most impactful factors of biodiversity loss in terrestrial and freshwater ecosystems (IPBES, 2019), generating habitat fragmentation or loss (Fahrig, 2003), introduction of invasive species (Doherty et al., 2016), direct interactions between humans and wildlife (e.g. exploitation, hunting) and pollution. Increasingly, studies have shown that land use intensification leads to changes in species composition across trophic groups (Etard et al., 2022; Gossner et al., 2016). However, species are not independent of each other. Instead they interact in complex food webs that reflect the flow of energy and biomass in the system, and the interdependency among species (Link et al., 2005). The architecture of food webs, namely the configuration of trophic interactions between species in a community, can be summarized into key properties that have an impact on food-web dynamics (e.g. degree of omnivory, generalism, compartmentalization, trophic chain lengths, see Botella et al., 2022). Changes in food-web architecture following land use intensification might be indicative of the potential for ecosystem collapse (Evans et al., 2013; Keyes et al., 2021; Saint-Béat et al., 2015). Food webs sustain a number of ecosystem functions and services, such as pest control (Montoya et al., 2003), seed dispersal (Corlett, 2017) or nutriment cycling in soils (De Vries et al., 2013), and their architecture partly determines community stability (Mestre et al., 2022; Saint-Béat et al., 2015; Tylianakis et al., 2010). We thus urgently need to understand how changes in land use will modify the architecture of food webs (Li et al., 2018; Rigal et al., 2022). While local studies focusing on specific land uses or taxonomic groups can help formulate hypotheses on how land management intensity affects food-web architecture (Agostini et al., 2020; de Visser et al., 2011; Gossner et al., 2016; Hallmann et al., 2014; Heger & Jeschke, 2018; Herbst et al., 2013), we lack a macroecological assessment of these hypotheses and their context dependence.

Local-scale studies have shown that land use intensification favours a limited set of synanthropic and generalist species, in terms of habitat (Clavel et al., 2011) and trophic interactions (McKinney & Lockwood, 1999), at the expense of more specialist ones, leading to biotic homogenization (Gossner et al., 2016; McKinney & Lockwood, 1999). On the one hand, intensive grassland management reduces plant diversity and induces local extinction cascades in higher trophic levels (Herbst et al., 2013). Likewise, increased use of pesticides indirectly affects species feeding on plants or invertebrates and is a well-known cause of the loss of basal vertebrate species, such as in birds (Geiger et al., 2010; Hallmann et al., 2014) and

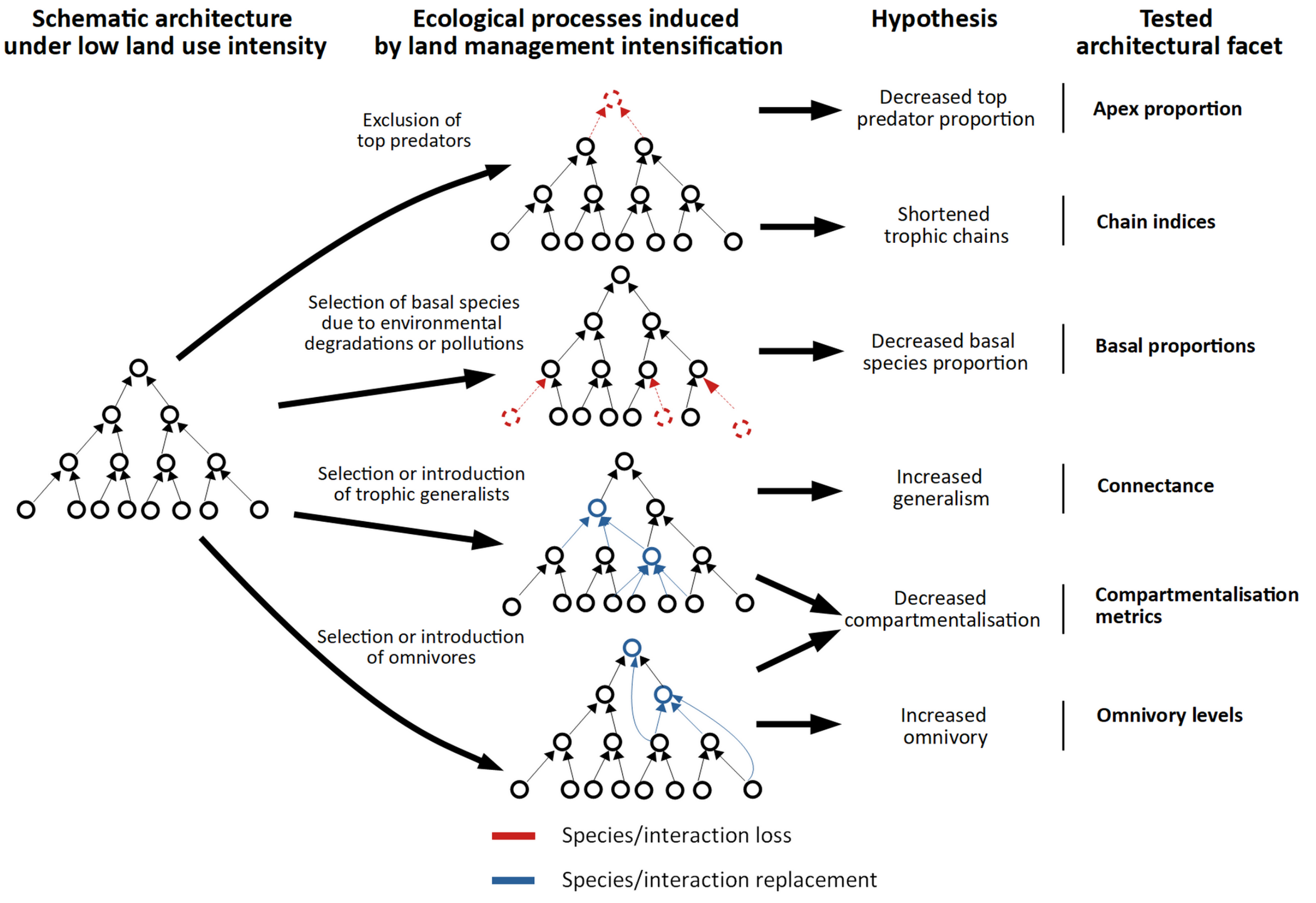


FIGURE 1 Hypothetical food-web architecture changes related to the ecological processes associated with land use intensification. However, our general assumptions could be contradicted by the context dependence of these processes, that is, intensification does not necessarily enhance all these processes under all land uses or climates, their interactions and the effect of other unknown processes.

amphibians (Agostini et al., 2020; Sparling et al., 2001). On the other hand, human activities and habitat loss often negatively affect top predators even more drastically than lower trophic levels (de Visser et al., 2011; Dobson et al., 2006; Estes et al., 2011). This might lead to a loss of top-down control of mesopredators in trophic communities, called mesopredator release (Prugh et al., 2009), and offer opportunities for new mesopredators to establish (Heger & Jeschke, 2018). The mesopredator release could indirectly generate negative pressure on basal species (Estes et al., 2011). The decrease in richness of both basal species and top predators could induce shorter trophic chains and denser networks through the replacement of specialists by generalists or omnivores. These more frequent generalists and omnivores should also make networks less compartmentalized (i.e. groups of species interacting more together than with others are expected to be more rare). These ecological processes related to intensification should thus translate into the following changes on six different facets of food-web architecture (Figure 1) that we test here: decreased proportions of (1) apex and (2) basal species, higher proportions of (3) trophic generalists and (4) omnivores, (5) shorter trophic chains and (6) decreased compartmentalization.

We build on a recent macro-scale study on European terrestrial vertebrate food-web architectures (Braga et al., 2019) that found a decreased connectance and increased compartmentalization in landscapes more strongly influenced by humans. These trends contradict our general expectations, motivating further investigations accounting for context dependency. We used a recent high-resolution classification of land management intensity for different land uses (Dou et al., 2021), along with massive presence-only observations collected across Europe (GBIF, iNaturalist) and knowledge of trophic interactions between all European terrestrial vertebrates, hereafter called the metaweb (Maiorano et al., 2020). Through a thorough spatial sampling analysis, we reconstructed 67,051 local meta food webs containing all potential interactions among the species present in a 1-km^2 resolution. These local meta food webs had a total of 756 vertebrate species and spanned five bioclimatic regions (Atlantic, Continental, Mediterranean, Alpine or Boreal) and six land uses (forest, grasslands, arable and permanent croplands, agricultural mosaics or human settlements) across Europe. We quantified the six above-mentioned architectural facets (Figure 1) in each local meta food-web, and evaluated how they were influenced by land management intensity. To investigate the context dependence of the response to intensification, we tested this response per land use and bioclimatic region.

2 | MATERIALS AND METHODS

2.1 | Data

2.1.1 | Species presence/absence/uncertainty rasters

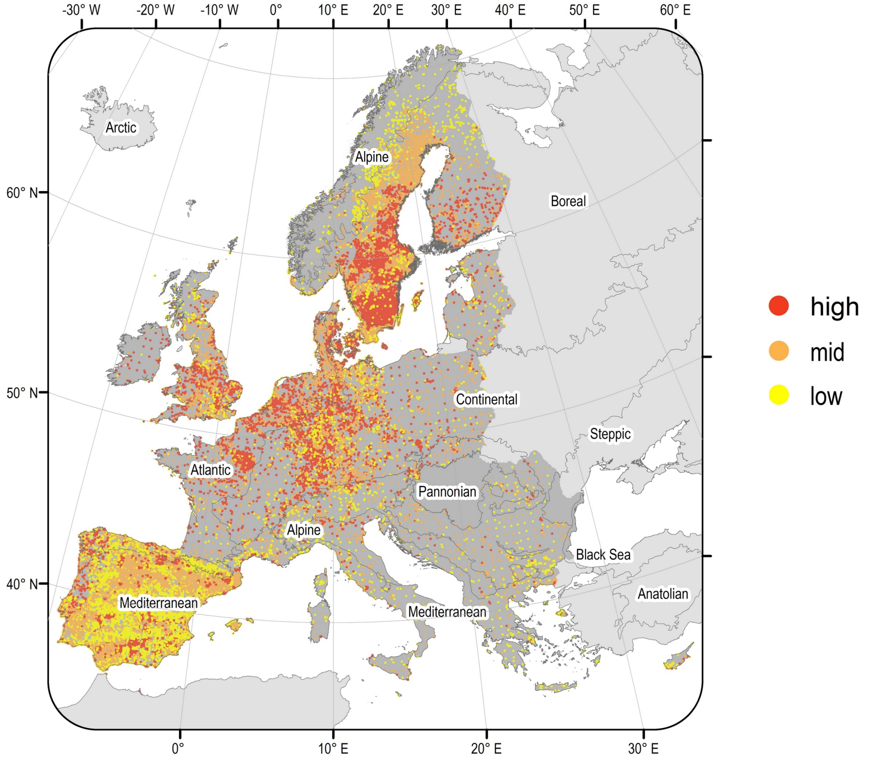
To quantify the effects of land management intensity on European tetrapods trophic networks, we gridded species occurrences from GBIF and iNaturalist. We chose to use these occurrences to complement the extent of occurrence from IUCN or BirdLife, commonly used previously (e.g. Braga et al., 2019; O'Connor et al., 2020), which cannot be interpreted as an area of certain presence at our resolution. We considered 756 terrestrial vertebrate (hereafter vertebrate) species with at least one geolocated occurrence after data cleaning (see Appendix S1) across continental Europe (35 countries). Since most data in GBIF and iNaturalist are presence-only data, we subselected cells to minimize the impact of false absences. More specifically, for each species, we built a raster indicating the presence, absence or uncertain status of that species in each 1 km by 1 km cell of the land use raster described below (as shown in box 2 of Figure S1.1). As a conservative strategy, we first considered a species as absent in a cell if it was out of the species' distribution range provided by the IUCN Red List, including both native and invasive ranges (IUCN, 2021). Within the IUCN range, cells having at least one occurrence of the focal species were considered as presences. The remaining cells for that species (inside the IUCN range but without occurrence) were considered as absences if the sampling effort in the cell exceeded a defined species-specific threshold, or uncertain otherwise. The sampling effort in a cell for a given species was approximated by the total number of occurrences across all species of the same taxonomic class (Aves, Mammalia, Amphibia or Reptilia). The sampling effort threshold to consider this species as absent when undetected was defined as the first decile of sampling effort values across all presence cells of that species. The sensitivity of our main results to the stringency of the sampling effort threshold and taxonomic sampling bias (e.g. favouring Aves compared to Reptilia/Amphibia) were investigated in Appendix S8. We excluded from the study all cells where more than 30% of all 756 species (i.e. 227 species) had uncertain status or the observed richness was lower than 20 (box 3 of Figure S1.1), because a lower richness is rare in tetrapod communities studied at comparable scale (Braga et al., 2019; Gaüzère et al., 2022) and would likely be due to imperfect detection.

After this filtering process, cells were grouped per combination of bioclimatic region and land use (explained further below) only retaining combinations containing enough cells to compare land management intensity levels (see box 4 of Figure S1.1 for more detail). After cell filtering, we retained 67,051 cells which are shown in Figure 2, that is, 1.3% of our study area (EU28+ filled with dark grey in Figure 2).

2.1.2 | Metaweb of tetrapod trophic interactions

We used the metaweb of potential trophic interactions between European tetrapod species (Maiorano et al., 2020), which we restricted to 756 selected species with enough observations. The metaweb of these species is fully represented in Figure S2.2 of the appendix, highlighting its decomposition into 46 trophic groups. These 46 trophic groups assembled by O'Connor et al. (2020) are synthesized in Table S2.1. We also provide a simplified visualization in Figure 3 where species were aggregated per trophic group.

(a) Land system intensity



(b) Richness

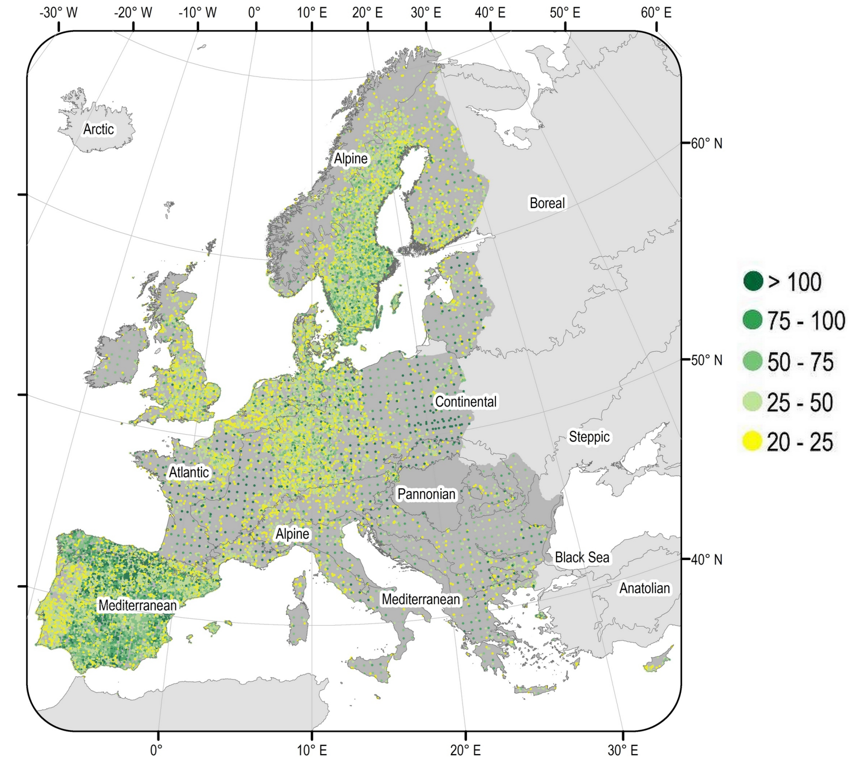


FIGURE 2 Map of the 67,051 studied local meta food webs (1 km^2 cells). (a) Cell locations coloured by land management intensity. (b) Cell locations coloured by observed species richness. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

2.1.3 | Local meta food webs

The metaweb was used to reconstruct what we call here the local meta food-web associated with the set of species present in each retained cell. Two species were assumed to interact locally if they are both observed in the cell and if they are known to interact in the metaweb. This representation of food webs can be also seen as a local realization of the metaweb interactions based on trusted species presences and absences, consistently with many related studies (e.g. Braga et al., 2019; Kortsch et al., 2019; O'Connor et al., 2020;

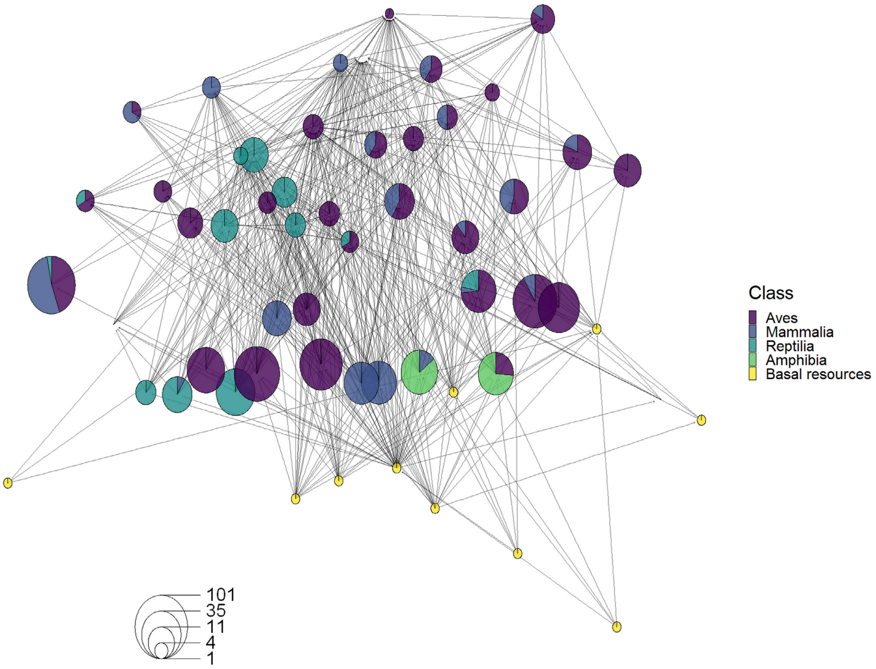


FIGURE 3 The metaweb of trophic interactions of our 756 European tetrapods aggregated per trophic groups (O'Connor et al., 2020). Each node is one of the 46 trophic groups (detailed in Table S2.1), its size represents the number of species while the colours represent the proportion of classes. The trophic groups were automatically positioned vertically according to their trophic level and horizontally so that connected groups are more aligned than non-connected ones (TL-tsne layout method of the R package metanetwork: https://marcohlmann.github.io/metanetwork/). Basal resources (i.e. diets that are not wild vertebrates) were included as yellow nodes.

Poisot et al., 2012). Species having locally no prey and predator were kept, as they can feed on non-tetrapod species (aquatic vertebrates, invertebrates, fungi, plants), without affecting most network metrics (see architecture facets' section below).

2.1.4 | Land use and management intensity

We used a new land system map that integrates land use data with intensity of use for the past decade over Europe at 1-km^2 resolution (Dou et al., 2021), which covers EU28+ (including the EU, the United Kingdom, Norway, Switzerland and the Western Balkans, but excluding Iceland, Turkey and Macaronesia). We considered six land uses: forest, grassland (except grass wetlands), permanent cropland (vineyards, olive groves, fruit gardens), arable cropland, agricultural mosaic (cropland and grassland) and human settlement (cities and peri-urban landscapes). Dou et al. (2021) decomposed each land use into different levels of land management intensity (low/high for permanent croplands, low/medium/high for others) based on criteria that (i) depend on the land use (see Table S3.2) and (ii) have documented impacts on biodiversity, which make these land use classifications suitable to our purpose.

2.1.5 | Bioclimatic regions

As climate influences tetrapod food webs (Braga et al., 2019), we integrated it to control for the influence of its spatial variations in our analysis. We considered the biogeographical regions defined by the European Environment Agency (EEA, 2021). These bioclimatic regions represent large-scale biodiversity units reflecting climatic contrasts and are based on an interpretation of geobotanical data. Among the 11 original regions, five were used in our study, the Alpine, Atlantic, Boreal, Continental and Mediterranean regions, for which we had enough sampled cells, as illustrated by the count of cells by bioclimatic region, land use and management intensity in Figure S3.3. To validate that our cell selection procedure minimized the biases due to spatial variations in sampling effort in our analysis, we plotted the sampling effort per bioclimatic region, land use and management intensity for each taxonomic class in Figure S3.4.

2.2 | Analysis methods

To evaluate the effect of land management intensity on six facets of food-web architecture (see Figure 1), we selected one or several network metrics summarizing each facet. We measured the mean deviation per metric related to an increase of land management intensity and tested, for each facet, the statistical significance of the multivariate deviation between intensity levels per combination of bioclimatic region and land use (which we refer to as context below, for instance mediterranean forests).

2.2.1 | Network architecture facets

The network metrics composing each architecture facet are summarized in Table 1. They were computed for each local meta food-web. Detailed explanations are presented in Appendix S4. For apex proportion, we computed the proportion of observed species that are apex predators (pApexMeta), which is determined from species trophic levels (MacKay et al., 2020) in the metaweb completed by species diets as additional nodes (as recommended in Maiorano et al., 2020). Diets were represented along with tetrapod trophic

TABLE 1 Architectural facets and their constituent metrics computed for all local food webs in this study.

Architecture facet	Metric acronym	Description	Range of values
Apex proportion	pApexMeta	Proportion of species that are apex predators in the metaweb.	[0,0.3]
Basal proportions	pBasalMeta	Proportion of species that are basal in the metaweb.	[0,1]
	pBasal	Proportion of species that are basal in the local meta food-web (have no preys).	[0.1,1]
Connectance	dirCon	Directed connectance: density of interactions in the local meta food-web.	[0,0.3]
Omnivory levels	omniProp	Proportion of general omnivore species among non-basal and non-top species.	[0.3,1]
	omniLvl	Mean standard deviation of prey trophic levels of the non-basal and non-top species.	[0.1,0.7]
Chain indices	maxPath	Maximum length across shortest paths from basal to apex species in the local meta food-web.	[0,12]
	meanPath	Mean length across shortest paths from basal to apex species in the local meta food-web.	[0,3.8]
	sdPath	Standard deviation of lengths across shortest paths from basal to apex species in the local meta food-web.	[0,2.4]
Compartmentalization metrics	modul	Modularity (Newman, 2006): A measure of densely interconnected groups of species being less connected with other species.	[−1,0.4]
	meanShortDist	Mean path distance across species pairs in the undirected transform of the local meta food-web.	[1,4.3]

groups in the full metaweb visualization of Figure 3. For basal proportions, we computed two metrics: pBasalMeta and pBasal are the proportion of observed species having no tetrapod prey in the metaweb or local meta food-web, respectively. Both versions of the metric were considered because some of a species' potential prey (metaweb) might have not been detected in local meta food webs. For connectance, we computed the density of directed trophic interactions among tetrapod species in a local meta food-web (dirCon). For omnivory levels, we computed two metrics based on a continuous or categorical view of trophic levels: omniLvl is the average, over non-basal and non-apex species in the metaweb, of the standard deviation of their prey's trophic levels, while omniProp is the proportion of non-basal and non-apex species in the metaweb predating several levels (basal/intermediary/apex, see Appendix S4). For chain indices, we computed the longest (maxPath), mean (meanPath) and standard deviation (sdPath) of the shortest paths from locally basal species to top species. Finally, for compartmentalization, we computed the local modularity (modul, Newman, 2006), and the mean distance (meanShortDist) between species on the (undirected) local meta food-web. Several metrics were chosen for one facet when one dimension alone could not capture the ecological meaning well. As a logical consequence, metrics inside each facet were positively correlated but weakly correlated between facets (see Figure S5.6). We later interpret land management intensity as influencing a given facet only if all its metrics were influenced in the same way.

2.2.2 | Mean metric deviations related to land management intensity

To assess the influence of land management intensity on architecture facets and its context- dependence, we measured the mean deviation of each metric related to an increase in land management intensity per context. We fitted a multivariate linear regression (Johnson & Wichern, 1992) over local meta food webs where the metrics were set as dependent variables, and the combination of context and land management intensity as categorical explanatory variable with nested contrasts, so that the deviation related to a higher intensity level (high or medium compared to low) is nested per context (i.e. estimated for each context). More precisely, these nested contrasts are implemented with the R formula: metric ~ bioclimatic region/land use/intensity. We obtained one mean deviation related to an increase of intensity (high vs. low, or mid vs. low) for each network metric and for each context (bioclimate and land use). Some combinations were not considered due to a lack of well-sampled cells (see Figure S3.3). We obtained 38 mean deviations per metric, including deviations from low to medium intensity cells for 20 contexts, and from low to high intensity for 18 contexts, spanning a total of 21 contexts (see Figures S6.7–S6.12, where each table shows one facet). The fit of the linear models (R^2) per metric and relative influence of climate, land use and its intensity is reported in Table S7.3. We also tested the robustness of these general results to several potential biases, namely the choice of our sampling effort threshold for species detection, taxonomic detection bias and outlier food webs, in Appendix S8.

2.2.3 | Tests of multivariate deviation significance

We tested whether the mean deviations related to an increase of intensity were significant for each facet and context. We tested the equality between the two multivariate distributions of food-web metrics (high vs. low intensity, or medium vs. low intensity) included in the facet, and detected significant deviations when the null hypothesis was rejected (i.e. no effect of higher land management intensity). This was done using a nonparametric multivariate test based on Wilk's Lambda statistics, which accounts for the unbalanced number of cells between intensity levels (Liu et al., 2011, implemented in the *npmv* R package, Burchett et al., 2017). We defined the risk of detecting at least one false non-equality across our six facets to 5% per context, as explained in Appendix S6. The significance of the deviation in each context is indicated by a white background of the cells in Figures S6.7–S6.12.

3 | RESULTS

The influence of land management intensity was overall weaker than those of climate and land use but accounting for land management intensity yielded a greater explanatory power of food-web variability based on the model partial R^2s (Table S7.3). The general influence of land management intensity was quite strongly negative for apex proportions, with a mean relative deviation below −10% (Figure 4a), and substantial on all other facets (around ±5%), except omnivory, as explained below per facet.

Apex predator proportion decreased strongly under higher land management intensity. In agreement with our hypothesis, apex predator proportion (pApexMeta) decreased with increasing land management intensity and had the strongest mean deviation of all food-web metrics (greater than 10% of the interquartile range, Figure 4a). In other words, the decrease of apex proportion in high land use intensity compared to low intensity represents >10% of the inter-quartile range of the overall metric variation among the 70,000 local meta food webs when correcting for the effect of climate and land use. This trend was robust with a nearly constant magnitude across sensitivity analyses (Appendix S8). This decrease concerned eight of the nine highest trophic groups which included only apex predators (Figure 5). Negative deviations spanned 15 of the 21 contexts, represented 68% of all deviations, while positive deviations were mostly small (Figure 4b; Figure S6.7).

Basal species proportions decreased under higher land management intensity. In agreement with our hypothesis, the two metrics of basal species proportions were lower, with a relative deviation of −5% in the most intensively managed landscapes averaging over both metrics (Figure 4a) while controlling for context. This trend was also robust in all sensitivity analyses (Appendix S10). These decreases included 12 of the 16 trophic groups containing basal species (Figure 5). Fifty per cent of the 34 significant mean deviations showed a decrease of both pBasal and pBasalMeta metrics, spanning half of the 21 contexts (Figure 4b). This decrease was particularly strong in continental and boreal contexts (Figure 6). Contrary to our expectation, pBasal and pBasalMeta increased with land management intensity in 26.5% of the significant contexts (Figure 6; Figure S6.8). In contrast, two contexts showed a strong increase of basal proportions under higher intensity, that is, Atlantic croplands and Mediterranean forests (Figure S6.8). Even though basal tetrapod diversity decreased under high intensity compared to low

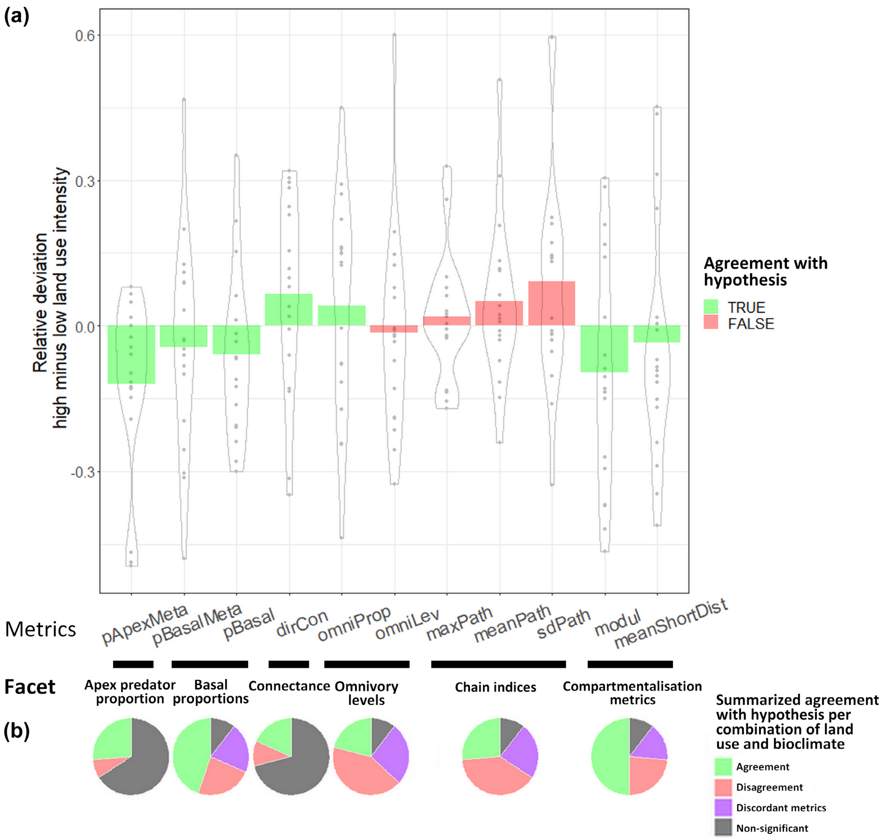


FIGURE 4 Food-web metric deviations related to higher land management intensity per architecture facet and agreement with the initial hypothesis. (a) For each metric (*x*-axis), the relative deviation (barplot on *y*-axis) is the average over 18 contexts (grey dots) of the mean deviation from low- to high-intensity food webs divided by the interquartile range of the global metric distribution. This relative deviation indicates the general response to land management intensity while controlling for context dependence. The bar plot's colour indicates if the deviation is confirming (green) or contradicting (red) the initial hypothesis on the corresponding facet (see Figure 1). (b) For each facet, a pie plot summarizes the tests of deviation significance over the 38 contexts and intensity level comparisons (high vs. low and medium vs. low) into agreements (green) or disagreements (red) with the hypothesis, discordant metrics (purple) or non-significant, based on the multivariate test.

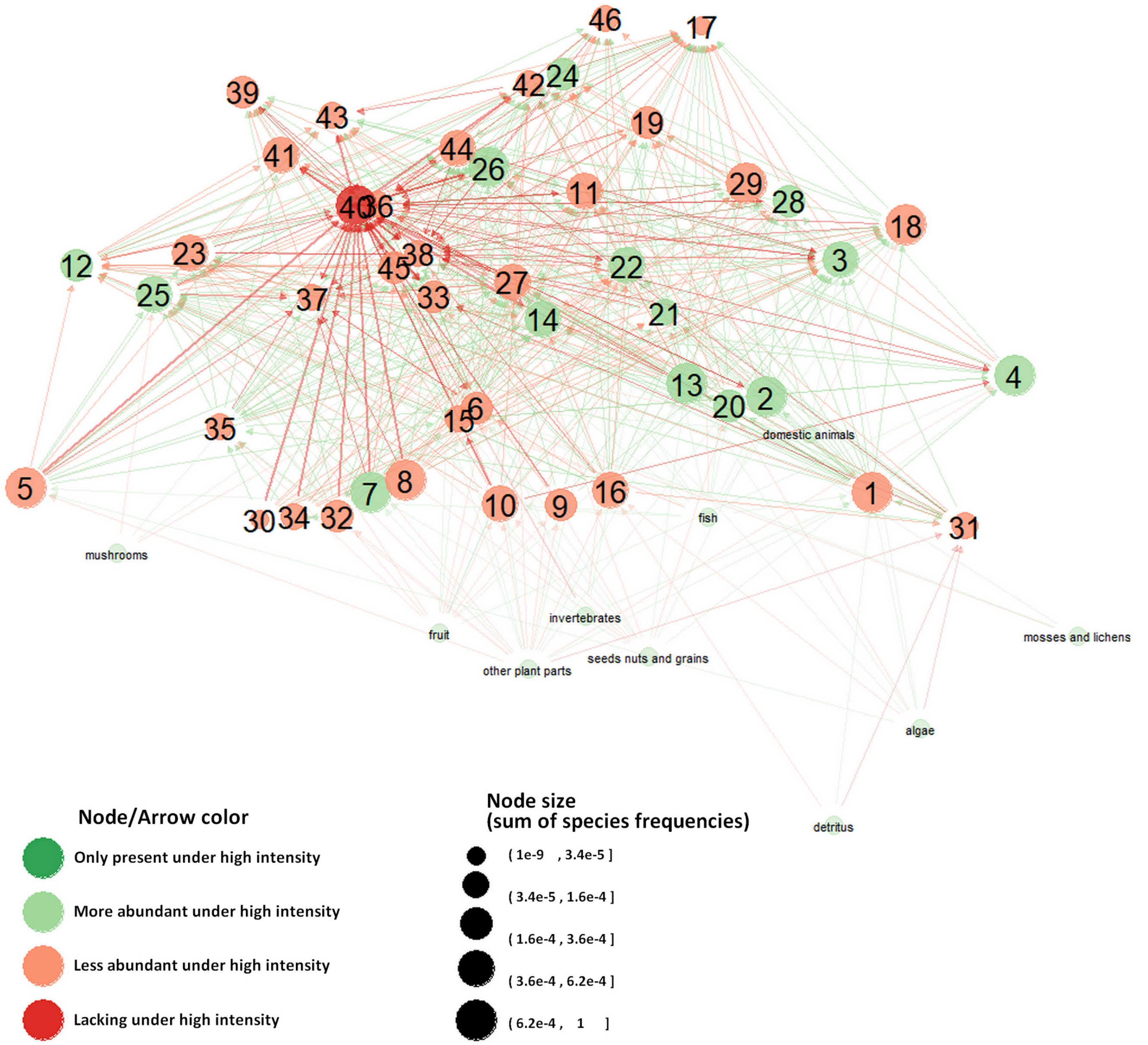


FIGURE 5 Changes of trophic group frequencies when increasing land management intensity. This difference plot between average networks in high and low land management intensity cells is produced by the diff_plot function in metanetwork R package. As in Figure S2.2, each node is one trophic group and its size represents the sum of species frequencies across the 67,051 local meta food webs. A red (resp. green) node colour indicates a decrease (resp. increase) of the group frequency in high-intensity cells compared to low-intensity cells. More details on the trophic group compositions are provided in Table S2.1.

intensity in these contexts (−12% for Atlantic croplands and −31% for Mediterranean forests, respectively), the diversity of mesopredators (−16% and −46%, respectively) and top predators (−25% and −35%, respectively) decreased more strongly. Indeed, the total loss in tetrapod species richness was strong in these contexts (−15% and −37%, respectively).

Connectance substantially increased under higher land management intensity. Connectance substantially increased in general with land management intensity with a relative deviation greater than +5% (Figure 4a). Positive mean deviations spanned 17 of the 21 contexts, represented 74% of all deviations and were notably strong in all forests except the Mediterranean ones (Figure S6.9). Mediterranean contexts hosted most significant negative mean deviations. However, when considering only the most sampled cells for all taxonomic classes, the influence of a higher land management intensity on connectance was negative (Appendix S8, Figure S8.14), due to the selection of Spanish Mediterranean cells.

Omnivory showed contrasted responses to land management intensity. OmniLev and omniProp had context-dependent responses to land management intensity (Figure 4a) across bioclimates and land uses. While most mean deviations were significant

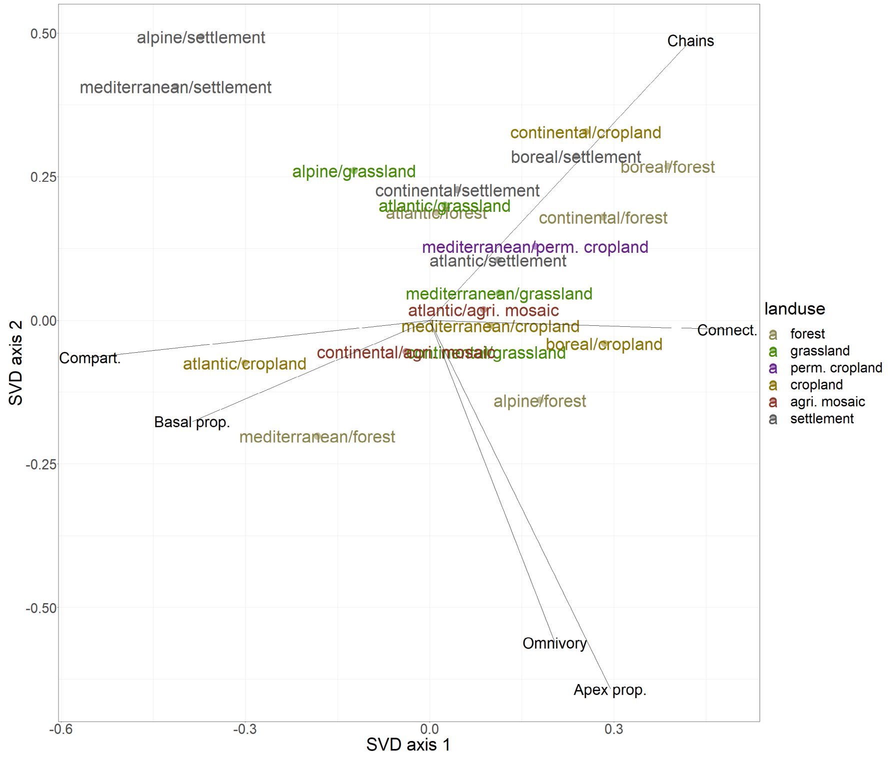


FIGURE 6 Summary of the relative deviations per context and facet directions in a summary 2-dimensional plane. The multivariate responses of the six facets relative deviations (averaged for high and mid intensities) over the 21 contexts were summarized in two axes using a singular value decomposition (SVD), explaining 55% of the total variability.

(34/38), only 23.5% of them showed an increase of both omnivory levels (Figure 4b), challenging our expectations. These spanned six contexts, including three forest contexts where strong deviations of both metrics were observed under the highest intensity level (Figure S6.10). In contrast, omnivory levels both decreased in 47.1% of the significant mean deviations, including all settlement contexts where deviations were particularly strong. These unexpected negative responses might be partly due to the taxonomic sampling bias because both metric mean deviations became positive and increased in magnitude when minimizing this bias in a complementary analysis (Appendix S8, Figure S8.14).

Trophic chain lengths increased under high land management intensity in human settlements. Contrary to our expectations, the three metrics describing trophic chain length increased on average with land management intensity but with a moderate magnitude, that is, the relative deviations were inferior to +10% for the three metrics (Figure 4a). Local meta food webs under low land management intensity had relatively more shortest paths of length 1 (direct predation on a basal species), while local meta food webs under high land management intensity had more shortest paths of length 2–5 (see Figure S9.18). This general trend concealed a strong context dependence. Indeed, four of the nine contexts where we measured significant positive deviations were in human settlements and the relative deviations were strong for the Boreal, Continental and Atlantic settlements (Figure S6.11). Outside cities, significant positive deviations covered fewer contexts than significant negative deviations (5 vs. 6). Besides, the general increase of the three metrics was softer with a more stringent sampling effort quantile for cell selection (Figure S8.13) or when removing outlier food webs (Figure S8.17).

Compartmentalization overall decreased under high land management intensity. Both compartmentalization metrics decreased in general with increasing land management intensity with a moderate magnitude as relative deviations were superior to −10% for both metrics (Figure 4a). This general trend is confirmed by a higher proportion of disconnected pairs of basal and apex species in low-intensity food webs compared to the high intensity ones (Figure S9.18), that is, more frequent disconnected trophic chains or species. The decrease was robust in all sensitivity analyses and larger in magnitude for both metrics when correcting for taxonomic bias or removing outlier food webs (Appendix S10). Of the 34 significant mean deviations, 56% showed a decrease and 27% an increase in both metrics, half of which were located in the Mediterranean region (see Figure S6.12).

The influence of land management intensity was strongly context dependent. The general influence of land management intensity concealed larger, contrasting effects across different climatic and land-use contexts, as shown by the very spread out relative deviations per contexts, often greater than 20% in absolute value, for all facets (Figure 4a). The sign of mean deviations varied across land uses and bioclimatic regions for all facets, except for apex proportions whose relative deviation was rarely positive and weak in these contexts (lower than +10%). Forests, croplands and settlements showed particularly strong responses in comparison to agricultural mosaic and grasslands: The labels are often further from the centre in Figure 6 for forest and settlements contexts. The response of Mediterranean food webs diverged from the general trends described above and was quite consistent among forest, settlements and croplands of this region: Connectance strongly and significantly decreased while compartmentalization strongly and significantly increased when land management was more intense (illustrated in Figure 6, detailed deviations in Figures S6.9 and S6.12). Mediterranean forests and settlements also showed strongly and significantly increased basal proportions, contrary to most other contexts including Mediterranean croplands (Figure S6.8). Even though other settlement contexts followed the general trends, Alpine and Mediterranean settlements strongly differed from it regarding connectance, with a strongly negative deviation (Figure 6; Figure S6.9). The influence of intensification was most opposed to the general trends in Mediterranean forests and Atlantic croplands (Figure 6), as both contexts showed a sharp increase of basal proportions (Figure S6.8), compartmentalization (Figure S6.11) and a strong decrease of connectance (Figure S6.9) and chain indices (Figure S6.10).

4 | DISCUSSION

We demonstrated that, in addition to more commonly considered climatic factors (Braga et al., 2019; Kortsch et al., 2019), the architecture of local meta food webs is significantly influenced by land use and management intensity. Although the overall impact of land management intensity was less pronounced compared to climate and land use, it still exerted a notable influence on specific trophic groups. Land management intensity generally strongly reduced the proportion of top predators. Furthermore, we observed a substantial negative general influence of intensification on basal tetrapods and compartmentalization, along with a positive influence on connectance and the trophic chain lengths. However, for these latter architecture facets, the influence of intensification was highly contingent on the context. Notably, intensification sharply decreased connectance in Mediterranean and Alpine settlements, and it increased basal proportions and compartmentalization in Mediterranean forests and Atlantic croplands. Besides, we observed a sharp decrease of omnivory in all settlement contexts.

Food webs architecture was more hierarchical in less intensively used landscapes. Indeed, local meta food webs under lower land management intensity were made of a higher proportion of apex and basal tetrapod species and with a greater compartmentalization. This combination of properties strongly suggests that food webs became topologically more hierarchical (Clauset et al., 2008, see network on left of Figure 1 as an illustration) in response to intensification, namely networks that are similar to a tree. These findings support those of Mestre et al. (2022), who showed that low human pressures favours scale-free architectures, that is, where the node degree distribution follows a power-law. A scale-free architecture combined with a high compartmentalization results in a hierarchical architecture (Barabási et al., 2003). This hierarchical architecture tends to limit the number of predators per basal species. Apex predators were also relatively more diverse under lower human pressures, suggesting a better regulation of mesopredators, which might indirectly limit the predation pressure on the basal layer (Prugh et al., 2009).

Intensification concentrated species diversity among mesopredators, potentially participating in basal tetrapod decline. In intensive environments, food webs exhibited a reduced proportion of apex predator species, a phenomenon often attributed to direct human interference (de Visser et al., 2011; Estes et al., 2011; Prugh et al., 2009). Additionally, human activities led to a decline in the proportion of basal tetrapod species, so that the proportion of mesopredator species increased. This redistribution of species diversity between trophic layers suggests a role played by mesopredator release (Soulé et al., 1988). A lack of regulation by top predators could induce a growth of mesopredators, itself provoking local extinctions of basal prey species, as observed with coyotes in coastal southern California (Crooks & Soulé, 1999; Soulé et al., 1988). Mesopredator release is indeed thought to be common in our context of land use change and habitat fragmentation (Prugh et al., 2009) and its impact on basal tetrapods decline would be likely given that predation is the primary cause of their mortality (Hill et al., 2019). However, we lack abundance measures to assess whether the increased relative diversity of mesopredators translates into a higher predation pressure on basal tetrapods. The decline of basal tetrapods can be attributed to a combination of other factors tied to human activity: hunting, transport and agricultural practices account for a significant proportion of tetrapod prey mortality (Hill et al., 2019). Our results fuel the pressing question of the drivers and extent of future basal tetrapod collapse due to global changes. Further decline of basal tetrapods could incur further losses of crucial ecosystem services already threatened by climate change, as for instance the control of mosquito-borne diseases (Brugueras et al., 2020), and of crop pests (Civantos et al., 2012).

Beyond general trends, food-web architecture showed strongly context-dependent responses to land use intensification. In Atlantic croplands and Mediterranean forests, we observed a sharp increase in the proportion of basal species (Figure 6). However, this increase in proportion concealed a decline in the diversity of basal species, accompanied by an even greater decline in the diversity of other trophic levels, including mesopredators. The decline in local tetrapod richness in Atlantic croplands is a cause for concern. This region shows by far the largest proportion of intensive croplands (60%, Figure S3.3), which may have contributed to this decline, given that the generalization of intensive agriculture has contributed, for example, to the decline of birds in Europe (Rigal et al., 2023). Besides, we observed a decrease of omnivory and an increase of trophic chain lengths in response to higher land management intensity in cities and peri-urban areas, partly explaining the unexpected general trends for these two facets. These results support trophic dynamics phenomena previously documented in urbanized habitats called prey specialization and predator subsidy consumption (Fischer et al., 2012): Dense urban habitats may select mesopredator species specializing on prey adapted to such habitat (prey specialization), such as certain small bird and rodent species, or mesopredators consuming anthropogenic food (predator subsidy consumption) such as garbage.

Context dependencies and discrepant results could also be explained by other forms of human impacts that do not always act in concert with intense land management. For instance, higher habitat fragmentation and diversity were significantly associated with higher intensity only in Mediterranean and Alpine forests (Figure S10.19). This may partly explain the singular response of Mediterranean forests, that is, the decreased connectance and increased compartmentalization. A higher agglomeration of diverse land uses at a small spatial scale is thought to host more diverse independent trophic chains even though empirical evidence is still rare (Gonzalez et al., 2011; Kortsch et al., 2015). Braga et al. (2019) showed, in the same area, that the increase of human footprint was related to a higher compartmentalization, in contradiction with our results. This discrepancy might be due to not only the difference between land management intensity and human footprint (which incorporate different factors such as night light intensity, road and population density) but also the differences in the analysis methods, such as our choice to control for the context and to use food-web metrics normalized for species richness. When not accounted for, food-web size variability drives important variations in most metrics (Botella et al., 2022), which are not interesting in our context because the effects of human pressures on species richness have been well studied.

Much of the variability of food web architecture remained unexplained. Indeed, most of the variations in food web metrics could not be explained by the explanatory factors included in our model (R^2 ranged from 0.01 to 0.20 across metrics, Table S7.3). This is a consequence of our approach: We included a limited number of factors, corresponding to expectations identified from ecological theory, hence limiting the risk of capturing spurious correlations, but yielding a relatively simple model compared to the number of food webs, diversity of contexts and spatial scale. Many more unknown factors are likely to impact food web architecture. Yet, this unexplained variability should not per se challenge our interpretations. Indeed, a substantial part of the unexplained variability was due to 10% of outliers in our food webs, whose removal nearly doubled the coefficient of determination on average when refitting our model (0.068 vs. 0.112, Table S7.3). Besides our general interpretations were robust to various potential sources of bias, that is, the stringency of the species detection threshold, the taxonomic sampling bias and outlier food webs (Appendix S8). Lastly, we highlighted that the effect size of intensification is much greater in many contexts compared to its general effects, which is not reflected in the general R^2.

We acknowledge several limitations in our study stemming from constraints related to the data, spatial resolution and food-web representation. We used a space-for-time substitution strategy (Blois et al., 2013; Walker et al., 2010) to examine the effects associated with varying land management intensity across space. These spatial effects likely reflect historical changes in intensification occurring over several decades. However, spatial patterns may not always accurately mirror the effects of land use intensification or other global changes (Gaüzère & Devictor, 2021). While we compared areas with similar large-scale bioclimates and land uses, we recognize that small-scale environmental variations covarying with land management intensity, such as elevational gradients in mountain regions, could also impact food webs architecture and bias our results. Another limitation of our study pertains to the spatial scale used to reconstruct the local meta food webs (1 km^2). Some species may have much larger home ranges (e.g. wolf, bear), and interact with other species in neighbouring cells, the extent of which depends not only on the species itself but also on landscape structure. Our cell selection process favoured areas with intense and multi-year sampling efforts, which facilitated the detection of highly mobile species in each occupied cell. Nevertheless, it is possible that we underestimated the presence of the largest and most mobile species, potentially introducing a negative bias in our estimates of apex proportions.

Moreover, our study did not account for the dynamic nature of species distributions, primarily relying on species observations over the past 30 years. Consequently, we may have overlooked local declines of species during this period. Improving control for spatial sampling biases could also be achieved through statistical modelling of species detection and absence probabilities (Guillera-Arroita, 2017). Yet, even though such modelling was successfully used with presence-only data from crowdsourcing (Van Strien et al., 2013), a better understanding of opportunistic sampling behaviours would be necessary to implement it effectively in our context.

Unlike sampled interaction networks, our local meta food webs are neither snapshots frozen in time nor limited by the imperfect detection of interactions. Instead, they represent a 'maximum' depiction of all the interactions that likely occurred locally over several years, which makes sense in the context of our study (Thuiller et al., 2023). However, these potential trophic interactions may not necessarily manifest locally due to factors like phenological mismatches or low abundances of one or both interacting partners. As a result, we may unintentionally overemphasize certain rare trophic interactions. Furthermore, local meta food webs ignore how the realization of interactions depends on the environment, which might bias our results. To enhance our approach, it would be valuable to conduct a critical comparison with sampled food webs. Another broader perspective is to integrate non-trophic interactions (Kéfi et al., 2016), interaction strengths (Saint-Béat et al., 2015) and feeding behaviours (Heckmann et al., 2012) into future attempts to characterize interaction network architecture changes.

5 | CONCLUSION

Land use intensification has already changed the architecture of food webs, likely affecting ecosystem functions, services, stability and resilience. The general influence of intensification on European tetrapod food webs consistently undermines top predators. It often decreased the proportion of basal tetrapod species, compartmentalization and increased connectance and trophic chain lengths. However, some contexts showed marked discrepant responses, such as an increase of basal tetrapod proportions and compartmentalization in Mediterranean forest and Atlantic croplands. Intensive urbanization especially favoured longer trophic chains and lower omnivory. In summary, intensification has the potential to disrupt the regulation of mesopredators and heighten predation pressure on the basal layer of food webs. This underscores the importance of protecting top predators and raises questions about the long-term stability of food webs in the face of human-induced pressures.

AUTHOR CONTRIBUTIONS

Christophe Botella: Conceptualization; data curation; formal analysis; investigation; methodology; software; validation; visualization; writing – original draft; writing – review and editing. **Pierre Gaüzère:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing. **Louise O'Connor:** Conceptualization; data curation; methodology; validation; visualization; writing – review and editing. **Marc Ohlmann:** Methodology; software; validation; visualization; writing – review and editing. **Julien Renaud:** Data curation; visualization; writing – review and editing. **Yue Dou:** Conceptualization; data curation; methodology; writing – review and editing. **Catherine Graham:** Conceptualization; funding acquisition; validation; writing – review and editing. **Peter H. Verburg:** Funding acquisition; validation; writing – review and editing. **Luigi Maiorano:** Funding acquisition; validation; writing – review and editing. **Wilfried Thuiller:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data used in this study are available at https://zenodo.org/record/7741947, and the R scripts to reproduce figures and results are provided at https://github.com/ChrisBotella/foodwebs_vs_land_use.

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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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