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Land-use intensity influences European vertebrate food-webs

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Statement of authorship: CB, PG, LO and WT conceptualised the study. CB, JR, YD, LM and PV collected and preprocessed the data. CB developed the code and analysis. CB, PG, MO and JR made the Figures. All authors validated the results. CB wrote the first draft together with WT. All authors read and reviewed the manuscript.

Data accessibility 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.

Funding statement: This study has received funding from the ERA-Net BiodivERsA—Belmont Forum, with the national funder Agence Nationale de la Recherche (ANR-18- EBI4-0009), The Dutch Research Council NWO (grant E10005), and the Swiss National Science Foundation (20BD21_184131/1), part of the 2018 Joint call BiodivERsA-Belmont Forum call (project 'FutureWeb'). WT, JR, LOC, LM and PHV also acknowledge support from the European Union's Horizon Europe under grant agreement number 101060429 (project NaturaConnect). CB was funded by the French Agence Nationale de la Recherche (ANR) through the EcoNet (ANR-18-CE02-0010) project. WT acknowledges support from MIAI@Grenoble Alpes (ANR-19-P3IA-0003) and FORBIC (ANR-18-MPGA-0004). CG also acknowledges funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (grant 787638).

Number of words: 149 words in abstract, 5172 words in main text. **5 Figures and 1 Table** in main text. **Number of references:** 58. **Running title:** Intensification impacts food-web architecture. **Type of article:** Letter.

Keywords: Trophic networks; food-webs; anthropization; land use ; intensification ; tetrapods ; biotic homogenization; crowdsourcing

Abstract

Land use intensification favours particular trophic groups which can induce architectural changes in food-webs. These changes can impact ecosystem functioning and stability. However, the imprint of land management intensity on food-web architecture has rarely been characterised across large spatial extent and various land uses. We investigated the influence of land management intensity on six facets of food-web architecture for 67,051 European terrestrial vertebrate communities and its dependency on land use and climate. We found that, in general, intensification tended to lower proportions of both apex and basal species, favoured mesopredators and decreased food-webs compartmentalisation. These general trends were particularly strong in forests and settlements, but some contexts, like Mediterranean forest or Atlantic croplands, showed strong and discrepant responses. By favouring mesopredators in most contexts, intensification could undermine basal tetrapods, the cascading effects of which need to be assessed. Our results support apex predator diversity protection where possible.

Introduction

Land use intensification and change have been identified as the most impactful factors of biodiversity loss in terrestrial and freshwater ecosystems (Diaz et al., 2019), generating habitat fragmentation or loss (Fahrig et al., 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 (Gossner et al., 2016, Etard et al., 2022). 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 summarised 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 (Tylianakis et al., 2010, Saint-Béat et al., 2015, Mestre et al., 2022). 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., 2021). 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 et al., 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 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 affect 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 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 (Dobson et al., 2006, Visser et al., 2011, 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 et al., 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 replacement of specialists by generalists or omnivores. These more frequent generalists and omnivores should also make networks less compartmentalised (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 1km² 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.

Material and methods

Data

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 can not 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 sub-selected cells to minimise 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 1km by 1km 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 S11**. 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, Gaüzere 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 summarised by bioclimatic region, land use and management intensity in **Figure S3.4**.

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 (the same as in O'Connor et al., 2020); we also provide a simplified visualisation in **Figure 2** where species were aggregated per trophic group.

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 realisation of the metaweb interactions based on trusted species presences and absences, consistently with many related studies (e.g., Poisot et al., 2012, Kortsch et al., 2019, Braga et al., 2019, O'Connor et al., 2020). 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).

Land use and management intensity. We used a new land system map that integrates various land use and land cover data with intensity of use for Europe at 1km^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 graves, 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.

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 (European Environmental 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, 5 were used in our study, the Alpine, Atlantic, Boreal, Continental and Mediterranean regions, for which we had enough sampled cells (**Figure S3.4**).

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 summarising each facet. We measured the mean deviation per metric related to an increase of land management intensity (**Figure 4**) 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).

Network architecture facets

The network metrics composing each architecture facet are summarised in **Table 1.** They were computed for each local meta food-web**.** Detailed explanations are presented in the 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 groups in the full metaweb

visualisation of **Figure 2**. 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 et al., 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.

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 versus low, or mid versus 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 S3.4**). 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 Tables **S6.7 to S6.12**, where each table shows one facet). 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 **S10**.

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 versus low intensity, or medium versus 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 non-parametric 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 blue background of cells in Tables **S6.7** to **S6.11**.

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 4-top**), 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 4-top**). 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 thousand 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 S10**). This decrease concerned 8 of the 9 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 4-bottom** and **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 -5% in the most intensively managed landscapes averaging over both metrics (**Figure 4-top**) 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 percent of the 34 significant mean deviations showed a decrease of both pBasal and pBasalMeta metrics, spanning half of the 21 contexts (**Figure 4-bottom,** Table 3). This decrease was particularly strong in continental and boreal contexts (**Figure S6.13**).

Contrary to our expectation, pBasal and pBasalMeta increased with land management intensity in 26.5% of the significant contexts (**Figure S6.13 and Figure S6.8**).

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 4-top)**. 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 S10, Figure S11.17**), 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 4-top**) across bioclimates and land uses. While most mean deviations were significant (34/38), only 23.5% of them showed an increase of both omnivory levels (**Figure 4-bottom**), challenging our expectations. These spanned 6 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 S10, Figure S11.17**).

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, i.e. the

relative deviations were inferior to +10% for the three metrics (**Figure 4-top**). 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 to 5 (see **Figure S8.13**). This general trend concealed a strong context dependence. Indeed, four out 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 versus 6). Besides, the general increase of the three metrics was softer with a more stringent sampling effort quantile for cell selection (**Figure S11.16**) or when removing outlier food-webs (**Figure S11.20).**

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 4-top**). 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 S7.12**), i.e. 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 4-top**). 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 S6.13** 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 S6.13**, 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 (**Figures 6 and S6.9**). The influence of intensification was most opposed to the general trends in Mediterranean forests and Atlantic croplands (**Figure S6.13**), 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**).

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 compartmentalisation in Mediterranean forests and Atlantic croplands. Besides, we observed a sharp decrease of omnivory in all settlement contexts.

Less intensively used landscapes tend to host local meta food-webs 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, i.e. 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).

High land management intensity resulted in a concentration of species diversity among mesopredators. In these environments, food webs exhibited a reduced proportion of apex predator species, a phenomenon often attributed to direct human interference (Prugh et al., 2009, De Visser et al., 2011, Estes et al., 2011). Additionally, human activities led to a decline in the proportion of basal tetrapod species. Consequently, the proportion of mesopredator species increased, aligning with the concept of mesopredator release as proposed by Prugh et al. (2009).

The decline of basal tetrapods can be attributed to a combination of direct and indirect drivers. Human activities, including hunting, transportation or agricultural practices, account for a significant portion of tetrapod prey mortality (Hill et al., 2019). Moreover, the mesopredator release phenomenon, amplified by top predators decline (Prugh et al., 2009), may increase predation pressure on basal tetrapods, considering that predation is the primary cause of their mortality (Hill et al., 2019).

Beyond these general trends of food-web architecture response to land management intensity, we observed a variety of more specific responses depending on the bioclimatic regions and land uses. For instance, 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 urbanised habitats called prey specialisation and predator subsidy consumption (Fischer et al., 2012): Dense urban habitats may select mesopredator species specialising on prey adapted to such habitat (prey specialisation), 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 s9.14**). This may partly explain the singular response of Mediterranean forests, i.e. 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.

406 This discrepancy might be due to the difference between land management intensity and
407 human footprint (which incorporate different factors such as night light intensity, road and
408 population density), but also to differences in the analysis methods, such as our choice to
409 control for the context and to use food-web metrics normalised for species richness. When not
410 accounted for, food-web size variability drives important variations in most metrics (Botella et
411 al., 2022), which are not interesting in our context because the effects of human pressures on
412 species richness have been well studied.

413 We acknowledge several limitations in our study stemming from constraints related to the data,
414 spatial resolution, and food-web representation. We used a space-for-time substitution strategy
415 (Walker et al., 2010, Blois et al., 2013) to examine the effects associated with varying land
416 management intensity across space. These spatial effects likely reflect historical changes in
417 intensification occurring over several decades. However, spatial patterns may not always
418 accurately mirror the effects of land use intensification or other global changes (Gaüzère &
419 Devictor, 2021). While we compared areas with similar large-scale bioclimates and land uses,
420 we recognize that small-scale environmental variations covarying with land management
421 intensity, such as elevational gradients in mountain regions, could also impact food-webs
422 architecture and bias our results. Another limitation of our study pertains to the spatial scale
423 used to reconstruct the local meta food-webs (1km²). Some species may have much larger
424 home ranges (e.g. wolf, bear), and interact with other species in neighbouring cells, the extent
425 of which depends not only on the species itself but also on landscape structure. Our cell
426 selection process favoured areas with intense and multi-year sampling efforts, which facilitated
427 the detection of highly mobile species in each occupied cell. Nevertheless, it is possible that we
428 underestimated the presence of the largest and most mobile species, potentially introducing a
429 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 over-emphasize certain rare trophic interactions. Further, local meta food-webs ignore how the realisation 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 characterise interaction network architecture changes.

Despite these limitations, our observations fuel the pressing question of the 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).

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 undermine 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 urbanisation 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.

Acknowledgments:

We dedicate this work to the memory of Marc Ohlmann, whose pioneering ideas felt like strong footholds for this modest ascent on the long climbing route towards a biogeography of ecological interaction networks. CB thanks Catherine Matias, Vincent Miele, Stéphane Dray, David M Richardson and Cang Hui for enabling the finalisation of this study.

References:

Agostini, M. G., Roesler, I., Bonetto, C., Ronco, A. E., & Bilenca, D. (2020). Pesticides in the real world: The consequences of GMO-based intensive agriculture on native amphibians. *Biological Conservation*, *241*, 108355.

Ballouard, J. M., Kauffman, C., Besnard, A., Ausanneau, M., Amiguet, M., Billy, G. et al. (2021). Recent invaders in small Mediterranean islands: Wild boars impact snakes in Port-Cros National Park. *Diversity*, *13*(10), 498.

Barabási, A. L., Dezső, Z., Ravasz, E., Yook, S. H., & Oltvai, Z. (2003, April). Scale-free and hierarchical structures in complex networks. In *AIP Conference Proceedings* (Vol. 661, No. 1, pp. 1-16). American Institute of Physics.

Blois, J. L., Williams, J. W., Fitzpatrick, M. C., Jackson, S. T., & Ferrier, S. (2013). Space can substitute for time in predicting climate-change effects on biodiversity. *Proceedings of the National Academy of Sciences*, *110*(23), 9374-9379.

Botella, C., Dray, S., Matias, C., Miele, V., & Thuiller, W. (2022). An appraisal of graph embeddings for comparing trophic network architectures. *Methods in Ecology and Evolution,* 13(1), 203-216. doi:10.1111/2041-210X.13738

Braga, J., Pollock, L. J., Barros, C., Galiana, N., Montoya, J. M., Gravel, D., ... & Thuiller, W. (2019). Spatial analyses of multi-trophic terrestrial vertebrate assemblages in Europe. *Global Ecology and Biogeography*, *28*(11), 1636-1648.

Brugueras, S., Fernández-Martínez, B., Martínez-de la Puente, J., Figuerola, J., Porro, T. M., Rius, C. et al. (2020). Environmental drivers, climate change and emergent diseases transmitted by mosquitoes and their vectors in southern Europe: A systematic review. *Environmental research*, *191*, 110038.

Burchett, W. W., Ellis, A. R., Harrar, S. W., & Bathke, A. C. (2017). Nonparametric inference for multivariate data: the R package npmv. *Journal of Statistical Software*, *76*(1), 1-18.

Carpio, A. J., Guerrero-Casado, J., Ruiz-Aizpurua, L., Vicente, J., & Tortosa, F. S. (2014). The high abundance of wild ungulates in a Mediterranean region: is this compatible with the European rabbit?. *Wildlife Biology*, *20*(3), 161-166.

Civantos, E., Thuiller, W., Maiorano, L., Guisan, A., & Araújo, M. B. (2012). Potential impacts of climate change on ecosystem services in Europe: the case of pest control by vertebrates. *BioScience*, *62*(7), 658-666.

Clauset, A., Moore, C., & Newman, M. E. (2008). Hierarchical structure and the prediction of missing links in networks. *Nature*, *453*(7191), 98-101.

Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species: toward a global functional homogenization?. *Frontiers in Ecology and the Environment*, *9*(4), 222-228.

Corlett, R. T. (2017). Frugivory and seed dispersal by vertebrates in tropical and subtropical Asia: an update. *Global Ecology and Conservation*, *11*, 1-22.

Diaz, S., Settele, J., Brondizio, E., et al (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services.

Dobson, A., Lodge, D., Alder, J., Cumming, G. S., Keymer, J., McGlade, J. et al. (2006). Habitat loss, trophic collapse, and the decline of ecosystem services. Ecology, 87(8), 1915-1924.
Doherty, T. S., Glen, A. S., Nimmo, D. G., Ritchie, E. G., & Dickman, C. R. (2016). Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences*, *113*(40), 11261-11265.

De Visser, S. N., Freymann, B. P., & Olff, H. (2011). The Serengeti food web: empirical quantification and analysis of topological changes under increasing human impact. *Journal of animal ecology*, *80*(2), 484-494.

De Vries, F. T., Thébault, E., Liiri, M., Birkhofer, K., Tsiafouli, M. A., Bjørnlund, L., ... & Bardgett, R. D. (2013). Soil food web properties explain ecosystem services across European land use systems. *Proceedings of the National Academy of Sciences*, *110*(35), 14296-14301.

Dou, Y., Cosentino, F., Malek, Z. *et al.* A new European land systems representation accounting for landscape characteristics. *Landscape Ecology* **36,** 2215–2234 (2021). https://doi.org/10.1007/s10980-021-01227-5

European Environmental Agency, EEA (2021). Biogeographical regions. https://www.eea.europa.eu/data-and-maps/data/biogeographical-regions-europe-3

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J. et al. (2011). Trophic downgrading of planet Earth. *science*, *333*(6040), 301-306.

Etard, A., Pigot, A.L. & Newbold, T. (2022). Intensive human land uses negatively affect vertebrate functional diversity. Ecology Letters 25: 330-343. DOI:10.1111/ele.13926.

Evans, D. M., Pocock, M. J., & Memmott, J. (2013). The robustness of a network of ecological networks to habitat loss. *Ecology letters*, *16*(7), 844-852.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual review of ecology, evolution, and systematics*, *34*(1), 487-515.

Fischer, J. D., Cleeton, S. H., Lyons, T. P., & Miller, J. R. (2012). Urbanization and the predation paradox: the role of trophic dynamics in structuring vertebrate communities. *Bioscience*, *62*(9), 809-818.

Gaüzère, P., & Devictor, V. (2021). Mismatches between birds' spatial and temporal dynamics reflect their delayed response to global changes. *Oikos*, *130*(8), 1284-1296.

Gaüzère, P., O'Connor, L., Botella, C., Poggiato, G., Münkemüller, T., Pollock, L. J., ... & Thuiller, W. (2022). The diversity of biotic interactions complements functional and phylogenetic facets of biodiversity. *Current Biology*, *32*(9), 2093-2100.

Geiger, F., Bengtsson, J., Berendse, F., Weisser, W. W., Emmerson, M., Morales, M. B. et al (2010). Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. Basic and Applied Ecology, 11(2), 97-105.

557 Gonzalez, A., Rayfield, B., & Lindo, Z. (2011). The disentangled bank: how loss of habitat
558 fragments and disassembles ecological networks. *American journal of botany*, *98*(3), 503-516.

559 Gilarranz, L. J., Mora, C., & Bascompte, J. (2016). Anthropogenic effects are associated with a
560 lower persistence of marine food webs. *Nature communications*, *7*(1), 1-5.

561 Gossner, M. M., Lewinsohn, T. M., Kahl, T., Grassein, F., Boch, S., Prati, D. et al. (2016). Land-
562 use intensification causes multitrophic homogenization of grassland communities. *Nature*,
563 *540*(7632), 266-269.

564 Guillera-Arroita, G. (2017). Modelling of species distributions, range dynamics and communities
565 under imperfect detection: advances, challenges and opportunities. *Ecography*, *40*(2), 281-295.

566 Hallmann, C. A., Foppen, R. P., Van Turnhout, C. A., De Kroon, H., & Jongejans, E. (2014).
567 Declines in insectivorous birds are associated with high neonicotinoid concentrations. *Nature*,
568 *511*(7509), 341-343.
569
570 Heckmann, L., Drossel, B., Brose, U., & Guill, C. (2012). Interactive effects of body-size
571 structure and adaptive foraging on food-web stability. *Ecology letters*, *15*(3), 243-250.
572
573 Heger, T., & Jeschke, J. M. (2018). Enemy release hypothesis. *Invasion Biology. Hypotheses*
574 *and Evidence. 1st ed. Boston, MA: CABI*, 92-102.
575
576 Herbst, C., Wäschke, N., Barto, E. K., Arnold, S., Geuß, D., Halboth, I. et al. (2013). Land use
577 intensification in grasslands: higher trophic levels are more negatively affected than lower
578 trophic levels. *Entomologia Experimentalis et Applicata*, *147*(3), 269-281.
579
580 Hill, J. E., DeVault, T. L., & Belant, J. L. (2019). Cause-specific mortality of the world's terrestrial
581 vertebrates. *Global Ecology and Biogeography*, *28*(5), 680-689.
582
583 IUCN (International Union for Conservation of Nature) 2021. The IUCN Red List of Threatened
584 Species. Version 2021-1. https://www.iucnredlist.org. Downloaded on 15 march 2021.
585
586 Johnson, R. A., and D. W. Wichern. 1992. Applied multivariate statistical analysis. Third edition.
587 Prentice–Hall, Englewood Cliffs, New Jersey, USA.
588
589 Kéfi, S., Miele, V., Wieters, E. A., Navarrete, S. A., & Berlow, E. L. (2016). How structured is the
590 entangled bank? The surprisingly simple organization of multiplex ecological networks leads to
591 increased persistence and resilience. *PLoS biology*, *14*(8), e1002527.
592
593 Keyes, A. A., McLaughlin, J. P., Barner, A. K., & Dee, L. E. (2021). An ecological network
594 approach to predict ecosystem service vulnerability to species losses. *Nature communications*,
595 *12*(1), 1-11.
596
597 Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A. V., & Aschan, M. (2015). Climate change
598 alters the structure of arctic marine food webs due to poleward shifts of boreal generalists.
599 *Proceedings of the Royal Society B: Biological Sciences*, *282*(1814), 20151546.
600
601 Kortsch, S., Primicerio, R., Aschan, M., Lind, S., Dolgov, A. V., & Planque, B. (2019). Food-web
602 structure varies along environmental gradients in a high-latitude marine ecosystem. *Ecography*,
603 *42*(2), 295-308.

Lange, H. J. D., Lahr, J., Van der Pol, J. J., Wessels, Y., & Faber, J. H. (2009). Ecological vulnerability in wildlife: an expert judgment and multicriteria analysis tool using ecological traits to assess relative impact of pollutants. *Environmental Toxicology and Chemistry: An International Journal*, *28*(10), 2233-2240.

Li, D., Poisot, T., Waller, D. M., & Baiser, B. (2018). Homogenization of species composition and species association networks are decoupled. *Global Ecology and Biogeography*, *27*(12), 1481-1491.

Link, J. S., Stockhausen, W. T., & Methratta, E. T. (2005). Food-web theory in marine ecosystems. *Aquatic food webs: an ecosystem approach. Oxford University Press, Oxford*, 98-114.

Liu, C., Bathke, A. C., & Harrar, S. W. (2011). A nonparametric version of Wilks' lambda—Asymptotic results and small sample approximations. *Statistics & probability letters*, *81*(10), 1502-1506.

MacKay, R. S., Johnson, S., & Sansom, B. (2020). How directed is a directed network?. *Royal Society open science*, *7*(9), 201138.

Maiorano, L., Montemaggiori, A., Ficetola, G. F., O'connor, L., & Thuiller, W. (2020). TETRA-EU 1.0: A species-level trophic metaweb of European tetrapods. *Global Ecology and Biogeography*, *29*(9), 1452-1457.

McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in ecology & evolution*, *14*(11), 450-453.

Mestre, F., Rozenfeld, A., & Araújo, M. B. (2022). Human disturbances affect the topology of food webs. *Ecology Letters*.

Montoya, J. M., Rodríguez, M. A., & Hawkins, B. A. (2003). Food web complexity and higher-level ecosystem services. *Ecology letters*, *6*(7), 587-593.

Newman, M. E. (2006). Modularity and community structure in networks. *Proceedings of the national academy of sciences*, *103*(23), 8577-8582.

O'Connor, L. M., Pollock, L. J., Braga, J., Ficetola, G. F., Maiorano, L., Martinez-Almoyna, C. et al. (2020). Unveiling the food webs of tetrapods across Europe through the prism of the Eltonian niche. *Journal of Biogeography*, *47*(1), 181-192.

Poisot, T., Canard, E., Mouillot, D., Mouquet, N., & Gravel, D. (2012). The dissimilarity of species interaction networks. *Ecology letters*, *15*(12), 1353-1361.

Prugh, L. R., Stoner, C. J., Epps, C. W., Bean, W. T., Ripple, W. J., Laliberte, A. S., & Brashares, J. S. (2009). The rise of the mesopredator. *Bioscience*, *59*(9), 779-791.

Rigal, S., Devictor, V., Gaüzère, P., Kéfi, S., Forsman, J. T., Kajanus, M. H. et al. (2021). Biotic homogenisation in bird communities leads to large-scale changes in species associations. *Oikos*.

644 Saint-Béat, B., Baird, D., Asmus, H., Asmus, R., Bacher, C., Pacella, S. R. et al. (2015). Trophic
645 networks: How do theories link ecosystem structure and functioning to stability properties? A
646 review. *Ecological indicators*, *52*, 458-471.

647 Sparling, D. W., Fellers, G., & McConnell, L. (2001). Pesticides are involved with population
648 declines of amphibians in the California Sierra Nevadas. *The scientific world journal*, *1*, 200-201.

649 Thuiller, W., Calderon-Sanou, I., Chalmandrier, L., Gaüzere, P., O'Connor, L., Ohlmann, M.,
650 Poggiato, G. & Münkemüller, T. (2023). Navigating the integration of Biotic Interactions in
651 Biogeography. *Journal of Biogeograhy.* [In press]

652 Tylianakis, J. M., Laliberté, E., Nielsen, A., & Bascompte, J. (2010). Conservation of species
653 interaction networks. *Biological conservation*, *143*(10), 2270-2279.

654 Van Strien, A. J., Van Swaay, C. A., & Termaat, T. (2013). Opportunistic citizen science data of
655 animal species produce reliable estimates of distribution trends if analysed with occupancy
656 models. *Journal of Applied Ecology*, *50*(6), 1450-1458.

657 Walker, L. R., Wardle, D. A., Bardgett, R. D., & Clarkson, B. D. (2010). The use of
658 chronosequences in studies of ecological succession and soil development. *Journal of ecology*,
659 *98*(4), 725-736.

660 Wermelinger, B. and Herrmann, M. (2015). Chapter 7 - Natural Enemies of Bark Beetles:
661 Predators, Parasitoids, Pathogens, and Nematodes. (Pages 247-304)
662
663

Figures

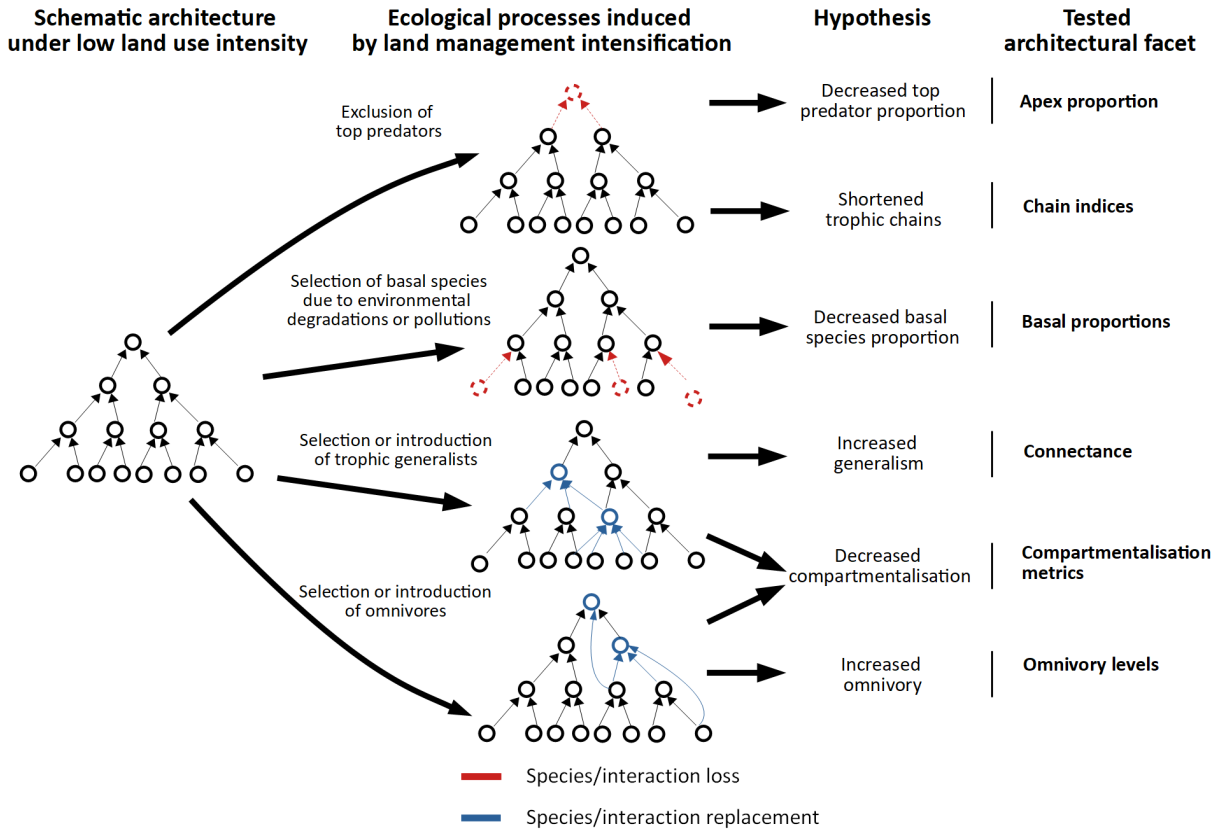
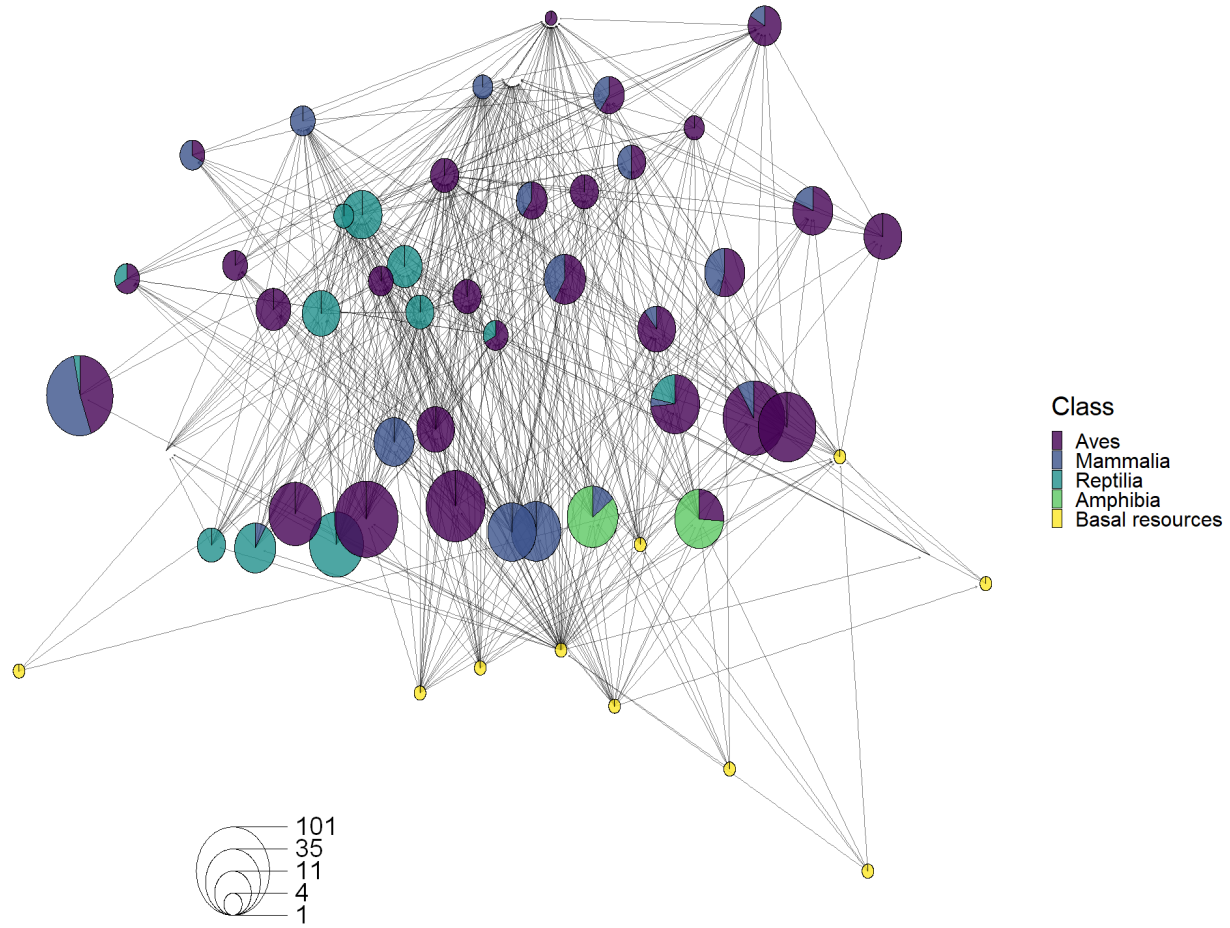
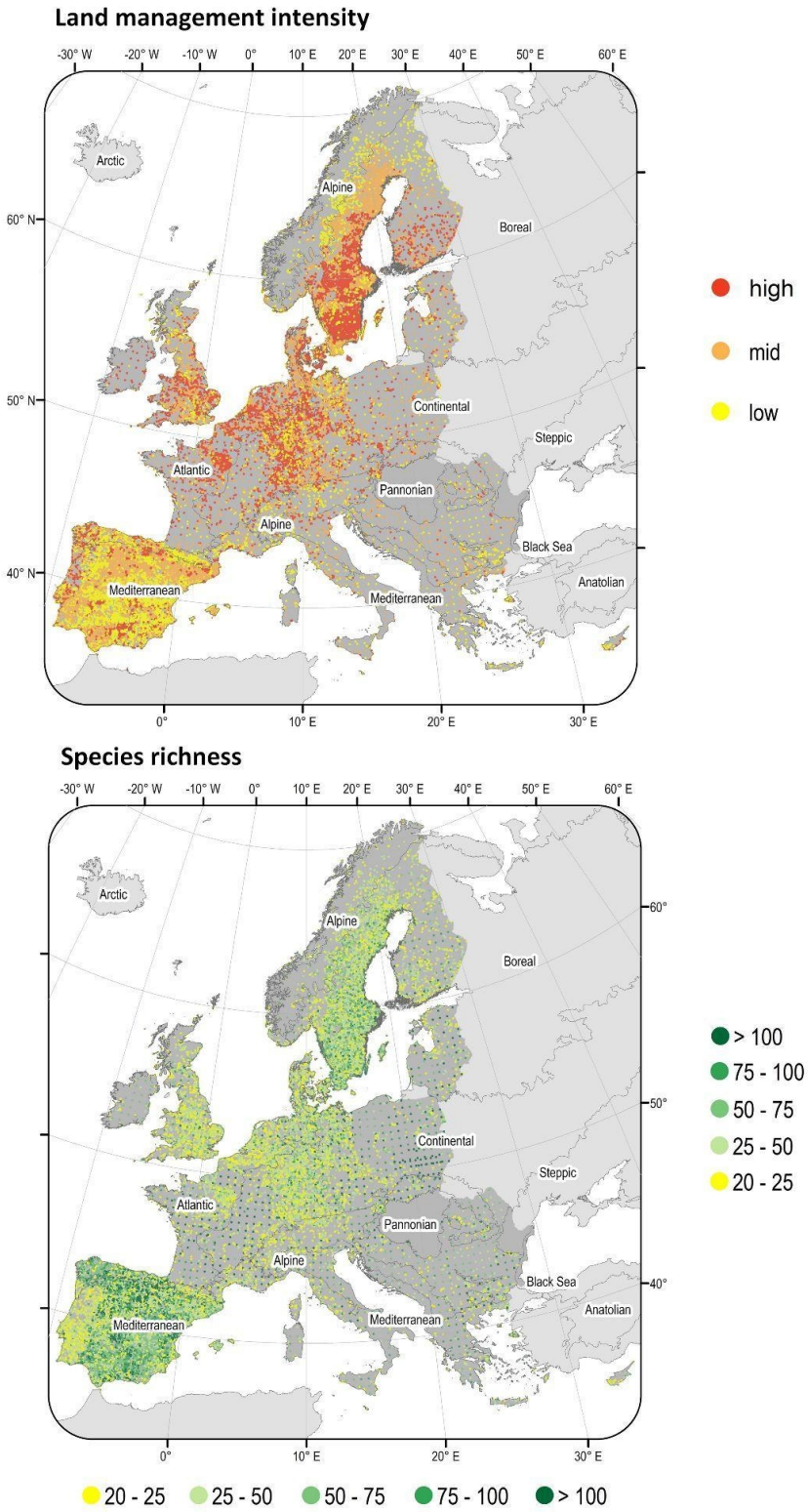


Figure 1. Hypothetical food-web architecture changes related to the ecological processes associated with land use intensification. However, our general assumptions could be contradicted by the context dependence of these processes, i.e. intensification does not necessarily enhance all these processes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



673

674 **Figure 2.** The metaweb of trophic interactions of our 756 European tetrapods aggregated per
675 trophic groups (O'Connor et al., 2020). Each node is one of the 46 trophic groups (detailed in
676 Table **S2.1**), its size represents the number of species while the colours represent the
677 proportion of classes. The trophic groups were automatically positioned vertically according to
678 their trophic level and horizontally so that connected groups are more aligned than non-
679 connected ones (TL-tsne layout method of the R package **metanetwork:**
680 https://marcohlmann.github.io/metanetwork/). Basal resources (i.e diets that are not wild
681 vertebrates) were included as yellow nodes.



682

683 **Figure 3.** Map of the 67,051 studied local meta food-webs (1km² cells). **Top:** Cell locations
684 colored by land management intensity. **Bottom:** Cell locations colored by observed species
685 richness.

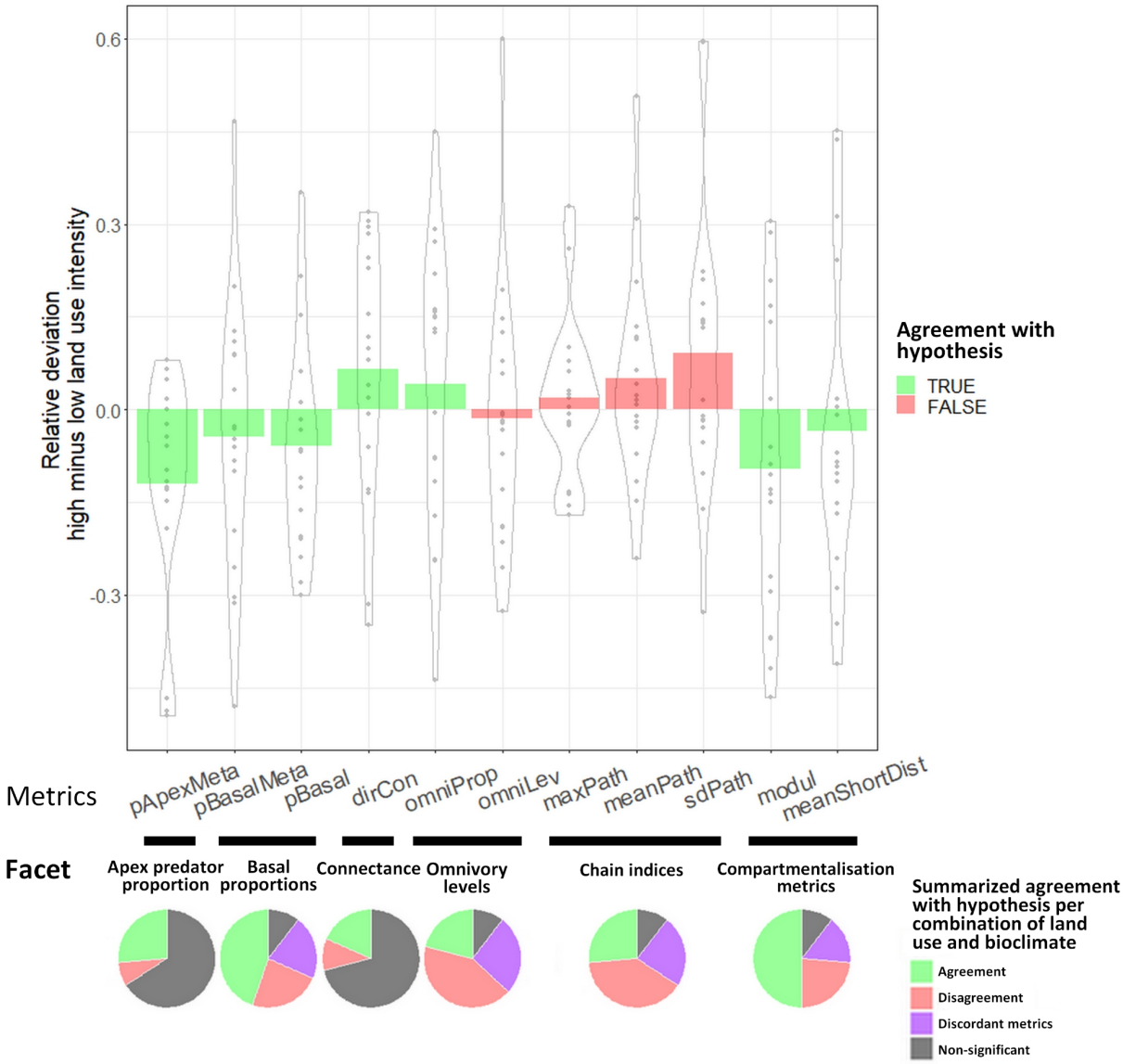


Figure 4. Food-web metric deviations related to higher land management intensity per architecture facet and agreement with the initial hypothesis. **Top:** For each metric (x-axis), the relative deviation (barplot on y-axis) is the average over 18 contexts (grey dots) of the mean deviation from low to 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**). **Bottom:** For each facet, a pie plot summarises the tests of deviation significance over the 38 contexts and intensity level comparisons (high versus low and medium versus low) into agreements (green) or disagreements (red) with the hypothesis, discordant metrics (purple) or non-significant, based on the multivariate test.

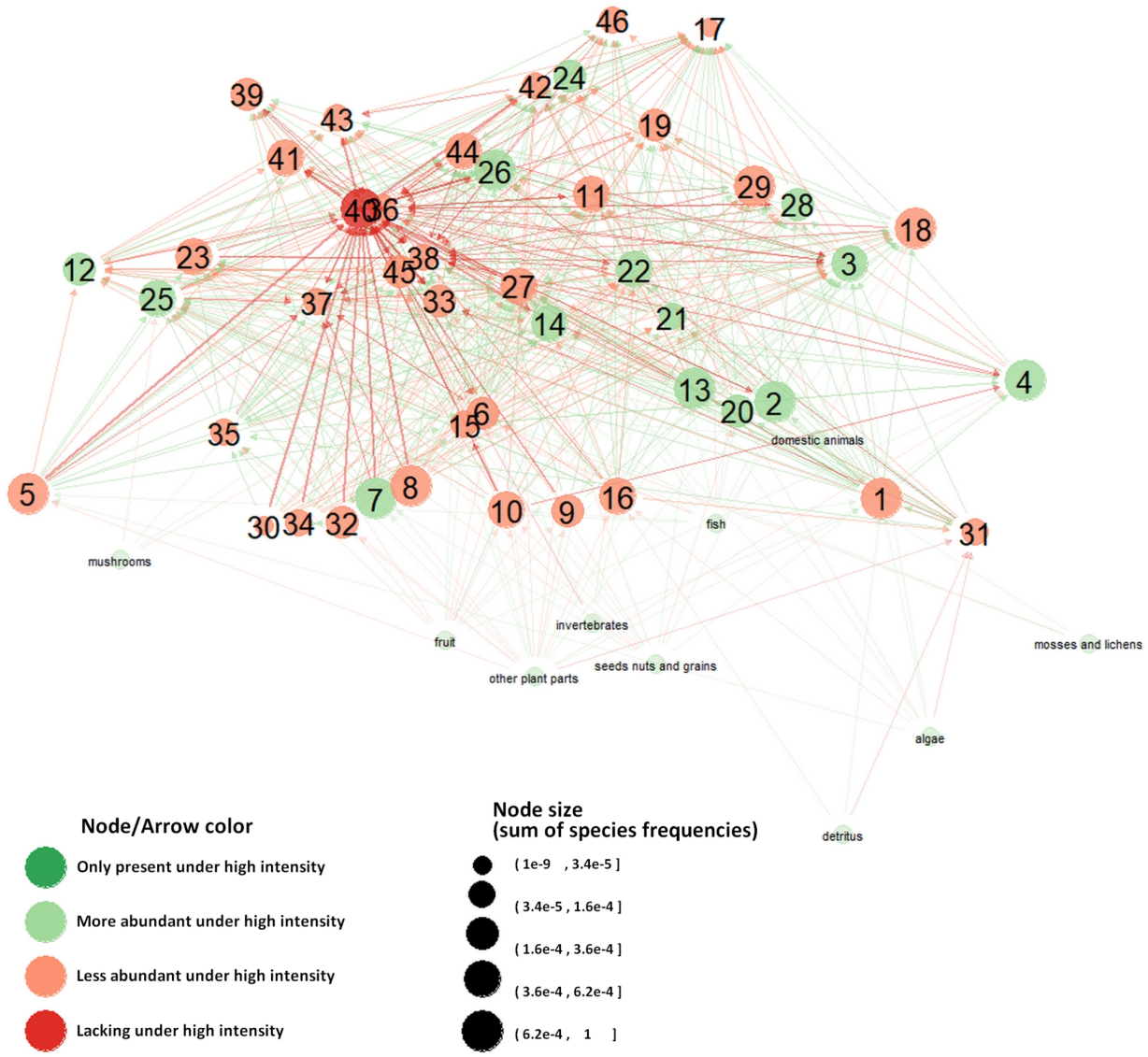


Figure 5. Changes of trophic group frequencies when increasing land management intensity. This difference plot between average networks in high and low land management intensity cells is produced by the diff_plot function in **metanetwork** R package. As in **Figure S2.2**, each node is one trophic group 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**.

Tables

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 et al., 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]

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

Appendices

Appendix S1 - Data preprocessing

Figure S1.1 summarizes the 4 steps of our data preprocessing pipeline leading to the selection of the species, cells and combinations of bioclimatic region, land use and land management intensity in this study. In the text below, we also present in more detail the first step, namely

data cleaning of the GBIF/iNaturalist occurrences. Finally, we explain how to reproduce the data preprocessing steps for transparency (optional) and the manuscript Figures using our online repositories.

Data cleaning (step 1 of Figure S1.1). We extracted all tetrapod geolocated occurrences from the GBIF (except iNaturalist dataset) with date posterior to 1980, including only human observations, a geolocation uncertainty below 1km (resolution of our study cells). Besides, we extracted the tetrapod iNaturalist research grade occurrences using the rinat R package to add them to the GBIF ones. Then, we removed duplicates, and occurrences suffering from various coordinates errors using the **CoordinateCleaner** R library:

- Degree-minute to decimal degree conversion error (cd_ddmm function)
- Location too close to gbif headquarters or other biodiversity institutions, country capitals, country centroids.
- Occurrences outside of the IUCN range, if available and including the invasive range (spatial ranges are assessed in the context of the IUCN red list of threatened species, IUCN, 2021), for the corresponding species. Indeed, we assumed that species presence outside of the IUCN range was either an identification error, a geolocation error, or a vagrant specimen not proving the existence of a local population.

We fully removed the datasets for which the **`cd_round`** function of **CoordinateCleaner** detected a spatial rasterization pattern in their coordinates with a periodicity superior to 1km. However, we acknowledge that this automatic detection algorithm was not sufficient to detect all rasterized datasets as for instance one of them is visible from Figure 3-bottom. Finally, the 756 species included in this study were those with at least one occurrence remaining and present in the tetrapod meta-web of trophic interactions (Maiorano et al., 2020).

Reproduction. To reproduce our result Figures, one can simply download **preprocessed_data** and **TrophicNetworksList** Rdata files from our Zenodo repository (https://zenodo.org/record/5831144) and run R script **analyse_preprocessed_data.R** provided in our Github repository (https://github.com/ChrisBotella/foodwebs_vs_land_use). It will generate the Figures of this manuscript locally. To reproduce steps 2 to 4 of the data preprocessing pipeline given in **Figure S1.1** from the cleaned GBIF/iNaturalist occurrences, it is possible to download the **raw_data** Rdata file from Zenodo (several Gb file) and run the **preprocess_data.R** script from our Github. It will re-generate **preprocessed_data** and **TrophicNetworksList** locally, which are the inputs for **analyse_preprocessed_data.R.**

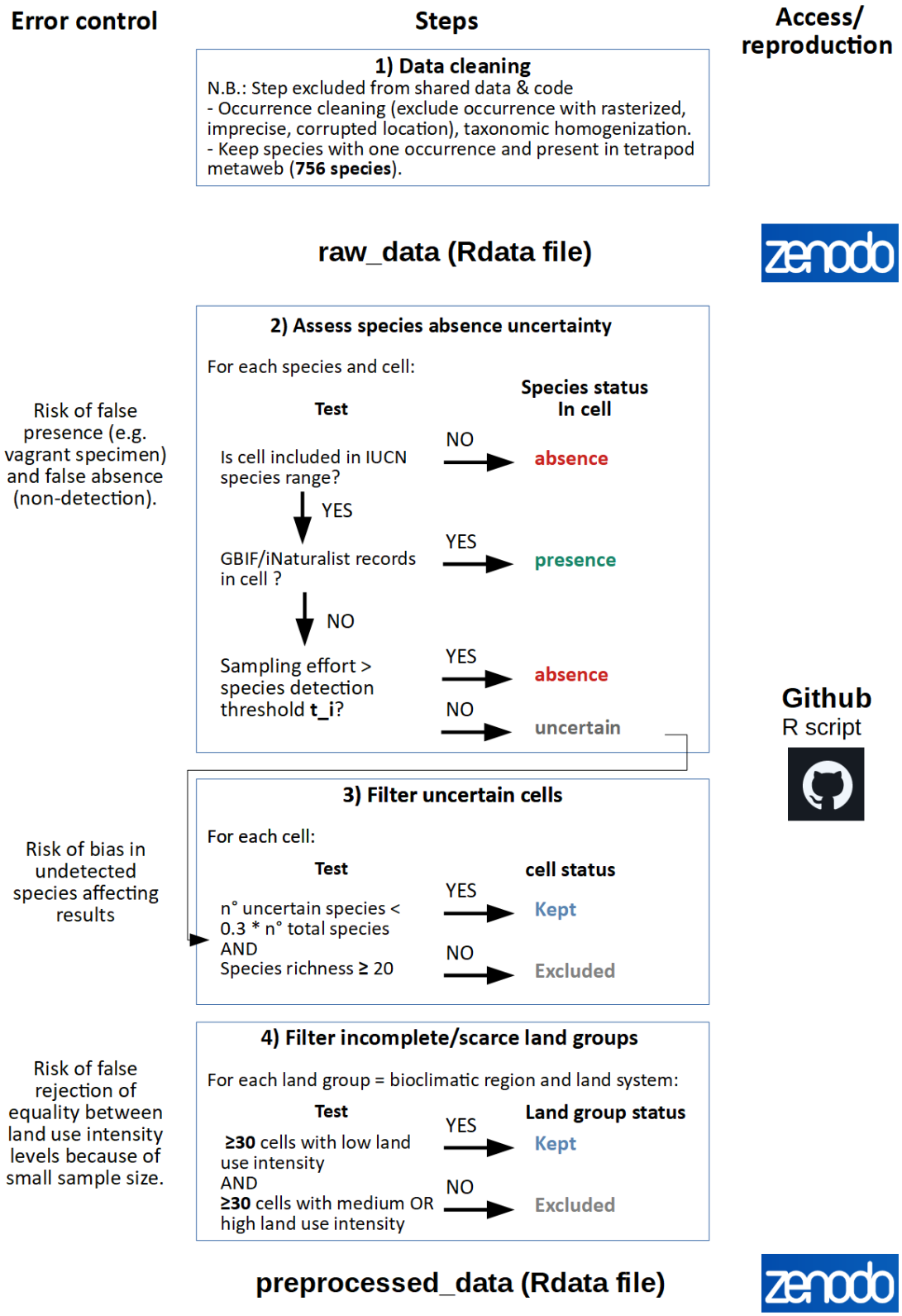
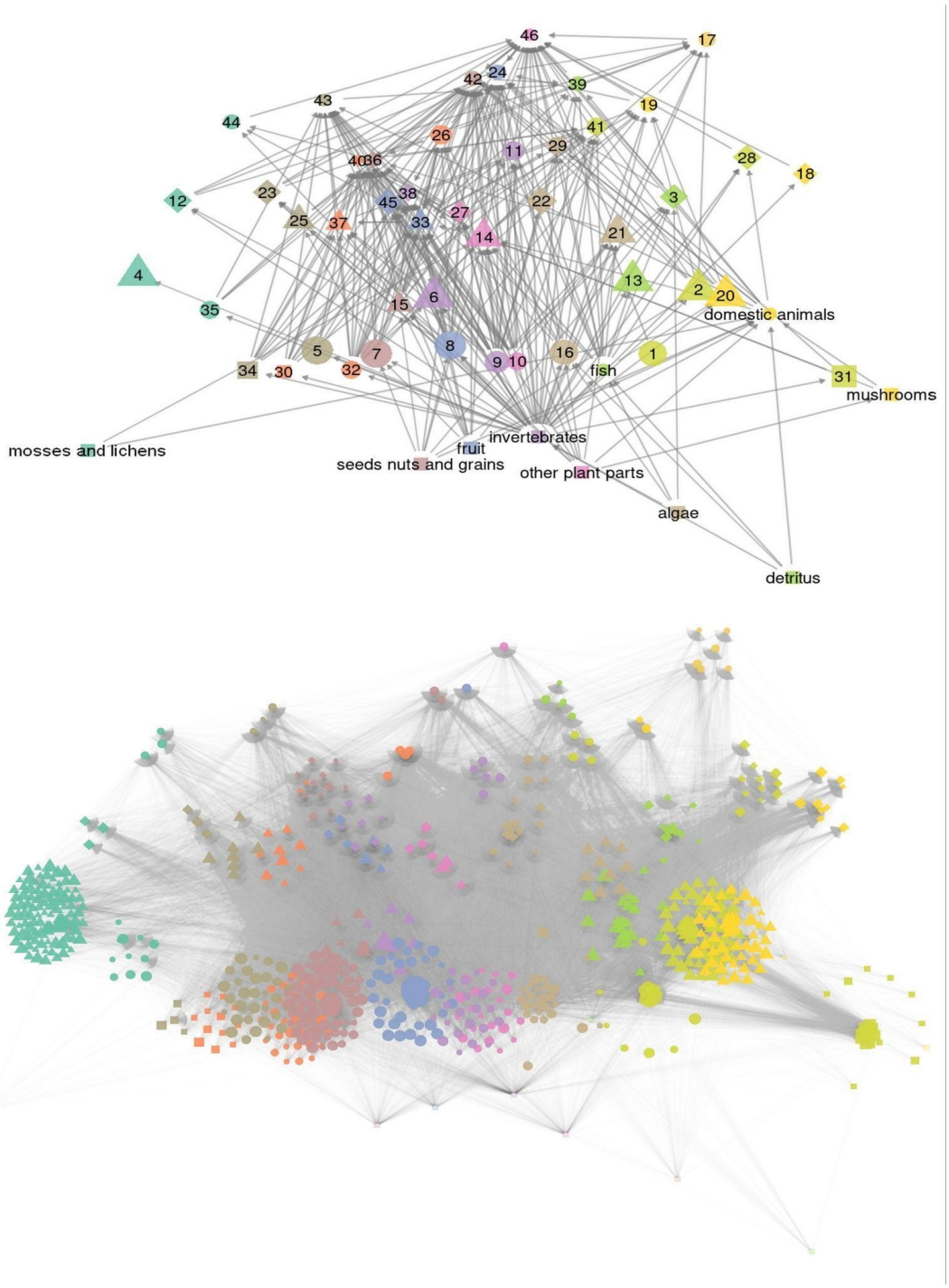


Figure S1.1. Data preprocessing pipeline (center), potential errors that each step is meant to control (left) and the websites where our material is provided for reproduction (right).

Appendix S2 - metaweb details



764

765 **Figure S2.2** The metaweb of trophic interactions of our 756 European tetrapod species and
766 their 46 trophic groups. Top: The meso-scale metaweb where each node is one trophic group
767 numbered as in Table S2.1, and identified by a combination of shape and colour. The vertical
768 positioning is based on the trophic level, while the horizontal one is based on the proximity in
769 the network (more connected groups are more aligned than non-connected ones). Diets are
770 included as basal nodes. Each arrow indicates trophic interactions between species of two
771 groups (going from prey to predator). Bottom: The micro scale metaweb where each node is
772 one species and species belonging to a same trophic group are aggregated into clusters (group-

TL-tsne method of the R package metanetwork) with the same trophic group shape and colour code as in the above Figure.

Group	nSpecies	Most frequent species	Most common class
46	1	Bubo bubo	Aves
17	6	Accipiter gentilis	Aves
24	1	Strix aluco	Aves
42	2	Vulpes vulpes	Mammalia
39	5	Aquila chrysaetos	Aves
43	3	Felis silvestris	Mammalia
19	2	Falco peregrinus	Aves
44	3	Circaetus gallicus	Mammalia
41	4	Ciconia ciconia	Aves,Mammalia
26	4	Corvus corone	Aves
29	4	Milvus milvus	Aves
11	5	Buteo buteo	Aves
28	11	Circus aeruginosus	Aves
36	11	Malpolon monspessulanus	Reptilia
40	2	Dolichophis caspius	Reptilia
18	9	Hieraaetus pennatus	Aves
23	3	Athene noctua	Aves
38	7	Vipera berus	Reptilia
3	11	Larus canus	Aves
12	3	Accipiter nisus	Aves
22	12	Chroicocephalus ridibundus	Aves
45	3	Lanius excubitor	Aves
27	4	Lanius collurio	Aves
25	7	Nucifraga caryocatactes	Aves
33	4	Timon lepidus	Reptilia
37	9	Coronella girondica	Reptilia
21	9	Ardea cinerea	Aves
14	3	Garrulus glandarius	Aves
4	101	Cuculus canorus	Mammalia
13	23	Vanellus vanellus	Aves
2	67	Columba palumbus	Aves
20	48	Gallinago gallinago	Aves
6	9	Turdus merula	Aves
15	11	Eliomys quercinus	Mammalia
35	11	Anguis fragilis	Reptilia
8	54	Fringilla coelebs	Aves
5	31	Hirundo rustica	Aves
16	27	Bufo bufo	Amphibia
1	23	Gyps fulvus	Amphibia
7	77	Parus major	Aves
10	24	Crocidura russula	Mammalia
9	22	Apodemus sylvaticus	Mammalia
32	35	Zootoca vivipara	Reptilia
34	4	Chalcides striatus	Reptilia
30	12	Chalcides bedriagai	Reptilia
31	29	Lissotriton vulgaris	Amphibia

Table S2.1. The 46 trophic groups of the European tetrapod metaweb as defined in O'Connor et al. (2020) and represented in Figure S2.2-bottom above and Figure 4 of the main manuscript.

Groups are ordered by decreasing average trophic level. The table also shows their number of species (of the 756 studied here), the most frequently present species across the 67,051 local meta food-webs and the most common taxonomic class of the group.

Appendix S3- Land systems and study area coverage

land uses	Composition	Land management intensity classes	Indicators of intensity used
1. Forest	All forests except some clear cuts	Low, medium, high	Wood production, probability of primary forest
2. Grassland	All grasslands excluding grassed wetlands	Low, medium, high	Inorganic fertilizer input, mowing frequency, livestock density
3. Permanent cropland	vineyards, olive graves, fruit gardens	Extensive (low), Intensive (high)	Understory vegetation
4. Arable cropland	Annual crops (wheat, etc)	Low, medium, high	Inorganic fertilizer input, field size
5. Agricultural mosaic	cropland and grassland	Low, medium, high	Inorganic fertilizer input, field size, livestock density
6. Human settlement	Cities and surrounding urban areas	Low, medium, high	Population density, distance from urban core, imperviousness

Table S3.2. Classification of land uses and land management intensity.

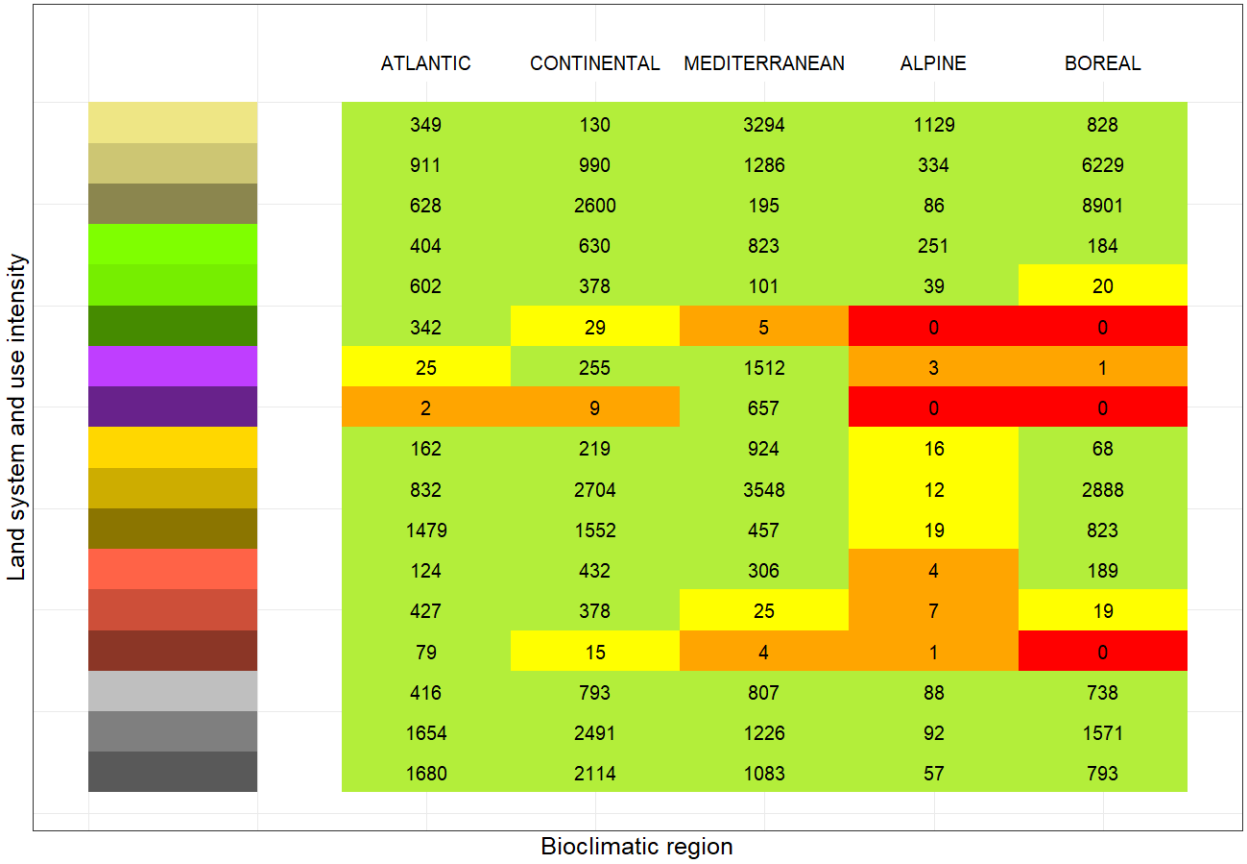
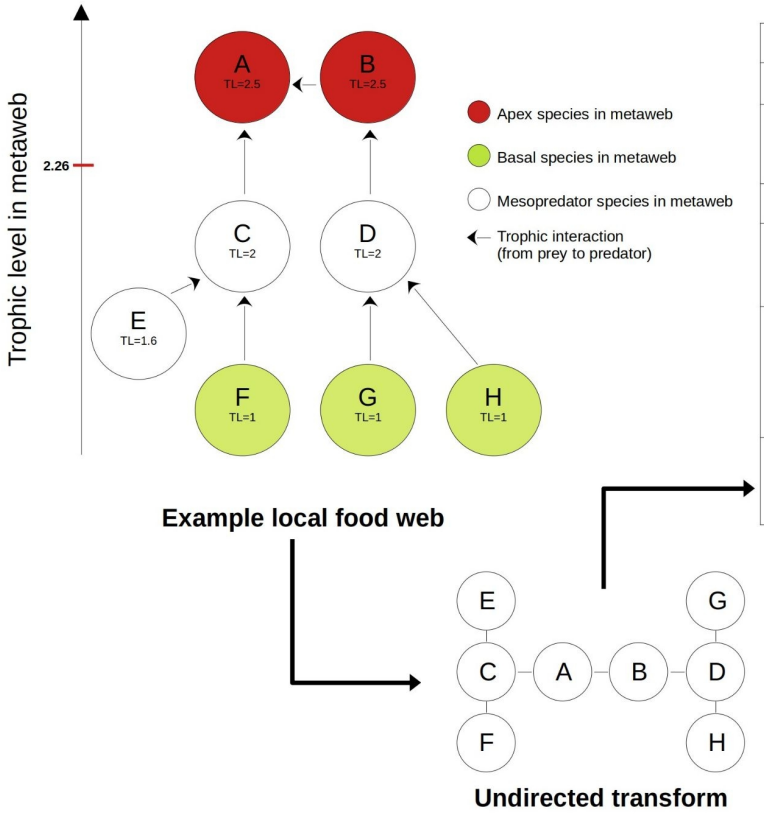


Figure S3.4. Numbers of 1km² cells per land group (combination of bioclimatic region, land use and land management intensity included in the study) with >70% of all tetrapod species certainly present or absent and a richness >20. Land groups are colored based on their number of cells: No cell (red), 1 to 9 cells (orange), 10 to 29 (yellow) and more than 29 cells (green). We finally kept a total of 67,051 cells for our study, including only the green combinations above and discarding Black Sea and Pannonian regions because they lacked intensity levels for comparison.

Appendix S4- Detailed network metrics per architecture facet

Apex proportion: To define apex species, we first computed species trophic levels (MacKay et al., 2020) in the metaweb completed with species diets (**Figure S2.2**), as recommended by

Maiorano et al. (2020). There are 10 diets (1) “algae”, (2) “fish”, (3) “invertebrates”, (4) “domestic animals”, (5) “mushrooms”, (6) “mosses and lichens”, (7) “detritus”, (8) “fruit”, (9) “seed, nuts and grains” and (10) “other plant parts”. They were integrated as additional nodes in the metaweb along with trophic relationships between them, that is: (1), (7) is eaten by (2) and (3). (3) is eaten by (2) and (4). (5), (6), (7), (8), (9), (10) are eaten by (4). (10) is eaten by (5). This makes the trophic levels more meaningful, especially for the many tetrapod species that otherwise have no prey among tetrapods, because they can have variable height in the whole trophic chains including non-tetrapod species. We define that species with trophic level above 2.262 are apex predators, so that the 59 selected species fitted best to those generally qualified as apex predators, including wolf, brown bear, wolverine, foxes, badger, wild cat, eagles, falcons, owls, and macro vipers. We then computed, in each local network, the proportion of apex predators, hereafter called **pApexMeta**. In the example local meta food-web of **Figure S4.5,** there are two species that are apex in the metaweb (their trophic level is higher than 2.26) so **pApexMeta**=2/8=0.25.



Facet	Metric	Value
Apex proportions	pApexMeta	0.25
Basal proportions	pBasalMeta	0.375
	pBasal	0.5
Connectance	dirCon	0.194
Omnivory levels	omniProp	-
	omniLvl	-
Chain indices	maxPath	3
	meanPath	2.5
	sdPath	0.557
Compartmentalization metrics	modul	0.258
	meanShortDist	2.643

Figure S4.5. Virtual example of a local food-web and the values of our metrics. Eight species are present in this virtual trophic community, and they are positioned vertically according to their

trophic level in the metaweb of tetrapod species. If a species has no tetrapod prey in the metaweb, it is a basal species (filled in green), if its trophic level is above 2.26, it is an apex predator (filled in red), otherwise it is a mesopredator. The compartmentalization metrics are computed from the undirected transform of the food-web, which is represented in the bottom.

Basal proportions: We computed the proportion of basal species in the local network (species with no prey), called **pBasal,** and the proportion of species that are basal in the metaweb (species without any tetrapod prey in the metaweb), called **pBasalMeta**. This gives a different perspective as a non-basal species in the metaweb can be locally observed without its prey. In the example local food-web of **Figure S4.5,** there are three species that are basal in the metaweb (F, G, H) so **pBasalMeta**=3/8=0.375, but there are four species that have no prey in the local food-web (E, F, G, H) so **pBasal**=4/8=0.5. By comparing proportions of basal and proportions of apex species between two sets of networks, we can also deduce the variation of proportion of mesopredator species.

Connectance: We computed the directed connectance of the local network as the average number of prey per species (i.e. the average in-degree, reflecting trophic generalism) divided by species richness, called **dirCon**. This metric captures the density of trophic interactions in the local network and enables to compare the level of generalism independently of richness. We preferred it to the actual average in-degree which tends to scale linearly with species richness and may thus bias our signal here as observed richness is partially biased by heterogeneous sampling effort. Note that we only accounted here for predation on terrestrial vertebrates as we lack data for assessing the full trophic generalism on non-tetrapod species (e.g. invertebrates, marine vertebrates, plants, fungi).

Omnivory levels: We computed two metrics for each local network. **omniLvl** takes the average, over locally present mesopredator species in the metaweb (non-basal nor apex), of the standard deviation of their prey trophic levels in the metaweb. This metric is based on a continuous view of omnivory. In the example local food-web of **Figure S4.5**, the mesopredator species are E, C and D. For each of these species, we must gather the trophic levels of its prey in the metaweb and compute their standard deviation (which can't be done from the information available in this virtual example). omniLvl is then the average of these three standard deviations. **omniProp** computes the proportion of locally present mesopredator species in the metaweb (non-basal nor apex) that are classified as omnivores, namely feeding on several trophic level intervals in the metaweb. We considered three trophic level intervals: basal (0 to the maximum trophic level of

basal species in the metaweb, i.e. 1.572), mesopredators (from the latter to the apex trophic level threshold, explained above), and apex (above the apex trophic level threshold). In the example local food-web of **Figure S4.5**, This definition enables us to locally detect surpluses of species that have a potentially broader trophic niche, even though many of their prey are not locally present. As defined here, our omnivory metrics are insensitive to species richness, basal and apex proportions in the local community. Our choice to exclude apex predators from the computation of omnivory levels is a consequence of the fact that most tetrapod apex predators are very omnivore so that including them would induce a strong correlation with apex proportion and carry no information about the omnivory of mesopredators, which are the main focus of this facet.

Chain indices: For each local network, we computed the longest, the mean, and the standard deviation of trophic chain lengths linking basal and top species, based on directed shortest-path lengths. More precisely, we computed the matrix of shortest-path lengths between basal and top species only. Each row of this matrix corresponds to a basal species (no prey in local network), each column to a top species (no predator in local network) and the coefficient (i,j) indicates the length of the shortest path in the network (trophic chain) starting from basal species i and going to top species j. When no path exists from i to j, it is indicated by an infinite coefficient. Note that species without any prey or predator are excluded. Then, we turned this matrix to a vector, removing infinite coefficients, and summarized it with its maximum (**maxPath**), mean (**meanPath**) and standard deviation (**sdPath**) values. For instance, in the example local food-web of Figure S4.5, there are four existing paths from the four local basal species (E, F, G, H) to the single local top predator A. The associated four shortest-path lengths are: 2 (E->A), 2 (F->A), 3 (G->A), 3 (H->A). Then, maxPath is the largest (3), meanPath is their mean (2.5) and sdPath is their standard deviation (~0.577).

Compartmentalization: We hypothesized that the replacement of trophic specialists with trophic generalists and omnivores would tend to break up compartments within networks, i.e. sets of species with denser interactions between them than with the rest of the network. It should translate into a decrease of network modularity (Newman et al., 2006), and a decrease of mean distance between species in the **undirected network** (where the initial directed edges are replaced by undirected ones). Thus, we computed those two metrics, respectively called **modul, meanShortDist**, in this architectural facet. More precisely, **modul** is the sum (over all pairs of nodes belonging to a same compartment) of the number of edges between two nodes (zero or one here) minus its expectation if edges were placed at random, standardised by the number of

edges. There are several ways to detect communities in a network. We first divided the network into its connected components (sets of nodes between which there exist a path through edges) and for each of them, we detected communities inside it with the **cluster_spinglass** function of the igraph R package (spinglass model with simulated annealing, see Reichardt & Bornholdt, 2006), so that the network communities are the union of communities across its connected components. Then, the exact formula of the modularity Q for a network of **n** nodes and **m** edges is given below:

$$Q = \frac{1}{4m} \sum_{i,j} \mathrm{com}(i,j)(A_{ij} - \frac{k_i k_j}{2m})$$

Where **k_i** is the degree (number of edges) of node **i**, **A_ij** equals one if there is an edge between **i** and **j** or zero otherwise, and **com(i,j)** equals one if **i** and **j** belong to the same community or zero otherwise. The modularity of a network lies between -1 and 1, with a value above zero if nodes inside each community are more connected than expected by chance. This is the case in the example local food-web of Figure S4.5 which has a modularity of 0.248. The spinglass algorithm detected three node communities: (E,C,F), (A,B) and (G,D,H). These communities make sense visually given the topology of the network undirected transform in the bottom of Figure S4.5.

References:

MacKay, R. S., Johnson, S., & Sansom, B. (2020). How directed is a directed network?. *Royal Society open science*, *7*(9), 201138.

Maiorano, L., Montemaggiori, A., Ficetola, G. F., O'connor, L., & Thuiller, W. (2020). TETRA-EU 1.0: A species-level trophic metaweb of European tetrapods. *Global Ecology and Biogeography*, *29*(9), 1452-1457.

Newman, M. E. (2006). Modularity and community structure in networks. *Proceedings of the national academy of sciences*, *103*(23), 8577-8582.

Reichardt, J., & Bornholdt, S. (2006). Statistical mechanics of community detection. *Physical review E*, *74*(1), 016110.

Appendix S5- Relationships between network metrics

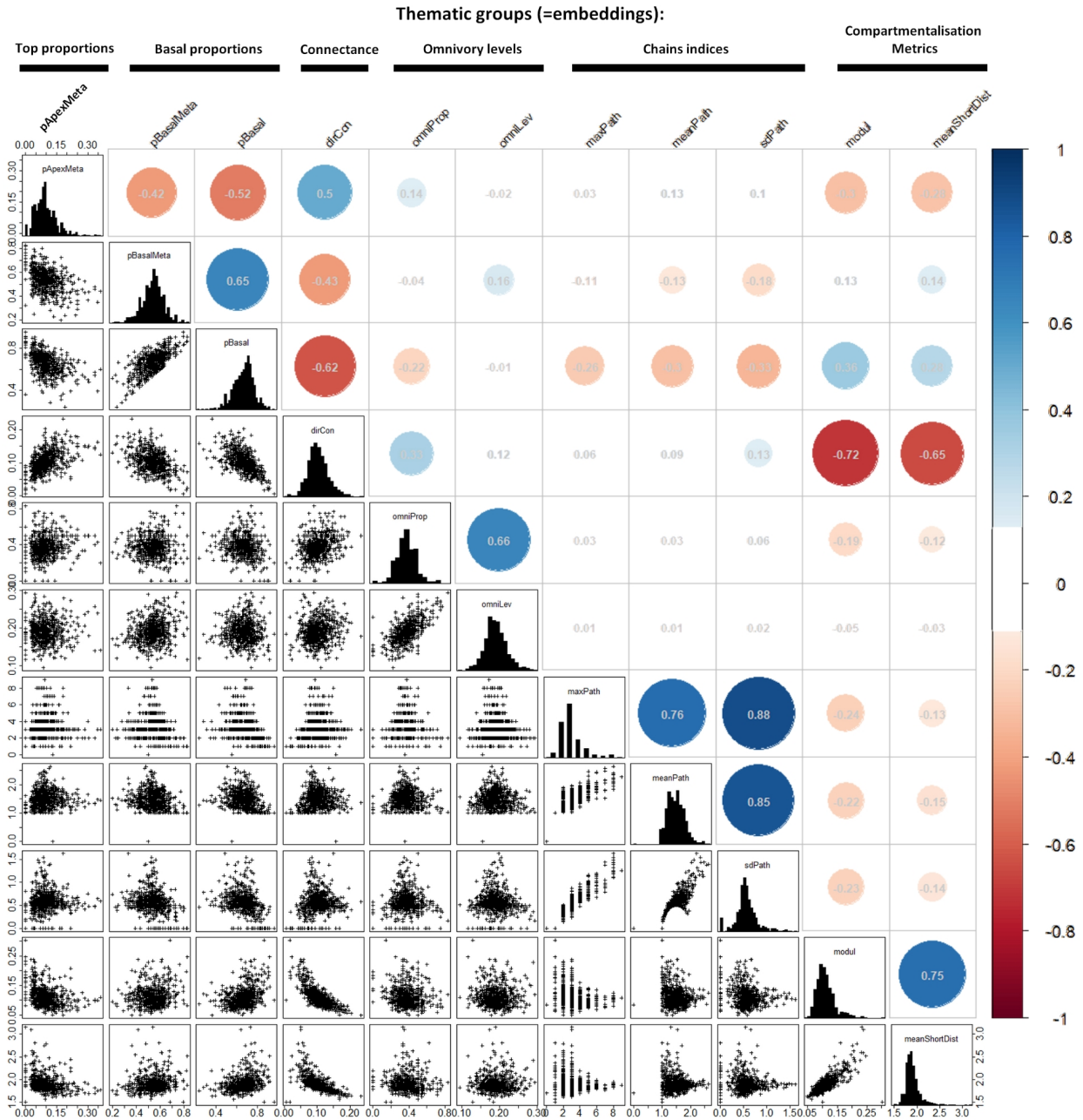


Figure S5.6. Relationships between food-web metrics used in this study. Lower triangle: Scatter plots of metrics values over 650 randomly sampled cells. Upper triangle: Pearson correlations between metric pairs over all cells.

Appendix S6- Quantifying and testing effects of land management intensity on food-webs architecture per land use and bioclimatic region

We notably 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 versus low intensity, or medium versus 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 non-parametric 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). For every context, we set the first order risk α of detecting at least one false non-equality across our 6 facets to 5%, which translates into a risk of $1-(1-\alpha)^{(1/6)} \approx 0.009$ in each facet, a rather conservative choice. Following the procedure of Burchett et al. (2017), when three intensity levels were available for a context, we first tested the equality between the three distributions with risk α, and if equality was rejected, we tested the equality between each pair with risk $2\alpha/3$, to maintain a strong control of the familywise error rate. The significance of the deviation in each context is indicated by a blue background of cells in Tables **S6.7** to **S6.11**.

	ATLANTIC	CONTINENTAL	MEDITERRANEAN	ALPINE	BOREAL
medium intensity forest	-0.372	-0.074	+0.009	-0.038	+0.043
high intensity forest	-0.467	-0.126	+0.081	-0.059	+0
medium intensity grassland	-0.101	-0.083	-0.059	-0.346	
high intensity grassland	-0.116	-0.098			
intensive perma. cropland			+0.017		
medium intensity cropland	-0.14	-0.032	+0.146		+0.065
high intensity cropland	-0.192	+0.049	+0.017		-0.129
medium intensity agri. mosaic	+0	+0.048			
high intensity agri. mosaic	-0.045				
medium intensity settlement	-0.014	-0.087	-0.588	-0.437	+0.055
high intensity settlement	-0.024	-0.148	-0.495	-0.487	+0.065

Figure S6.7. Food-web metrics deviations related to land management intensity, **Part 1: Apex proportion embedding (pApexMeta).** For each bioclimatic region (columns), land use and land management intensity level (rows), we show the index of variation along each metric between the considered intensity level (medium/high) and the reference one (low). This index is the centroid coordinate of the highest intensity group minus the centroid coordinate of the lower intensity group, divided by the interquartile range of the metric across all studied cells (as in **Figure 2**). It indicates the direction of the deviation and its importance compared to the dataset variability. Cells with a number over a white background indicate a significant multivariate

deviation in the corresponding context, established with a non-parametric multivariate test, while cells with a grey background indicate a non-significant deviation and empty cells indicate no data. A significant deviation is written in pale green when its direction confirms our initial expectation, in dark red when it contradicts it, and in black for discordant deviations.

	ATLANTIC	CONTINENTAL	MEDITERRANEAN	ALPINE	BOREAL
medium intensity forest	+0.044;-0.073	-0.283;-0.09	+0.175;+0.171	+0.142;+0.014	-0.213;-0.265
high intensity forest	+0.11;-0.033	-0.256;-0.064	+0.465;+0.351	+0.127;-0.24	-0.195;-0.3
medium intensity grassland	-0.217;-0.049	+0.023;+0.093	+0.096;+0.003	+0.013;+0.292	
high intensity grassland	-0.1;-0.069	+0.088;-0.033			
intensive perma. cropland			-0.061;-0.205		
medium intensity cropland	+0.073;+0.076	-0.268;-0.217	-0.325;-0.171		-0.082;-0.228
high intensity cropland	+0.198;+0.153	-0.303;-0.279	-0.479;-0.162		-0.028;-0.111
medium intensity agri. mosaic	-0.205;-0.129	-0.112;-0.024			
high intensity agri. mosaic	+0.032;-0.015				
medium intensity settlement	-0.291;-0.214	-0.041;-0.035	+0.109;+0.195	+0.2;+0.273	+0.049;-0.12
high intensity settlement	-0.312;-0.208	-0.083;+0.012	+0.09;+0.216	-0.049;+0.063	-0.032;-0.126

Figure S6.8. Food-webs modifications related to land management intensity, **Part 2: Basal proportion facet** (pBasalMeta; pBasal).

	ATLANTIC	CONTINENTAL	MEDITERRANEAN	ALPINE	BOREAL
medium intensity forest	+0.163	+0.14	-0.129	+0.083	+0.17
high intensity forest	+0.23	+0.284	-0.135	+0.245	+0.305
medium intensity grassland	+0.03	+0.094	+0.131	+0.018	
high intensity grassland	+0.039	+0.32			
intensive perma. cropland			+0.117		
medium intensity cropland	-0.152	+0.184	+0.114		+0.29
high intensity cropland	-0.13	+0.296	-0.062		+0.099
medium intensity agri. mosaic	+0.153	+0.043			
high intensity agri. mosaic	+0.155				
medium intensity settlement	+0.039	+0.022	-0.233	-0.329	+0.043
high intensity settlement	+0.081	+0.019	-0.348	-0.315	-0.006

Figure S6.9. Food-webs modifications related to land management intensity, **Part 3: Connectance embedding** (dirCon).

	ATLANTIC	CONTINENTAL	MEDITERRANEAN	ALPINE	BOREAL
medium intensity forest	-0.025;-0.045	+0.027;-0.036	+0.101;-0.025	+0.183;+0.186	+0.044;-0.053
high intensity forest	+0.131;+0.126	+0.163;+0.058	+0.292;-0.032	+0.45;+0.599	+0.159;-0.009
medium intensity grassland	-0.078;-0.175	-0.053;-0.001	-0.076;+0.126	-0.22;-0.172	
high intensity grassland	-0.077;-0.19	+0.272;+0.079			
intensive perma. cropland			-0.078;-0.004		
medium intensity cropland	+0.133;-0.112	-0.377;-0.298	+0.13;-0.11		+0.2;+0.196
high intensity cropland	+0.125;-0.13	-0.245;-0.214	+0.219;-0.017		+0.15;+0.193
medium intensity agri. mosaic	-0.131;-0.139	-0.085;-0.104			
high intensity agri. mosaic	+0.148;+0.147				
medium intensity settlement	+0.045;-0.029	-0.091;-0.109	-0.105;-0.17	-0.464;-0.218	-0.054;-0.026
high intensity settlement	-0.005;-0.022	-0.172;-0.189	-0.243;-0.326	-0.438;-0.255	-0.116;-0.073

966
967 **Figure S6.10.** Food-webs modifications related to land management intensity, **Part 4:**
968 **Omnivory levels facet** (omniLev; omniProp).

	ATLANTIC	CONTINENTAL	MEDITERRANEAN	ALPINE	BOREAL
medium intensity forest	-0.046;-0.052;+0.047	+0.148;+0.144;+0.283	-0.084;-0.098;-0.078	-0.05;+0.102;+0.036	+0.292;+0.332;+0.655
high intensity forest	-0.156;-0.149;-0.104	+0.1;+0.064;+0.211	-0.137;-0.117;-0.03	-0.025;+0.207;+0.224	+0.261;+0.308;+0.596
medium intensity grassland	+0.104;+0.075;+0.201	-0.091;-0.063;-0.106	+0.016;+0.042;+0.054	-0.027;-0.161;-0.127	
high intensity grassland	-0.019;-0.01;-0.019	-0.134;-0.072;-0.162			
intensive perma. cropland			+0.1;+0.134;+0.171		
medium intensity cropland	-0.137;-0.191;-0.282	+0.201;+0.27;+0.418	+0.029;-0.021;+0.053		+0.01;-0.003;-0.013
high intensity cropland	-0.17;-0.24;-0.328	+0.005;+0.042;+0.139	+0.063;+0.022;+0.133		+0.019;+0.007;-0.01
medium intensity agri. mosaic	-0.006;-0.06;-0.007	-0.098;-0.135;-0.211			
high intensity agri. mosaic	-0.006;+0.015;-0.016				
medium intensity settlement	+0.017;+0.096;+0.115	+0.054;+0.057;+0.079	+0.002;-0.065;-0.051	+0.029;+0.044;+0.179	+0.284;+0.396;+0.442
high intensity settlement	+0.03;+0.113;+0.142	+0.079;+0.118;+0.145	-0.021;-0.03;-0.053	+0.024;-0.02;+0.015	+0.329;+0.508;+0.595

969
970 **Figure S6.11.** Food-webs modifications related to land management intensity, **Part 5: Chains**
971 **indices facet** (maxPath; meanPath;sdPath).

	ATLANTIC	CONTINENTAL	MEDITERRANEAN	ALPINE	BOREAL
medium intensity forest	-0.214;-0.02	-0.25;-0.169	+0.129;+0.099	-0.219;-0.049	-0.243;+0.011
high intensity forest	-0.271;-0.085	-0.371;-0.412	+0.305;-0.093	-0.42;+0.018	-0.465;-0.168
medium intensity grassland	-0.007;+0.055	-0.161;-0.161	-0.051;-0.354	+0.016;-0.243	
high intensity grassland	-0.089;+0.004	-0.295;-0.241			
intensive perma. cropland			-0.138;-0.116		
medium intensity cropland	+0.238;+0.371	-0.115;-0.266	-0.056;-0.08		-0.491;-0.509
high intensity cropland	+0.168;+0.312	-0.13;-0.289	+0.208;+0.241		-0.368;-0.347
medium intensity agri. mosaic	-0.026;-0.066	+0.085;-0.013			
high intensity agri. mosaic	+0.017;-0.152				
medium intensity settlement	+0.003;+0.091	-0.116;-0.076	+0.181;+0.363	+0.08;+0.381	-0.21;-0.192
high intensity settlement	-0.061;-0.008	-0.15;-0.07	+0.286;+0.436	+0.141;+0.451	-0.105;-0.104

Figure S6.12. food-webs modifications related to land management intensity, **Part 6: Compartmentalization metrics facet** (modul; meanShortDist).

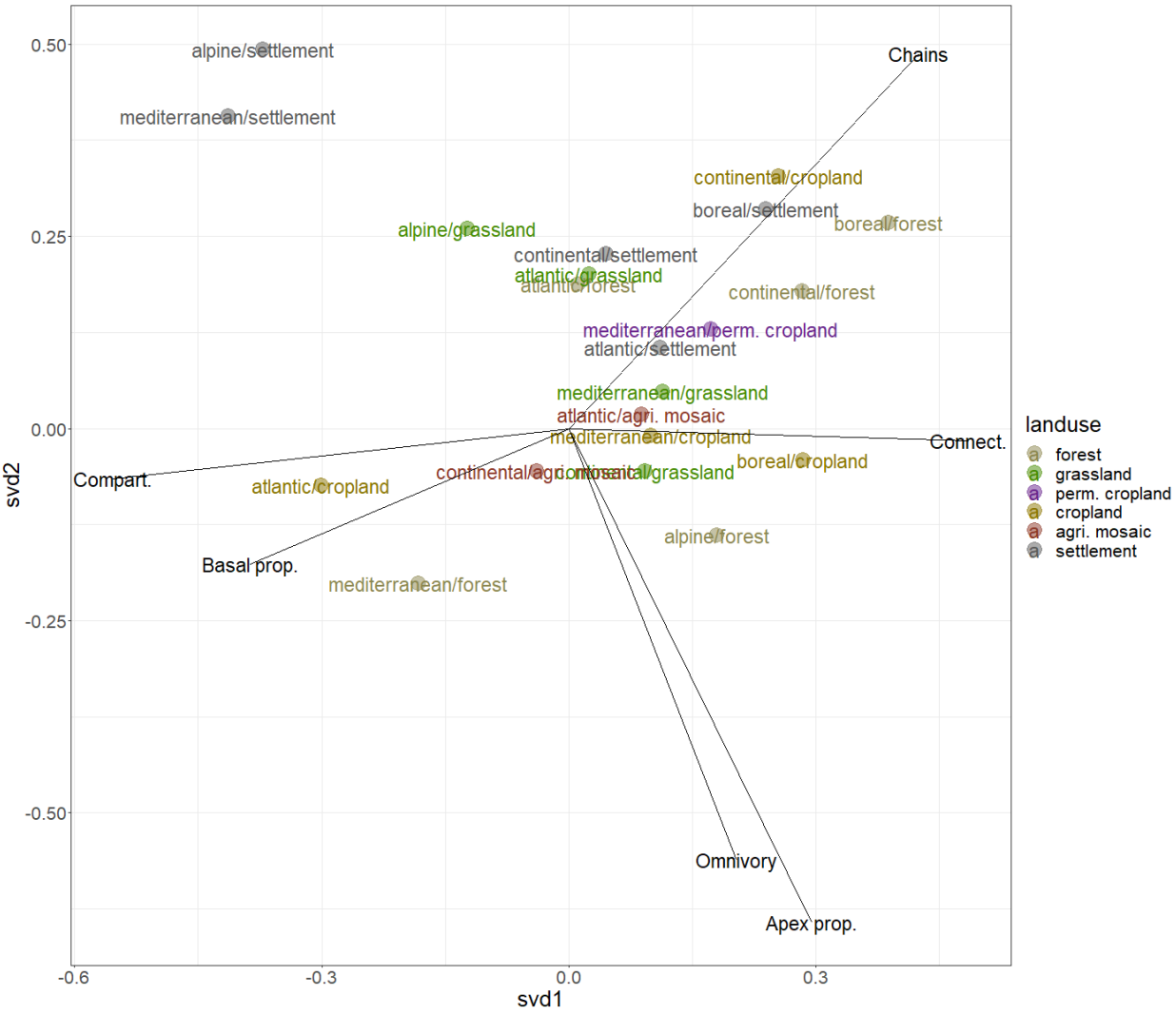


Figure S6.13. Summary of the relative deviations per context and facet directions in a summary 2 dimensional plane. The multivariate responses of the six facets relative deviations (averaged for high and mid intensities) over the 21 contexts were summarised in two axes using a Singular Value Decomposition (SVD), explaining 55% of the total variability.

Appendix S7- Fit of linear models per metric and the relative influence of climate, land use, and land management intensity

Table S7.3. Coefficient of determination (R^2) per metric for the full linear model with all explanatory factors (climate, land use and land management intensity, see column 3) and partial R^2s for the sequential addition of the factors: the R^2 with climate only (column 2), and the partial R^2 related to the addition of land use (column 3) and to the addition of intensity compared to climate and land use only (column 4). The full model was also re-fitted (4th column) by excluding the 10% most outliers local meta food-webs, namely the 5% most negative and 5% most positive residuals.

Metric	R^2 climate	Part. R^2 Use | climate	Part. R^2 intensity | use, climate	R^2 all	R^2 (-10% outliers)
pApexMeta	0.163	0.034	0.008	0.198	0.319
pBasalMeta	0.032	0.046	0.007	0.083	0.135
pBasal	0.042	0.032	0.007	0.078	0.131
dirCon	0.009	0.019	0.007	0.034	0.055
omniProp	0.024	0.008	0.004	0.037	0.055
omniLev	0.069	0.025	0.004	0.097	0.161
maxPath	0.015	0.030	0.007	0.052	0.072
meanPath	0.018	0.045	0.009	0.071	0.14
sdPath	0.019	0.030	0.007	0.055	0.072
modul	0.007	0.012	0.009	0.027	0.056
meanShortDist	0.002	0.008	0.004	0.014	0.032
Average	**0.036**	**0.026**	**0.007**	**0.068**	**0.112**

Appendix S8- Shortest-Path lengths distribution in low vs high land management intensity

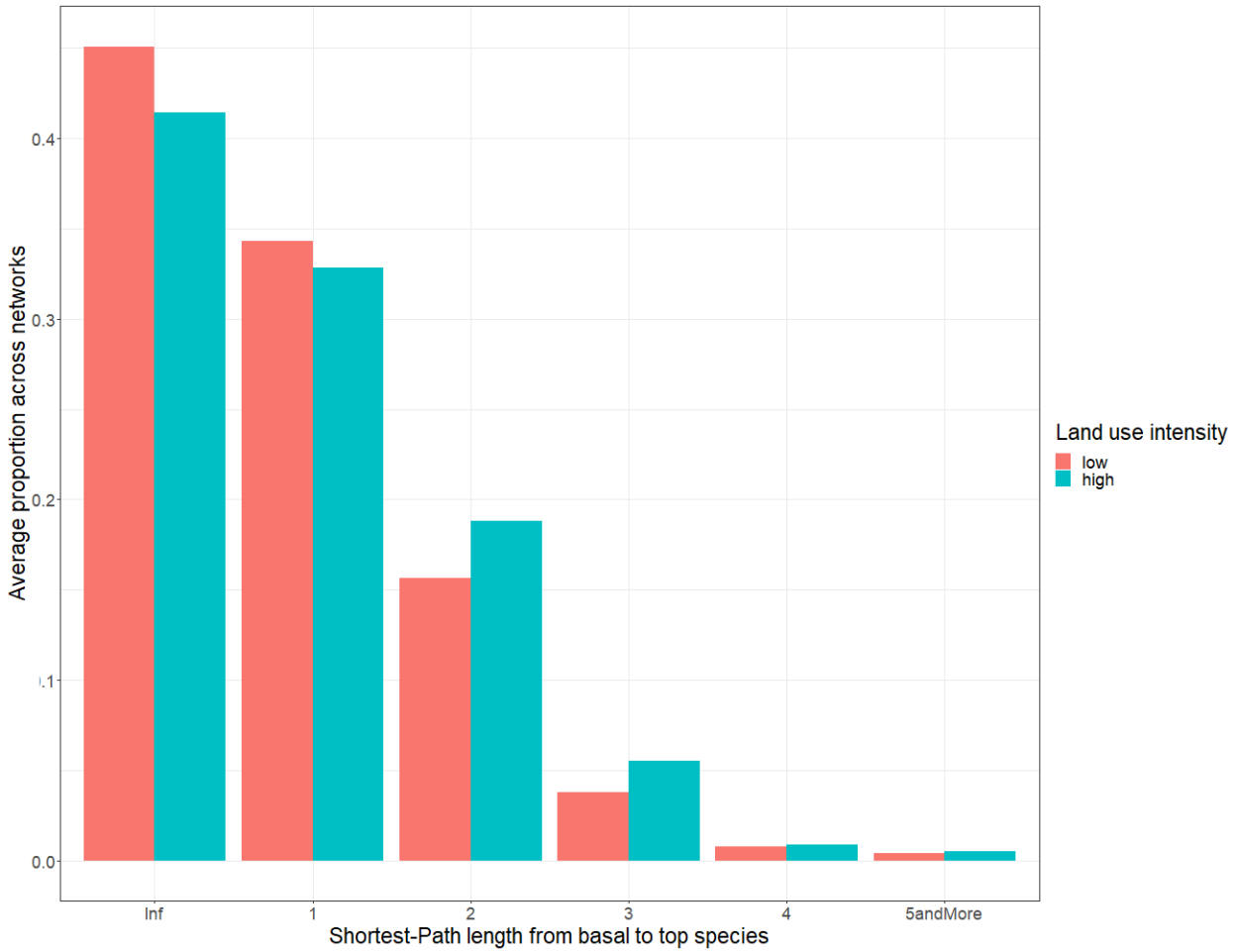


Figure S8.13. Average proportions of shortest-path lengths from basal to top species in european tetrapods food-webs under low (red) or high (blue) land management intensity. We used a weighted average to give an equal weight to each bioclimatic region and land use, i.e. we averaged proportions over networks in the same bioclimatic region, land use and land management intensity, before averaging over all networks in the same land management intensity.

Appendix S9- Effect of land management intensity on landscape fragmentation and diversity per land use and bioclimatic region

We computed for each cell three complementary metrics of landscape fragmentation and diversity based on the 36km² square window of cells (9x9 cells) centered on the focal cell: **patchAntiArea, proxToBorder** and **divLandUse**. **patchAntiArea** is the opposite of the number of cells contained in the homogeneous patch of land system (land use and management intensity) containing the focal cell. **proxToBorder** is the opposite of the euclidean distance (in cells) to the closest cell border of this patch. We took the opposite of the last two quantities to ensure that an increase of value indicates higher fragmentation. **divLandUse** is the number of distinct land system (land use and management intensity) in the 8 adjacent cells to the focal one. The mean variation of each fragmentation metric related to higher land management

intensity and the significance of the multivariate deviation are reported per land group in **Figure S9.14.**

	ATLANTIC	CONTINENTAL	MEDITERRANEAN	ALPINE	BOREAL
medium intensity forest	+4.297;+0.008;+0.438	+8.927;+0.153;+0.244	+17.538;+0.202;+0.591	+16.725;+0.15;+0.757	+0.03;+0.017;+0.215
high intensity forest	-3.742;-0.038;-0.021	-4.378;+0.093;-0.087	+14.011;+0.196;+0.669	+19.688;+0.115;+1.092	-13.593;-0.083;+0.053
medium intensity grassland	-7.735;-0.039;-0.235	-4.638;-0.007;-0.084	+6.102;+0.04;+0.281	+4.603;+0.022;-0.231	
high intensity grassland	-20.038;-0.131;-0.704	-20.301;-0.227;-0.968			
intensive perma. cropland			-5.296;-0.061;-0.207		
medium intensity cropland	-13.167;-0.085;-0.361	-15.126;-0.154;-0.72	-17.607;-0.203;-0.725		-8.957;-0.03;-0.474
high intensity cropland	-20.349;-0.134;-0.551	-7.232;+0.004;-0.277	-4.596;-0.069;-0.358		-0.821;+0.004;-0.114
medium intensity agri. mosaic	-2.918;-0.012;-0.409	-0.704;+0.002;-0.224			
high intensity agri. mosaic	-4.142;+0;-0.318				
medium intensity settlement	-8.373;-0.014;-0.116	-6.621;-0.01;-0.205	-7.076;-0.01;-0.322	-5.337;-0.022;+0.042	-8.227;-0.028;-0.293
high intensity settlement	-24.051;-0.289;-1.069	-18.785;-0.229;-1.127	-14.258;-0.144;-0.891	-3.864;-0.035;+0.025	-7.714;-0.048;-0.68

Figure S9.14. Landscape fragmentation and diversity metrics modifications related to land management intensity (patchAntiArea; proxToBorder; divLandUse)**.** For each bioclimatic region (columns), land use and land management intensity level (rows), we show the mean variation of each fragmentation metric related to higher intensity (when taking the low intensity level as reference). Cells with a number over a white background indicate a significant multivariate deviation in the corresponding context, established with a non-parametric multivariate test, while cells with a grey background indicate a non-significant deviation and empty cells indicate no data. A significant deviation is written in pale green when positive for the three metrics and dark red when negative.

Appendix S10- Residual sampling effort variations across land management intensity levels

Our general results arised from the analysis of mean metric deviations related to variations of land management intensity for 21 contexts (combinations of land use and bioclimatic region). The residual spatial sampling bias can only bias the estimated mean deviation for a given context if the sampling effort varies between land management intensity levels. We plot in Figure **S10.15** the distribution of log-sampling effort (number of records across cells, the log was plotted to visualise to facilitate the comparison across classes) per land management intensity (bar colour), taxonomic class (x-axis) and context (plots). The sampling effort varies consistently across classes, with birds always showing the highest sampling effort, and among cells per context and intensity level, we observe no relationship between land management intensity and the median sampling effort, whatever the taxonomic class, except in some rare cases. Hence, spatial sampling effort variations should not bias our mean deviation estimates.

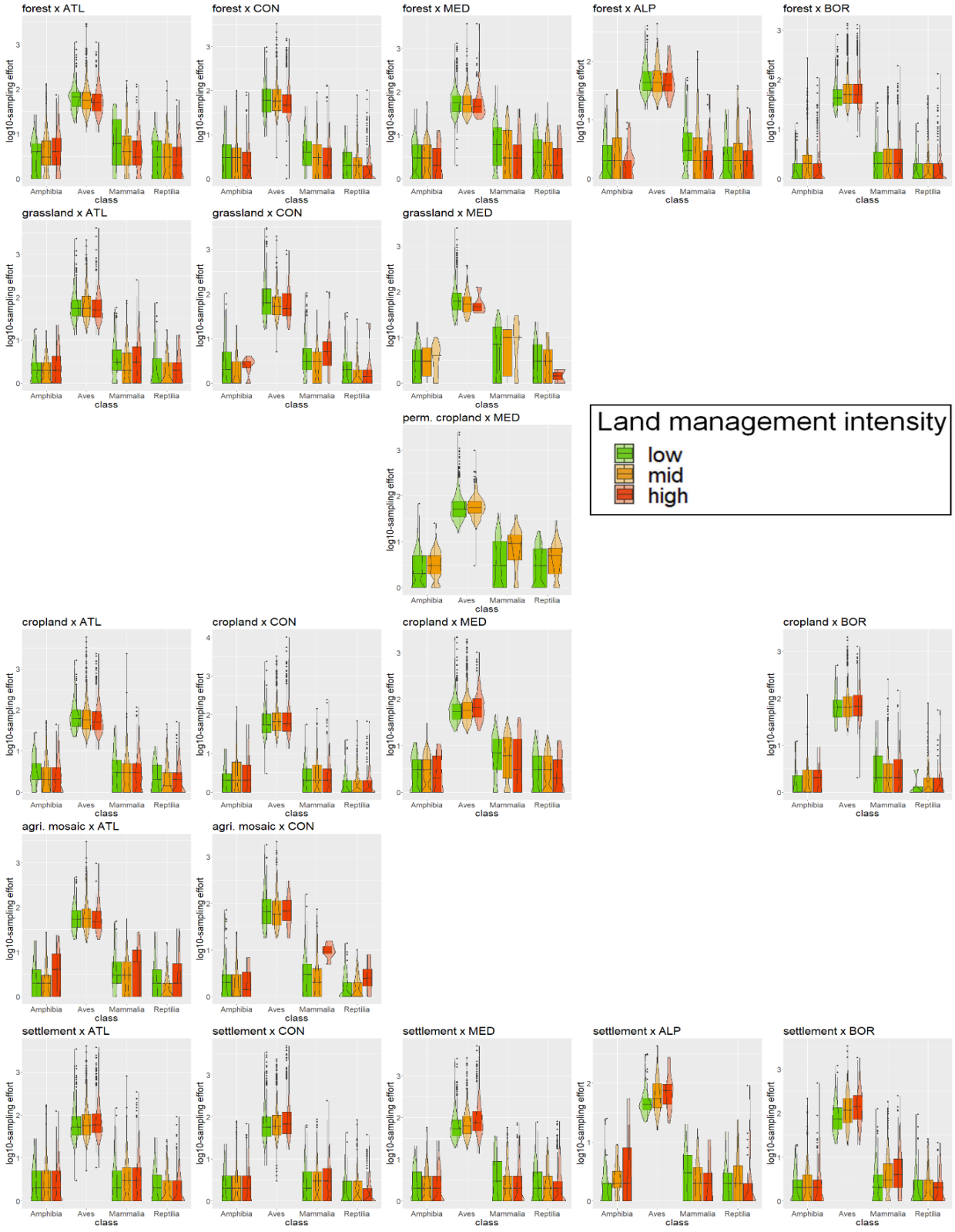


Figure S10.15. Sampling effort per taxonomic class, land management intensity for the 21 contexts, namely combinations of land use (row) and bioclimatic regions (column).

Appendix S11- Robustness of general results to various potential biases

Even though our main analysis was run on the most sampled cells, our cell selection criteria might potentially allow certain biases to affect our general results. Hence, we carried three independent sensitivity analyses to test the robustness of our main results to three bias factors: The stringency of the assumed species detection threshold, the overall sampling bias toward some taxonomic classes and the outlier food-webs.

For each type of bias, our approach was to subselect smaller set of cells among the 67,051 initially selected cells, where the potential bias is minimised and to measure if our main result was preserved on this cell subselection, namely the sign and magnitude of the mean deviation of each metric between high and low intensity cells (as in **Figure 4-top**).

Sensitivity to the quantile of the detection threshold. With the cell selection of our main analysis, the number of species with uncertain absence were generally a small proportion of the richness per cell, i.e. less than 20% of the observed richness in 84% of cells and less than 10% in 63% of cells. However, the number of uncertain species in a cell depends on the stringency of the sampling effort threshold above which a given species is considered truly absent. Hence, we investigated here the effect of the quantile chosen to generate the species-specific sampling effort thresholds, determining when the species is assumed absent if not detected. In our manuscript, we took the first decile (probability=0.1 in **Figure S11.16**) of the sampling effort values among the species presence cells as the species-specific sampling effort threshold. This might not be stringent enough to ensure that the species is truly absent for any species. Hence, we compared here the results obtained when the cell subselection was based on the third decile (probability=0.3 in **Figure S11.16**) and the median (probability=0.5 in **Figure S11.16**). The number of selected cells decreased with 64,349 cells remaining when choosing the median. As a result, the metric deviations are almost unchanged when increasing the quantile, except for omniLev and maxPath, for which the deviations collapse. Given that our main results were not sensitive to the quantile choice, we kept the first decile in our main analysis to maximise our cell sample size and hence our ability to detect significant deviations of architecture facets in the weakly sampled contexts (e.g., see Figure).

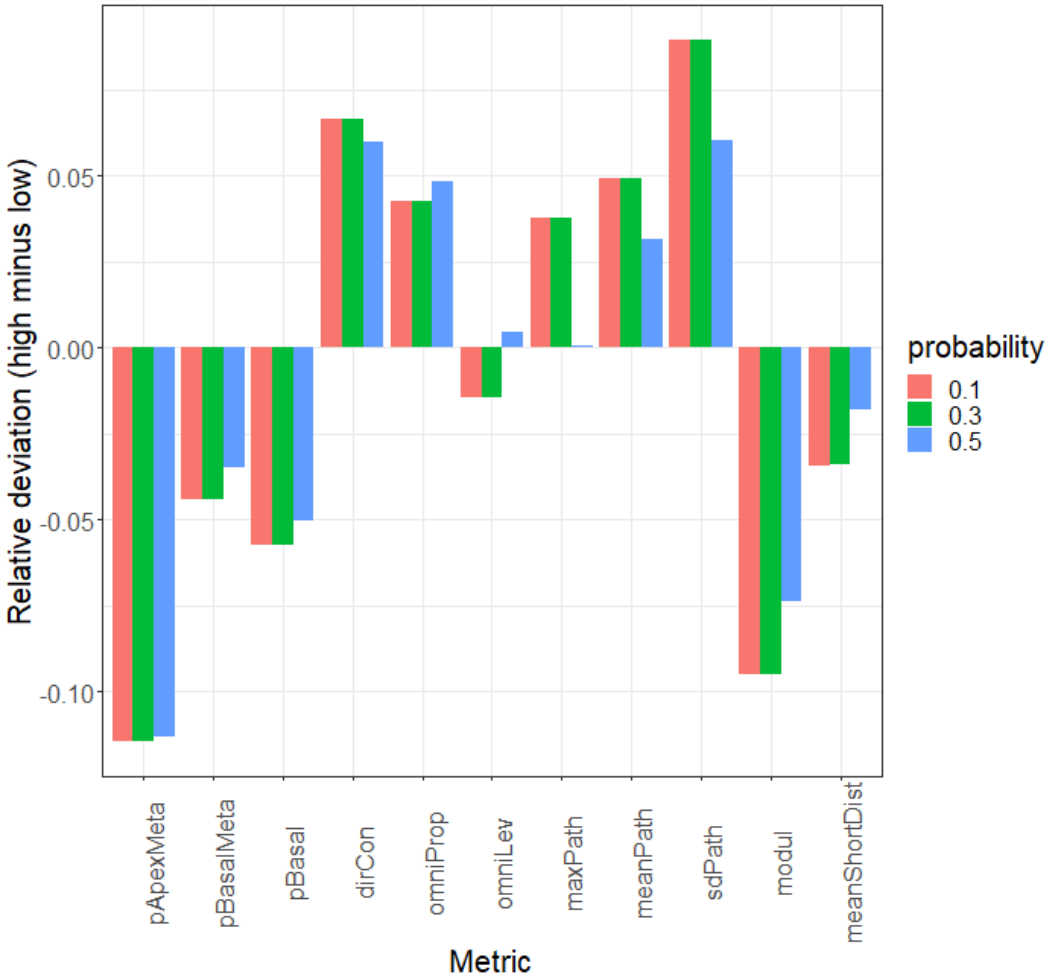


Figure S11.16. Food-web metric deviations related to higher land management intensity per architecture facet and per choice of quantile value (0.1, in red, is the reference value of our main results), determining the sampling effort needed for any given species to be considered absent when not observed. For each metric (x-axis), the mean relative deviation (y-axis) is the average of the mean deviation per context of high versus low intensity food-webs divided by the interquartile range of the global metric distribution, as in **Figure 4**.

Sensitivity to taxonomic bias. Hence, our network metrics (described below) are likely more representative of interaction among birds and mammals, and may hence underestimate the effect of other important interactions such as birds predating diverse amphibians and reptiles.

Birds (Aves) and Mammals were overall much more intensively sampled than other classes (Reptilia, Amphibia) in our data, due to the large proportion of crowdsourcing data. Even though we imposed that 70% of the 751 tetrapod species must be certainly present or absent for a cell to be selected, the 30% remaining species may still concentrate a large part of *Reptilia* and *Amphibia* species due to this taxonomic sampling bias. This could potentially affect food-web metrics as for instance most *Amphibia* are actually basal species in the metaweb of trophic interactions (see **Figure 3**). To minimise this potential bias, we subselected the initially selected cells with the constraint that the four taxonomic classes were well sampled. More precisely, we

first computed the minimum sampling effort value such that more than 500 cells had a higher sampling effort in all four taxonomic classes for both low and high management intensity cells (this minimum value was 3). Then, we subselected the associated cells (1329 low intensity and 561 high intensity cells) and re-computed the 18 mean deviation per metric and compared it with our main manuscript result in **Figure S11.17**. It shows that the sign of the deviation is unchanged for most metrics, except for dirCon and omniLev.

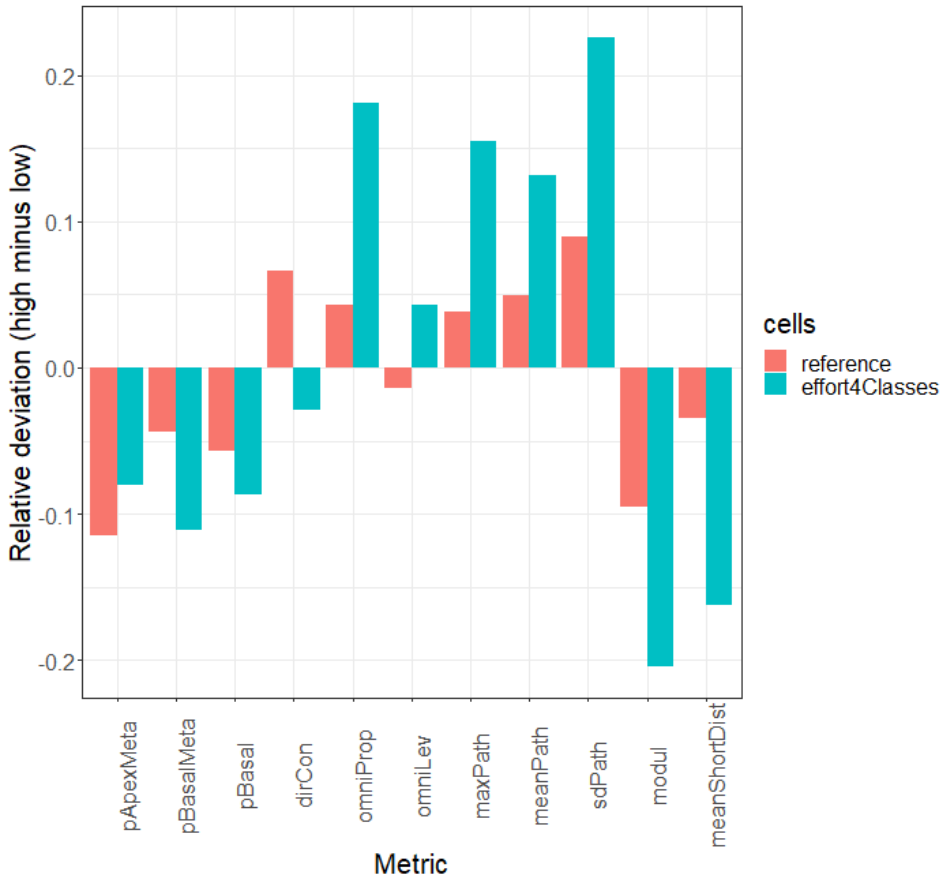


Figure S11.17. Food-web mean relative metric deviations related to higher land management intensity per architecture facet for our reference cell selection (red, 67,051 cells) versus a subselection with high sampling effort on the four taxonomic classes (blue, 1,890 cells). For each metric (x-axis), the mean relative deviation (y-axis) is the average of the mean deviation per context of high versus low intensity food-webs divided by the interquartile range of the global metric distribution, as in **Figure 4**.

Sensitivity to the outlier food-webs. For each metric, some local food-webs had extreme metric values (|standardised residuals| >3), challenging the gaussian assumption on the residuals in linear regressions on the metrics used to estimate their mean deviation per context. These outlier food-webs are visible on the quantile-quantile (q-q) plots in the central panel of **Figures S11.18 and S11.19**. Most of the q-q plots showed a fat tailed distribution in the residuals (except pBasalMeta, pBasal, dirCon), often with a skewness on the right (pApexMeta,

path length and compartmentalisation metrics), mostly due to the 0 lower bound on these metrics whose value are low in our context. This is not problematic for our significance test on the multivariate deviation per architecture facet because we tested it using a non-parametric approach which doesn't rely on the gaussian assumption. However, these outlier food-webs might potentially bias the deviations in our main results (**Figure 4-top**). Hence, for each food-web metric, we re-computed the mean relative deviation when removing the outlier food-webs (in blue in **Figure S11.20**) and compared it to our main results (in red in **Figure S11.20**). Our main results appear robust to the removal of the outliers responsible for these long tails. Indeed, for each metric, the mean relative deviations are almost unchanged when removing the outliers before fitting the linear regression (**Figure S11.20)**.

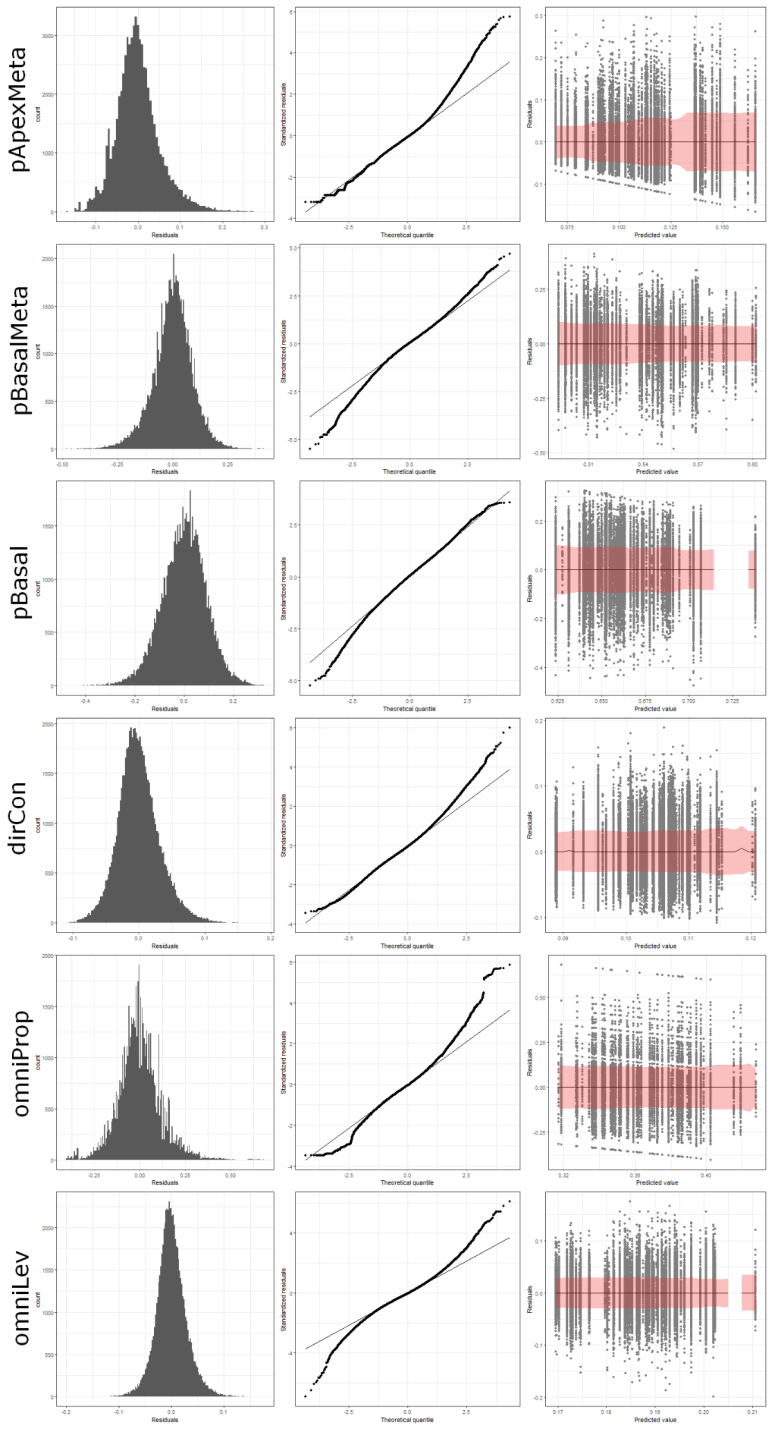


Figure S11.18. Part 1 diagnostic plots of the multivariate multiple regression. For each metric (row), the left panel shows the histogram of residuals, the central panel shows the quantile-quantile plot to compare the deviation of the residual distribution to a gaussian distribution, and the right panel shows the mean and standard deviation with a sliding window along the axis of predicted values, enabling to check for homoscedasticity.

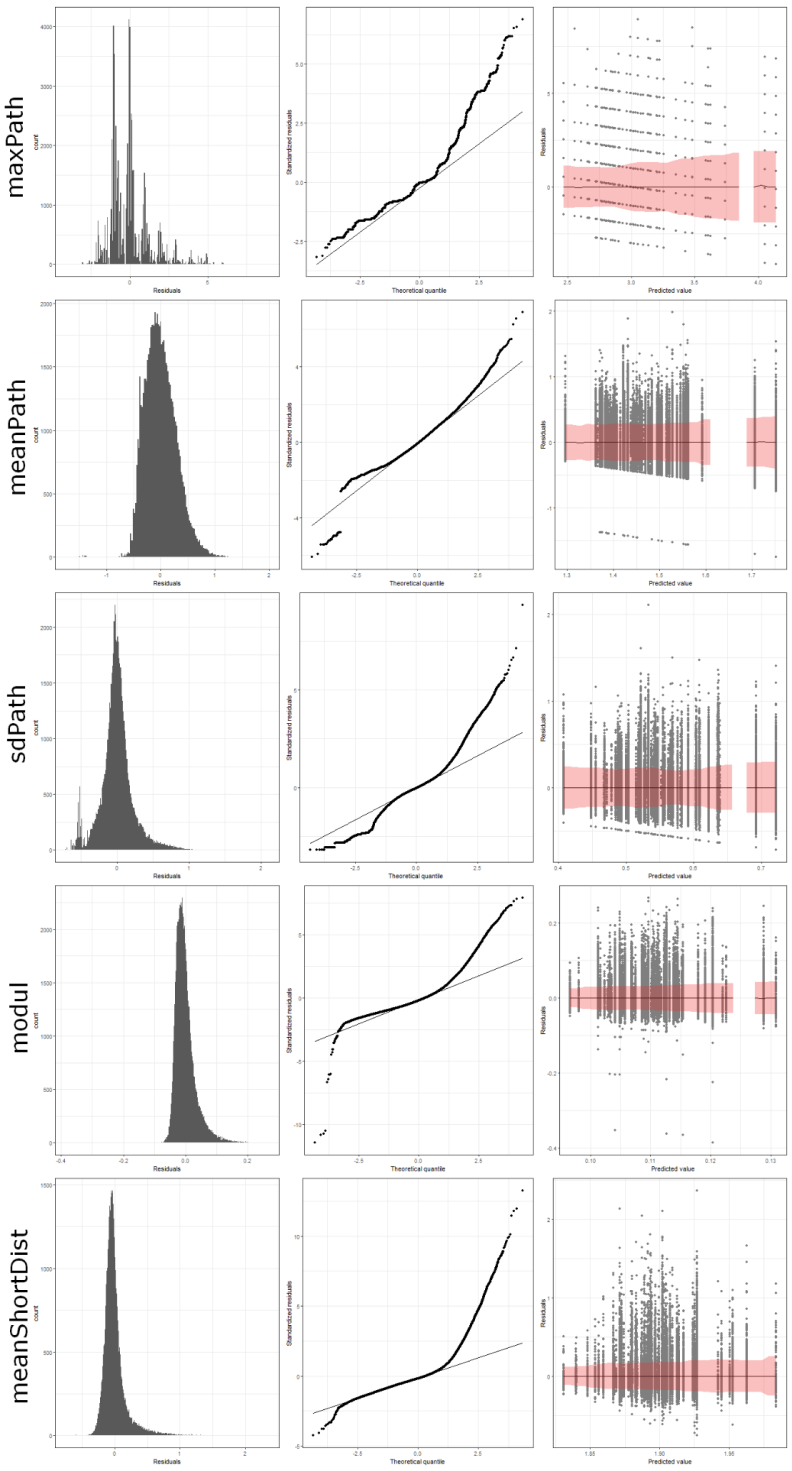


Figure S11.19. Part 2 of diagnostic plots of the multivariate multiple regression. Same principle for the last 5 metrics.

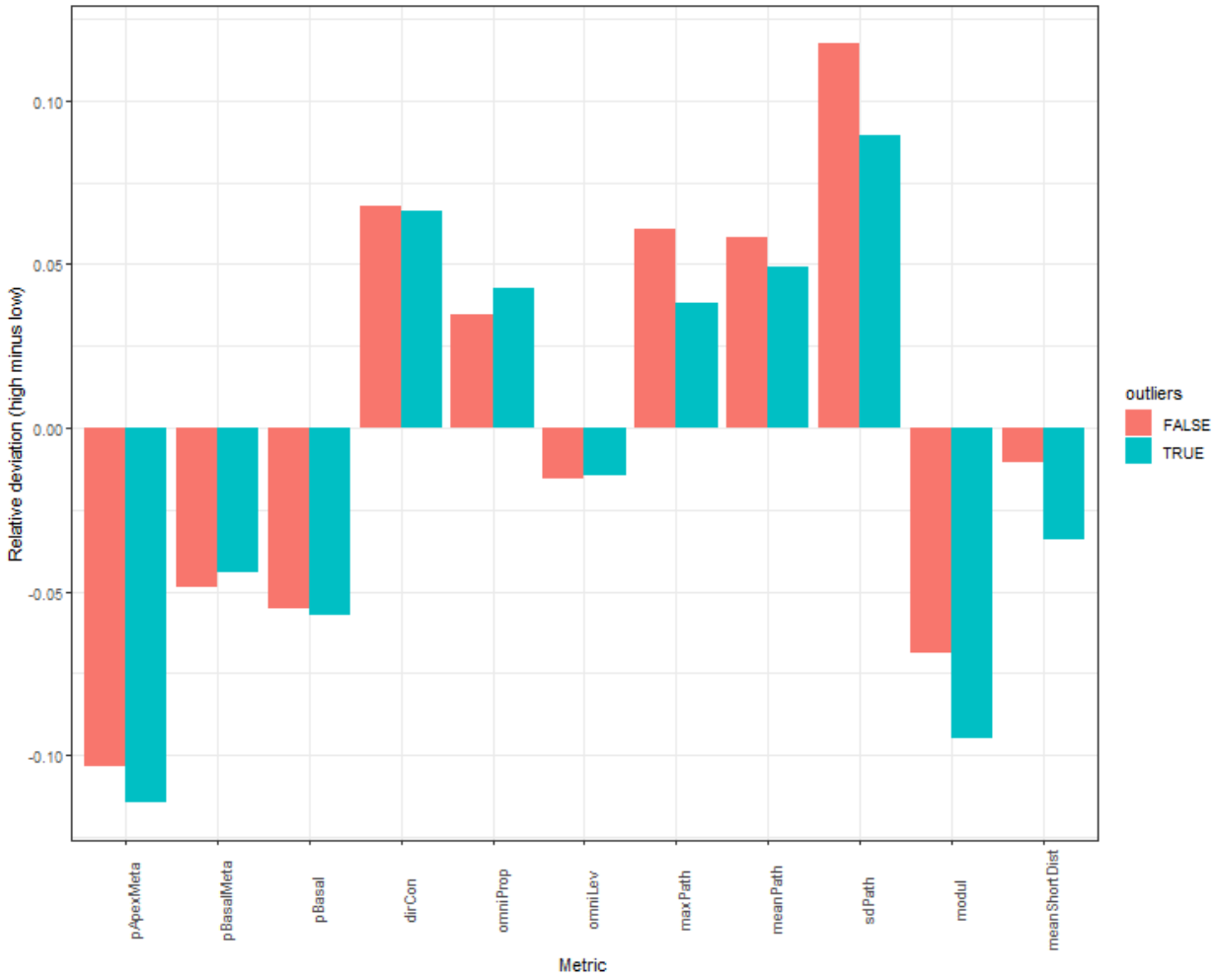


Figure S11.20. Food-web metric deviations related to higher land management intensity per metric (same as in Figure 4 of main manuscript) for the 67,512 initially studied local food-webs including outliers (blue bars) and for the filtered food-webs excluding the outliers of each linear regression (|standardised residuals| >3).