



OPEN ACCESS

EDITED BY

Manoj Kumar Jhariya,
Sant Gahira Guru Vishwavidyalaya, India

REVIEWED BY

Somanath Sarvade,
Jawaharlal Nehru Agricultural University, India
Nirius Jenan Ekka,
Sambalpur University, India

*CORRESPONDENCE

José Carlos Pérez-Girón
✉ jcperezgiron@ugr.es

RECEIVED 07 May 2025

ACCEPTED 22 July 2025

PUBLISHED 04 August 2025

CITATION

Pérez-Girón JC, López-Bao JV,
Díaz-Varela E and Álvarez-Álvarez P (2025)
Predicting climate-related compositional
shifts in nut-producing species that are
important for bears during hyperphagia.
Front. For. Glob. Change 8:1624612.
doi: 10.3389/ffgc.2025.1624612

COPYRIGHT

© 2025 Pérez-Girón, López-Bao, Díaz-Varela
and Álvarez-Álvarez. This is an open-access
article distributed under the terms of the
[Creative Commons Attribution License](#)
(CC BY). The use, distribution or reproduction
in other forums is permitted, provided the
original author(s) and the copyright owner(s)
are credited and that the original publication
in this journal is cited, in accordance with
accepted academic practice. No use,
distribution or reproduction is permitted
which does not comply with these terms.

Predicting climate-related compositional shifts in nut-producing species that are important for bears during hyperphagia

José Carlos Pérez-Girón^{1*}, José Vicente López-Bao²,
Emilio Díaz-Varela³ and Pedro Álvarez-Álvarez⁴

¹Inter-University Institute for Research on the Earth System in Andalucía (IIITA), University of Granada, Granada, Spain, ²Biodiversity Research Institute, University of Oviedo-CSIC-Principado de Asturias, Mieres, Spain, ³Higher Polytechnic School of Engineering, University of Santiago de Compostela, Lugo, Spain, ⁴Department of Organisms and Systems Biology, Polytechnic School of Mieres, University of Oviedo, Mieres, Asturias, Spain

Introduction: Climate change represents an escalating threat to wildlife globally, disrupting ecosystems and altering species interactions. Key nut-producing forest species in the Cantabrian Mountains may be affected, with consequences for Cantabrian brown bears (*Ursus arctos*) during hyperphagia. Understanding such changes may help to improve conservation strategies to ensure that bears may be able to adapt to changing environmental conditions.

Methods: With this aim, we assessed the current and future habitat suitability of all nut-producing trees in the Cantabrian Mountains. We fitted species distribution models using a down-sampling random forest ensemble approach to create comprehensive maps and species flows, identifying key hotspots of nut production under the SSP3-7.0 and SSP5-8.5 climate change scenarios. Based on bear mobility patterns, we identified areas where individuals lacked access to at least two fruit-producing species, thereby identifying potential areas of nuts shortage for bears during hyperphagia.

Results and discussion: We anticipate a potential decline in beech (*Fagus sylvatica*) and Atlantic oaks (*Quercus petraea*), with a compositional shift towards thermophilic species, such as sweet chestnuts (*Castanea sativa*) and Mediterranean oaks (e.g. *Quercus ilex*). The area unsuitable for any nut-producing species is likely to increase over time, reaching 25% within the current bear range. The diversity of nut-producing species is projected to decline over time, leaving large areas within the bear's range with access to only one or two species. Bears may be able to gain access to food resources owing to their dietary plasticity and their ability to move and track energy-rich food resources. Ensuring the long-term accessibility of nuts to bears in some areas could be based on the establishment of Chestnut plantations apart from human settlements, as well as actions to enhance fruiting for oaks, such as the case of Pyrenean oaks.

KEYWORDS

climate change, habitat suitability, species distribution models, stacked species distribution models, nuts, Cantabrian Mountains

Highlights

- Climate change can impact the survival and productivity of nut-producing species.
- In some regions, brown bears feed mainly on nuts during hyperphagia.
- Bear adaptability and mobility may ensure future access to nut-producing species.
- Chestnut plantations far from humans may favor bears' access to chestnuts.
- Actions to enhance fruiting for oaks could improve nut availability in some areas.

Introduction

Human-induced global warming has led to extreme weather events and unprecedented climate records worldwide, resulting in the emergence of what has been described as a new global climate domain (Harvey et al., 2023). Changes in temperature and precipitation patterns and the increased frequency of extreme weather events are expected to impact ecosystem functioning in multiple ways. Species with greater adaptability are likely to cope more effectively with these changing conditions. In this respect, the brown bear (*Ursus arctos*) is very mobile and has a broad trophic niche (Bojarska and Selva, 2012; Martin et al., 2012). This dietary flexibility may enhance its capacity to adapt to the consequences of climate change (Navarro et al., 2021). Nevertheless, during the hyperphagia period (late summer and autumn, before hibernation) brown bears are particularly sensitive to food availability, as they must accumulate sufficient fat reserves to support reproduction in the case of adult females (Costello et al., 2003; Di Domenico et al., 2012; López-Alfaro et al., 2013) and ensure survival in winter season (Ryan et al., 2007; Schwartz et al., 2006). During this period, bears across central-southern Europe and the Middle East feed on different nut-producing species such as beech (*Fagus sylvatica*), various oak species (*Quercus* sp.) and sweet chestnut (*Castanea sativa*) (e.g., Ambarlı, 2016; Bojarska and Selva, 2012; Ciucci et al., 2014; De Angelis et al., 2021; Naves et al., 2006; Paralikiidis et al., 2010; Rodríguez et al., 2007), some of which are threatened by the effects of climate change (del Río et al., 2021; Dyderski et al., 2025, 2017; Kasper et al., 2022; López-Tirado et al., 2018; Rubio-Cuadrado et al., 2018; Uri et al., 2015).

Climate change severely impacts forest ecosystems, as prolonged droughts, heatwaves and heavy rainfall compromise primary productivity (Nussbaumer et al., 2018), a key factor in the fruiting success of nut-producing species (Journé et al., 2021). Climate change alters the phenology of nut-producing trees, affecting the timing of phenological events (e.g., flowering and fruiting); it lengthens the growing season, which favors increased productivity but also makes irregular yields more likely due to extreme weather events. Thus, phenology has been suggested to be a key factor in determining future species distribution, as climate-driven shifts in timing can lead to decline or expansion of suitable habitats for many plant species (Piao et al., 2019; Vitasse et al., 2011). Several nut-producing species, such as beech and oaks, show remarkable interannual variability in fruit production inherent to the species, although mast years (Gea-Izquierdo et al., 2006; Nussbaumer et al., 2018, 2016) may also be associated with the effects of climate change (Hacket-Pain and

Bogdziewicz, 2021). For example, Clevenger et al. (1992) observed fruiting failure in *Quercus* spp. and *F. sylvatica* in northern Spain for up to 4 consecutive years, in some cases overlapping among species in the same year.

Bears relying on nut-producing trees for food during hyperphagia have to adapt to the aforementioned changes, such as in the case of bears in the Cantabrian Mountains (northern Spain) (Lucas et al., 2025; Navarro et al., 2021; Pérez-Girón et al., 2022). Here, the long-term climate-related changes in the availability of food resources, such as a decrease in the availability of *Vaccinium* fruits, have already been linked to an increase in the consumption of nuts by Cantabrian bears (Rodríguez et al., 2007). The non-territorial character of bears (Swenson et al., 2023) allows them to increase their use of space or to carry out long-distance movements searching for food resources across the landscape (De Angelis et al., 2021). Indeed, bears can aggregate, sometimes in remarkable numbers, at clustered food sources during hyperphagia (Ballesteros et al., 2018; Ciucci et al., 2014). For example, during the 2017 hyperphagia period, Ballesteros et al. (2018) reported exceptional bear aggregations linked to a large variation in the availability of nuts; at least 31 different bears were feeding on oak acorns in an area of ca. 3 km² (with the main concentration observed in about 50 ha) where good acorn production occurred for orographic and microclimatic reasons, in a year when there was generalized fruiting failure in nut-producing species caused by heavy frosts in spring throughout most of the bear range. The dependency on nut-producing trees could become even greater, as warming conditions may lead to a further reduction in the hibernation period in addition to that already observed (e.g., Pigeon et al., 2016; Planella et al., 2019), increasing energy demands and intensifying reliance on stable, year-round food sources. Additionally, if these resources become scarce, bears may increasingly turn to anthropogenic food sources, potentially intensifying human-wildlife conflicts (Kurth et al., 2024).

Under the current scenario of climate change, the distribution and productivity of species such as thermophilic oaks (*Q. faginea*, *Q. ilex*, and *Q. suber*) and sweet chestnut may increase (Benito Garzón et al., 2008; Pérez-Girón et al., 2020) as a result of a better tolerance, adaptation and competitive capacity of these tree species, compared to beech or Atlantic oaks (Duque-Lazo et al., 2018; Dyderski et al., 2025; Uri et al., 2015). Although a shift in dominant species may ultimately occur, hybridization among oak species (Sánchez De Dios et al., 2006) and the gradual development of mixed stands are also likely. Mixed stands are up to 30% more productive in biomass than pure stands (Pretzsch et al., 2013), thus potentially increasing available resources to bears. Dietary plasticity is expected to help bears to cope with the effect of interannual variability in nut production among tree species (Ambarlı, 2016; Bojarska and Selva, 2012; Ciucci et al., 2014; De Angelis et al., 2021; Naves et al., 2006; Paralikiidis et al., 2010; Rodríguez et al., 2007). However, as some species are more constant in producing nuts (e.g., sweet chestnut; Petit and Larue, 2022), the potential impact of climate change on the distribution of nut-producing species could generate new scenarios of food availability and shortage for bears during hyperphagia (Navarro et al., 2021). In such scenarios, spatial complementarity among nut-producing species may be essential to ensure a minimum availability of food to bears at a landscape level. Spatial complementarity in our case is understood as the spatial and

temporal availability of multiple nut-producing species, which can collectively support the dietary needs of brown bears during hyperphagia. However, to date, the different responses of these nut-producing species and their complementary provision of food for the brown bear under different climatic scenarios has not been evaluated.

Assessing the potential effects of climate change on nut-producing species during hyperphagia is key to understand the adaptation of Cantabrian brown bears to changing environmental conditions, and its potential impacts on its recovery (Lucas et al., 2025). However, despite growing evidence of climate-driven changes in forest composition, little is known about how these shifts may affect the availability and spatial distribution of key trophic resources for the Cantabrian brown bear during critical stages such as hyperphagia. In particular, the spatial complementarity of nut-producing species, where the presence of multiple species may offset local deficits, remains understudied. The Cantabrian Mountains offer a particularly suitable setting for investigating these dynamics, given the region's ecological complexity and the heightened sensitivity of mountain ecosystems to climate change. Projected climate change impacts are expected to drive rapid ecological shifts in these habitats, including a significant decline in suitable habitat and upward shifts in ecological niches (Dyderski et al., 2025, 2017; Lenoir et al., 2008; Pérez-Girón et al., 2024).

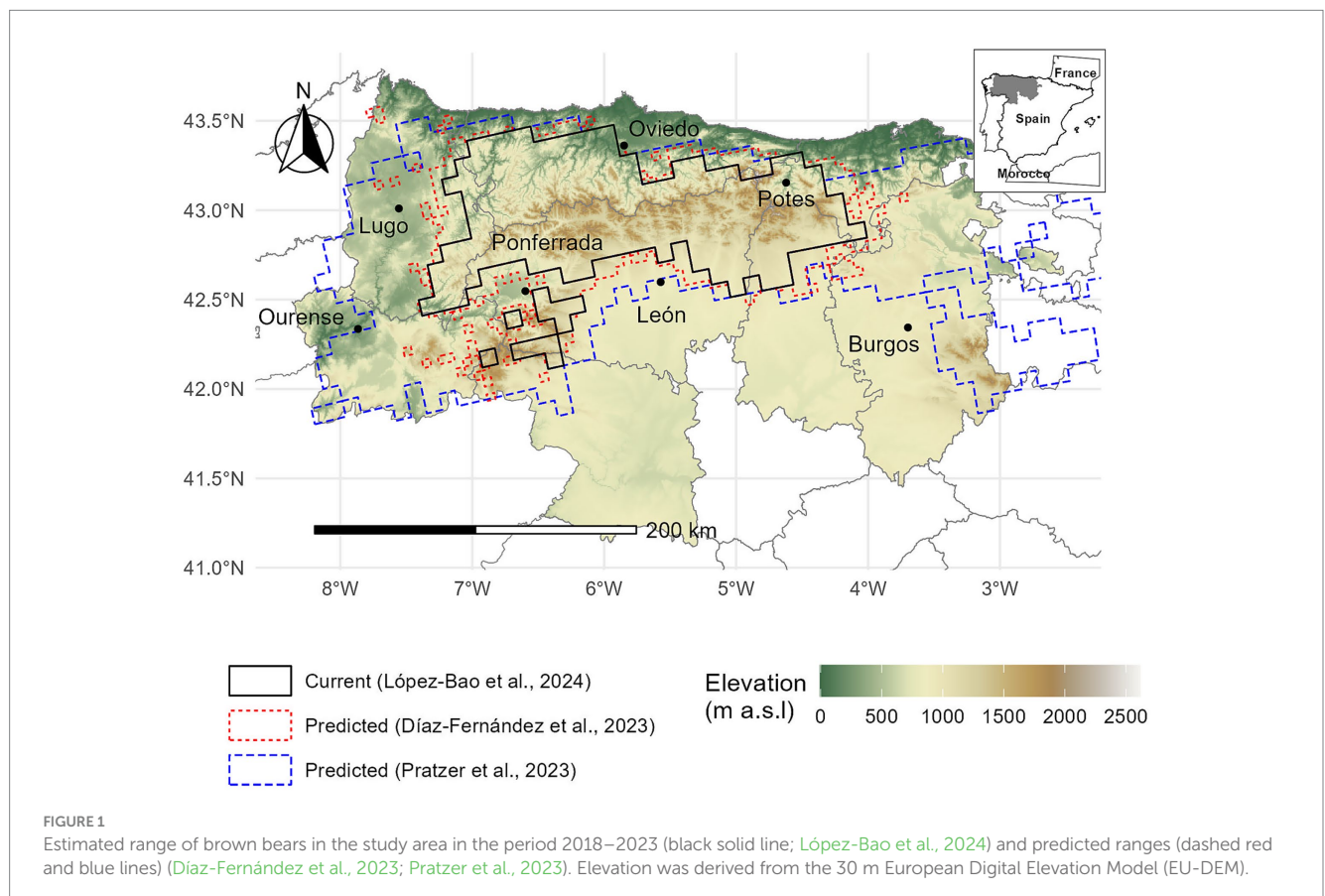
In this context, the objectives of this study are: (i) to evaluate the impact of climate change on nut-producing species that are important to the diet of the brown bear (*Ursus arctos*) during the hyperphagia

period; (ii) to analyze functional complementarity among species through species richness; and (iii) to identify vulnerable areas to better understand the challenges faced by the brown bear in adapting to changing environmental conditions. Additionally, conservation strategies are proposed to safeguard key trophic resources critical for the survival and well-being of the brown bear. Together, this work aims to provide a comprehensive understanding of the interactions between climate change, food resource availability, and the ecological requirements of the brown bear during hyperphagia, ultimately contributing to its long-term conservation under increasing environmental pressure.

Materials and methods

Study area

The study area encompasses the provinces of Lugo, Ourense, León, Zamora, Asturias, Cantabria, Palencia and Burgos, covering the entire range of the brown bear in the Cantabrian Mountains (Figure 1). The study area extends approximately from 41°N to 43.5°N latitude and from 3°W to 7°W longitude. Elevation ranges from sea level to high mountain peaks exceeding 2,500 m a.s.l., creating pronounced topographic heterogeneity. This mountain range also serves as a transitional zone between the Atlantic and Mediterranean biogeographical regions and has a unique climate gradient. The Cantabrian Mountains are characterized by an oceanic



climate, heavily influenced by their proximity to the Atlantic Ocean and their geographical orientation. The northern side supports forest dominated by broadleaved Atlantic species, whereas in the southern side tree species adapted to greater temperature variability and drier conditions predominate. Soils are generally acidic in the western and central parts of the range, while the eastern sector and some localized areas within the study region contain calcareous soils, which support distinct vegetation communities. In terms of nut-producing species, the study area hosts several taxa known to be important in the brown bear's diet during hyperphagia. Based on their nutritional relevance, we included the following nine species in our analysis: beech, pedunculate oak (*Quercus robur*), sessile oak (*Quercus petraea*), hazel (*Corylus avellana*), Pyrenean oak (*Quercus pyrenaica*), Portuguese oak (*Quercus faginea*), sweet chestnut, holm oak (*Quercus ilex*) and cork oak (*Quercus suber*) (Navarro et al., 2021; Naves et al., 2006; Rodríguez et al., 2007).

Presence of nut-producing species

Although our study was focused on northern Spain, which is characterized by an Atlantic climate, we gathered georeferenced occurrences of nut-producing species relevant to the brown bear across the entire Iberian Peninsula. This approach ensured that we captured the full range of climatic conditions in which these species can occur, including Mediterranean environments. Occurrences were compiled from the 3rd and 4th National Forest Inventory of Spain (NFI3 and NFI4), the 6th National Forest Inventory of Portugal (NFI6), the Continuous Forest Inventory of Galicia (IFCG), and the Global Biodiversity Information Facility (GBIF) (GBIF, 2024; ICNE, 2015; MITECO, 2022; Xunta de Galicia, 2022). Those plots from the NFIs where no individuals of the targeted nut-producing species were recorded were treated as true absences. The NFIs employ a systematic sampling approach, surveying all plots and documenting all species present. Consequently, the absence of a species in a plot reliably indicates its true absence. To improve data accuracy, we filtered the GBIF presences, retaining only those locations with <25 m of coordinate uncertainty. Subsequently, only those occurrences located outside of areas subject to human management, such as parks, gardens or agricultural lands, were considered. For this purpose, we intersected all occurrences with CORINE land cover 2018. Finally, to avoid any spatial bias arising from the integration of multiple data sources, we applied geographical filtering using the *ecoinfo* R package (Carlisle and Albeke, 2016), in which only those occurrences separated from each other by >200 m were retained, while a threshold distance of >1,000 m, consistent with the NFI sampling resolution, were used for true absences (Álvarez-Álvarez et al., 2025). As a result, we compiled 1,921 occurrences of *C. avellana*, 4,360 of *C. sativa*, 5,110 of *F. sylvatica*, 4,755 of *Q. faginea*, 17,586 of *Q. ilex*, 1,258 of *Q. petraea*, 6,244 of *Q. pyrenaica*, 5,669 of *Q. robur* and 5,909 of *Q. suber*.

Current and future habitat suitability for nut-producing species

Given the range of species considered, we selected generalist topographic, soil, and climatic variables with ecological significance

across multiple species (Supplementary Table S1). We derived slope and aspect from the 30 m European Digital Elevation Model (EU-DEM), and to prevent redundancy in aspect values at 0° and 360°, we transformed aspect into northness (cosine of aspect) and eastness (sine of aspect). Soil-related parameters included soil pH and soil organic carbon content (SOC) in the 5–15 cm layer, sourced from SoilGrids250m version 2.0 (Poggio et al., 2021). To account for potential climate change effects, we used bioclimatic variables from the CHELSA V2.1 dataset, excluding variables 8, 9, 18, and 19 due to known spatial discontinuities (Álvarez-Álvarez et al., 2025; Booth, 2022; Karger et al., 2017).

To project future habitat suitability, we replaced current information on climate variables with future projections of the same ones on the basis of climate scenarios derived from the Coupled Model Intercomparison Project Phase 6 (CMIP6) provided by CHELSA V2.1 (Karger et al., 2017). Specifically, we used five high-performance General Circulation Models (GCMs) (GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0, and UKESM1-0-LL) and two Shared Socioeconomic Pathways (SSPs) (SSP3-7.0, Regional Rivalry, and, SSP5-8.5, Fossil-fueled Development) spanning three distinct periods: 2011–2040, 2041–2070 and 2071–2100 (Lange, 2021). Since the SSP5-8.5 scenario represents an unlikely and high-risk future (Hausfather and Peters, 2020), we focused on the SSP3-7.0 scenario, highlighting its greater relevance for climate change research and policy-making. Consequently, analyses based on SSP5-8.5 are provided in Supplementary material. Additionally, to assess climatic extrapolation risks, we employed the Mobility-Oriented Parity (MOP) test (Owens et al., 2013), which identifies areas with high climatic dissimilarity relative to a reference set. Specifically, we sampled the current climatic conditions occupied by each species and normalized the results. Higher MOP distances indicate greater dissimilarity or “non-analogous” conditions, suggesting a higher risk of extrapolation when transferring ecological models to that area.

All predictors were cropped to fit the study area, reprojected to GRS84 (EPSG:4326) and resampled to a 100 m resolution using bilinear interpolation. These processes were completed using the *terra* package (Hijmans et al., 2022) and graphically plotted using the *tidyterra* and *tidyverse* R packages (Hernangómez, 2023; Wickham et al., 2019). The MOP analysis was conducted using the *mop* package in R (Cobos et al., 2025).

Species distribution modeling: evaluation and ensembling

We fitted species distribution models (SDMs) for each tree species and then combined these into stacked species distribution models (SSDMs), to create comprehensive maps and flows highlighting forest diversity hotspots and areas of potential species overlap. In the present context, SSDMs could be used to help identify vulnerable areas for bears in terms of the potential availability of nuts, as well as areas where less climate-sensitive species of interest for bears, such as chestnut, could potentially be established (Navarro et al., 2021; Pérez-Girón et al., 2022, 2020). We employed a down-sampled Random Forest (RF) algorithm to develop the SDMs, as this approach has been shown to be particularly effective when used as a standalone modeling method (Valavi et al., 2022). This method addresses class imbalance by equalizing the number

of majority-class samples (absences) with the minority-class samples (presences) (Liu et al., 2009).

The RF model was trained on a balanced sample using 80% of the occurrences, with the $mtry$ value set as the square root of the number of predictors, and 1,000 trees. For each species model, we excluded those variables with a Spearman's pairwise correlation coefficient $> |0.7|$ or a Variance Inflation Factor (VIF) > 5 (Sillero et al., 2021). The predictive accuracy and discriminative capacity of the down-sampled Random Forest (RFdown) models were evaluated using the area under the precision-recall curve (PR-AUC), applied to the remaining 20% of the occurrence data. We selected PR-AUC instead of the commonly used AUC-ROC metric to avoid the inflation of model performance scores that can occur when modeling over large spatial extents (Sillero et al., 2021). Finally, spatial predictions were binarized using the minimum training presence threshold (Liu et al., 2016), and future projections were derived using the median value for each scenario and time interval.

Post-processing of SDMs

First, we used the brown bear range in the Cantabrian Mountains as a framework to analyze changes in the spatial distribution of environmentally suitable habitats for each species under current and future climatic conditions, across different scenarios and time intervals. For this purpose, we used three ranges: the estimated range for the 2018–2023 period (López-Bao et al., 2024) and the future

ranges predicted by Díaz-Fernández et al. (2023) and Pratzner et al. (2023) (Figure 1).

Second, we computed an SSDM by combining each of the previously calculated individual binary SDMs to measure predicted species richness, where pixels with the highest values indicated regions of greatest expected availability of nut-producing species. We tracked species richness dynamics at pixel level from the current state through three future periods, by using a Sankey diagram (Sjöberg, 2024).

Third, we searched for potential vulnerable areas for bears by using a circular moving window analysis of the resulting species richness maps, to identify broader areas of potential food-shortage for bears. The value assigned to each target pixel was determined by the maximum species richness within a window size approximating the use of space by adult female bears. As home range estimates were limited in the study area (average minimum convex polygon for 4 adult females: 30.8 km²; Mateo-Tomás et al., 2024), we assumed a conservative area of 75 km², similar to the average home range described for adult female bears in Eurasian regions similar to the Cantabrian Mountains (i.e., 78.5 km²; extracted from Ambarlı and Bilgin, 2012; Gavrilov et al., 2015; Huber and Roth, 1993; Mertzanis et al., 2005). Finally, given reports of exceptional bear aggregations during years of widespread nut production failure (Ballesteros et al., 2018), we defined potentially vulnerable areas as pixels where < 2 nut-producing species were accessible, and we also tracked the transitions of expected species availability from the current state through three future periods (Figure 2).

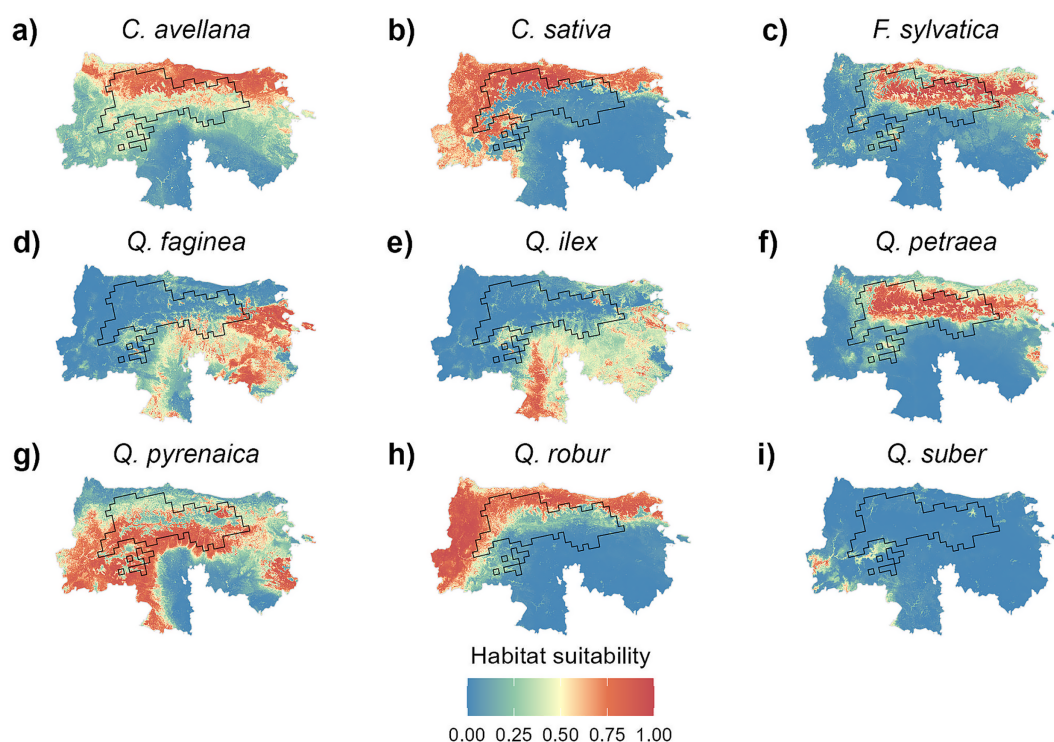


FIGURE 2

Current projections of habitat suitability for (a) *Corylus avellana*, (b) *Castanea sativa*, (c) *Fagus sylvatica*, (d) *Quercus faginea*, (e) *Quercus ilex*, (f) *Quercus petraea*, (g) *Quercus pyrenaica*, (h) *Quercus robur*, and (i) *Quercus suber*. Each panel represents the current spatial distribution of habitat suitability (values from 0 to 1). Habitat suitability is color-coded from low suitability (blue, 0) to high suitability (red, 1). The black lines represent the estimated distribution range of the Cantabrian brown bear for the 2018–2023 period in the Cantabrian Mountains (López-Bao et al., 2024).

Results

Current and future habitat suitability

The RF models performed well for all nut-producing species (validation PR-AUC values ≥ 0.90 , with the exception of PR-AUC = 0.77 for *Q. ilex*; [Supplementary Table S2](#)). At present, within the current estimated bear range for the period 2018–2023, the proportion of estimated suitable habitat was above 30% for three species: *Q. pyrenaica* (44%), *Q. petraea* (40%), and *F. sylvatica* (32%) ([Table 1](#)). By contrast, considering the predicted bear ranges proposed by [Díaz-Fernández et al. \(2023\)](#) and [Pratzer et al. \(2023\)](#), the highest figures corresponded to *Q. pyrenaica* (49 and 34%, respectively), *C. sativa* (39 and 26%, respectively), and *Q. robur* (31 and 25%, respectively) ([Table 2](#)).

Under the different climate change scenarios, predicted habitat suitability varies significantly among nut-producing species over time ([Supplementary Figures S1–S9](#) for individual spatial predictions, and [Supplementary Figures S10–S19](#) for the associated GCM uncertainty

for each species). Within the bear range, a decrease in the suitable habitat is predicted for Atlantic species, such as *C. avellana*, *F. sylvatica*, *Q. robur*, and *Q. petraea*, while suitable habitat for thermophilic species, such as *C. sativa*, *Q. ilex*, and *Q. suber*, are expected to increase ([Table 1](#)). The habitat suitability for sweet chestnut is projected to increase remarkably by 2071–2100, particularly in the western and central areas of the bear range ([Supplementary Figure S2](#)), whereas *Q. pyrenaica* is expected to maintain most of its suitable habitat and even expand slightly in the short term. Suitable habitat for the other thermophilic *Quercus* spp. is also expected to increase ([Supplementary Figures S5–S9](#)). By contrast, suitable habitat for Atlantic tree species is predicted to decrease in all scenarios, with *C. avellana* and *Q. petraea* experiencing near-complete losses. Considering the predicted bear range ([Table 2](#)), the suitable habitat for *C. sativa* would mainly occupy areas to the northwest and southwest ([Supplementary Figure S2](#)), whereas *Q. ilex* would occupy the eastern side ([Supplementary Figure S5](#)). The corresponding values for the SSP5-8.5 scenario are provided in [Supplementary Tables S3, S4](#).

TABLE 1 Habitat suitability estimates and changes over time for nine tree species under the Shared Socioeconomic Pathway SSP3-7.0 (Regional Rivalry) within the current distribution range of Cantabrian brown bears ([López-Bao et al., 2024](#)).

Specie	Current range (km ²)	Years	Stable (%)	Loss (%)	Gain (%)	Change (%)
<i>C. avellana</i>	5,205.55	2011–2040	53.14	46.85	8.13	–38.73
		2041–2070	23.73	76.27	5.30	–70.97
		2071–2100	5.17	94.83	1.81	–93.02
<i>C. sativa</i>	4,799.03	2011–2040	97.47	2.53	25.15	22.63
		2041–2070	92.26	7.74	33.72	25.97
		2071–2100	94.67	5.33	57.66	52.33
<i>F. sylvatica</i>	6,066.27	2011–2040	52.28	47.72	10.90	–36.82
		2041–2070	20.51	79.49	9.49	–70.00
		2071–2100	2.29	97.72	7.47	–90.24
<i>Q. faginea</i>	817.82	2011–2040	83.06	16.94	88.07	71.13
		2041–2070	50.70	49.30	88.42	39.12
		2071–2100	0.11	99.89	10.96	–88.92
<i>Q. ilex</i>	260.23	2011–2040	78.68	21.32	484.08	462.75
		2041–2070	57.42	42.58	646.79	604.21
		2071–2100	57.56	42.44	867.95	825.51
<i>Q. petraea</i>	7,462.25	2011–2040	65.70	34.30	5.07	–29.24
		2041–2070	36.31	63.69	5.71	–57.98
		2071–2100	9.71	90.29	2.95	–87.33
<i>Q. pyrenaica</i>	8,219.59	2011–2040	78.45	21.55	41.63	20.08
		2041–2070	53.82	46.18	52.91	6.72
		2071–2100	7.92	92.08	34.02	–58.06
<i>Q. robur</i>	4,008.02	2011–2040	76.67	23.33	10.05	–13.28
		2041–2070	61.69	38.31	5.96	–32.35
		2071–2100	46.61	53.39	4.20	–49.19
<i>Q. suber</i>	0.23	2011–2040	0.00	100.00	9,691.30	9,591.30
		2041–2070	4.35	95.65	15,269.57	15,173.91
		2071–2100	0.00	100.00	22,113.04	22,013.04

Values for stability, loss, gain and percentage change are expressed relative to the current distribution range.

TABLE 2 Habitat suitability estimates and changes over time for nine tree species under the Shared Socioeconomic Pathway SSP3-7.0 (Regional Rivalry) within the predicted distribution ranges of the Cantabrian brown bear according to Díaz-Fernández et al. (2023) and Pratzer et al. (2023).

Species	Current range (km²) (Díaz-Fernández et al., 2023)	Current range (km²) (Pratzer et al., 2023)	Period	Predicted changes based on Díaz-Fernández et al. (2023)		Predicted changes based on Pratzer et al. (2023)	
				Stable (%)	Change (%)	Stable (%)	Change (%)
<i>C. avellana</i>	1,632.49	4,430.34	2011–2040	73.56	–20.98	68.25	–23.80
			2041–2070	48.99	–46.75	40.21	–55.93
			2071–2100	11.69	–85.17	8.29	–89.29
<i>C. sativa</i>	2,545.16	10,465.24	2011–2040	96.07	10.02	80.51	–5.32
			2041–2070	81.53	2.08	57.23	–27.02
			2071–2100	86.13	17.68	56.38	–20.74
<i>F. sylvatica</i>	1,243.44	3,411.58	2011–2040	45.65	–51.06	49.29	–48.50
			2041–2070	15.80	–81.25	16.04	–82.53
			2071–2100	1.71	–95.49	1.27	–97.53
<i>Q. faginea</i>	606.89	4,462.2	2011–2040	77.89	18.45	81.24	–0.36
			2041–2070	60.43	–16.55	35.99	–52.68
			2071–2100	0.65	–98.62	0.19	–97.50
<i>Q. ilex</i>	309.9	2,401.94	2011–2040	81.00	292.37	82.94	132.20
			2041–2070	90.69	425.23	88.40	200.29
			2071–2100	89.54	430.29	77.18	189.43
<i>Q. petraea</i>	910.19	2,410.69	2011–2040	62.72	–29.38	64.37	–29.44
			2041–2070	32.40	–58.52	31.07	–60.83
			2071–2100	8.76	–80.59	6.24	–87.54
<i>Q. pyrenaica</i>	3,216.19	13,634.17	2011–2040	57.98	–22.41	56.01	–27.28
			2041–2070	24.46	–63.45	21.26	–71.73
			2071–2100	1.17	–96.08	0.95	–97.83
<i>Q. robur</i>	2,046.1	10,115.05	2011–2040	90.35	–2.95	82.26	–13.40
			2041–2070	66.89	–27.80	54.13	–42.10
			2071–2100	45.36	–51.86	34.08	–63.88
<i>Q. suber</i>	0.04	57.76	2011–2040	0.00	62,400.00	67.88	504.48
			2041–2070	25.00	28,700.00	43.59	550.68
			2071–2100	0.00	24,125.00	23.23	226.63

Values for stability and percentage change are relative to the current distribution range.

Species richness and dynamics over time

Under the SSP3-7.0 scenario, it was estimated that 35% of the current bear range would be suitable for more than 2 nut-producing species (Figure 3a; see Supplementary Figure S19 for SSP5-8.5 scenario). However, this proportion is projected to decrease over time, reaching 23% by the end of the century. The suitable habitat for *C. sativa*, and combinations with other species like *Q. pyrenaica* and *Q. robur*, is predicted to increase gradually over time. In the predicted bear ranges (Figures 3b,c), the suitable habitat for *Q. pyrenaica* fluctuate between 13 and 7% in the short term, becoming unsuitable by the end of the century. An increase in suitable habitat for *C. sativa* and Mediterranean oaks (*Q. ilex*) over time is also predicted. By the end of the century, the suitable areas for *C. sativa* and *Q. ilex* would be around 32–21% and 25–26%, respectively. Importantly, we estimated that the area unsuitable for any of these tree species is likely to increase over time, reaching 25%

within the current bear range, and 19–34% in the predicted ranges. Spatially, the highest richness of nut-producing species is concentrated along the central and northern areas of the Cantabrian Mountains, which are expected to undergo a gradual contraction over time (Figure 4; see Supplementary Figure S20 for spatial projections under SSP5-8.5 scenario).

Forecasting areas of potential food shortage for bears

Under the SSP3-7.0 scenario (Figure 5; see Supplementary Figure S12 for SSP5-8.5 scenario), more than 90% of both current and predicted bear ranges are expected to provide access to more than 2 nut-producing species to bears. This proportion is predicted to decrease over time, although it is not expected to drop below 68% within the current brown

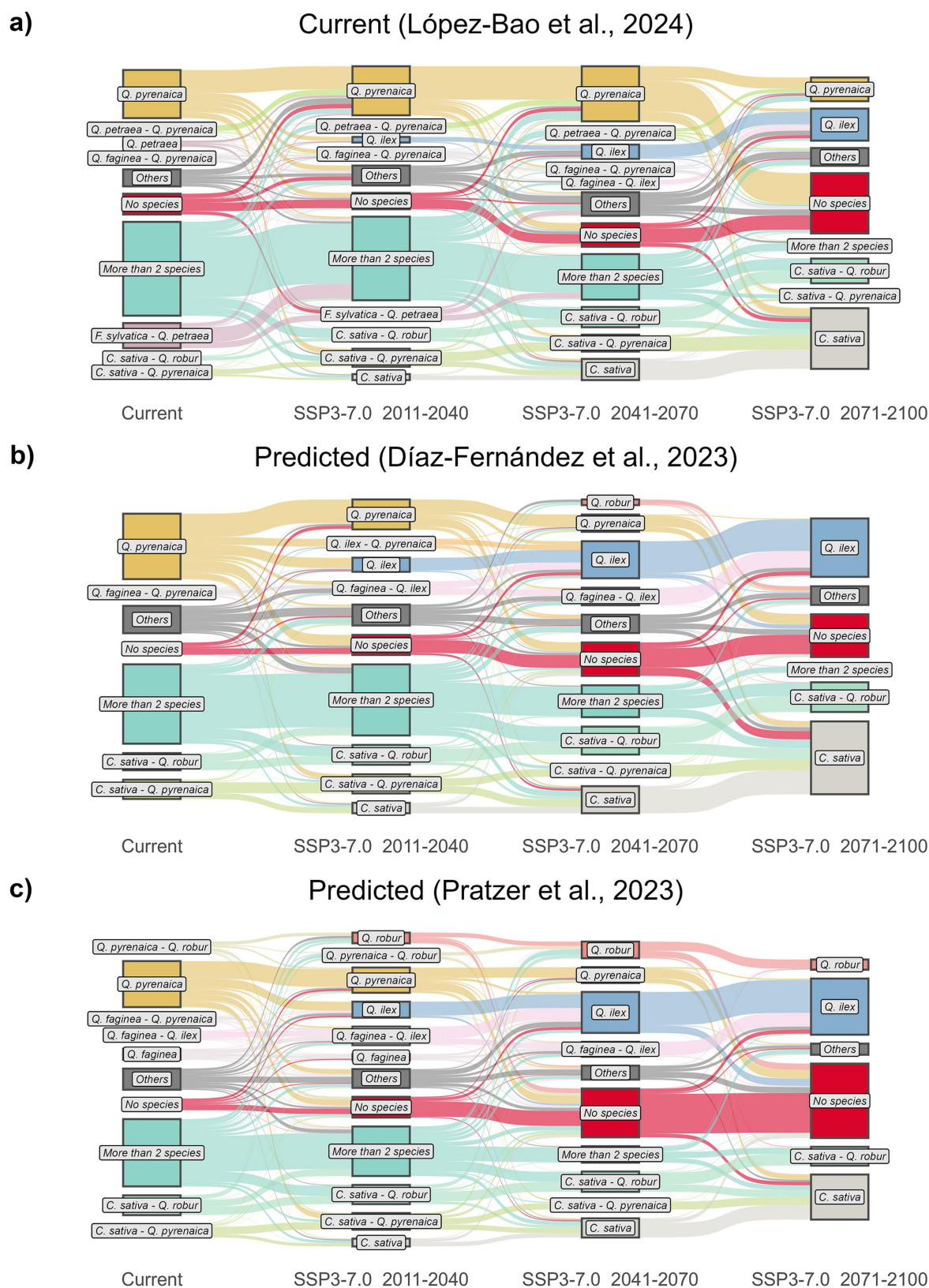


FIGURE 3

Pixel-level transitions in dominant nut-producing species compositions under the Shared Socioeconomic Pathway SSP3-7.0 (Regional Rivalry). The flow diagrams illustrate temporal changes in the dominant nut-producing tree species (or co-dominant species pairs) at the pixel level across four time periods: current conditions, and three future projections (2011–2040, 2041–2070, and 2071–2100). Transitions are shown within three different spatial frameworks based on brown bear (*Ursus arctos*) distribution ranges in the Cantabrian Mountains: **(a)** the current distribution for the 2018–2023 period (López-Bao et al., 2024), **(b)** the predicted distribution by Díaz-Fernández et al. (2023), and **(c)** the predicted distribution by Pratzer et al. (2023). Each

(Continued)

FIGURE 3 (Continued)

colored band represents the number of pixels shifting from one dominant species composition to another over time, with the width of the band proportional to the magnitude of change. Categories include individual species (e.g., *Q. pyrenaica*, *C. sativa*), dominant species pairs (e.g., *C. sativa*—*Q. pyrenaica*), “More than 2 species” (pixels with three or more co-occurring nut-producing species), and “No species” (pixels where none of the considered species are present). Rare species combinations (<2% of the total area in each time step) were grouped under “Others” for visual clarity.

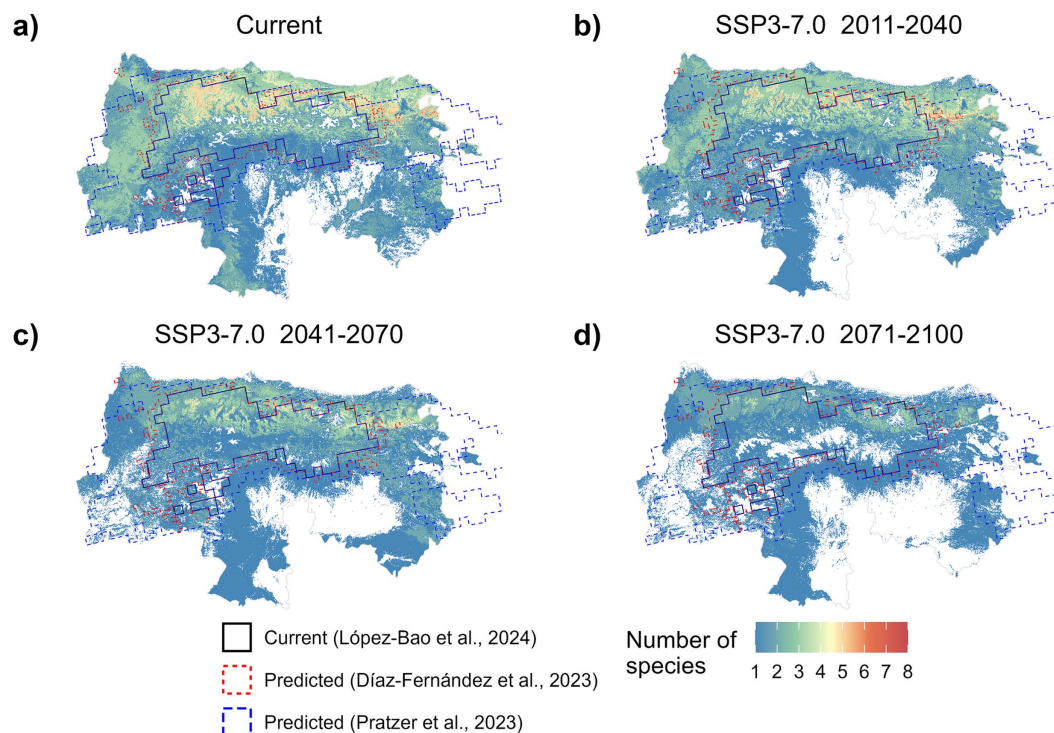


FIGURE 4

Projected changes in nut-producing tree species richness under the Shared Socioeconomic Pathway SSP3-7.0 (Regional Rivalry). Species richness is calculated as the number of nut-producing tree species (from a total of nine) present in each pixel. Richness values range from 0 (no species, shown in white) to 8 species per pixel (highest richness, shown in dark red). Projections are displayed across four timeframes: (a) current conditions, (b) 2011–2040, (c) 2041–2070, and (d) 2071–2100. The black lines represent the current (black solid line) and predicted (red and blue dashed lines) distribution of the Cantabrian brown bear (Díaz-Fernández et al., 2023; López-Bao et al., 2024; Pratzer et al., 2023).

bear range, and remains above 52 and 40% in the predicted future distributions, respectively. Bears would have increased access to species combinations dominated by *C. sativa* and *Q. pyrenaica* in the currently bear occupied area and in the predicted distribution ranges (Figures 5b,c). Toward the end of the century, access to *Quercus ilex* and to combinations involving *C. sativa* with *Q. ilex* and *Q. suber* becomes particularly notable. Only by the end of the century, some very small areas in the southern part of the bear range are expected to not have access to any species (0.2% for SSP3-7.0 scenario, <2% for SSP5-8.5 scenario). The areas most vulnerable for bears in terms of shortage of nut-producing species would be located in the southern side of the Cantabrian Mountains, which may also be the first to undergo shrinkage under expected climate change (Figure 6; see Supplementary Figure S13 for spatial projections under SSP5-8.5 scenario).

Discussion

Understanding the potential impacts of climate change on nut-producing species distributions requires acknowledging the

limitations inherent to modeling approaches used in this study. Our SDMs assume static ecological niches over time, thereby not accounting for potential adaptive responses, or ecological plasticity of tree species under changing climatic conditions. Additionally, we did not incorporate dynamic vegetation feedbacks, such as species interactions, interspecific competition, ecological succession, or natural disturbances (e.g., wildfires, pest), all of which can significantly alter community composition and influence future species assemblages (Hao et al., 2025; Harvey et al., 2023; Wisz et al., 2013). Our models also do not consider species dispersal limitations, potentially overestimating the availability of suitable habitat in regions that may not be colonized within the projected timeframe. Finally, projections are subject to uncertainties inherent in climate models (GCMs) and emission scenarios (SSPs), which, although we have attempted to minimize through median ensemble approaches, may still influence the robustness of future predictions. For these reasons, our results should be interpreted as plausible trajectories under a specific set of assumptions, rather than precise forecasts, and are best used to inform adaptive and precautionary conservation strategies under future climate uncertainty.

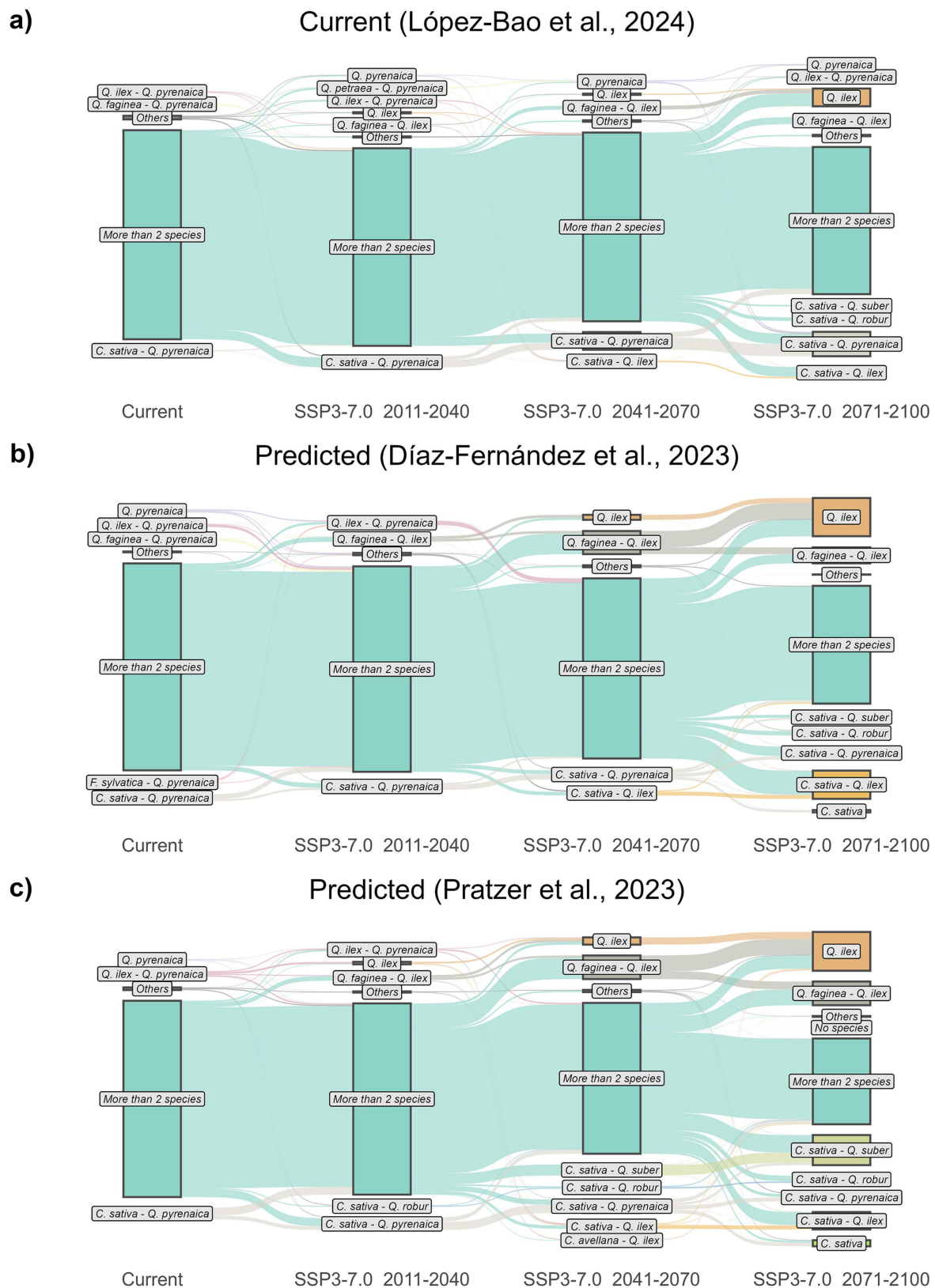


FIGURE 5

Nut-producing species availability for bears under the Shared Socioeconomic Pathway SSP3-7.0 (Regional Rivalry). This figure illustrates how the availability of nut-producing species changes over time within the distribution ranges of the brown bear (*Ursus arctos*) in the Cantabrian Mountains. Availability was assessed using a 75 km² circular moving window across four time periods: current conditions, 2011–2040, 2041–2070, and 2071–2100. Three different spatial frameworks based on brown bear distribution ranges were considered: (a) the current distribution for the 2018–2023

(Continued)

FIGURE 5 (Continued)

period (López-Bao et al., 2024), (b) the predicted distribution by Díaz-Fernández et al. (2023), and (c) the predicted distribution by Pratzer et al. (2023). Each colored flow band represents transitions in the dominant availability class for a given area: individual species (e.g., *Q. pyrenaica*, *C. sativa*), dominant species pairs (e.g., *C. sativa*—*Q. pyrenaica*), “More than 2 species” (areas with three or more co-occurring species), and “No species” (areas without any of the nine nut-producing species). Rare combinations accounting for less than 0.5% of the total area in each time step are grouped under “Others” for clarity.

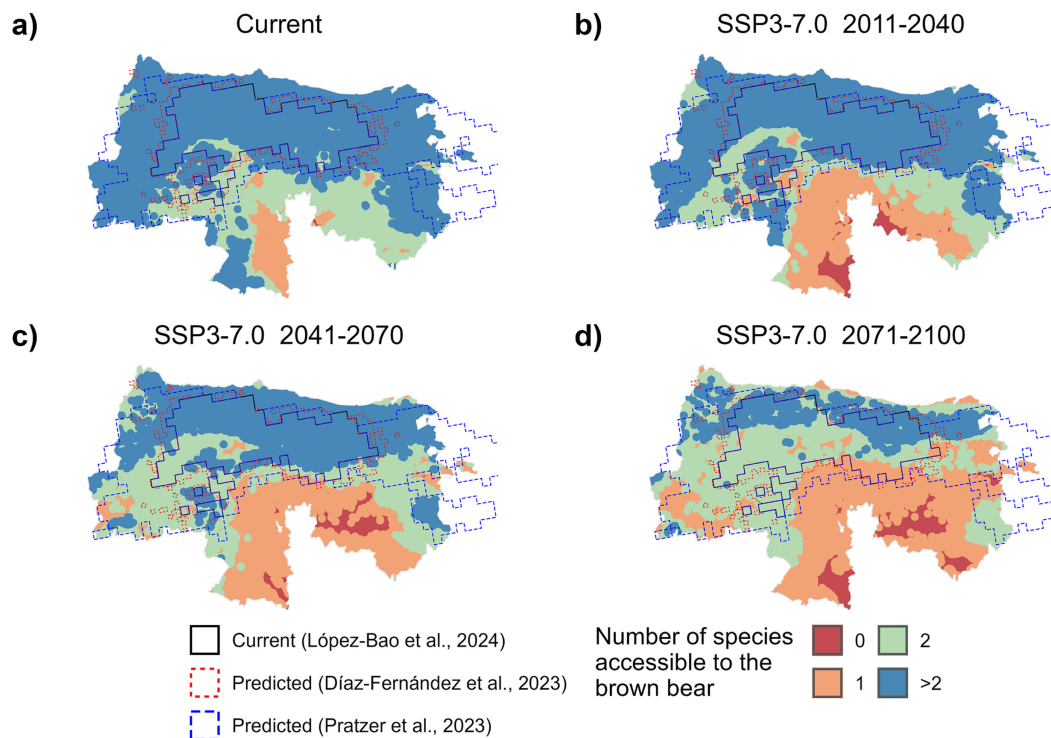


FIGURE 6

Maps of nut-producing species availability for bears under the Shared Socioeconomic Pathway SSP3-7.0 (Regional Rivalry). Availability was assessed using a 75 km² circular moving window across four time periods: (a) current conditions, (b) 2011–2040, (c) 2041–2070, and (d) 2071–2100. The black lines represent the current (black solid line) and predicted (red and blue dashed lines) distribution ranges of the Cantabrian brown bear (Díaz-Fernández et al., 2023; López-Bao et al., 2024; Pratzer et al., 2023).

The projected changes in habitat suitability for the main nut-producing species in the Cantabrian Mountains, influenced by climate change, may have implications for forest composition under different scenarios (SSP3-7.0 and SSP5-8.5) and for the availability of food for bears. Our findings, which are consistent with those of Benito Garzón et al. (2008); del Río et al. (2021); Dyderski et al. (2025, 2017) and López-Tirado et al. (2018), suggest that the Atlantic species located at the margins of their distribution, such as *F. sylvatica*, Atlantic oaks (*Q. petraea*) and *C. avellana*, are projected to experience substantial shrinkage of their area of distribution as a shift in the ecological niche shifts to higher elevations or more northerly latitudes is not feasible (Lenoir et al., 2008). As an aggravating factor, some of these species may be considered more resistant or tolerant than others to certain climate factors such as drought. For instance, *Q. petraea* would be better able to tolerate drier conditions than *F. sylvatica* (Kunz et al., 2018), possibly indicating a loss of competitiveness of the latter (Kasper et al., 2022; Rubio-Cuadrado et al., 2018). By contrast, the suitable habitat for thermophilic and Mediterranean nut-producing species, such as *C. sativa* or *Q. ilex*, is expected to undergo expansion

in the Cantabrian Mountains (Álvarez-Álvarez et al., 2025; Pérez-Girón et al., 2020). These species may be more tolerant, adaptable and competitive under changing climatic conditions. Consequently, they are likely benefit from the decline in Atlantic species (Duque-Lazo et al., 2018; Dyderski et al., 2025, 2017; Urli et al., 2015). Consequently, a gradual shift in forest composition toward thermophilic and Mediterranean species is expected, accompanied by a reduction in the richness of nut-producing species, decreasing the diversity of nut resources for bears over time, which would have only two species (or less) available across wide areas within the estimated bear range. The effects of climate change are expected to occur gradually, leading species to first reduce or cease fruiting and eventually enter a survival phase, ultimately resulting in their replacement by other species.

These changes may, to some extent, reflect the scenario that bears have historically encountered in most of peninsular Spain, where Mediterranean acorns probably constituted a primary food source (Nores and Naves, 1993; Viana et al., 2022). Indeed, holm oaks are already present in many parts of the Cantabrian Mountains, and bears already feed on their fruits in their current

range (Navarro et al., 2021). Both, Atlantic and Mediterranean oaks show a high variability in nut production both between individuals and within individuals between years, as well as synchronous nut production within species, even in mast years (Gea-Izquierdo et al., 2006; Nussbaumer et al., 2018, 2016), which could increase the risk of nutritional stress for bears relying solely on acorns in years of production failure (Ciucci et al., 2014). Such risks have been highlighted by observations of exceptional bear aggregations linked to a high level of variation in food availability, as reported by Ballesteros et al. (2018). The primary concern arising from these limitations lies in their implications for reproduction: female bears must accumulate substantial fat reserves, estimated at a minimum of 19% body fat, to support successful female bear reproduction (López-Alfaro et al., 2013; Welch et al., 1997). Additionally, although the approach of Cantabrian brown bears to humanized areas has been primarily attributed to intraspecific competition rather than a direct shortage of food (Blanco et al., 2021), it cannot be ruled out that increasing scarcity and unpredictability of food sources may intensify such competition. This, in turn, could lead to a greater reliance on anthropogenic food sources, thereby elevating the risk of human–wildlife conflict (Kurth et al., 2024).

By contrast, asynchronous nut production across different oak species increases the likelihood that at least one species is producing at any given time, helping to buffer interannual fluctuations in food availability (Gea-Izquierdo et al., 2006). This temporal complementarity, combined with the higher overall productivity typically observed in mixed-species stands (Pretzsch et al., 2013), may help moderate the nutritional concerns associated with mast failure years by smoothing fruiting variability across the landscape. In this regard, the projected stability or slight increase in the habitat suitability of *Q. pyrenaica* could favor the formation of such mixed stands. This fact not only contributes to structural forest diversity but also provides potential refuge areas for bears, especially in landscapes where acorn production from Mediterranean oaks is expected to be low and scattered (Quintano et al., 2016). Furthermore, brown bears have been shown to preferentially use large and diverse highly aggregated mixed deciduous forest stands to feed on acorns (Pérez-Girón et al., 2022), and the presence of mixed stands could therefore reduce the risk of food shortages.

Sweet chestnut emerge as an important food source for bears during the hyperphagia and winter time, when other nuts are scarce (Navarro et al., 2021; Pérez-Girón et al., 2022; Rodríguez et al., 2007). Our results suggest that the habitat suitable of sweet chestnut may increase toward areas in the northwest and southwest of the Cantabrian Mountains, coinciding with the current bear range and with a large part of the projected expansion areas. Chestnuts have the advantage of relatively consistent fruit production (Petit and Larue, 2022) compensating for variations in other nut-producing trees during the hyperphagia while possibly benefiting from climate change (Álvarez-Álvarez et al., 2025; Pérez-Girón et al., 2020). However, chestnut stands are currently strongly linked to human settlements, which influences bear foraging behavior: for instance, bears tend to spend significantly less time foraging in chestnut orchards than in other forest ecosystems, presumably due to higher human activities in chestnut stands (Pérez-Girón et al., 2022). A wider availability of chestnut trees apart from human settlements may favor the accessibility for

bears to sweet chestnuts, especially during years when other food sources, such as acorns and beech nuts, are less abundant.

From a conservation standpoint, the high mobility and the wide trophic niche of brown bears (Ambarlı, 2016; Ambarlı and Bilgin, 2012; Bojarska and Selva, 2012; Ciucci et al., 2014; De Angelis et al., 2021; Gavrilo et al., 2015; Huber and Roth, 1993; Lucas et al., 2025; Martin et al., 2012; Mertzanis et al., 2005; Naves et al., 2006; Paralikidis et al., 2010; Rodríguez et al., 2007) are expected to help bears to cope with food shortages. However, special attention should be paid to areas characterized by high species richness, as reflected in Figure 4, because they constitute biodiversity hotspots that require specific sustainable management and conservation efforts (Ramachandra et al., 2018). The establishment of chestnut trees in areas of both low and high species richness areas may enhance available nut production during hyperphagia. In addition, for Pyrenean oak trees, for which habitat suitability is projected to be stable or showing a slight increase, actions to enhance fruiting and thereby improve food availability could benefit bears. For example, silvicultural management that increases light availability by reducing stand density, which would promote fruiting and thereby improve food availability across these ecosystems (Gea-Izquierdo et al., 2006; Martiník et al., 2013).

In this context, the recovery of the Cantabrian brown bear in Spain stands as a remarkable conservation success, but it also brings new challenges for coexistence with local communities. As bear populations expand and their range increases, the likelihood of encounters with humans, livestock, and agricultural activities inevitably grows (Bombieri et al., 2019). Effective management strategies must balance the conservation of this iconic species with the needs of rural communities. Restoring and managing forests, particularly those with chestnut and other native species, as part of ecological connectivity networks (Díaz-Varela et al., In Press) and area-based conservation measures (Díaz-Varela et al., 2018) can strategically reduce human–bear conflicts. Such habitat management serves as a proactive approach, complementing financial compensation for damages and public awareness campaigns (Bautista et al., 2019). Ultimately, long-term success will depend on fostering a culture of coexistence, where both bears and people thrive in shared landscapes. Sustainable chestnut forest management and ecosystem restoration could play a pivotal role in achieving this balance. This is especially important taking into account that the conservation status of chestnut forests (Habitat 9260) in Spain is currently assessed as “Unfavourable-Inadequate” in the Atlantic region and “Unfavourable-Bad” in both the Mediterranean and Alpine regions, highlighting the urgent need for targeted restoration and sustainable management efforts (European Environment Agency, 2023).

Conclusion

Our results suggest that climate change will lead to marked shifts in the distribution of nut-producing tree species in the Cantabrian Mountains, with important ecological implications for forest composition and brown bear conservation. Specifically, thermophilic and Mediterranean species such as *C. sativa* and *Q. ilex* are projected to expand, while Atlantic species such as

F. sylvatica, *C. avellana*, and *Q. petraea* are likely to contract significantly due to their limited climatic tolerance and geographic constraints. These transitions could result in reduced nut species richness across large portions of the brown bear's current and future range, potentially increasing the risk of nutritional stress and food shortages, particularly during years of mast failure.

Despite these risks, our projections also highlight opportunities for proactive management. For instance, promoting sweet chestnut plantations in areas of both low and high species richness, particularly on mid-elevation slopes with minimal human disturbance in the western regions, could enhance the availability of reliable nut resources during hyperphagia. Within ecological corridors and connectivity networks where chestnut populations are present, prioritizing the conservation, restoration, and promotion of chestnut forest is essential. Moreover, in regions where *Q. pyrenaica* is projected to persist or expand, implementing targeted silvicultural interventions, such as thinning to increase light availability, may boost acorn production. This would not only improve seasonal food supply but also help maintain structurally diverse forest habitats preferred by bears. Therefore, collectively, these measures have the potential to enhance food availability, mitigate human-bear conflicts, and contribute to reversing the unfavorable conservation status of *Castanea* habitats throughout Spain.

Finally, it is important to acknowledge that our predictions carry inherent uncertainty due to modeling assumptions and climate change projections. Therefore, they should be interpreted as plausible trajectories rather than deterministic forecasts. Further research aimed at refining species distribution models, incorporating potential adaptive responses, integrating dynamic vegetation feedbacks, and synchronizing bear presence with the phenology of nut-producing species, will be essential to improve the predictive capacity and ecological relevance of future scenarios.

Data availability statement

The original contributions presented in the study are included in the article/[Supplementary material](#), further inquiries can be directed to the corresponding author.

Author contributions

JP-G: Conceptualization, Data curation, Methodology, Writing – review & editing, Writing – original draft, Formal analysis. JL-B: Methodology, Project administration, Writing – review & editing, Conceptualization, Funding acquisition. ED-V: Methodology, Writing – review & editing. PÁ-Á: Formal analysis, Writing – original draft, Project administration, Data curation, Methodology, Funding acquisition, Writing – review & editing, Conceptualization.

References

- Álvarez-Álvarez, P., Aviñoa-Arias, A., Díaz-Varela, E., López-Bao, J. V., and Pérez-Girón, J. C. (2025). Impact of climate change over distribution and potential range of chestnut in the Iberian Peninsula. *Front. For. Glob. Change* 8:1561027. doi: 10.3389/ffgc.2025.1561027
- Ambarlı, H. (2016). Litter size and basic diet of brown bears (*Ursus arctos*, Carnivora) in northeastern Turkey. *Mammalia* 80, 235–240. doi: 10.1515/mammalia-2014-0111
- Ambarlı, H., and Bilgin, C. (2012). Spatio-temporal ecology of brown bears in northeastern Turkey: evaluation of HR sizes and movement rate by sex, in: 21st international conference on bear research and management, New Delhi, India.
- Ballesteros, E., López-Bao, J. V., Blanco, J. C., Palomero, G., and Planella, A. (2018). Exceptional aggregation of Cantabrian brown bears during hyperphagia, in: Abstract-

Funding

The author(s) declare that financial support was received for the research and/or publication of this article. This study was conducted within the framework of the LIFE19 NAT/ES/000913 “Bears with Future” project, funded by the European Union, and coordinated by the Brown Bear Foundation. This research received additional financial support from the Spanish Ministry for the Ecological Transition and the Demographic Challenge of the Government of Spain. JL-B was supported by the Spanish Ministry of Science and Innovation (PID2023-149634OB-I00).

Acknowledgments

We sincerely thank the Instituto da Conservação da Natureza e das Florestas (ICNF) in Portugal for their generous provision and authorization to use the data from the 6th National Forest Inventory (IFN) for our research project.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of *Frontiers*, at the time of submission. This had no impact on the peer review process and the final decision.

Generative AI statement

The authors declare that no Gen AI was used in the creation of this manuscript.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/ffgc.2025.1624612/full#supplementary-material>

book of the 26th international conference on bear research and management. Ljubljana, Slovenia, p. 108.

Bautista, C., Revilla, E., Naves, J., Albrecht, J., Fernández, N., Olszańska, A., et al. (2019). Large carnivore damage in Europe: analysis of compensation and prevention programs. *Biol. Conserv.* 235, 308–316. doi: 10.1016/j.biocon.2019.04.019

Benito Garzón, M., Sánchez de Dios, R., and Sainz Ollero, H. (2008). Effects of climate change on the distribution of Iberian tree species. *Appl. Veg. Sci.* 11, 169–178. doi: 10.3170/2008-7-18348

Blanco, J., Palomero, G., Ballesteros, F., and López-Bao, J. V. (2021). “Habituation, food-conditioning and attacks on humans” in Cantabrian bears. Demography, coexistence and conservation challenges. (Barcelona: Brown Bear Foundation. Lynx Edicions), 65–90. Available online at: <https://www.lynxeds.com/>

Bojarska, K., and Selva, N. (2012). Spatial patterns in brown bear *Ursus arctos* diet: the role of geographical and environmental factors. *Mammal Rev.* 42, 120–143. doi: 10.1111/j.1365-2907.2011.00192.x

Bombieri, G., Naves, J., Penteriani, V., Selva, N., Fernández-Gil, A., López-Bao, J. V., et al. (2019). Brown bear attacks on humans: a worldwide perspective. *Sci. Rep.* 9:8573. doi: 10.1038/s41598-019-44341-w

Booth, T. H. (2022). Checking bioclimatic variables that combine temperature and precipitation data before their use in species distribution models. *Austral Ecol.* 47, 1506–1514. doi: 10.1111/aec.13234

Carlisle, J., and Albeke, S. (2016). ecoinfo: Assorted tools for the management and analysis of ecological information. R package version 0.9.3

Ciucci, P., Tosoni, E., Di Domenico, G., Quattrocchi, F., and Boitani, L. (2014). Seasonal and annual variation in the food habits of Apennine brown bears, Central Italy. *J. Mammal.* 95, 572–586. doi: 10.1644/13-MAMM-A-218

Clevenger, A. P., Purroy, F. J., and Pelton, M. R. (1992). Food habits of brown bears (*Ursus arctos*) in the Cantabrian Mountains, Spain. *J. Mammal.* 73, 415–421. doi: 10.2307/1382077

Cobos, M. E., Owens, H. L., Soberón, J., and Peterson, A. T. (2025). mop: Mobility oriented-parity metric.

Costello, C. M., Jones, D. E., Inman, R. M., Inman, K. H., Thompson, B. C., and Quigley, H. B. (2003). Relationship of variable mast production to American black bear reproductive parameters in New Mexico. *Ursus* 14, 1–16.

De Angelis, D., Kusak, J., Huber, D., Reljić, S., Gužvica, G., and Ciucci, P. (2021). Environmental and anthropogenic correlates of seasonal migrations in the Dinaric-Pindos brown bear population. *J. Zool.* 314, 58–71. doi: 10.1111/jzo.12864

del Río, S., Canas, R., Cano, E., Cano-Ortiz, A., Musarella, C., Pinto-Gomes, C., et al. (2021). Modelling the impacts of climate change on habitat suitability and vulnerability in deciduous forests in Spain. *Ecol. Indic.* 131:108202. doi: 10.1016/j.ecolind.2021.108202

Di Domenico, G., Tosoni, E., Boitani, L., and Ciucci, P. (2012). Efficiency of scat-analysis lab procedures for bear dietary studies: the case of the Apennine brown bear. *Mamm. Biol.* 77, 190–195. doi: 10.1016/j.mambio.2012.01.002

Díaz-Fernández, M., Naves, J., and Revilla, E. (2023). Conservation implications of range dynamics in endangered populations: an example with brown bears. *Conserv. Sci. Pract.* 5:e12894. doi: 10.1111/csp2.12894

Díaz-Varela, E. R., Álvarez-Álvarez, P., Pérez-Girón, J. C., López-Bao, J. V., Ballesteros, F., Gómez, M., et al. (In Press). “Management in SEPLs to ensure high-quality connectivity for brown bear in the western Cantabrian Mountains (northwestern Spain)” in Satoyama initiative thematic review. eds. Unu-Ias and Iges, Ensuring ecological connectivity in socio-ecological production landscapes and seascapes (SEPLS), vol. 10 (Singapore: Springer Nature). Available online at: <https://link.springer.com/book/9789819514731>

Díaz-Varela, E., Álvarez-Álvarez, P., Rocas-Díaz, J. V., and Rodríguez-Morales, B. (2018). “The contribution of chestnut orchard recovery projects for effective area-based conservation: two cases in Asturias (North-West Spain)” in Sustainable use of biodiversity in socio-ecological production landscapes and seascapes (SEPLS) and its contribution to effective area-based conservation. (Tokyo: United Nations University), 26–37.

Duque-Lazo, J., Navarro-Cerrillo, R. M., and Ruiz-Gómez, F. J. (2018). Assessment of the future stability of cork oak (*Quercus suber* L.) afforestation under climate change scenarios in Southwest Spain. *For. Ecol. Manag.* 409, 444–456. doi: 10.1016/j.foreco.2017.11.042

Dyderski, M. K., Paž, S., Frelich, L. E., and Jagodziński, A. M. (2017). How much does climate change threaten European forest tree species distributions? *Glob. Change Biol.* 24, 1150–1163. doi: 10.1111/gcb.13925

Dyderski, M. K., Paž-Dyderska, S., Jagodziński, A. M., and Puchalka, R. (2025). Shifts in native tree species distributions in Europe under climate change. *J. Environ. Manag.* 373:123504. doi: 10.1016/j.jenvman.2024.123504

European Environment Agency. (2023). Conservation status and trends of habitats and species [WWW Document]. Available online at: <https://www.eea.europa.eu/en/analysis/maps-and-charts/conservation-status-and-trends-article-17-national-summary-dashboards-archived> (Accessed June 13, 2025).

Gavrilov, G., Zlatanova, D., Racheva, V., Valchev, K., and Dutsov, A. (2015). Home range and habitat use of brown bear in Bulgaria: the first data based on GPS-telemetry. *Acta Zool. Bulg.* 67, 493–499.

GBIF (2024). Occurrence download. doi: 10.15468/DL.9ZHUR7

Gea-Izquierdo, G., Cañellas, I., and Montero, G. (2006). Acorn production in Spanish holm oak woodlands. *For. Syst.* 15, 339–354. doi: 10.5424/srf/2006153-00976

Hacket-Pain, A., and Bogdziewicz, M. (2021). Climate change and plant reproduction: trends and drivers of mast seeding change. *Philos. Trans. Roy. Soc. B Biol. Sci.* 376:20200379. doi: 10.1098/rstb.2020.0379

Hao, X., Holyoak, M., Zhang, Z., and Yan, C. (2025). Global projection of terrestrial vertebrate food webs under future climate and land-use changes. *Glob. Change Biol.* 31:e70061. doi: 10.1111/gcb.70061

Harvey, J. A., Tougeron, K., Gols, R., Heinen, R., Abarca, M., Abram, P. K., et al. (2023). Scientists’ warning on climate change and insects. *Ecol. Monogr.* 93:e1553. doi: 10.1002/ecm.1553

Hausfather, Z., and Peters, G. P. (2020). Emissions – the ‘business as usual’ story is misleading. *Nature* 577, 618–620. doi: 10.1038/d41586-020-00177-3

Hernangómez, D. (2023). Using the tidyverse with terra objects: the tidyterra package. *J. Open Source Softw.* 8:5751. doi: 10.21105/joss.05751

Hijmans, R. J., Bivand, R., Forner, K., Ooms, J., Pebesma, E., and Sumner, M. D. (2022). Package ‘terra’.

Huber, D., and Roth, H. U. (1993). Movements of European brown bears in Croatia. *Acta Theriol.* 38, 151–159. doi: 10.4098/ATArch.93-13

ICNF (2015). 6–6° Inventário Florestal Nacional. Portugal: ICNF-Instituto da Conservação da Natureza e das Florestas.

Journé, V., Caignard, T., Hacket-Pain, A., and Bogdziewicz, M. (2021). Leaf phenology correlates with fruit production in European beech (*Fagus sylvatica*) and in temperate oaks (*Quercus robur* and *Quercus petraea*). *Eur. J. For. Res.* 140, 733–744. doi: 10.1007/s10342-021-01363-2

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., et al. (2017). Climatologies at high resolution for the earth’s land surface areas. *Sci Data* 4:170122. doi: 10.1038/sdata.2017.122

Kasper, J., Leuschner, C., Walentowski, H., Petritan, A. M., and Weigel, R. (2022). Winners and losers of climate warming: declining growth in *Fagus* and *Tilia* vs. stable growth in three *Quercus* species in the natural beech-oak forest ecotone (western Romania). *For. Ecol. Manag.* 506:119892. doi: 10.1016/j.foreco.2021.119892

Kunz, J., Löffler, G., and Bauhus, J. (2018). Minor European broadleaved tree species are more drought-tolerant than *Fagus sylvatica* but not more tolerant than *Quercus petraea*. *For. Ecol. Manag.* 414, 15–27. doi: 10.1016/j.foreco.2018.02.016

Kurth, K. A., Malpeli, K. C., Clark, J. D., Johnson, H. E., and van Manen, F. T. (2024). A systematic review of the effects of climate variability and change on black and brown bear ecology and interactions with humans. *Biol. Conserv.* 291:110500. doi: 10.1016/j.biocon.2024.110500

Lange, S. (2021). ISIMIP3b bias adjustment fact sheet. Potsdam: Inter-Sectoral Impact Model Intercomparison Project.

Lenoir, J., Gégout, J. C., Marquet, P. A., de Ruffray, P., and Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320, 1768–1771. doi: 10.1126/science.1156831

Liu, C., Newell, G., and White, M. (2016). On the selection of thresholds for predicting species occurrence with presence-only data. *Ecol. Evol.* 6, 337–348. doi: 10.1002/ece3.1878

Liu, X.-Y., Wu, J., and Zhou, Z.-H. (2009). Exploratory undersampling for class-imbalance learning. *IEEE Trans. Syst. Man Cybern. B Cybern.* 39, 539–550. doi: 10.1109/TSMCB.2008.2007853

López-Alfaro, C., Robbins, C. T., Zedrosser, A., and Nielsen, S. E. (2013). Energetics of hibernation and reproductive trade-offs in brown bears. *Ecol. Model.* 270, 1–10. doi: 10.1016/j.ecolmodel.2013.09.002

López-Bao, J. V., Banco, J. C., and Palomero, G. (2024). Actualización del área de distribución del oso pardo en la Cordillera Cantábrica (in Spanish). España: Fundación Oso Pardo.

López-Tirado, J., Vessella, F., Schirone, B., and Hidalgo, P. J. (2018). Trends in evergreen oak suitability from assembled species distribution models: assessing climate change in South-Western Europe. *New For.* 49, 471–487. doi: 10.1007/s11056-018-9629-5

Lucas, P. M., Thuiller, W., Talluto, L., Polaina, E., Albrecht, J., Selva, N., et al. (2025). Trophic interactions are key to understanding the effects of global change on the distribution and functional role of the Brown bear. *Glob. Change Biol.* 31:e70252. doi: 10.1111/gcb.70252

Martin, J., van Moorter, B., Revilla, E., Blanchard, P., Dray, S., Quenette, P.-Y., et al. (2012). Reciprocal modulation of internal and external factors determines individual movements. *J. Anim. Ecol.* 82, 290–300. doi: 10.1111/j.1365-2656.2012.02038.x

Martiník, A., Dobrovolný, L., and Palátová, E. (2013). Tree growing space and acorn production of *Quercus robur*. *Dendrobiology* 71, 101–108. doi: 10.12657/denbio.071.010

Mateo-Tomás, P., Rodríguez-Pérez, J., Fernández-García, M., Bravo, E., García, E., Rivas, O., et al. (2024). Study of monitored specimens of griffon vultures and brown bears and their effectiveness in the Sentinel Network against poaching. Principality of Asturias Unpublished report. 25 p.

- Mertzanis, Y., Ioannis, I., Mavridis, A., Nikolaou, O., Riegler, S., Riegler, A., et al. (2005). Movements, activity patterns and home range of a female brown bear (*Ursus arctos*, L.) in the Rodopi Mountain range, Greece. *Belg. J. Zool.* 135:217.
- MITECO. (2022). Cuarto Inventario Forestal Nacional [WWW Document]. Available online at: https://www.miteco.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-forestal-nacional/cuarto_inventario.aspx (Accessed November 17, 2022).
- Navarro, A., García-Codrón, J., Álvarez Álvarez, P., Ballesteros, F., and López-Bao, J. (2021). "Climate change and brown bear conservation" in Cantabrian bears. demography, coexistence and conservation challenges. (Barcelona: Brown Bear Foundation. Lynx Edicions), 125–155. Available online at: <https://www.lynxeds.com/>
- Naves, J., Fernández-Gil, A., Rodríguez, C., and Delibes, M. (2006). Brown bear food habits at the border of its range: a long-term study. *J. Mammal.* 87, 899–908. doi: 10.1644/05-mamm-a-318r2.1
- Nores, C., and Naves, J. (1993). Distribución histórica del oso pardo en la Península Ibérica. *El oso pardo*, 13–33.
- Nussbaumer, A., Waldner, P., Apuhtin, V., Aytar, F., Benham, S., Bussotti, F., et al. (2018). Impact of climate change on wild cherry distribution and associated consequences on brown species in Europe. *For. Ecol. Manag.* 429, 336–350. doi: 10.1016/j.foreco.2018.07.011
- Nussbaumer, A., Waldner, P., Etzold, S., Gessler, A., Benham, S., Thomsen, I. M., et al. (2016). Patterns of mast fruiting of common beech, sessile and common oak, Norway spruce and scots pine in central and northern Europe. *For. Ecol. Manag.* 363, 237–251. doi: 10.1016/j.foreco.2015.12.033
- Owens, H. L., Campbell, L. P., Dornak, L. L., Saupe, E. E., Barve, N., Soberón, J., et al. (2013). Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. *Ecol. Model.* 263, 10–18. doi: 10.1016/j.ecolmodel.2013.04.011
- Paralikiadis, N. P., Papageorgiou, N. K., Kontsiotis, V. J., and Tsiompanoudis, A. C. (2010). The dietary habits of the Brown bear (*Ursus arctos*) in western Greece. *Mamm. Biol.* 75, 29–35. doi: 10.1016/j.mambio.2009.03.010
- Pérez-Girón, J. C., Álvarez-Álvarez, P., Ballesteros, F., and López-Bao, J. V. (2024). Potential impacts of climate change on wild cherry distribution and associated consequences on brown bears. *Biol. Conserv.* 289:110390. doi: 10.1016/j.biocon.2023.110390
- Pérez-Girón, J. C., Álvarez-Álvarez, P., Díaz-Varela, E. R., and Mendes Lopes, D. M. (2020). Influence of climate variations on primary production indicators and on the resilience of forest ecosystems in a future scenario of climate change: application to sweet chestnut agroforestry systems in the Iberian Peninsula. *Ecol. Indic.* 113:106199. doi: 10.1016/j.ecolind.2020.106199
- Pérez-Girón, J. C., Díaz-Varela, E. R., Álvarez-Álvarez, P., Hernández Palacios, O., Ballesteros, F., and López-Bao, J. V. (2022). Linking landscape structure and vegetation productivity with nut consumption by the Cantabrian brown bear during hyperphagia. *Sci. Total Environ.* 813:152610. doi: 10.1016/j.scitotenv.2021.152610
- Petit, R. J., and Larue, C. (2022). Confirmation that chestnuts are insect-pollinated. *Bot. Lett.* 169, 370–374. doi: 10.1080/23818107.2022.2088612
- Piao, S., Liu, Q., Chen, A., Janssens, I. A., Fu, Y., Dai, J., et al. (2019). Plant phenology and global climate change: current progresses and challenges. *Glob. Chang. Biol.* 25, 1922–1940. doi: 10.1111/gcb.14619
- Pigeon, K. E., Stenhouse, G., and Côté, S. D. (2016). Drivers of hibernation: linking food and weather to denning behaviour of grizzly bears. *Behav. Ecol. Sociobiol.* 70, 1745–1754. doi: 10.1007/s00265-016-2180-5
- Planella, A., Jiménez, J., Palomero, G., Ballesteros, F., Blanco, J. C., and López-Bao, J. V. (2019). Integrating critical periods for bear cub survival into temporal regulations of human activities. *Biol. Conserv.* 236, 489–495. doi: 10.1016/j.biocon.2019.05.051
- Poggio, L., de Sousa, L. M., Batjes, N. H., Heuvelink, G. B. M., Kempen, B., Ribeiro, E., et al. (2021). SoilGrids 2.0: producing soil information for the globe with quantified spatial uncertainty. *Soil* 7, 217–240. doi: 10.5194/soil-7-217-2021
- Pratzer, M., Nill, L., Kuemmerle, T., Zurell, D., and Fandos, G. (2023). Large carnivore range expansion in Iberia in relation to different scenarios of permeability of human-dominated landscapes. *Divers. Distrib.* 29, 75–88. doi: 10.1111/ddi.13645
- Pretzsch, H., Bielak, K., Block, J., Bruchwald, A., Dieler, J., Ehrhart, H.-P., et al. (2013). Productivity of mixed versus pure stands of oak (*Quercus petraea* (Matt.) Liebl. And *Quercus robur* L.) and European beech (*Fagus sylvatica* L.) along an ecological gradient. *Eur J Forest Res* 132, 263–280. doi: 10.1007/s10342-012-0673-y
- Quintano, P., Caudullo, G., and de Rigo, D. (2016). Quercus pyrenaica in Europe: distribution, habitat, usage and threats. In European Atlas of Forest Tree Species. eds. J. San-Miguel-Ayaz, D. de Rigo, G. Caudullo, T. Houston Durrant and A. Mauri. EU, Luxembourg, pp. e01f807+.
- Ramachandra, T. V., Setturu, B., Vinay, S., Tara, N. M., Subashchandran, M. D., and Joshi, N. V. (2018). "Conservation and sustainable management of local hotspots of biodiversity" in Geospatial infrastructure, applications and technologies: India case studies. eds. N. L. Sarda, P. S. Acharya and S. Sen (Singapore: Springer), 365–383.
- Rodríguez, C., Naves, J., Fernández-Gil, A., Obeso, J. R., and Delibes, M. (2007). Long-term trends in food habits of a relict brown bear population in northern Spain: the influence of climate and local factors. *Environ. Conserv.* 34, 36–44. doi: 10.1017/S0376892906003535
- Rubio-Cuadrado, Á., Camarero, J. J., del Río, M., Sánchez-González, M., Ruiz-Peinado, R., Bravo-Oviedo, A., et al. (2018). Drought modifies tree competitiveness in an oak-beech temperate forest. *For. Ecol. Manag.* 429, 7–17. doi: 10.1016/j.foreco.2018.06.035
- Ryan, C. W., Pack, J. C., Igo, W. K., and Billings, A. (2007). Influence of mast production on black bear non-hunting mortalities in West Virginia. *Ursus* 18, 46–53. doi: 10.2192/1537-6176(2007)18[46:IOMPOB]2.0.CO;2
- Sánchez De Dios, R., Benito-Garzón, M., and Sainz-Ollero, H. (2006). Hybrid zones between two European oaks: a plant community approach. *Plant Ecol.* 187, 109–125. doi: 10.1007/s11258-006-9136-1
- Schwartz, C. C., Haroldson, M. A., White, G. C., Harris, R. B., Cherry, S., Keating, K. A., et al. (2006). Temporal, spatial, and environmental influences on the demographics of grizzly bears in the greater Yellowstone ecosystem. *Wildl. Monogr.* 161, 1–8. doi: 10.2193/0084-0173(2006)161[1:TSAEIO]2.0.CO;2
- Sillero, N., Arenas-Castro, S., Enriquez-Urzelai, U., Vale, C. G., Sousa-Guedes, D., Martínez-Freiria, F., et al. (2021). Want to model a species niche? A step-by-step guideline on correlative ecological niche modelling. *Ecol. Model.* 456:109671. doi: 10.1016/j.ecolmodel.2021.109671
- Sjöberg, D. (2024). ggsankey: Sankey, Alluvial and Sankey bump plots.
- Swenson, J. E., Ciucci, P., Huber, D., Penteriani, V., and Zedrosser, A. (2023). "Brown bear *Ursus arctos* Linnaeus, 1758" in Handbook of the mammals of Europe. (Cham: Springer International Publishing), 1–36.
- Urlí, M., Lamy, J. B., Sin, F., Burlett, R., Delzon, S., and Porté, A. J. (2015). The high vulnerability of *Quercus robur* to drought at its southern margin paves the way for *Quercus ilex*. *Plant Ecol.* 216, 177–187. doi: 10.1007/s11258-014-0426-8
- Valavi, R., Guillera-Arroita, G., Lahoz-Monfort, J. J., and Elith, J. (2022). Predictive performance of presence-only species distribution models: a benchmark study with reproducible code. *Ecol. Monogr.* 92:e01486. doi: 10.1002/ecm.1486
- Viana, D. S., Blanco-Garrido, F., Delibes, M., and Clavero, M. (2022). A 16th-century biodiversity and crop inventory. *Ecology* 103:e3783. doi: 10.1002/ecy.3783
- Vitasse, Y., François, C., Delpierre, N., Dufrêne, E., Kremer, A., Chuine, I., et al. (2011). Assessing the effects of climate change on the phenology of European temperate trees. *Agric. For. Meteorol.* 151, 969–980. doi: 10.1016/j.agrformet.2011.03.003
- Welch, C. A., Keay, J., Kendall, K. C., and Robbins, C. T. (1997). Constraints on frugivory by bears. *Ecology* 78, 1105–1119. doi: 10.1890/0012-9658(1997)078[1105:COFBB]2.0.CO;2
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., et al. (2019). Welcome to the tidyverse. *J. Open Source Softw.* 4:1686. doi: 10.21105/joss.01686
- Wis, M. S., Pottier, J., Kissling, W. D., Pellissier, L., Lenoir, J., Damgaard, C. F., et al. (2013). The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biol. Rev.* 88, 15–30. doi: 10.1111/j.1469-185X.2012.00235.x
- Xunta de Galicia. (2022). Inventario Forestal Continuo de Galicia [WWW Document]. Available online at: <https://invega.xunta.local/invega/> (Accessed November 17, 2022).