Research Paper

Linking landscape structure and vegetation productivity with nut consumption by the Cantabrian brown bear during hyperphagia

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HIGHLIGHTS

- The Cantabrian brown bear mainly consumes nuts during the hyperphagia period
- A predictive model based on landscape pattern, relief and productivity was developed
- Model predictions for acorn consumption highlight areas of great importance
- Bears prefer to feed on acorns in relatively large, highly aggregated forest stands
- The findings are important for brown bear management and conservation programmes

GRAPHICAL ABSTRACT
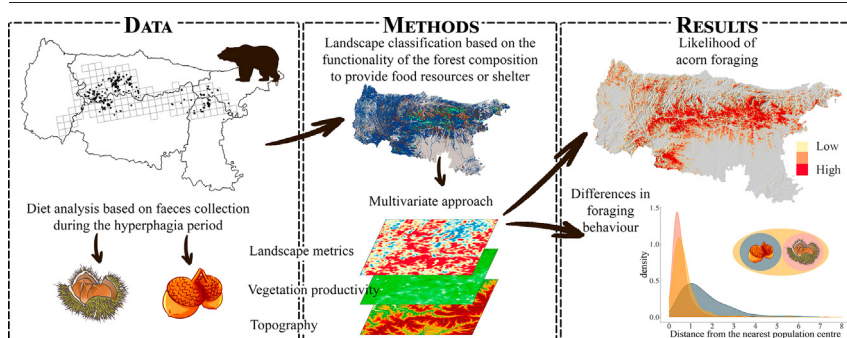
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ABSTRACT

In bears, reproduction is dependent on the body reserves accumulated during hyperphagia. The Cantabrian brown bear mainly feeds on nuts during the hyperphagia period. Understanding how landscape heterogeneity and vegetation productivity in human-dominated landscapes influence the feeding habits of bears may therefore be important for disentangling species-habitat relationships of conservation interest. We determined the spatial patterns of nut consumption by brown bears during the hyperphagia period in relation to landscape structure, characteristics of fruit-producing patches and vegetation productivity. For this purpose, we constructed foraging models based on nut consumption data (obtained by scat analysis), by combining vegetation productivity data, topographical variables and landscape metrics to identify nut foraging patterns during this critical period for bears. The average wooded area of patches where scats were collected and where the nuts that the bears had consumed were produced was larger than that of the corresponding patches where nuts were not produced. For scats collected outside of nut-producing patches, the distance between the scats and the patches was greatest for chestnut-producing patches. Elevation, Gross Primary Production (GPP) and the Aggregation Index (AI) were good predictors of acorn consumption in the models. Good model fits were not obtained for data on chestnut consumption in bears. The findings confirm that brown bears feeding on nuts show a preference for relatively large, highly aggregated patches with a high degree of diversity in the landscape pattern, which may help the bears to remain undetected. The nut prediction model highlights areas of particular importance for brown bears during hyperphagia. The human presence associated with sweet chestnut forest stands or orchards may make bears feel more vulnerable when feeding.

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1. Introduction

Landscape heterogeneity influences multiple processes, such as ecosystem functioning, population persistence and animal movements (Fahrig et al., 2011; Fahrig and Nuttle, 2005; Johnson et al., 1992; Matthiopoulos et al., 2020). Habitat conditions and resource supply are unevenly distributed across the landscape, affecting the spatial ecology of animal species (Avgar et al., 2013; Doherty and Driscoll, 2018; Nathan et al., 2008; Roshier et al., 2008; With, 2019) and conditioning choices such as those made by frugivorous species about what to eat and where to move (Fryxell et al., 2008). At the landscape scale, animal distributions are affected by two components of landscape heterogeneity (Fahrig et al., 2011; Fahrig and Nuttle, 2005): composition, i.e. the number of land cover types and their relative importance (Fahrig, 2003; Walz, 2011), and configuration, i.e. the spatial organization of the landscape elements (Bevanda et al., 2015; Villard and Metzger, 2014). Both components determine the availability of resources for animal species, which can therefore be affected in space and time by the level of productivity of the resources. The resource productivity thus constitutes an important factor for species distributions in critical seasons, such as periods of high nutritional requirements.

The importance of each component is highly dependent on the specific response of the species and the fragmentation threshold of the habitat (Bascompte and Sole, 1996; Pardini et al., 2010; Ritchie et al., 2009; Smith et al., 2011; Wiegand et al., 2005). The spatial heterogeneity of a landscape is sensitive to scale (Díaz-Varela et al., 2016; Díaz-Varela et al., 2009; Turner et al., 1989; Wu, 2004), thus affecting species-habitat relationships (Gastón et al., 2017; Mateo-Sánchez et al., 2014; Wheatley and Larsen, 2018), which on the other hand may reflect seasonal differences in resource availability and use (McLoughlin et al., 2010).

For long-lived species with low reproductive rates, such as the brown bear (*Ursus arctos* L.), reproduction is determined by nutritional status (Hertel et al., 2018; López-Alfaro et al., 2013). Brown bears accumulate fat reserves during hyperphagia (Di Domenico et al., 2012), before the hibernation period, when reproductive females give birth in dens. It has been estimated that at least 19% of body fat reserves are required to support female bear reproduction (López-Alfaro et al., 2013). The diet of the European brown bear is composed of a variety of types of food (Bojarska and Selva, 2012; Naves et al., 2006). However, during hyperphagia, the Cantabrian brown bear population, fragmented into eastern and western subpopulations (Gonzalez et al., 2016; Pérez et al., 2014) and located at the southwestern limit of its distribution, mainly consumes nuts produced by trees such as *Quercus* sp. and *Fagus sylvatica* L. (Bojarska and Selva, 2012; Naves et al., 2006). Long-term climate related changes in the availability of some other resources, such as the decrease in the availability of *Vaccinium* fruits, are already increasing the contribution of nuts to the bear diet (Rodríguez et al., 2007).

Bears are particularly sensitive to food availability during hyperphagia due to the high energy requirements associated with reproduction (Welch et al., 1997). Nut-producing species show high interannual variability in nut production: fruiting may fail in some years, while it will be normal in other years, and bumper crops will occur in other years, referred to as mast years (Pemán et al., 2013). Clevenger et al. (1992) observed fruiting failure in *Quercus* sp. and *F. sylvatica* in the Cantabrian Mountains for up to 4 consecutive years, in some cases coinciding in both species. Further studies claim that some tree species located at the limits of their distribution, such as beech (*F. sylvatica*) and Atlantic oaks (*Q. petraea* (Matt.) Liebl. and *Q. robur* L.), may suffer a drastic reduction in the Cantabrian Mountains in the context of climate change (Dyderski et al., 2017), thus further intensifying the changes in the bear diet (Navarro et al., 2021). Climate change is known to affect primary productivity, one of the most important ecosystem functions (Stocker et al., 2019; Tang et al., 2019) and on which fruiting depends (Journé et al., 2021). An increase in the frequency of extreme events, such as prolonged droughts, heatwaves and heavy rainfall, is also expected and could negatively affect forest productivity, as already demonstrated (Nussbaumer et al., 2018). However, the productivity of species such as thermophilic oaks (*Q. faginea* Lam., *Q. ilex* L.) and sweet

chestnut (*Castanea sativa* Mill.), the nuts of which already form part of the bear diet (Naves et al., 2006; Rodríguez et al., 2007), may even increase under future climate change scenarios (Pérez-Girón et al., 2020).

In autumn, bears can both increase the size of their home range and vary the elevational gradient at which they live, in the search for food resources rich in digestible energy that meet their dietary needs (Pop et al., 2018). Bears particularly favour acorns (Di Domenico et al., 2012; Naves et al., 2006) and chestnuts (Rodríguez et al., 2007), which are efficiently converted to body fat (Pritchard and Robbins, 1990). However, Angelis et al. (2021) suggested that this behaviour corresponds to seasonal migrations driven by years in which fruiting fails, and it therefore does not occur every year. In this context, exceptional bear aggregations have been associated with occurrences of large variations in food availability during hyperphagia, particularly in micro-regions where oak acorn production remains high despite widespread fruiting failure across the landscape (Ballesteros et al., 2018).

Remote sensing provides continuous, powerful information on plant productivity that can be used as a good proxy for assessing the availability of food resources to animals (Radeloff et al., 2019). Previous studies on brown bears in the Cantabrian Mountains have used remote sensing approaches such as the normalized difference vegetation index (NDVI), which is specifically related to ecosystem productivity and has proved useful for understanding general species-habitat relationships (Wiegand et al., 2008). However, this is not the only index related to ecosystem productivity. Dynamic habitat indexes (DHIs) summarize cumulative productivity, minimum productivity and seasonality, three key measures of plant productivity (Radeloff et al., 2019), and provide valuable information about ecosystem productivity that could be used to explain long-term habitat use patterns (Razenkova et al., 2020). Thus, given the predominantly frugivorous nature of brown bears during hyperphagia, vegetation productivity indices may be useful for explaining nut consumption, as nut productivity is related to ecosystem productivity (Fernández-Martínez et al., 2017; Herbst et al., 2015). Nonetheless, individual DHIs have low predictive power in habitat selection modelling and must be combined with environmental variables (Razenkova et al., 2020).

The aims of the present study were (*i*) to analyse the spatial distribution of brown bear faeces during hyperphagia to understand the nut foraging patterns in relation to the characteristics of nut-producing patches and (*ii*) to evaluate and model how vegetation productivity, topographical variables and landscape metrics are related to nut (particularly acorn and chestnut) consumption by the Cantabrian brown bear during the hyperphagia season.

2. Materials and methods

2.1. Study area

The reference area considered in this study covers the provinces of Lugo, León, Asturias, Cantabria and Palencia, comprising the entire range of the Cantabrian Mountains in the NW Iberian Peninsula (see Fig. 1). The Cantabrian Mountains are located in a transitional zone between the Atlantic and Mediterranean biogeographical regions, and they are characterised by an oceanic climate that is conditioned by the proximity to the ocean and by their geographic orientation. The northern faces of the mountains are characterised by a higher rainfall rate that is constant throughout the year; the climate is temperate, and snowfall is low, with little accumulation. This contrasts with the characteristically high oscillations in temperature and precipitation of the southern faces, with cooler and long winters with heavy snowfall and short summers without droughts (Lamamy et al., 2019; Naves et al., 2006; Ortega Villazán and Morales Rodríguez, 2015).

The heterogeneous landscape pattern has traditionally resulted from socio-ecological relationships established through millennia (López-Merino et al., 2009; Pérez-Díaz et al., 2016). This pattern has been caused by the gradual clearing of forests for agricultural and livestock husbandry
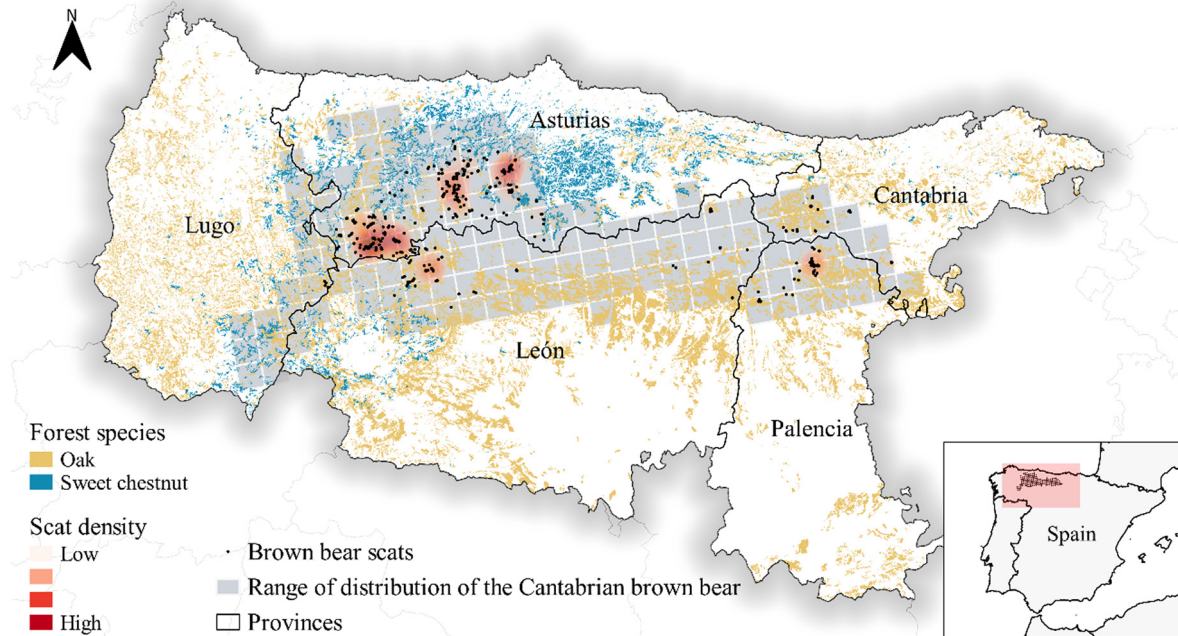
Fig. 1. Location and density of brown bear scats sampled within the study area. Forest species presence was extracted from the Forest Map of Spain (MFE) and only the predominant species is represented, although co-occurrence of species is possible. The oak category comprises *Quercus pyrenaica* Willd., *Quercus faginea* Lam., *Quercus petraea* (Matt.) Liebl., *Quercus robur* L., *Quercus ilex* L. and *Quercus suber* L..

and by the influence of climatic and topographic conditions (Muñoz Sobrino et al., 2005; Roces-Díaz et al., 2015). However, this heterogeneous pattern has changed in the last few decades, due to agricultural abandonment and land consolidation in the most productive areas, towards forest expansion (García-Llamas et al., 2019). In this context, the low/midlands are used for agricultural crop production or livestock grazing, with isolated patches of woodland of native species (*Q. robur* and *C. sativa*) and forest plantations destined for timber production (*Eucalyptus globulus* Labill., *Pinus pinaster* Aiton and *P. radiata* D. Don). In the highlands, deciduous forests dominated by sweet chestnut (*C. sativa*), oaks (*Q. robur*, *Q. petraea*), beech (*F. sylvatica*) or birch (*Betula pubescens* Ehrh.) predominate on northern slopes, while south-facing slopes are usually covered by deciduous sessile oaks (*Q. petraea* and *Q. pyrenaica*) or beech (*F. sylvatica*) forests and shrubland.

The species of interest in this study, i.e. *C. sativa* and *Quercus* (including *Quercus pyrenaica*, *Q. faginea*, *Q. petraea*, *Q. robur*, *Q. ilex* and *Q. suber* in the study area), are distributed throughout the entire distribution of the Cantabrian brown bear, but the eastern habitat only includes oaks (see Fig. 1). Together with beech and hazel (*Corylus avellana* L.), the aforementioned trees are the most important source of nuts during hyperphagia. However, although flowering occurs regularly every year, this does not necessarily indicate nut production. Acorn production varies greatly from year-to-year, tree-to-tree and also within species (e.g. in *Q. ilex*, *Q. petraea* and *Q. pyrenaica* acorn production tends to be high about once every 2–3 years, while in *Q. robur* high production is expected to occur every 8–10 years) (Pemán et al., 2013). By contrast, although bumper crops of sweet chestnut generally occur every 2–5 years, in what are referred to as mast years, nut production is very regular as a large number of sweet chestnut cultivars undergo asynchronous production. In this regard, nut production generally failed in 2017 due to heavy frosts that affected flowering and production. However, evidence of nuts being produced was observed in some small and localized patches, apparently due to favourable microclimate or orographic characteristics (Ballesteros et al., 2018). By contrast, 2019 and 2020 were good acorn-producing years.

2.2. Collection of bear faeces and analysis of dietary components

To explore the relationship between the nut-based diet of bears and landscape and vegetation productivity, we used data already available in the area. We used bear faeces collected across the range of Cantabrian bears during population monitoring surveys conducted in 2017, 2019 and 2020 (López-Bao et al., 2021; López-Bao et al., 2020). As bears do not use faeces for territorial marking, we used the spatial location of faeces as a proxy for bear habitat use during hyperphagia. Sample collection was based on 5 × 5 km UTM grid cells (see López-Bao et al., 2021, López-Bao et al., 2020 for details). In total, 148 grid cells covering a distance of 624 km were sampled in the eastern subpopulation in 2017, and 282 cells covering a distance of 1678 km were sampled in the western subpopulation in 2019 (López-Bao et al., 2021). In the eastern subpopulation, faeces were sampled between November and December 2017, while in the western subpopulation, sampling was conducted between October and December 2019 (López-Bao et al., 2021). Within each cell, transects were established in the best sites for detecting bear signs according to potential feeding areas in autumn. We also included scat samples collected in 2020 by the rangers of the Regional Government of Asturias during ongoing bear monitoring activities (the samples were collected following the approach described above). Overall, we analysed 677 scat samples: 128 collected in 2017, 455 collected in 2019, and 94 collected in 2020. Bear scats were georeferenced using a GPS and preserved in 96% ethanol. Each scat was subsequently classified by visual inspection according to the content, into four categories: i) presence of acorn remains (*Quercus* sp.); ii) presence of chestnut remains (*C. sativa*); iii) presence of both acorn (*Quercus* sp.) and chestnut remains (*C. sativa*); and iv) other.

2.3. Vegetation productivity data

The gross primary production (GPP) allocated to fruit production by forest species represents a small fraction of the total C balance in forest ecosystems. The values reported for European Fagaceae species range between 0.5 and 10% of the GPP, increasing to 23% in mast years (Fernández-Martínez et al., 2017; Herbst et al., 2015). A low proportion is allocated

by oak species, accounting for 0.9 and 1.3% of the GPP in *Q. petraea* and *Q. robur* respectively (Fernández-Martínez et al., 2017); however, there is evidence that the C balance in previous years can affect nut production and can therefore act as a limiting factor (Journé et al., 2021).

The global MODIS data were obtained from the Land Processes Distributed Active Archive Center (LP DAAC) data pool. We used the MOD17A2HGF.006 and MOD17A3HGF.006 products (Running and Zhao, 2019a, 2019b), which provide GPP and net primary production (NPP) data (in kg carbon m^{-2}) respectively, for the years 2017, 2019 and 2020, at 500 m resolution. The GPP and NPP were computed individually (Running et al., 2004). GPP and NPP values for non-vegetated or artificial areas were excluded from the analysis (Zhang et al., 2014), and the land pixel values were multiplied by a scale factor of 0.0001 (Running and Zhao, 2015), as ordered in the metadata file, to return the original value at the corresponding pixels.

The GPP data set (originally one for every 8 days) was used to calculate both the Dynamic Habitat Indices (DHIs) (Radeloff et al., 2019) and the Carbon Use Efficiency (CUE) (Pérez-Girón et al., 2020). DHIs comprise the following indices (Radeloff et al., 2019): (a) cumulative GPP, where the GPP is summed for all time periods over a year; (b) minimum GPP, where each pixel represents the minimum productivity value during the year evaluated; (c) GPP variation, which indicates the seasonality of the productivity over a year and is calculated as the standard deviation (σ) divided by the mean (μ). CUE was annually calculated as the NPP/GPP ratio, representing the efficiency of plants to sequester carbon from the atmosphere via photosynthesis.

2.4. Topographically derived information

Topographical variables are often used to explain the relationships with tree species distribution along elevational ranges, slopes and aspects (e.g. *Q. robur* and *C. sativa* occupying low-midlands), and they are also frequently used to fit brown bear habitat models (García et al., 2007; Mateo-Sánchez et al., 2016; Mateo-Sánchez et al., 2014). We selected 25 m EU-DEM v1.1 (Bashfield and Keim, 2011), which is distributed by the European Environment Agency (EEA) within the framework of the Copernicus programme.

In addition to extracting the elevational information, we used Horn's method (Horn, 1981) to compute slope and aspect, and we also calculated the surface curvature (profile, plan and general curvature) to determine changes in concavity or convexity in the direction of or perpendicular to the slope (Kienzle, 2004) and thus address slope, orientation and elevational changes that may affect the species-habitat relationships. We computed the topographic position index (TPI), terrain ruggedness index (TRI) and vector ruggedness measure (VRM) by using a moving window of 3 × 3 pixels, i.e. 75 × 75 m due to the pixel size, to address changes in ruggedness and morphology. The TPI (Jenness, 2006) determines whether the focal cell is located higher than its surrounding area or vice versa. The TRI (Riley et al., 1999) quantifies the total elevational change relative to its surrounding area. The VRM (Sappington et al., 2007) quantifies terrain ruggedness (i.e. local variations in terrain slope) by measuring the dispersion of vectors orthogonal to the terrain surface within a neighbourhood.

All topographically derived information was calculated using the QGIS geographic information system (QGIS Development Team, 2020).

2.5. Landscape source layers and classification

The vector format of the Forest Map of Spain (*Mapa Forestal de España*, MFE) (Ministerio para la Transición Ecológica y el Reto Demográfico, 2020) was used as the main source of information regarding the distribution of Spanish forest ecosystems, providing detailed data on forest composition and structure in patches such as the patch size, the 3 tree species that occupy each patch, the percentage of the patch covered by trees (canopy cover) and the individual occupation by each of the species, among other variables. A patch is understood as an area of habitat differing from its

surroundings, and therefore in which the ecosystem is sufficiently homogenous to be identified as forest stand. Canopy cover determines the extent to which a forest stand is occupied by trees. The latest version of the Forest Map of Spain, MFE25, was developed at 1:25000 scale by combining photointerpretation and field inventory data, with a minimum mapping unit (MMU) of 1 ha for forest. However, due to its decennial periodicity, it was not fully available for the entire study area, and we therefore used the previous version (MFE50), developed at 1:50000 scale with an MMU of 2.25 ha, for the provinces of León and Palencia.

The approach was applied by focusing on the functionality of the forest composition to provide food resources or shelter for brown bears in the hyperphagia period (Naves et al., 2003; Ordiz et al., 2011). Based on the three main species that the MFE includes, we computed the percentage of forest areas that potentially produced nuts during the hyperphagia period, i.e. only the species in which fruiting occurs in autumn were considered, by considering the percentage occupation by each tree species in the landscape patch. When the percentage area with the capacity to produce nuts was equal to or more than 50%, the patch was categorized as nut-producing. The same approach was used to compute the presence of fleshy fruit, understood as pulp fruit produced by tree species during hyperphagia season, e.g. the fruits of *Arbutus unedo* L. and *Sorbus* spp. Fleshy and mixed fruit production was also classified but did not exceed 0.5% of the study area, as fleshy fruits are not commonly available during the hyperphagia season. We also considered that forest without the capacity to produce fruits/nuts was capable of providing shelter for bears (Naves et al., 2018).

Non-wooded areas, such as wetlands, grassland, water bodies, artificial areas and cropland, were established in the Third National Forest Inventory (TNFI). These areas included a treeless class categorized according to the structural type into shrubland, grassland, wetland, water bodies or artificial areas. Shrublands were also considered shelter areas. A total of 9 landscape classes were included in the map, as briefly described in Table 1.

As the analysis required raster format cartography, a rasterization process was developed. The cell size was chosen by exhaustively following the recommendations of Hengl (2006) regarding the size of the smallest spatial objects, the width of linear elements and frequency distribution of patch sizes. The spatial resolution finally chosen was 20 m.

2.6. Detection of scale effects in landscape

Landscape heterogeneity was studied using landscape metrics (Botequilha-Leitão et al., 2012; Uuemaa et al., 2013). A moving window approach was used to analyse the spatial distribution of the values of the landscape metrics (Díaz-Varela et al., 2009; Gaucherel, 2007). The first step consisted of determining the window size to characterize a representative extension (i.e. scale) for the spatial pattern in the study area. For this purpose, the previously classified landscape raster map was analysed using FRAGSTATS software (McGarigal et al., 2012) to compute an initial set of six landscape metrics in multiple square windows of N x N cells in 13 increasing sizes. The side length of the different windows ranged from 100 to 1620 m, starting at 7 × 7 cell window size (side length of 100 m) and ending at 81 × 81 cell window size (side length of 1620 m) in steps of

Table 1
Recoding of landscape patch classes and codes in the functional classification.

Class	Landscape code	Description
Wetland	1	
Grassland	2	Land use established by the TNFI and the structural forest type in non-wooded areas
Water	3	
Artificial areas	4	
Cropland	5	
Fresh fruit	6	% of area with capacity to produce fresh fruit ≥ 50%
Nuts	7	% of area with capacity to produce nuts ≥ 50%
Mixed fruit-nuts	8	% of area with capacity to produce fresh fruit and nuts <50% but together add up more than 50%
Shelter	9	Forest areas without capacity to produce fruit production

40 m to 220 m, and 200 m thereafter. The mean value and standard deviation of patch area distribution (AREA_MN and AREA_SD), total edge (TE), shape index distribution (SHAPE_MN), interspersion and juxtaposition index (IJI) and Shannon's diversity index (SHDI) were used to represent different aspects of the landscape pattern. A detailed description of the metrics can be found in McGarigal et al. (2012).

The resulting maps were then analysed to identify representative scales through the observed dissimilarity (S) (Díaz-Varela et al., 2009; O'Neill et al., 1996; Saura and Martínez-Millán, 2001) and the change in the slope of the curve S as a change in the scale domain (p_i). Thus, from extension of the moving window for which the map shows a change in the sign of p_i, the heterogeneity value was less dependent on the scale of analysis and can be considered a representative analytical scale (i.e. window size). A moving window of 61×61 pixels (side length of 1220 m) was finally selected as the reference window size (see detailed analysis in Supplementary Material).

2.7. Landscape indices

After identification of the reference scale (i.e. moving window), a total of 85 landscape metrics corresponding to the typologies of area-edge, shape, contrast, aggregation (except proximity, similarity and connectance index, due to the requirement of non-available additional data) and diversity metrics were computed on the landscape map generated, using a moving window of 61×61 pixels in the FRAGSTATS 4.2 software (McGarigal et al., 2012). Further details about calculating the landscape metrics can be found in McGarigal (2015).

A set of information theory-derived landscape metrics was also computed, as conditional entropy, marginal entropy, joint entropy, mutual information and relative mutual information in R software, version 4.0.0 (R Core Team, 2020) using the landscapemetrics package (Hesselbarth et al., 2019) and a moving window of 61×61 pixels. For detailed information about the calculation procedure, see Nowosad and Stepinski (2019). A detailed list of calculated landscape indices is provided in Table S1.

2.8. Modelling foraging habits

A total of 99 independent variables related to vegetation productivity (5), topographical (9) and landscape patterns (85) were evaluated as potential predictor variables to explain changes in the presence or absence of bear scats containing food scraps of chestnut or acorn. A Random Forest (RF) classifier algorithm was fitted to the data with the single aim of identifying the most important predictors of acorn and sweet chestnut foraging habits in Cantabrian brown bears during the hyperphagia period. Subsequently, a Logistic Regression (LR) model selection procedure was carried out to fit predictive models using only the most important variables identified from the RF classifier.

The RF classification and regression non-parametric methodology, proposed by Breiman (2001), comprises a large number of individual decision trees that work as an ensemble, known as a "forest". RF quantifies the importance of the input variables, through random permutation, which can be used to rank or select factors (e.g. Genuer et al., 2010). In this study, we used the cforest implementation, which uses the Conditional Inference Trees (CTree) algorithm (Hothorn et al., 2006a) to fit each of the trees to be grown for the forest. This approach utilizes permutation tests, with the aim of distinguishing between significant and non-significant improvements (Sardá-Espinosa et al., 2017) and addressing overfitting and variable selection biases by using a conditional distribution to quantify the relationship between the output and the input variables and taking distributional properties into account (Williams, 2011). To assess variable importance, a permutation importance measure of accuracy was applied. This measure yields more robust results when multifactorial variables are involved and is less biased than the mean decrease in Gini in the traditional RF algorithm (Gil-Tapetado et al., 2020; Strobl et al., 2008; Strobl et al., 2007). Although implementation of cforest does not completely remove the problem of multicollinearity, it resolves it to some extent, thus helping to assess the

importance of correlated predictor variables (Strobl et al., 2009). These characteristics make cforest useful, especially when the challenge is to identify a subset of relevant predictor variables from large sets of candidates (Strobl et al., 2007).

Although RF allows a binary classification (0 or 1, presence or absence), LR is a well-known parametric method for fitting habitat use models with presence/absence samples that returns the probability of use of the target cell or pixel as a function of one or more independent variables (Boyce et al., 2002). It has the advantage that the coefficients have a natural interpretation while they do not vary, and therefore is sufficient to know the fitted values of the regression coefficient to apply a LR-based prediction rule to make predictions. Due to the computational cost of model selection, the seven non-correlated most important variables provided by RF (using Spearman's rank-order correlation) were selected to fit a set of LR Models. The predictive performance of LR models was assessed with the area under ROC curve (AUC), Akaike information criterion (AIC) and confusion matrix (omission and commission errors, accuracy and sensitivity) and the most parsimonious models -based on AIC and the goodness of fit- were selected. Once the best model was selected, the interactions between the selected predictors were considered and each interaction model was again validated according to the above criteria. Finally, an annual goodness of fit validation was performed with the selected model by examining the confusion matrix.

The party library (Hothorn et al., 2006b; Strobl et al., 2008; Strobl et al., 2007) and glmnet library (Friedman et al., 2009) implemented in the R software environment (R Core Team, 2020) were used to fit RF and LR. Additionally, the dredge function of the MuMIn package was used for model selection (Barton, 2015). In RF, the number of variables tested at a given classification tree node split was set at 10 (the square root of the total number of variables), and the number of trees to be grown was set at 10000 to ensure the stability of the RF results. Variables were excluded from models when they were pairwise correlated or not statistically significant. Finally, ecological criteria, such as the impossibility of acorn foraging in a cereal crop or on a road, were used to mask crops, artificial areas and water bodies from the from the visual representation of the spatial model prediction.

Graphical analyses were conducted with box-and-whisker plots constructed with the ggplot2 package (Wickham, 2009). Significant differences were determined using the Wilcoxon-Mann-Whitney test (at $\alpha = 0.01$).

3. Results

3.1. Location of bear faeces

In total 677 scat samples were analysed (Fig. 2). Of these, 41.7% contained acorn (*Quercus* sp.) remains, and 13% contained chestnut (*C. sativa*) remains, while 45.1% contained other types of food. The presence of both types of nut remains in the same scat was very uncommon. The percentage of samples collected in 2017 and 2019 without acorn or chestnut remains, i.e. with other food, was the same in both years (52.3%), and no sample of this type was found in 2020. Of the 284 samples containing remains of *Quercus* sp. acorns, 70% were located in patches with the presence of at least one species of the genus, while of the 90 scat samples containing chestnut remains, only 26% were found in sweet chestnut patches. The distribution and abundance of scat in the nut-fruiting patches in relation to the spatial coverage of those areas differed significantly from the random distribution typical of the null model approach, i.e. randomly redistributing the same number of samples from each category in the study area and replicating the process 100 times (Table S2). Therefore, the observed patterns cannot be considered typical of a random distribution.

The average patch size was 46.2 ha for acorn-producing patches and 34.8 ha for chestnut-producing patches in the study area, with an average wooded area of 30.2 and 24.9 ha, respectively. The average wooded area of the patch differed depending on whether the scats were located inside or outside the nut-producing patch and was always higher when scats were collected inside the patch, independently of whether the scat
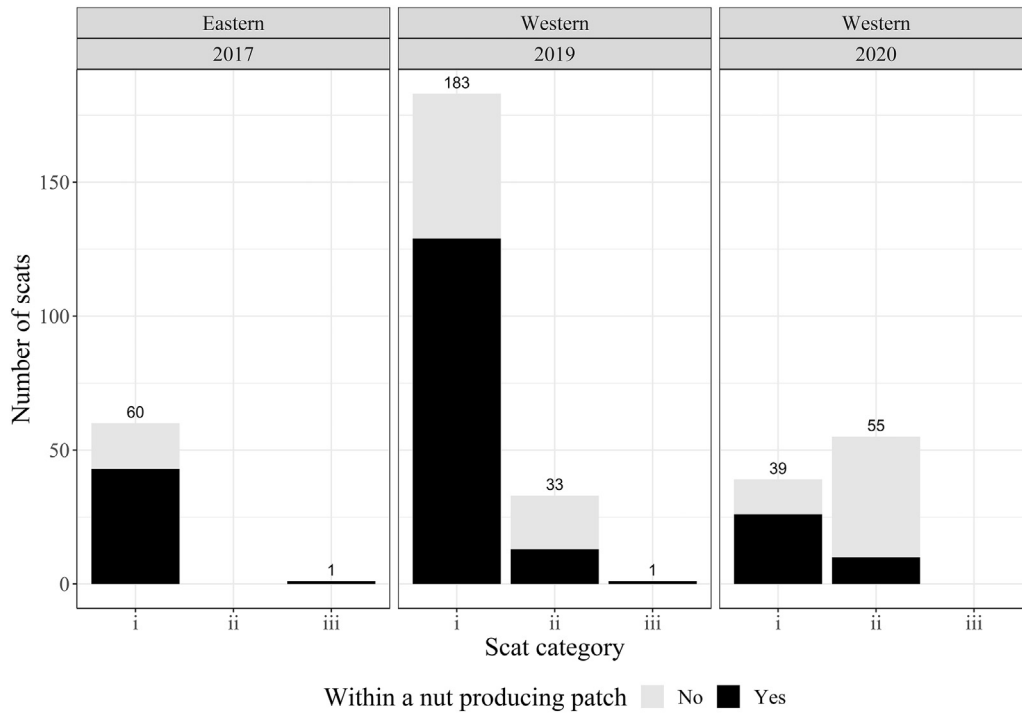
Fig. 2. Scat distribution in year and location categories within a nut-producing patch. The following categories were considered: i) presence of *Quercus* sp. acorn remains, ii) presence of *C. sativa* chestnut remains and iii) presence of both acorn (*Quercus* sp.) and chestnut (*C. sativa*) remains.
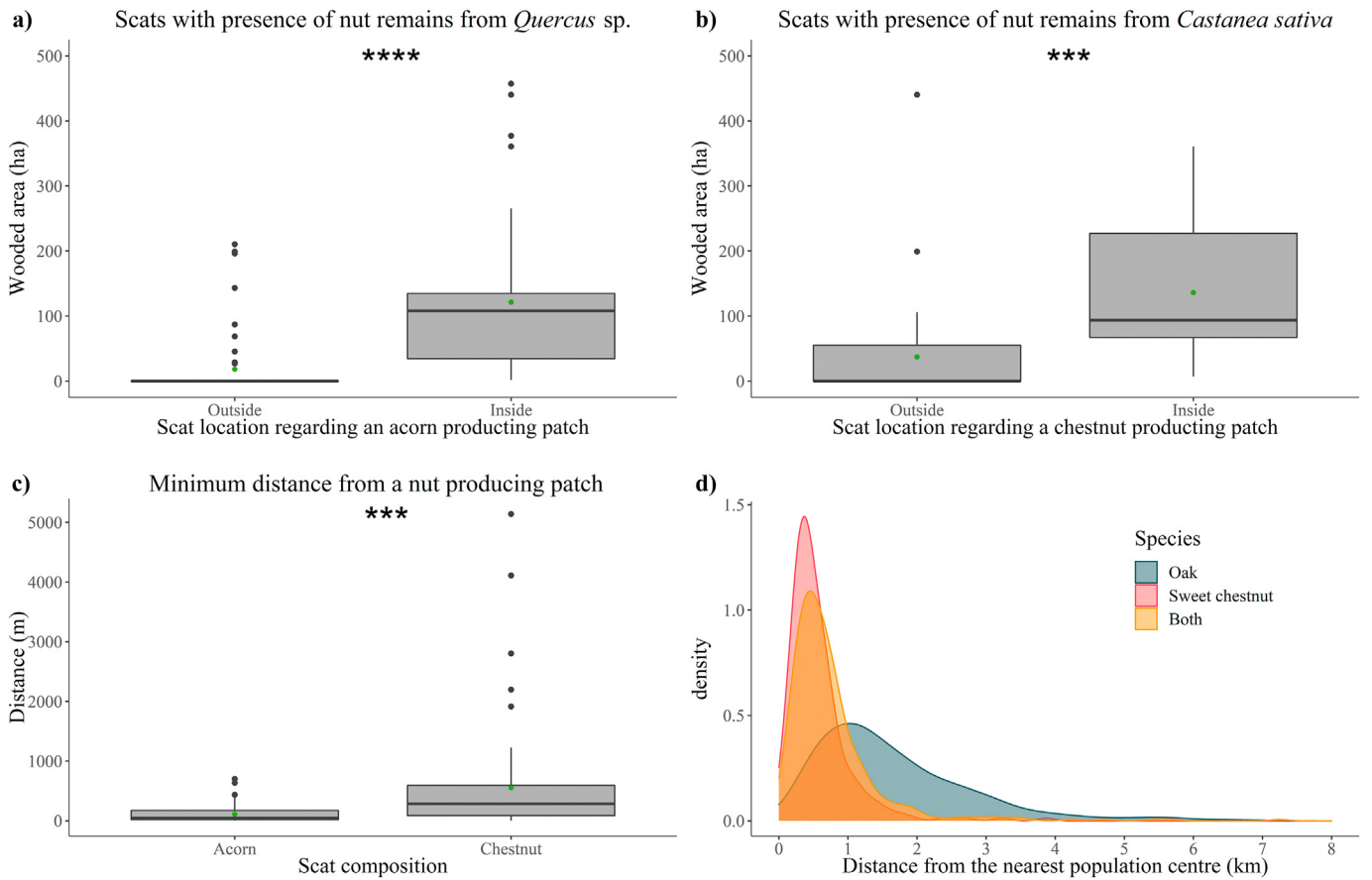

Fig. 3. Box-and-whisker plot comparing the average wooded area of the patch for scats found inside or outside the a) acorn- or b) chestnut-producing patch. c) Box-and-whisker plot comparing the minimum distance between scat containing nut remains and located outside of a forest patch with presence of *Quercus* sp. or *C. sativa* (as appropriate) and the nearest acorn- or chestnut-producing patch. d) Density plot of distance between the nut-producing patches and the nearest population centre. Statistical significance: *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$; ****: $p \leq 0.0001$. Green dots denote the mean values.

contained remains of acorn or chestnuts (Fig. 3a and b). The average patch size for scats containing acorn remains and located inside the nut-production patch was 161 ha, while the average wooded area was 121 ha. When these scats were located outside, the average patch size was 569 ha, while the average wooded area was 18 ha. Despite the low average wooded area, a large number of these samples located outside the patch were collected in patches categorized by the MFE as adult forest stands (pole or timber stage) and dense shrublands. Regarding scats containing chestnut remains, when those were located inside the nut-production patch, the average patch size was 177 ha while the average wooded area was 136 ha. When these scats were located outside, the average patch size was 314 ha, while the average wooded area was 37 ha. In the latter there are two trends: 33.8% of these scats were located in patches without trees and more than 55% in patches where trees represent 75% or more of the patch size.

A scat containing nut remains (acorn or chestnut) but located outside a forest patch that can produce this type of food may indicate that the bear has gone away from the place where it has eaten. Thus, for each scat containing nut remains (acorn or chestnut) and located outside a forest patch that produced the corresponding nut (acorn- or chestnut-producing patch as appropriate), the minimum distance (in a straight line) to the nearest patch that produced the corresponding nut was computed. The minimum distance was greatest for scats containing chestnut remains (Fig. 3c). The average minimum distance was 111 m for scats containing acorn remains and 552 m for scats containing chestnut remains. For the latter, in some cases the minimum distances were greater than 2500 m. Regarding the location of nut-fruiting patches, it was found that chestnut patches are located closer to the population centres than oak patches, while when both species co-occur, the distribution is similar to that of chestnut (Fig. 3d).

3.2. Modelling acorn consumption

3.2.1. Variable selection

The most important variable explaining the location of bear faeces containing acorn remains was the terrain elevation (Fig. 4). GPP was the most important vegetation productivity predictor, together with NPP. Landscape metrics also yielded some improvement. Specifically, the aggregation index (AI) was the best-positioned landscape variable (third position), followed by relative mutual information (relmutinf). The other variables comprising the top 20 in the variable importance plot were all landscape metrics, with the exception of CUE, which corresponds to vegetation productivity. We are

aware of the multicollinearity in most of the landscape metrics included in the analysis, and of the negative effects of such correlations in explanatory models (e.g. Cushman et al., 2008). However, we consider that multicollinearity was largely resolved by the use of the cforest algorithm and that the accuracy of predictive models was therefore not affected (Strobl et al., 2009).

The confusion matrix statistics for the acorn RF model revealed that the fitted model was very accurate, supporting its use for variable selection. Omission and commission errors represented respectively 5.1% and 18.7% of the errors. Thus, 89.3% of cases were correctly classified (overall error: 10.7%), with a sensitivity of 81.3% and an area under the ROC curve of 0.96.

Comparative box-and-whisker plots for scats containing acorn remains and the most important predictors showed different patterns for the presence or absence of acorn (Fig. 5). The Wilcoxon-Mann-Whitney results reinforced the hypothesis of significant differences between the presence or absence of scats containing acorn remains. In 2017, scats containing *Quercus* sp. acorn remains were located in forest patches with higher GPP and lower elevations than scats that did not contain *Quercus* sp. acorns. The opposite trend occurred in 2019, when scats containing acorn were found at higher elevations with lower GPP, while in 2020, only the elevation was statistically significant at $p < 0.05$. Predictor values for scats containing acorn remained constant between years and subpopulations. The average GPP values in scats containing acorn ranged from 1.47 to 1.50 kg C m^{-2} yr^{-1}, for elevation approximately from 850 to 1000 m and the AI remained stable at around 95%.

3.2.2. Predictive model

The LR acorn model selected was not the model with the lowest AIC (Δ AIC = 4.79), but it was the most parsimonious, as it includes only three predictors, GPP, elevation and aggregation index. The model yielded an acceptable fit (Table 2; Table S3 for complete model selection table), with an accuracy of 0.68, a sensitivity of 0.53 and an AUC of 0.75. In other words, the model correctly classified 68% of all samples and 53% of scats containing acorn remains. Omission and commission errors suggest over-prediction of acorn presence. Comparison of this model with a better candidate model (as indicated by ΔAIC = 0.25) including another variable (slope) showed that the additional variable added further complexity and did not improve the model fit sufficiently for this model to be considered further (see goodness of fit measures in Table S4). When interactions between predictors were considered, only the interaction between
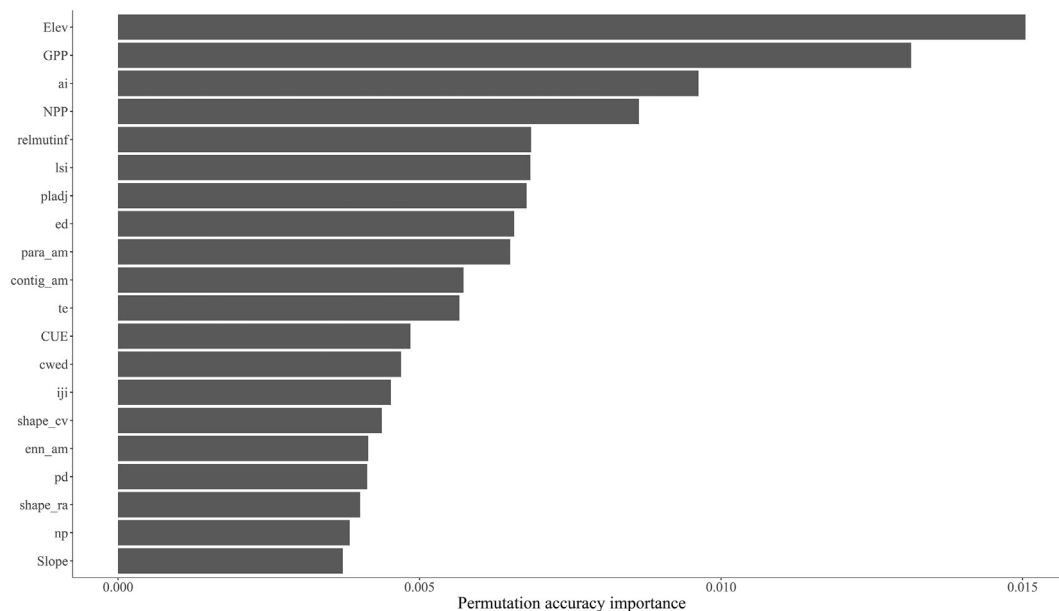

Fig. 4. Top 20 variables in regard to permutation importance for acorn scats, determined using the cforest algorithm.
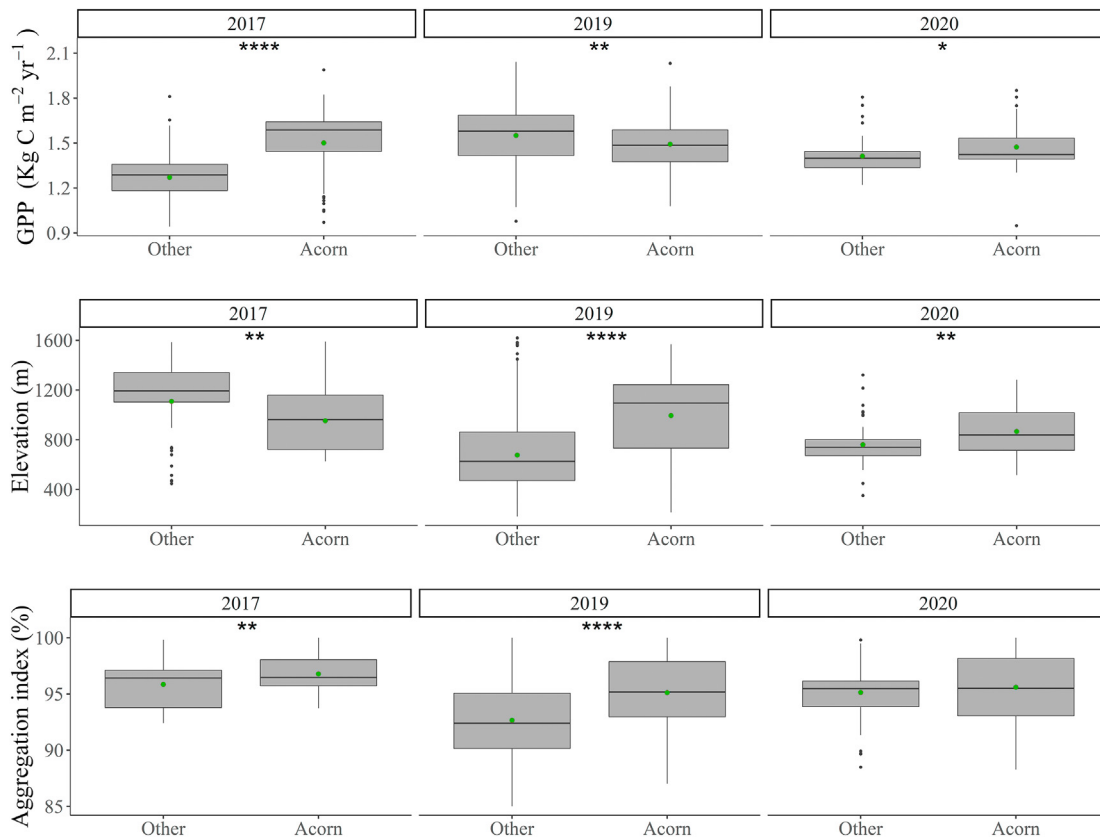
Fig. 5. Box-and-whisker plot comparing the presence and absence of scats containing acorns by years for the most important vegetation productivity, topographical and landscape variables. Statistical significance: *: $p \le 0.05$; **: $p \le 0.01$; ***: $p \le 0.001$; ****: $p \le 0.0001$. The black dots represent outliers. The green dots represent mean values.

aggregation index (ai) and elevation (interaction model 2; Table S5 for further details) slightly improved the model sensitivity (ca. 4%). Furthermore, there are more models with ΔAIC <2, so other models may perform similarly or may be of interest in relation to model averaging. However, with an ecological meaning in mind, the parsimonious initial model with only three variables and without interactions was selected, as adding new variables or considering interactions led to an increase in complexity with a slight improvement (ca. 4% in the best of cases), which was considered insufficient to assume greater complexity.

Annually, the LR acorn model showed a consistent and robust accuracy while the sensitivity varied slightly between years due to the lack of uniformity of the acorn samples (Table 3). In 2017, the sensitivity was above average for the general model, correctly classifying 79% of acorn samples. In 2019, when the bulk of samples were obtained, the goodness of fit was almost the same, while in 2020, despite the small number of acorn samples, the model correctly classified 36% of acorn scats.

The prediction model fits well with the most recent distribution of the Cantabrian brown bear, particularly in previous and permanent distribution cells (Fig. 6). The new areas occupied by bears between 2012 and 2016 also showed a high likelihood of being good habitats for hyperphagia, especially in the intermediate interpopulation corridor. Outside of the distribution of the Cantabrian brown bear, intermediate probabilities of presence were predicted for the surrounding area north of León and high probabilities in the southwest of León, where the Montes de León Mountain system connects with the province of Zamora and northern Portugal.

3.3. Modelling sweet chestnut consumption

For scats containing chestnut remains, the RF model yield an accuracy 0.88 and sensitivity of 0.18. Thus, the RF model correctly classified 88% of absences, but did not correctly predict more than 18% of the presence of scat containing chestnut. Omission errors represented 1.3% of the errors, and 82% of commission errors. Therefore, the models and the corresponding importance variable plots were not useful for explaining the presence of scats containing chestnut. Given the low predictive power of the predictors, no further analysis was performed with chestnut scats.

4. Discussion

The study findings highlight the association between Cantabrian brown bear food habits during hyperphagia and vegetation productivity, terrain elevation and landscape characteristics. One variable of each type was included in the final model for acorn. However, a good model fit was not obtained for the data on chestnut consumption by brown bears, which may be

Table 2
Fitting method and goodness of fit measures for the acorn model. Confusion matrix statistics are proportions.

Fitting method	Independent variable	Parameter estimate	Std. Error	AUC	AIC	Omission error	Commission error	Accuracy	Sensitivity
RF + LR	(Intercept)	−0.382	0.086	0.75	804.75	0.21	0.47	0.68	0.53
	GPP	0.662	0.109						
	Elev	0.733	0.118						
	ai	0.552	0.109						

Table 3
Annual goodness of fit measures for the acorn model. Confusion matrix statistics are proportions.

Year	AUC	Omission error	Commission error	Accuracy	Sensitivity
2017	0.69	0.46	0.21	0.66	0.79
2019	0.76	0.17	0.52	0.69	0.48
2020	0.69	0.15	0.64	0.65	0.36

explained by the bears' foraging behaviour and the spatial distribution of chestnut formations, which is strongly influenced by human management.

Elevation was the most important predictor variable in the acorn model. However, elevation cannot be assessed independently of DHI, as changes in the elevational range imply changes in vegetation structure and composition, as well as in climatic conditions, which affect vegetation productivity (Collalti et al., 2020). In other words, as elevation increases, the weather conditions become colder and harsher, which favours some species but not others, and therefore implies changes in vegetation. However, these changes do not necessarily imply changes in vegetation productivity, as when the productivity of one species is reduced this may favour another species. Nonetheless, in some transition zones productivity will not be good for either species as both will be at the extreme limits of their distribution. Thus, in 2017, in the eastern subpopulation and coinciding with low acorn and beechnut production due to harsh weather conditions (Ballesteros et al., 2018), the GPP was higher for locations of scats containing acorns at lower elevations than at higher elevations. Therefore, our interpretation is that bears moved to lower elevations to feed on acorns, predictably in patches that were not affected by frost. The other food consumed was characterised by less common fruits, such as fruits of Rosaceae (*Rosa* sp.), typical of areas recolonized by shrubs or open landscapes. By contrast, in the samples from 2019 and 2020, corresponding to the western subpopulation and good acorn-producing years, and therefore where all the patches produced acorn, *Quercus* sp. trees used by bears to feed on acorn were located at higher elevations than other food, e.g. chestnut, and the data can thus be interpreted in relation to the higher elevation and lower GPP values.

The most important landscape metrics were the aggregation index (AI) and the relative mutual information (relmutinf), which quantify respectively the degree of aggregation of the habitat classes (He et al., 2000) and the information that a given cell with class *y* provides about a given neighbouring cell with class *x* (Nowosad and Stepinski, 2019). The predictive ability of the aggregation index in the mixed forest has previously been reported (Mateo-Sánchez et al., 2014). Although AI is considered a configurational metric (McGarigal et al., 2012), we believe that as both metrics are positive and highly correlated, they indicate the preference of brown bears for relatively large, highly aggregated adjacent forest stands of diverse cover classes for feeding on acorns during the hyperphagia season. In this particular case, the relmutinf variable identified a high degree of diversity in the landscape pattern (Nowosad and Stepinski, 2019), which may emerge from the aggregation of a variety of land cover classes at a given spatial scale. This is also consistent with previous research in the area (Lamamy et al., 2019; Mateo-Sánchez et al., 2014), highlighting the importance of diverse types of forest and other land cover types in the selection of suitable habitat with access to resources. These stands may also act as refuges and would therefore be associated with the risk perceived by bears regarding human presence (Nellemann et al., 2007; Ordiz et al., 2011).

Food takes between 3 and 16 h to pass through the bear's digestive tract before being excreted (Elfström et al., 2013). As bears can walk an average distance of between 0.5 and 2 km in this time (Lalleroni et al., 2017), the scats can thus be deposited in the feeding area as well as in the bedding or refuge area and on the route between these areas. Regardless of the presence of *Quercus* sp. or *C. sativa*, the existence of large, highly aggregated adjacent and complex forest stands may act as refuges where bears can remain undetected. The bears may therefore spend more time in these patches, consuming nuts and resting, as indicated by the average wooded area for scats found inside the nut-producing patch, and the percentage of scats containing acorn remains inside the acorn-producing patches.

The resulting model has shown acceptable predictive capacity for areas with good conditions for bear feeding during hyperphagia, overlapping with some recent expansion of bear habitats (Di Domenico et al., 2012; López-Alfaro et al., 2013). The resulting model has a slight tendency to overestimate probabilities due to the higher commission than omission error, which means that the acorn presence may be overestimated. This implies that the probability may actually be a little lower and in the case of claiming classifications, the established LR threshold must be restrictive. However, the general trend given by those areas with a very high predictive power can be considered accurate. The predictions suggest a high probability of good quality hyperphagia habitat in the interpopulation corridor and towards the southwest of the western subpopulation, where bear presence has been expanding in recent years (Gonzalez et al., 2016; Palomero et al.,
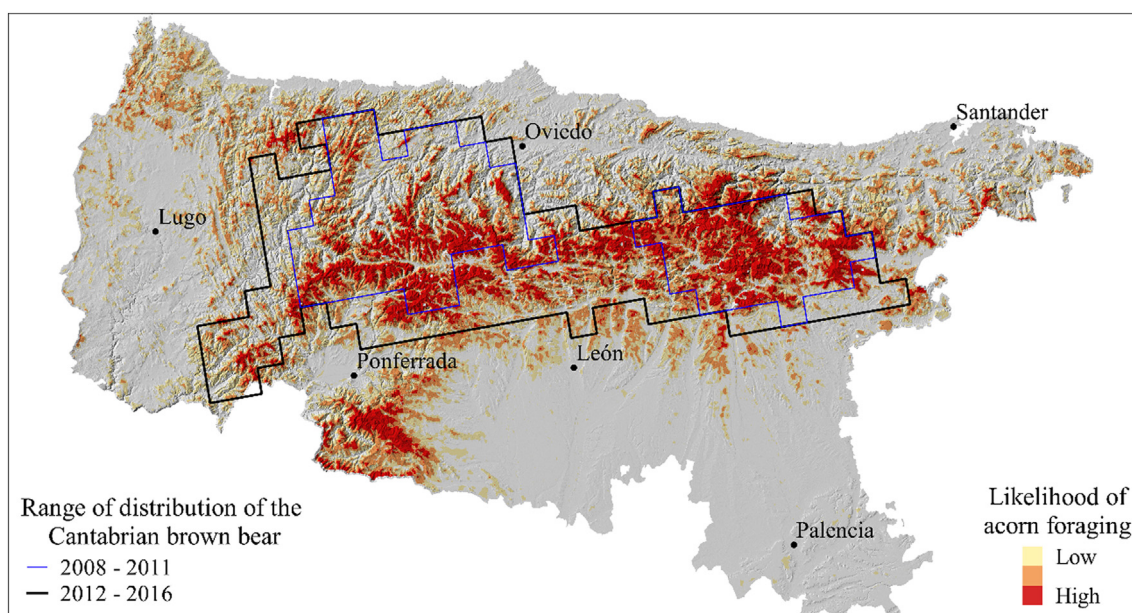

Fig. 6. Maps of probability of acorn foraging by brown bears during the hyperphagia period as determined by the logistic regression model.

2021). It also suggests a possible limitation in the eastern subpopulation, where beech trees and *Q. pyrenaica* dominate the landscape in the area occupied by bears. Therefore, years with low beechnut production or even the loss of beech trees (Dyderski et al., 2017), together with the probable scarcity of acorn production by *Q. pyrenaica* (Pemán et al., 2013), may affect bears during hyperphagia, due to the lack of other species such as *C. sativa*. In large areas of the southern Cantabrian slope, the presence and expansion of dense *Q. pyrenaica* patches may facilitate bear movements and land use during hyperphagia. Acorn production may be limited in *Q. pyrenaica*, in which mast episodes are common (Pemán et al., 2013).

Sweet chestnut constitutes an increasingly important source of food for brown bears during hyperphagia, particularly in the western subpopulation (Rodríguez et al., 2007), and the species may benefit from climate change, especially in the Cantabrian range (Pérez-Girón et al., 2020), thus compensating for variations in other nut/−producing trees during hyperphagia. However, we were unable to relate vegetation productivity, terrain elevation or landscape characteristics to chestnut consumption. The traditionally multifunctional agroforestry character of sweet chestnut trees, appearing in natural and semi-natural forest stands, as well as in managed stands, which vary from high-forest to grafted orchards, is always related to human presence (Míguez-Soto et al., 2019; Roces-Díaz et al., 2018), potentially making bears feel more vulnerable (Fig. A.1). Thus, we believe that bears feeding on chestnuts near villages or areas with human presence may perceive a high risk related to humans and human activity. As a consequence, after consuming the chestnuts, the bears will tend to move from these stands to quieter refuge areas. Therefore, different risk perception by bears may explain the observed differences in foraging patterns for acorn and chestnut in regard to the size and distance to the nut-producing patches. The current trend towards the abandonment of traditional chestnut orchards involves the evolution of the agroforestry system in different ways, varying from orchards (known as soutos, castañeros or castañeos in NW Spain and characterised by low tree density, open stand structure and high chestnut production) to abandoned orchards or mixed forests (Roces-Díaz et al., 2018), the likely stages at present and where sweet chestnut trees may occur in different proportions. This results in a high level of spatial variability in resource availability, which is difficult to map or predict. A clear example of this was given by Gil-Tapetado et al. (2020), who found that *C. sativa* trees were attacked by the chestnut gall wasp *Dryocosmus kuriphilus* throughout almost the entire region of Galicia, while even at the highest resolution available the MFE did not capture this change, as this would require tree-to-tree mapping.

5. Conclusions

In the light of our findings on acorn consumption by bears during hyperphagia, we suggest that bears prefer to feed on acorns, specifically in relatively large, highly aggregated deciduous mixed forest stands with a high degree of diversity in the landscape pattern, characterised by the presence of adjacent forest stands of diverse cover classes. This type of landscape will provide refuge areas where bears can remain undetected. This pattern was also reflected in the model predictions, as the areas predicted to be most important coincided with areas of high importance (e.g. permanent distribution cells) or where recent expansion has occurred (e.g. the interpopulation corridor or the southwest of the western subpopulation). We therefore encourage the preservation and maintenance of large patches of mature deciduous mixed forest that produce nuts, as well as patches of dense vegetation or scrub interspersed with or close to these forests, to ensure the nutritional needs of bears are met during hyperphagia and to promote bear reproduction.

Sweet chestnut forests and orchards (grafted trees organized in open stands) possibly acquire greater importance in the bear's diet during the hyperphagia season. Consumption of sweet chestnut also compensates for the variable production of other nuts. Recovery of abandoned orchards and promotion of new fruit chestnut plantations is of particular interest, mainly in the search for large patches or stands with chestnuts far from inhabited areas and human influence.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.152610.

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