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Trophic Interactions Are Key to Understanding the Effects of Global Change on the Distribution and Functional Role of the Brown Bear

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ABSTRACT

Biotic interactions are expected to influence species' responses to global changes, but they are rarely considered across broad spatial extents. Abiotic factors are thought to operate at larger spatial scales, while biotic factors, such as species interactions, are considered more important at local scales within communities, in part because of the knowledge gap on species interactions at large spatial scales (i.e., the Eltonian shortfall). We assessed, at a continental scale, (i) the importance of biotic interactions, through food webs, on species distributions, and (ii) how biotic interactions under scenarios of climate and land-use change may affect the distribution of the brown bear (*Ursus arctos*). We built a highly detailed, spatially dynamic, and empirically sampled food web based on the energy contribution of 276 brown bear food species from different taxa (plants, vertebrates, and invertebrates) and their ensemble habitat models at high resolution across Europe. Then, combining energy contribution and predicted habitat of food species, we modelled energy contribution across space and included these layers within Bayesian-based models of the brown bear distribution in Europe. The inclusion of biotic interactions considerably improved our understanding of brown bear distribution at large (continental) scales compared with Bayesian models including only abiotic factors (climate and land use). Predicted future range shifts, which included changes in the distribution of food species, varied greatly when considering various scenarios of change in biotic factors, providing a warning that future indirect climate and land-use change are likely to have strong but highly uncertain impacts on species biogeography. Our study confirmed that advancing our understanding of ecological networks of species interactions will improve future projections of biodiversity change, especially for modelling species distributions and their functional role under climate and land-use change scenarios, which is key for effective conservation of biodiversity and ecosystem services.

1 | Introduction

In the current biodiversity crisis (Pereira et al. 2024), understanding how the distribution of species will be impacted by global changes, such as climate and land-use changes (Chen et al. 2011; IPCC 2014), is critical for conserving biodiversity and securing associated ecosystem services (Urban et al. 2016) including human food systems (O'Neill et al. 2017). One of the major outstanding challenges is to capture the complexity of biological responses when making predictions about how species will respond to global changes, as their distributions are shaped by a complex set of abiotic (fundamental niche) and biotic factors (realized niche) (Hutchinson 1957; Nogues-Bravo 2009; Payne et al. 2024).

Species distribution shifts in response to global changes are highly variable (Lucas, González-Suárez, et al. 2016; Pacifici et al. 2020; Le Luherne et al. 2024), and species' ecological traits such as the climate niche, habitat specificity, and mobility determine the redistribution of species (Pacifici et al. 2017; Pacifici et al. 2020; Carroll et al. 2024). Furthermore, species within an ecological community can shift their habitat at different rates and directions, altering the original overlap of species, with congruous, convergent, divergent, or contracted shifts (Durant et al. 2007; Carroll et al. 2024). These differences in the redistribution of species within the same community can lead to a change in the spatial overlap between prey and predator, strengthening or weakening their interactions (Durant et al. 2007; Carroll et al. 2024). Predators will respond differently to prey redistribution depending on their ecological traits (e.g., trophic position and diet breadth) and environmental factors (e.g., availability of alternative prey) (Carroll et al. 2024). They can respond by prey-switching (diet generalist species), or the predator's fitness might be affected—change of predator realized niche—causing bottom-up effects

on the predator's population and, in the worst scenario, its local extinction (diet specialist species or absence of alternative preys) (Ferrerias et al. 2011; Carroll et al. 2024). At the community level, this can lead to changes in interaction strengths and food web topologies. In summary, communities and biotic interactions are dynamic over time and are influenced by global changes (Blois et al. 2013; Bartley et al. 2019). However, most existing biogeographical studies that aim to predict species responses to global changes rely primarily on abiotic factors, especially climate. This is, in part, a result of the perceived differences in scale, with abiotic factors thought to operate at larger spatial scales (Willis and Whittaker 2002), and biotic factors, such as species interactions, being considered more important at local scales within communities (Willis and Whittaker 2002). Such reliance on abiotic factors when explaining large-scale species distributions has also resulted from extremely sparse data on species interactions. This knowledge gap on species interactions, also termed the Eltonian shortfall (understood as the lack of knowledge on intra- and interspecific interactions, but also as the physiological tolerances of species, and the effects of species on ecosystems), severely limits our understanding of large-scale biodiversity patterns (Hortal et al. 2015).

Despite these limitations, studies are beginning to incorporate species interactions for understanding species distribution shifts due to global changes (Guisan and Thuiller 2005; Penteriani et al. 2019; Bas et al. 2025; Hao et al. 2025). These studies have demonstrated that adding information on other species significantly improves the understanding of distribution changes (Wisiz et al. 2013; Pollock et al. 2014) and allows assessing changes in the ecosystem structure and functioning (Bas et al. 2025; Hao et al. 2025), suggesting that species interactions are a valuable component in understanding the effects of global changes on biodiversity (Carroll et al. 2024;

Hao et al. 2025). However, the approaches used to include species interactions usually face three important limitations: (1) They typically only include spatial co-occurrence as a surrogate for species interactions (Meier et al. 2010; Belmaker et al. 2015), (2) they usually use a binary measure for interaction, for example, presence/absence of an interaction between *Species_A* and *Species_B*, and (3) it is assumed there is no spatial variation in the interaction, for example, interaction between *Species_A* and *Species_B* is considered constant in all ecosystems (Banašek-Richter et al. 2009). These assumptions could be improved with: (1) real data on ecological interactions, for example studying the trophic interactions among species; (2) describing the interactions among species with quantitative measures, for example, measuring the relative energy obtained from food/consumed species; and (3) incorporating the spatial variability of those interactions among different ecosystems (Dormann et al. 2018; Galiana et al. 2018; Blanchet et al. 2020), for example, measuring different values of the relative energy from food/consumed species across geographic space. Therefore, to advance our understanding of species distributions, it is necessary to adopt a cross-scale approach merging community ecology represented by local-scale biotic interactions over broader scales (Wisiz et al. 2013) with abiotic factors (Lavergne et al. 2010; Boulangeat et al. 2012) based on detailed community ecology knowledge (Figure 1) (Dudenhöffer et al. 2022; Carroll et al. 2024).

Here, we assess whether considering detailed diet data at large spatial scales helps to understand future consequences of global change for the redistribution of species and their role in the ecosystem structure and functioning. Specifically, we tested (i) how biotic interactions, based on diet, change over space, (ii) whether species' geographic distributions are better estimated by quantitative (continuous) or binary proxies of biotic interactions, (iii) whether species' geographic distributions are better explained when combining biotic (e.g., prey availability) and abiotic factors (e.g., climate and land use), and (iv) whether or not future range shifts differ when considering biotic interactions in addition to abiotic factors. Trophic interactions are among the most important biotic factors determining species distributions and are fundamental to ecosystems (Braga et al. 2019). We used as a model system a top predator and generalist omnivore species with a strong impact on ecosystems (Penteriani and Melletti 2020) and with several of its subpopulations at extinction risk (McLellan et al. 2017), the brown bear *Ursus arctos* in Europe and Türkiye (formerly known as Turkey). This model system has a broader applicability to understanding ecosystems in general, higher-level predators in particular, and could be extended to other species.

2 | Material and Methods

2.1 | Biotic Interactions

To obtain knowledge of biotic interactions, we reviewed studies of brown bear diet in Europe and Türkiye, constructed a unique, highly detailed, spatially explicit database of trophic interactions (*Trophic Database*; Figures 1a and 2; Tables S1–S4 and Figures S1; see Figure S2 for a detailed diagram of methods),

and calculated the relative energy contribution of each food item (Figure 1c).

2.2 | Review of Brown Bear Diet Studies

We reviewed 47 studies of brown bear diet by searching in SCI Journals, master's and PhD theses, and gray literature (research that is either unpublished or has been published in noncommercial form, for example, technical reports, conference proceedings; Tables S1 and S2 and Figure S1). For each study, we recorded three types of information: study area location; the type of samples, for example, brown bear scat or the stomachs of dead individuals; and the number of samples. Additionally, within each study and for each food item we recorded two parameters: (1) the relative frequency of occurrence (rF), calculated as the number of occurrences of food item i divided by the total number of occurrences of all food items, that is, $rF_i = f_i / \sum f_j$; and (2) the relative volume (rV), calculated as the volume of food item i divided by the total volume of all food items, that is, $rV_i = v_i / \sum v_j$.

2.3 | Calculating Energy Available From Food Items

Because not all studies reported estimates of rV , we used the strong relationship between rF and rV ($r = 0.86$, 0.81 – 0.90 95% CI from bootstrapped correlation coefficients; Figures S3–S5) to impute rV for those studies with missing data. Then, we used rV to calculate the relative estimated dietary energy content (rEDEC) (Hewitt and Robbins 1996) of each food item i in each study: $rEDEC_i = CF_{Ei} \times rEDC_i / \sum (CF_{Ei} \times rEDC_i)$ (Appendix S1, Tables S2–S4).

2.4 | Calculating Associations Between Diet and Environmental Variables

To address question (i), namely whether biotic interactions change over space and if they are explained by environmental factors, we used averaged linear models predicting the relative energy contribution of different food categories (i.e., reproductive plants, vegetative plants, unknown plants, invertebrates, and vertebrates; Table S5) and the diet diversity using these food categories as a function of climate (Karger et al. 2017) and land use (Schipper et al. 2020) variables. For consistency with climate and land-use data, we selected 31 studies conducted between 1989 and 2018 which had sufficient taxonomic resolution (genus and/or species; Table S1) to calculate the association between latitude, land cover, and climate variables and the rEDEC in each diet category. We first calculated the value of climate (Karger et al. 2017) and land use (Schipper et al. 2020) variables (the 19 bioclimatic variables and 8 variables describing the percentage of land use by cell; for a full description see of variables see Tables S6 and S7) within a buffer area of 18 km (an area of 1018 km²) around the site locations of the selected studies calculated using ArcMap 10.5 (Esri Inc. 2016). We eliminated highly correlated variables using the variance inflation function (VIF) (Dormann et al. 2013) in the R package usdm (Naimi 2017). Then, we calculated all possible linear

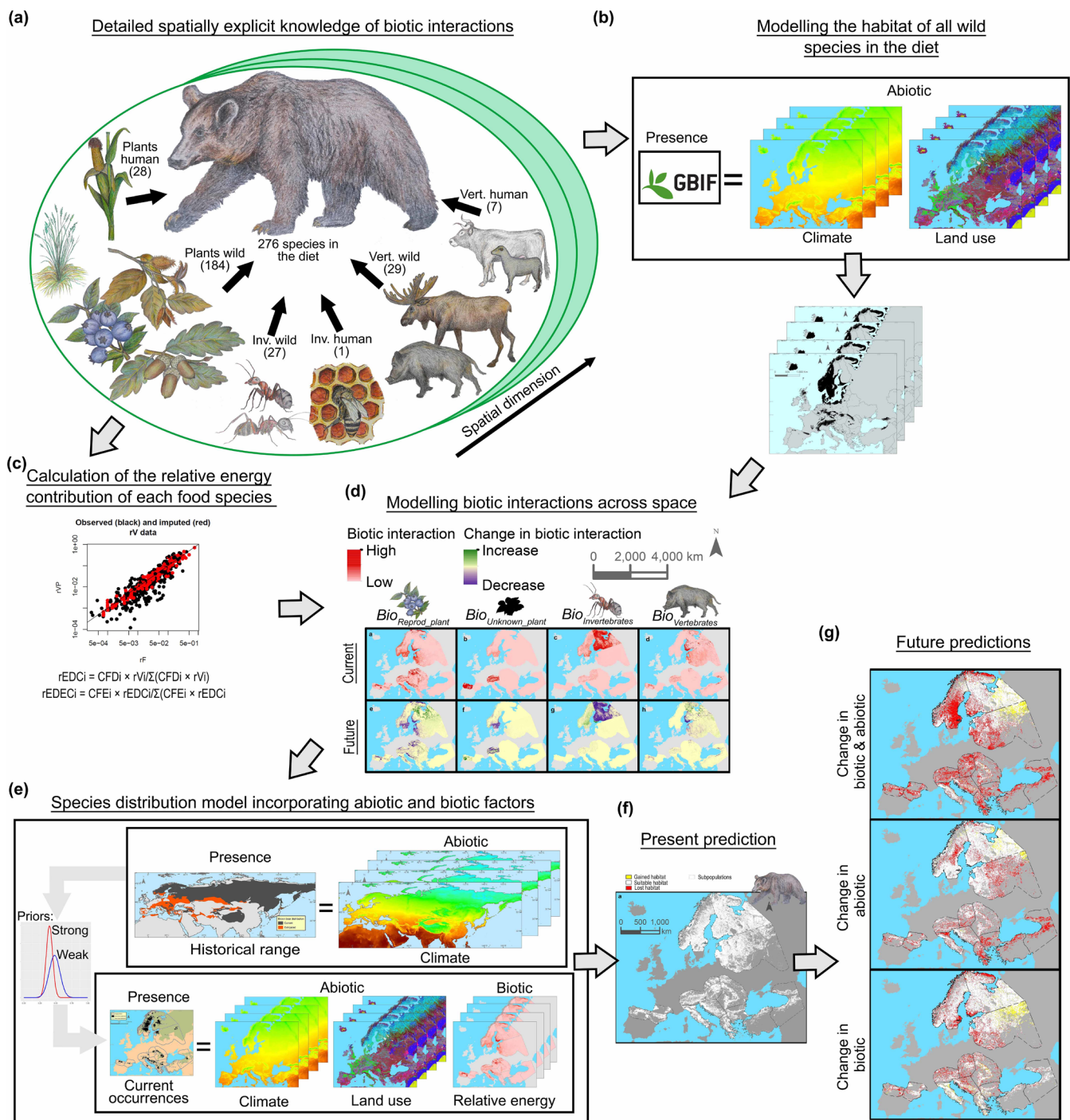


FIGURE 1 | Diagram showing our model system to assess the importance of biotic interactions for understanding the consequences of global change for biodiversity. (a) Construction of a database with detailed explicit knowledge of biotic interactions (in our model system, brown bear food species in Europe) based on a literature review which accounts for the spatial variability of interactions. (b) Fitting ensemble species distribution models (SDMs) for wild food species and calculation of habitat suitability for the current and three future (2040) shared socioeconomic pathways, which were included using predictions for climate (Karger et al. 2017) and land-use changes (Schipper et al. 2020). (c) Calculation of the relative energy contribution of each food species in different subpopulations/space. (d) Calculation of quantitative and binary proxies of biotic interactions across the space and predictions of the spatial biotic interactions for each scenario. (e) Fit of a species distribution model for the brown bear combining historical and current data and incorporating abiotic factors, which refer to the effects of global changes that directly impact the brown bear, including temperature changes (i.e., affecting hibernation and reproduction) and land-use changes (i.e., decreasing suitable habitat), and biotic factors, which refer to the effects of global changes through biotic interactions such as changes in the availability of other species as food sources. (f, g) Current and future predictions for brown bear distribution considering both abiotic and biotic factors.

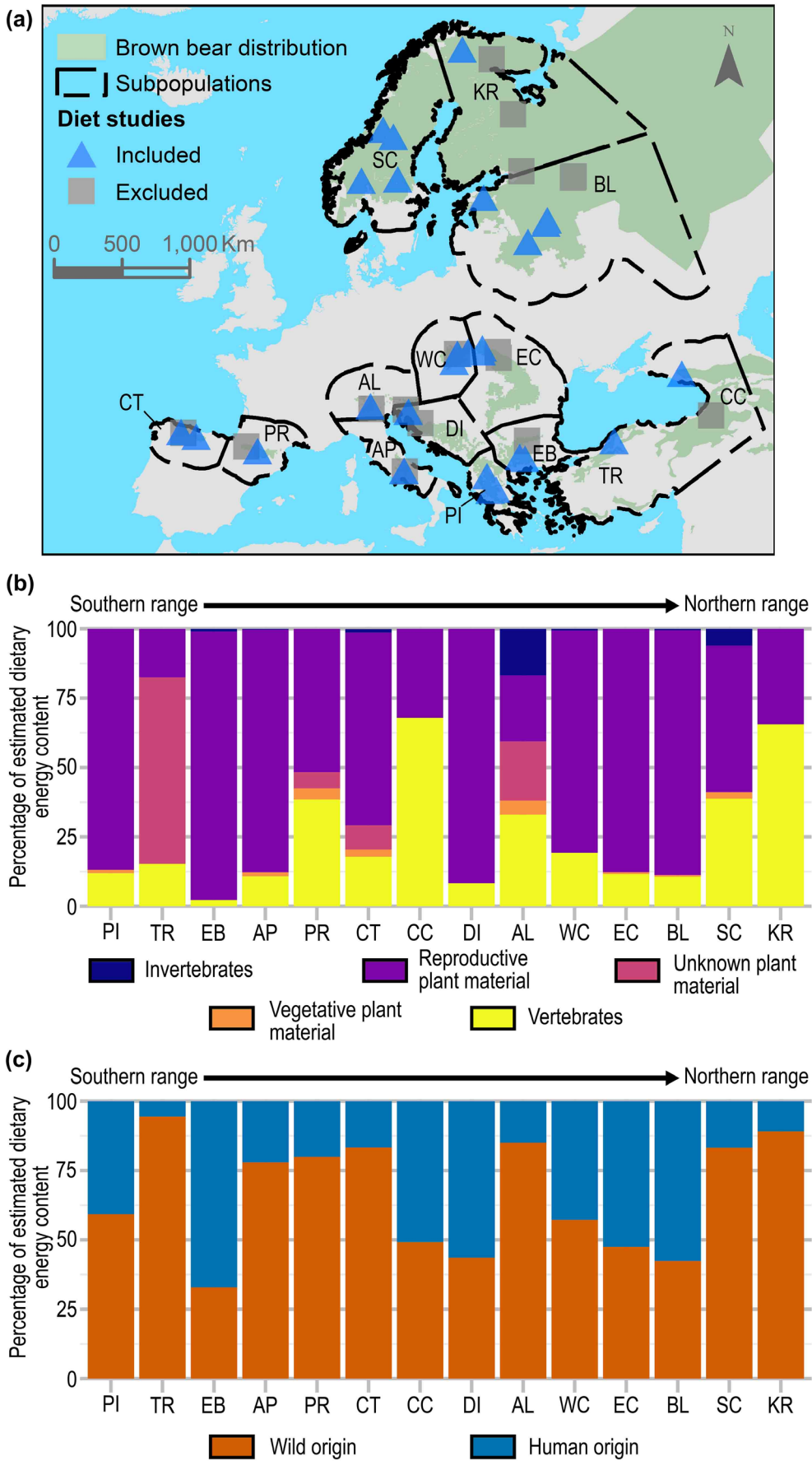


FIGURE 2 | Legend on next page.

FIGURE 2 | Brown bear diet in Europe. (a) Map showing the 14 brown bear subpopulations considered: Pindos (PI), Türkiye (TR), East Balkan (EB), Apennine (AP), Pyrenees (PR), Cantabrian (CT), Caucasian (CC), Dinaric (DI), Alpine (AL), Western Carpathian (WC), Eastern Carpathian (EC), Baltic (BL), Scandinavian (SC), and Karelian (KR). We also mark the location of all the studies of brown bear diet reviewed, indicating if they were ultimately included ($n = 31$) or not ($n = 16$) for the calculation of biotic interactions at species level and for the associations between diet and environmental variables; note that not all studies are visible due to the overlapping of locations. (b) Relative estimated dietary energy content (rEDEC, a proxy for the relative importance of each item in the diet) identified at the species level for each food category, for each of the 14 brown bear subpopulations in Europe. (c) Proportion of the rEDEC for wild species and those of human origin.

models explaining the percentage of each diet category using all possible combinations of the remaining uncorrelated variables as predictors, using the package MuMIn (Barton 2009) in R. Using the subset of best models (delta Akaike information criterion, corrected, $AICc < 3$) we calculated an average model using the subset option. We also calculated models explaining diet diversity (among the diet categories) as a function of land use and climate variables in the buffer areas. We first calculated three indexes of diversity for the diet categories (Simpson, Shannon, and Inverse Simpson) (Fisher et al. 1943; Hurlbert 1971) using the R package vegan (Oksanen et al. 2013). We fitted linear models explaining each diversity index as a function of the uncorrelated variables previously calculated. We calculated, for each index, all possible models using all possible combinations from the uncorrelated variables, and using the subset of best models (delta $AICc < 3$) we calculated an average model using the subset option.

2.5 | Calculation of a Representative Diet for Each Subpopulation

We used the selected 31 studies of brown bear diet (Table S1) to calculate the representative diet for each subpopulation (Appendix S1).

Similarly to Banašek-Richter et al. (2004), where consumed biomass was used as a quantitative descriptor for the flow of energy in the food system, we used the rEDEC previously calculated, which provides a more realistic version of the flow of energy in the brown bear food web system. From the diet studies within each subpopulation, Subp, we calculated for each food species (S), the $rEDEC_{SubpS}$, and assumed it to be a representative rEDEC in that subpopulation:

$$rEDEC_{SubpS} = \sum_{i=1}^n \frac{(Z_i \times rEDEC_{Si})}{\sum_{i=1}^n Z_i}$$

where $rEDEC_{SubpS}$ is the representative rEDEC in the subpopulation Subp for food species S , i is each diet study within the subpopulation Subp (Figure S1 and Table S1), n is the number of diet studies in the subpopulation Subp (Table S1), Z is the number of sampling units (n scats, or n of stomachs analysed) in each study (we use this term to give more importance to studies with more data; Table S1), and $rEDEC_{Si}$ is the rEDEC of food species S in diet study i (Table S4).

2.6 | Calculation of Habitat Suitability for Each Wild Food Species

We fitted ensemble species distribution models (SDMs) at 1 km² resolution for each wild food species in the *Trophic Database*

(Tables S5 and S8), using Global Biodiversity Information Facility (GBIF) occurrences (GBIF 2018, 2023). GBIF data are spatially biased, and this may produce wrong modelling of species distribution if it is not addressed correctly (Rondinini et al. 2006; Beck et al. 2014; Kittle et al. 2018). To reduce the spatial bias, we first reduced the number of occurrences in oversampled regions using spatial filtering by aggregating points of occurrence into presences into equal-area grid cells (Dormann et al. 2007; Phillips et al. 2009; Kramer-Schadt et al. 2013; Aiello-Lammens et al. 2015; Cimatti et al. 2021) of 1 × 1 km using a Conic Equal Area projection (Europe Albers Equal Area Conic). Each grid cell that contained at least one occurrence point was assigned a “1” (considering only once a pixel with one or more occurrences) (Cimatti et al. 2021). Furthermore, we excluded species with < 50 “presence” grid cells from the analyses. In addition, we applied a second technique/recommendation to reduce the spatial bias in GBIF data which consists in selecting the pseudo-absences following the same spatial bias as presence data (Phillips et al. 2009; Wisz and Guisan 2009; Iturbide et al. 2015). To that end, following previous studies (Chefaoui and Lobo 2008; Iturbide et al. 2018), for each species we selected pseudo-absences randomly among the 1 × 1 km grid cells within a 10 km buffer and outside a 3 km buffer around each pixel with presence calculated using Idrisi (Clark Labs 2012). Pseudo-absences were assigned a “0,” and we selected the same number of pseudo-absences as presences. We used climate and land-use variables (Karger et al. 2017; Schipper et al. 2020) as predictors selected the variables to calculate the habitat suitability of food species following a three-step procedure: (1) preselection of variables, (2) filtering of correlated variables, and (3) selection of best variables for each species (for a detailed description of the calculation of habitat suitability of food species see Appendix S1). Using these six selected variables, we modelled the habitat of each food species applying ensemble modelling, a statistical technique that improves the robustness of predictions (Araujo and New 2007), using the R package Biomod2 (Thuiller et al. 2016) (Appendix S1).

Using the fitted ensemble models, we predicted the habitat suitability of each food species for the current and three future coupled scenarios of climate and land use. Future scenarios coupled the climate data from the Institut Pierre Simon Laplace Model CM5A-MR (IPSL-CM5A-MR) (Mignot and Bony 2013) from the CHELSA (Karger et al. 2017) database and land-use forecasts from the GLOBIO 4 (Schipper et al. 2020) database for the year 2050 (Appendix S1).

From the IPSL-CM5A-MR from CHELSA, we selected the RCP2.6 scenario, RCP6.0 scenario, and the RCP8.5 scenario. Thus, combining the future scenarios from the GLOBIO 4 database and from CHELSA, we obtained three future socioeconomic shared pathways (SSPs); namely SSP1-2.6, SSP3-6.0, and SSP5-8.5.

2.7 | Brown Bear Presence Databases

We constructed two databases of brown bear presence: (1) a database of brown bear at the scale of its geographic range using historical distribution data, the *Range Database*, and (2) a database of brown bear using current data, the *Occurrence Database*.

The *Range Database* contains data, at a low spatial resolution (50 × 50 km), on the Eurasian historical distribution of brown bears, areas of current presence, and areas which were occupied in the past but where the species has been extirpated. We discarded the North American brown bear distribution due to large differences in life-history traits between Eurasian and North American subspecies (Zedrosser et al. 2011; Penteriani and Melletti 2020) (Appendix S1 and Figure S6). Across the pixels of presences and absences, we applied a random environmentally stratified sampling procedure following section 7.4.3 in Guisan et al. (2017). Environmentally stratified sampling design consists in designing a method to sample the environmental space (e.g., temperature, precipitation). First, it is necessary to create stratum, a subset of the environmental space where the sampling will be applied. We used climate variables (*Clim_3*, *Clim_4*, *Clim_8*, and *Clim_9*) to create stratum, subsets of the environmental space with similar climate conditions, and then we selected an equal number of presences and absences by stratum (equal number variant). This last selection was used to model the distribution of brown bears at the range scale. The environmental stratified sampling design, although it represents a more complex approximation, has the advantage over the spatially random approach of being more likely to include rare stratum (Guisan et al. 2017).

The *Occurrence Database* contains >3.2 million brown bear occurrences with an uncertainty of <1 km² in Europe and Türkiye, comprising data from 23 countries and 14 subpopulations (all European and Turkish subpopulations), and for the period 1989–2018 (Tables S9–S11 and Figures S2 and S6). Based on identified individuals and on estimations from each research group reporting the data, the *Occurrence Database* contains data from more than 3350 brown bear individuals (>900 linked to GPS and VHF collared individuals, >1200 linked to genetic analysis, and 1295 estimated based in expert knowledge; Appendix S1, Tables S9 and S10 show more information/detail of datasets including the number of individuals, original occurrences and sampling methods used). Most of these occurrences (98%) were obtained from telemetry, VHF, and GPS collars. The use of telemetry data within SDMs provides more objective information about species distribution compared to other methods (Dambach and Rödder 2011) but these data are highly spatially autocorrelated (SAC) and may produce pseudoreplication if this is not considered (Holloway and Miller 2017). Among the methods applied to reduce SAC and avoid pseudoreplication from telemetry data in SDMs, spatial filtering is probably the most widely used (Holloway and Miller 2017), and it allows avoiding this problem in other sources of data, for example, tracks or sightings (Lucas, Herrero, et al. 2016; Grilo et al. 2019), and the combination of different data sources (Bogdanović et al. 2023). Thus, we applied spatial filtering and aggregated the occurrences into presences in equal-area grid cells of 1 × 1 km using a Conic Equal Area projection (Europe Albers Equal Area Conic), considering only once a grid with one or more occurrences.

Each grid cell that contained at least one occurrence was assigned as “presence” (“1”). We obtained more than 100,000 grid cells with the presence of brown bears showing a spatial bias between the different subpopulations, with a minimum of 471 presences for the Türkiye subpopulation and a maximum of 45,119 presences for the Scandinavian subpopulation (Table S11 and Figure S2). Then, we excluded presences occurring in non-terrestrial systems (i.e., presences in lakes or seas). We applied a second filter to the grid cells with presences to reduce their SAC, to avoid overrepresentation of some subpopulations due to a larger number of individuals or greater sampling effort, and also because of computing limitations. Our second filter consisted in subsampling the presence data by selecting a maximum of 2000 presences for each subpopulation, and for subpopulations with less than 2000 presences available, we selected all presences available (Table S11). Pseudo-absences were extracted randomly within a 5 km buffer around pixels with brown bear presences, and we selected the same number of pseudo-absences as presences for each subpopulation. In total, we used 24,908 presences, which were split into two sets, one set to train the model (19,926 presences, 80%) and the other to validate the model (4982 presences, 20%). Proportionally, we reduced to a 0.77% our initial data, from 3.2 million occurrences to 24,908 grid presences. This reduction in filtering the data is between 1 and 3 orders of magnitude bigger than previous studies using GPS collar data to fit SDMs (Maiorano et al. 2015; Coxen et al. 2017; Chibeya et al. 2021; Bogdanović et al. 2023), and it supposes an average of approximately 7.4 grid presences per bear individual. The training data were used in all models using the *Occurrence Database* (for the comparison of biotic proxies explaining brown bear distribution and for modelling brown bear distribution at a fine scale with the Bayesian models, BMs).

2.8 | Modelling the Potential Energy Available to the Brown Bear Across Space

To assess (ii) whether species' geographic distributions are better explained by quantitative or binary proxies of biotic interactions, we calculated two proxies to calculate spatial variables describing the biotic interactions between the brown bear and food species in its diet. The first was a quantitative measure of biotic interactions (*Biotic variables*) obtained by multiplying the $rEDEC_{SubpS}$, the relative energy contribution described at the species level in each subpopulation (defined as parts of the distribution of the species that are isolated from others and/or present different environmental characteristics and/or conservation status; Figure 2a; See Appendix S1 and Figure S7) by the habitat suitability of each species, and then combining the values for each food category (Figure 2b). The second was a binary measure of biotic interactions (*Biotic binary variables*) calculated by multiplying the current habitat suitability by 1 or 0 depending on, respectively, whether or not an interaction with a given food species was observed in each subpopulation, and then combining the values for each food category. For each food category, we fitted and evaluated (Akaike information criterion, AIC, based) two univariable SDMs explaining brown bear distribution using the brown bear *Occurrence Database*: (a) a model using *Biotic variables* as predictors and (b) a model using *Biotic binary variables* as predictors.

2.9 | Bayesian Brown Bear Species Distribution Model

To assess (iii), whether species' geographic distributions are better explained when combining biotic and abiotic factors, we fitted and evaluated (widely applicable information criterion, WAIC, based) three Bayesian models (BMs) to explain brown bear distribution using data from the brown bear *Occurrence Database* as a response variable: (1) a model with abiotic (climate and land-use variables) and biotic predictors (using the best overall proxies, *Biotic variables* or *Biotic binary*, from the previous univariable SDMs), (2) a model with abiotic predictors only, and (3) a model with biotic predictors only (Figure 1e). To minimize bias or the truncation of the environmental space when using only current data (Thuiller et al. 2004; Talluto et al. 2016), two of these BMs utilized historical range data (*Range Database*): the abiotic and biotic BM, and the abiotic BM. Historical range data was included using a Bayesian hierarchical model (BHM) which combined models with historical geographic range as a response variable and historical climate variables as predictors (see Section 2.10) and models with current data (see Section 2.11). For the SDMs explaining brown bear distribution, we used as climate variables bioclimatic variables, which are variables derived from monthly temperature and precipitation values with a biological meaning. We included isothermality, which is the mean diurnal range divided by the temperature annual range (*Clim_3*), temperature seasonality (*Clim_4*), mean temperature of the wettest quarter (*Clim_8*), and mean temperature of the driest quarter (*Clim_9*; Karger et al. 2017 for a detailed description). For land use, we included the rate of urban areas (*Urban*), the rate of broadleaved forested areas (*Broadleaved Forest*), the rate of coniferous areas (*Coniferous Forest*), and a measure of the rate of natural areas at landscape scale (a 11 × 11 km window; *Natural Landscape*). To address (iv), whether future range shifts differ when considering biotic factors or not, we used the best BMs and assessed changes in the potential distribution of the brown bear combining the three previous SSPs with three scenarios of change: (1) change in abiotic and biotic variables, (2) change in abiotic variables, and (3) change in biotic variables (Figure 1d).

2.10 | Species Distribution Model of the Historical Range

We used a model of the historical distribution of the brown bear (based on historical range data and climate data) to inform models of the current distribution (Appendix S1). Specifically, we fitted a species distribution model with presences/absences from the *Range Database* (50 × 50 km resolution) as a function of historical bioclimatic variables (Appendix S1). We selected bioclimatic variables by first dropping those with a VIF over a threshold of 10 using the R package *usdm* (Guisan et al. 2017; Naimi 2017). We further refined the variables by selecting the four best historical climate variables (Table S12) on the basis of the AIC of univariate binomial GLMs (logit link) with linear and quadratic effects. We then fitted a final "historical" distribution model with a Bayesian binomial GLM using these four variables (*Clim_3*, *Clim_4*, *Clim_8* and *Clim_9*) and a stratified sampling of presences/absences from the brown bear *Range*

Database. We extracted the mean and standard deviation of the parameter estimates for use as an informed prior for the models described below (Tables S13–S17 and Figures S8–S10).

2.11 | Modelling and Predicting Brown Bear Distribution at a Fine Scale

We modelled the distribution of the brown bear at a high spatial resolution (1 × 1 km; Table S18) using the training selection of presences/pseudo-absences from the brown bear *Occurrence Database* as the response variable (N presences = 19,926; N pseudo-absences = 19,926; Tables S9–S11) and three types of predictor variables: climate, land-use, and biotic. We selected four variables to include within each type. For climate variables, we selected the same four variables used in the model of the historical brown bear distribution (but with values for the current climate, obtained from the CHELSA database (Karger et al. 2017)). For land-use and biotic variables, we selected the four best (AIC-based) uncorrelated variables determined by a univariable GLMM (Tables S19–S21).

We fitted three Bayesian models (BMs) explaining brown bear distribution using different combinations of factors (abiotic, biotic, or both): (1) a model with abiotic (climate and land-use variables) and biotic predictors (using biotic variables), (2) a model with abiotic predictors only, and (3) a model with biotic predictors only (Table S18). Note that only models including climate variables can use the historical priors, and thus the model based solely on biotic variables can only use current data. We also fitted a null model with only the intercept using only current presences/pseudo-absences.

The two Bayesian hierarchical models (BHMs) which used historical range data (the model with abiotic and biotic predictors and the model with biotic predictors only) used noninformative priors for land use and biotic variables and informative priors based on the historical distribution model as defined above. We assumed equal confidence for the historical and current data, and thus the mean and SD of the parameter estimates from the historical distribution model were not modified and used directly as priors. The biotic model used noninformative priors for all variables. All models were Bayesian binomial GLMMs calculated with a logit link, using the Hamiltonian Monte Carlo algorithm in Stan (Stan Development Team 2023, mc-stan.org). We used Stan with the *rstan*, *rstanarm*, and *loo* packages in R to fit and assess the diagnostics of the models (Stan Development Team 2020; Goodrich et al. 2022; Vehtari et al. 2022). Models were diagnosed by calculating the model coefficients (best estimates and their SE), Monte Carlo standard error (MCSE), confidence intervals (10%, 50% and 90%), number of effective sample size (N_{eff}), and the potential scale reduction factor on split chains (R_{hat} ; at convergence $R_{\text{hat}} = 1$). In addition, we plotted the Markov chain from each model parameter to check whether chains were stationary, whether the path stayed within the posterior distribution (the mean value of the chain is stable from the beginning to the end) and had a good mixing, whether each successive sample within each parameter is not highly correlated with the previous sample (there is a zig-zag motion of each path) (McElreath 2020). We evaluated and compared the models using the widely

applicable information criterion (WAIC) (Vehtari et al. 2017). The best model (based on the WAIC) was evaluated using the validation subset of the brown bear *Occurrence Database* (N presences = 4982; N pseudo-absences = 4982; Table S11). As we used pseudo-absences, we established a cutoff for the potential distribution based on the 90th percentile training presence (Liu et al. 2005; Bean et al. 2012), that is, leaving out 10% of the observed presences of the training dataset.

In addition to those models, and in order to evaluate whether there was an effect of combining different data, we fitted two simple Bayesian models (not hierarchical) for the two BHMs without considering the information of the historical range; we used noninformative priors for all predictors (Table S18).

We used the best model to predict the distribution of brown bear in all subpopulations for the current and nine future climate/land use change scenarios which considered combinations of three SSPs (SSP1-2.6, SSP3-6.0, and SSP5-8.5) with changes in (1) abiotic and biotic variables, (2) abiotic variables, and (3) biotic variables. For the biotic variables, the climate and land-use scenarios were used indirectly to predict the influence of climate and land use on the habitat of species in the brown bear diet, which was then summarized as energy available in the space as described above (Table S22). For the current and each of the nine future climate/land-use change scenarios for the distribution of brown bear, we calculated different descriptors related to the conservation status of species (Lucas et al. 2019; Ramírez-Delgado et al. 2022), such as area of the distribution, percentage of the distribution occupied, and distribution included in protected areas using the World Database of Protected Areas (UNEP and IUCN 2017).

To assess error propagation in the Bayesian hierarchical model using abiotic and biotic factors, we applied a sensitivity analysis over the biotic variables, a technique widely used in fields of ecology and climate change (Rogelj et al. 2012; Barabás et al. 2014). This technique allowed us to quantify how the uncertainty from the biotic variables affects the model's overall uncertainty. For this, we first find the extremes of the biotic variable input (i.e., Figure 1d), with a 95% confidence interval on the strength of the inputs. Then we rerun the Bayesian model with the two extremes to get an upper and lower bound for how much the biotic layer affects uncertainty in the outputs and calculated the current prediction for these new models. We found that estimates and predictions changed slightly (Tables S23–S26 and Figures S11 and S12); predictions showed a high correlation with the original prediction (correlation = 0.9999991 for the model using the lower bound and correlation = 0.9999994 for models using the upper bound). All statistical analyses were performed in the R program, versions 3.1.2 (R Development Core Team 2017) and 4.02 (R Development Core Team 2020) for Bayesian analysis.

3 | Results

3.1 | Spatial Variation of Biotic Interactions

From the literature search, we identified trophic interactions between the brown bear and 276 food species (Figure 1a; Table S5). In total, 76.8% of species were plants and 23.2%

were animals (13.0% vertebrates, 10.1% invertebrates). When focusing only on trophic interactions described at the species level, we found that the relative energy contribution of each food category varied among subpopulations; for example, in the Scandinavian subpopulation, 51% of the energy was of vertebrate origin compared to just 4% for the East Balkan subpopulation (Tables S27–S29). Also, the proportion of energy from human-derived sources ($n = 36$ species) strongly varied among subpopulations; for example, in the Karelian subpopulation, only 2% of the energy was from human-derived sources compared to 93% for the East Balkan subpopulation (Figure 2b,c; Table S30).

Using all food items in each study site ($n > 1300$; not only those described at the species level), we found that the relative energy contribution to the diet of the brown bear for all food categories (apart from the vegetative plant category), as well as the diversity of food categories, was driven by climate and land use (climate and land-use variables showed p values < 0.05 ; see Figure 3 and Tables S31–S50 for detailed model fits including parameter estimates and uncertainties and Appendix S2 for supplementary results). For example, bears consumed (based on the rDEEC) proportionally more reproductive plant parts (e.g., fleshy fruits and nuts) and fewer invertebrates in areas with more broad-leaved forest cover (Figure 3a,b, respectively), and proportionally more vertebrates in areas with climates exhibiting lower annual mean temperatures (Figure 3c) or a smaller diurnal temperature range (Figure 3d). Similarly, bears tend to have more diverse diets when they occur in areas with lower annual mean temperature (Figure 3e,f) or in areas with lower broadleaved forest cover (Figure 3g,h).

3.2 | Quantitative Versus Binary Proxies of Biotic Interactions to Explain Geographic Distributions

Among all wild food species ($n = 240$; Table S5), we were able to build robust SDMs and predict the current/future habitat suitability for 205 species (SDM_{Food} : average sensitivity of 78.4%, specificity of 69.2% and TSS of 0.48; see Tables S8 and S51–S56 for detailed model fits). We then contrasted, based on AIC, whether brown bear distribution was better explained by quantitative (*Biotic variables*) or binary proxies of biotic interactions (*Biotic_binary*). For the vegetative plant food category, we found that the binary proxy for the interaction was sufficient to best explain brown bear distribution. Conversely, for all other food categories (i.e., reproductive plants, unknown plants, invertebrates, and vertebrates), including a quantitative measure of the interactions with species better explained the distribution of brown bears (see Table S21 for model comparison based on AIC).

3.3 | The Role of Abiotic and Biotic Factors in Explaining Species' Geographic Distributions

When we compared the three Bayesian models (BMs), we found that the model combining abiotic and biotic factors was the best ($WAIC_{AbioticBiotic} = 52,675.0 \pm 93.1$; Figure 4) and significantly improved the understanding of brown bear distribution compared to models using either abiotic or biotic factors (delta

Climate and land use associations with brown bear diet

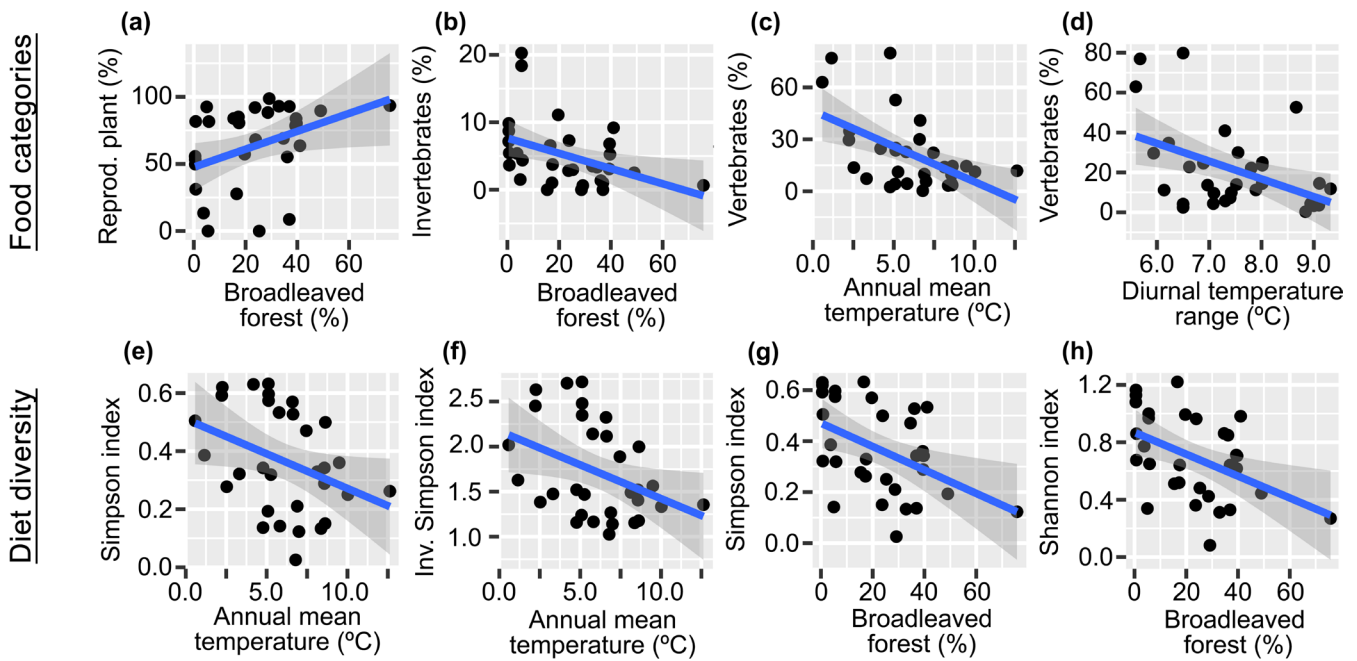


FIGURE 3 | Linear models associating brown bear diet with environmental variables. (a) Association of relative estimated dietary energy content (rEDEC) from reproductive plant with percentage of broadleaved forest. (b) Association of rEDEC from invertebrates with percentage of broadleaved forest. (c) Association of rEDEC from vertebrates with annual mean temperature. (d) Association of rEDEC from vertebrates with diurnal temperature range. (e) Association of Simpson index of diversity (rEDEC-based) with annual mean temperature. (f) Association of inverse Simpson diversity index (rEDEC-based) with annual mean temperature. (g) Association of Simpson diversity index (rEDEC-based) with percentage of broadleaved forest. (h) Association of Shannon diversity index (rEDEC-based) with percentage of broadleaved forest. All predictors of these models showed significant associations (p values < 0.05).

$WAIC_{Abiotic} = 340.0 \pm 95.5$; $\Delta WAIC_{Biotic} = 1679.9 \pm 59.1$; see Tables S18 and S57–S67 and Figures S11–S18 for detailed model fits including parameter estimates and uncertainties). The model combining abiotic and biotic factors showed a good performance compared with a Null model using only the intercept ($\Delta WAIC_{Null} = 2539.7 \pm 0.0$) and yielded a high rate to correctly classify the presences of brown bear (true positive rate = 0.90; Table S68), with a low rate to correctly classify the pseudo-absences of brown bear (true negative rate = 0.21), but see Leroy et al. (2018). The model threshold for classifying presence/absence was intentionally selected to have a true-positive rate = 0.90 to overestimate the current distribution of the species as it has locally been eliminated from potentially suitable areas (Faurby and Araújo 2018) (see Methods), and similarly to other studies of large carnivores which have suffered important range contraction (Grilo et al. 2019). The predictions showed a current potential distribution for the brown bear of 2,794,314 km² (Figure 5a; Table S69), with large areas that could host brown bears but currently do not.

In terms of species response to the selected abiotic and biotic variables, brown bear presence showed a bell-shaped response to most climate variables, but as expected, a negative response to the percentage of urban areas, and a positive association with forests and natural landscapes (Figure 4). While the response of brown bear presence to most biotic variables/food categories was positive (i.e., reproductive plants, unknown plants, and vertebrates), it showed a surprising negative association with the invertebrate food category (see Section 4 and Table S58).

3.4 | The Effect of Biotic Factors in Future Range Shifts

The predictions of biotic interactions, based on the best measures of interaction (*Biotic variables*), for future SSPs showed important differences. The potential available energy for the brown bear from all food species ($Bio_{All_species}$) was predicted to be reduced by 53% under SSP3-6.0. Importantly, when focusing on the different food categories, future predictions for biotic variables showed differences by food category and spatially varied by subpopulation (Figure 1d; Figure S19 and Table S22).

Those predicted future changes in biotic interactions affected the projected distribution of brown bears in the future. Our model showed a drastic range reduction that was more marked when considering both abiotic and biotic variables, with an overall reduction in 36%, as compared to either biotic (reduction in 13%) or abiotic (reduction in 20%) variables only. Range reduction was most pronounced in the south-eastern subpopulations, for example, 93% reduction in the East Balkan subpopulation and 86% reduction in the Türkiye subpopulation (Figure 5; Tables S69–S72). Importantly, the spatial variability of future changes in biotic interactions and by food category described above translated into different effects across the brown bear range, as abiotic and biotic factors acted differently among the different subpopulations. For example, according to the SSP3-6.0 scenario, in the Alpine subpopulation, biotic variables were associated with a habitat reduction in 44% compared to 32% for abiotic variables,

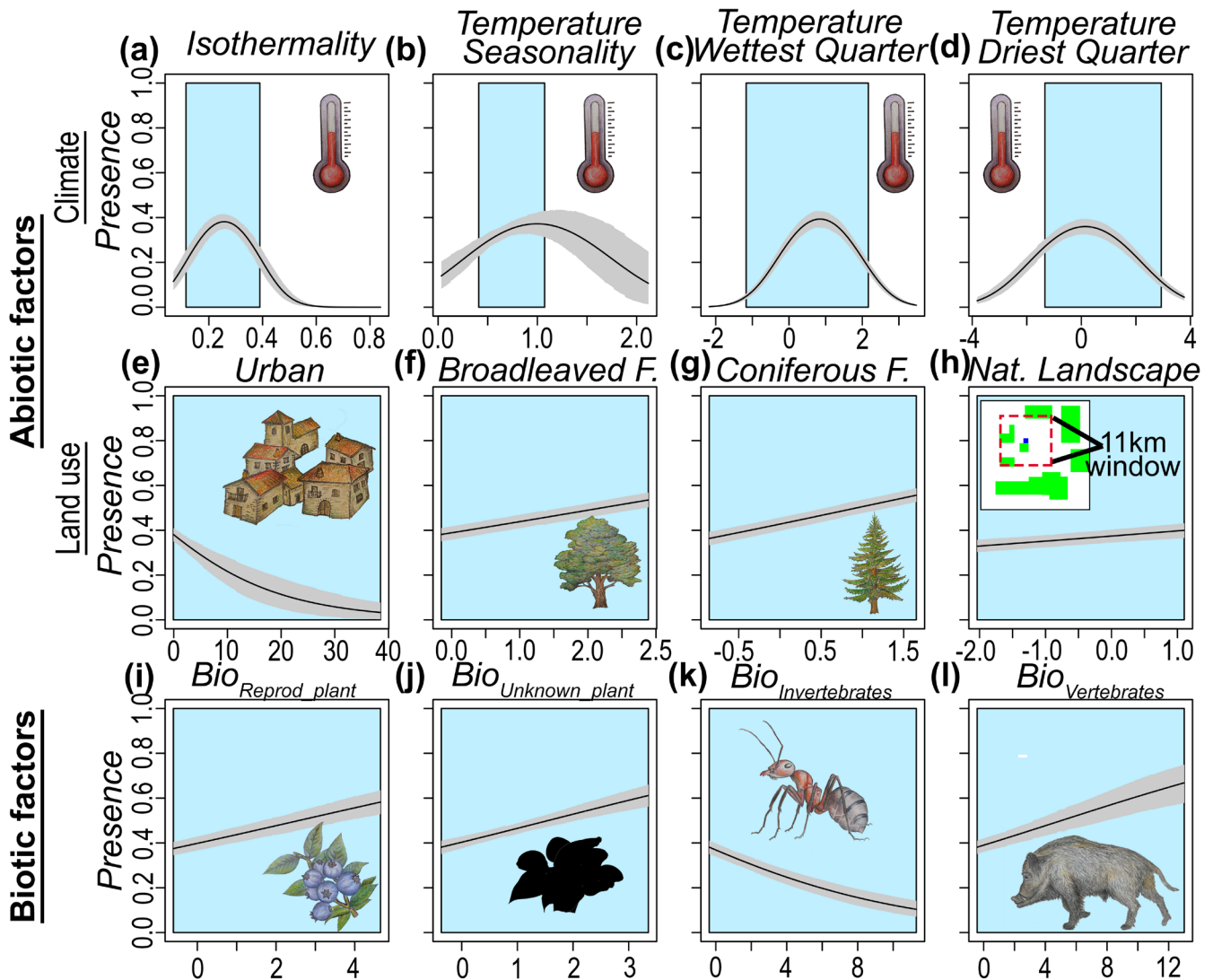


FIGURE 4 | Partial response plots of brown bear distribution to both abiotic and biotic variables. The distribution model for brown bear including both abiotic and biotic factors was fitted combining both historical (*Range Database*) and current data (*Occurrence Database*). The continuous line represents the mean response value, and the grey area shows the model uncertainty (95% confidence interval). The blue area indicates the range of values of the current data. Isothermality (*Clim_3*), temperature seasonality (*Clim_4*), mean temperature of the wettest quarter (*Clim_8*), and mean temperature of the driest quarter (*Clim_9*).

whereas in Türkiye, biotic variables explained a comparatively smaller habitat reduction in 6% (Tables S69–S72).

4 | Discussion

We demonstrate the importance of trophic interactions in explaining species distributions at large (continental) scales. Specifically, we found that (1) trophic interactions are highly variable across geographic space and are determined by climate and land-use variables, (2) reliably estimating these biotic factors requires accounting for quantitative measures of biotic interactions, (3) including biotic interactions significantly improves our understanding of species distributions, and (4) the consideration of biotic interactions in future projections has important effects on predicting future consequences of climate and land-use changes for species distributions and for ecosystem functioning. Our findings are based on a species

with a wide abiotic niche, and which is a top-predator diet generalist (Penteriani and Melletti 2020). Species with other ecological traits, such as different abiotic niche breadth, trophic position, diet breadth, or with a limited mobility capacity, might show different responses to land use and climate change (Carroll et al. 2024). Climate and human land use showed an association with biotic interactions through different ecosystems, suggesting that future scenarios of climate and land use may indirectly affect the brown bear diet. Climate and land use were used as proxies as they explain species richness and community (Coelho et al. 2023) which is the real/direct factor explaining biotic interactions. Future changes in brown bear food webs (our predator-energy system) are caused by/ based on overlap dynamics of predator abiotic niche and prey distributions (Durant et al. 2007; Carroll et al. 2024). At the continental level, two patterns prevail, divergent shifts, and contracted shifts, both causing a decrease in the available energy, but in some areas, we can observe congruous shifts, with

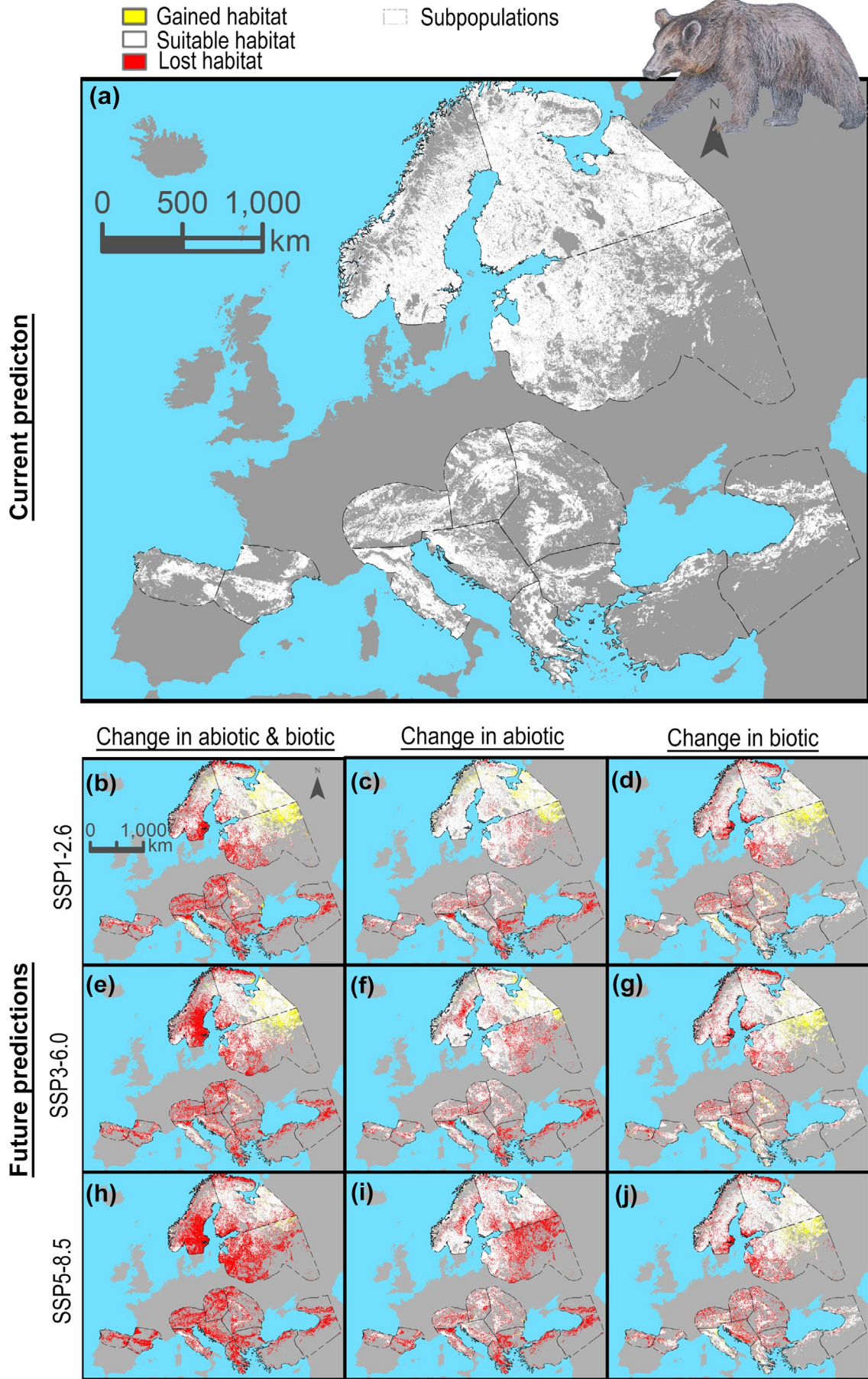


FIGURE 5 | Legend on next page.

FIGURE 5 | Brown bear habitat predictions. Prediction of brown bear habitat for current conditions (a). Future predictions of habitat for climate change scenarios SSP1-2.6, SSP3-6.0, and SSP5-8.5 considering changes in both abiotic and biotic factors (b, e, h), changes in abiotic factors only (c, f, i), and changes in biotic factors only (d, g, j). The predicted area only includes a buffer area of 200 km around the current distribution to avoid extrapolating biotic variables into an environmental space where there is no information about the trophic interactions of brown bears.

bears and energy redistributing in similar directions (e.g., Scandinavian subpopulation) and convergent shifts, with bear available energy increasing the overlap with bear abiotic niche (e.g., Karelian subpopulation) (Durant et al. 2007; Carroll et al. 2024). This spatial variability, among the different subpopulations, in the overlap dynamic shows the complexity of the indirect effects of biotic interactions over species distributions and may be caused by several factors: (1) different magnitudes and directions of global changes in the different communities, for example, subpopulations around the Mediterranean will face higher increases in temperature and a reduction in precipitation (Karger et al. 2017); (2) there are different prey species, with different ecological traits, among the different subpopulations, for example, Southern subpopulations depend more on plant species with a narrower niche, whereas northern subpopulations have a higher proportion of ungulates in their diet. We did not account for species mobility, which may increase the contracted shifts for prey species of lower mobility. Overall, we would expect increasing homogenization in the diet among the different subpopulations, with more importance of those species with certain ecological traits such as a wide abiotic niche or higher mobility and a reduction in the available energy to bears in general (Carroll et al. 2024). However, reorganization of food webs implies different responses for top-predators (Hoeks et al. 2020; Hao et al. 2025). As a diet generalist, the brown bear may switch to more available prey in response to a decline in overlap with important species in their diet (Ferrerás et al. 2011) which could imply changes in the trophic position of the brown bear. In certain areas, energy reductions may lead to a decrease in bear abundance, as it has been observed in black bears (Laufenberg et al. 2018), and in some cases can contribute to a local extinction, joining other factors, for example, in subpopulations currently at high extinction risk or subpopulations facing an intense contraction of the abiotic niche (e.g., Türkiye subpopulation) (Sıkdokur et al. 2025). Importantly, changes in brown bear food webs can result in an increase in human–wildlife conflict if wild prey species availability decreases and bears switch to a diet based on anthropogenic sources (Chynoweth et al. 2016; Laufenberg et al. 2018; Abrahms et al. 2023; Kurth et al. 2024; Sıkdokur et al. 2024), which is a problem for the conservation of species (Pooley et al. 2017).

Ecosystem structure and functioning will be importantly affected by the reorganization of food webs driven by global changes (Sinclair 2003; Preisser et al. 2007). As large carnivores play a key role in ecosystems, a change in their abundance or trophic position determine important cascade effects, such as changes in abundance of herbivores and mesopredators and a decrease in the autotroph biomass (Hoeks et al. 2020). In the case of European and Türkiye ecosystems, the important range contraction of the historical distribution of brown bear (see historical range in Figure 1e and Figure S6) and its low abundance in some areas (several European subpopulations at

extinction risk due to small population size) may have already caused an important change in ecosystem functionality and structure which should be considered for rewilding (Araújo and Alagador 2024).

The distribution of brown bears in Europe depends on climate variables, influencing the physiological functioning of the species (Bozinovic et al. 2011; Rogers et al. 2021; Kurth et al. 2024), as well as land use, such as forested areas and continuous natural areas which could be used as shelters (Grilo et al. 2019; Penteriani et al. 2019; Penteriani and Melletti 2020; Sıkdokur et al. 2025). This is in line with previous studies showing the importance for brown bear distribution of minimum temperature of the coldest month and annual mean temperature (Luna-Aranguré et al. 2020; Sıkdokur et al. 2025) and with the importance of forest cover (Penteriani et al. 2019; Sıkdokur et al. 2025). However, here we show that even biotic factors shape brown bear distribution, represented here as the relative energy derived from food resources available to the species. According to our results, brown bears select areas that maximize this available energy (i.e., positive response of brown bear to most biotic variables), which may be explained by the high energy requirements of the species (White and Seymour 2003)⁴⁴ and the absence of strong interspecific competition for food resources (Braz et al. 2020). The negative association with the availability of energy from invertebrates may be related to their negative correlation with isothermality (*Clim_3*; Correlation = -0.47), which has great importance for brown bear distribution and exhibits a bell-shaped response (Figure 4a). This could indicate that areas with high available energy from invertebrate species are located in less suitable environments. In addition, the low relative energy represented by invertebrates in the brown bear diet—an average of 2% among all subpopulations (Figure 2b and Table S29)—may suggest that they represent opportunistic consumption rather than intentional/preferred prey, which may not influence the distribution of brown bears. Our results showed that brown bears currently have a large amount of suitable habitat that could be occupied. While the potential adaptability of brown bears to diverse food resources and the challenges of predicting future energy availability are promising research avenues, it is paramount to underscore the significant impact of humans on brown bear distribution and their conservation (Morales-González et al. 2020; Ashrafzadeh et al. 2022). Furthermore, climate and land-use changes have the potential to greatly reduce suitable bear habitats. Hence, safeguarding forests, minimizing landscape fragmentation, and preserving the species communities that interact with brown bears play vital roles in mitigating the effects of these drivers (Li et al. 2020).

The use of SDMs is one of the most advanced and widely used tools to understand the factors delimiting species distributions and to predict the effects of global change on biodiversity (Guisan and Thuiller 2005). Our results show the importance

of additionally considering biotic factors and taking an ecosystem approach to properly understand species distributions (Romero et al. 2018; Antão et al. 2022), especially for modelling species distributions under climate and land-use change scenarios (Thuiller et al. 2018; O'Gorman et al. 2023). However, as biotic interactions are highly complex, their inclusion needs to be accounted for on the basis of ecological studies that consider the spatial heterogeneity of these interactions and provide quantitative estimates for them (Banašek-Richter et al. 2004; Banašek-Richter et al. 2009). Our approximation was a simplification of the true biotic interaction networks, and other aspects such as competition, parasitism, the potential plasticity of different subpopulations to alter their diet in future scenarios, and/or other dimensions including temporal variation at seasonal, interannual, and other spatial scales may be relevant and could be considered in future studies. For example, the important diet adaptability of the brown bear and food preferences were not considered. It is expected that future communities where brown bears will be present will be different in species composition but also in their abundance, and this will have an important role in the potential interactions; for example, we would expect that brown bears would select species with higher energy such as big ungulates (Hayward and Kerley 2008; Niedziałkowska et al. 2019). It is also possible that novel habitats suitable for brown bears in both abiotic and biotic conditions could emerge under different climate change scenarios in areas currently outside brown bear distribution. In general, implementation of projections including biotic interactions in other species currently faces two big challenges: (1) detailed and extended information about ecological interaction networks, and (2) high-quality data about species presences/occurrences. To overcome these challenges, global-scale monitoring initiatives with open-source principles, open-source databases on species ecology, and the reduction of spatial and taxonomic biases will be of primary importance (Meyer et al. 2015; Delgado-Baquerizo et al. 2016). This new generation of projections has a wider applicability over all species, allows decoupling abiotic and biotic factors, will better identify the drivers responsible for species distributions, and will enhance the predictions regarding the effects of global change on species, including agriculture or livestock species; overall they will generate important knowledge to conserve biodiversity, ecosystem services, and to secure the human food system.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and R code that support the findings of this study are openly available in Zenodo at <https://zenodo.org/records/15364702> (trophic interactions database), <https://zenodo.org/records/15375279> (range database), <https://doi.org/10.5281/zenodo.15336808> (R code) and Github at <https://github.com/PabloMLucas/Trophiclinks-shape-global-change-effects> (R code). This specimen represents an endangered or threatened species. The specific locality has been removed from the online record to protect this species from over-collection. These data may be supplied to researchers on request. The database of occurrences of species in the brown bear diet obtained from GBIF, has been mirrored on Zenodo (<https://doi.org/10.15468/dd.4whdmm>). Temperature and precipitation data were obtained from CHELSA via Dryad at <https://doi.org/10.5061/dryad.kd1d4>. Land use/cover was obtained from GLOBIO 4 at <https://www.globio.info/globio-data-downloads> (Land use versions for 2015 and scenarios 2050 SSP1 RCP2.6, 2050 SSP3 RCP6.0 and 2050 SSP5 RCP8.5 from Schipper et al. 2020). Protected areas were obtained from the World Database on Protected Areas at <https://www.protectedplanet.net/>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.