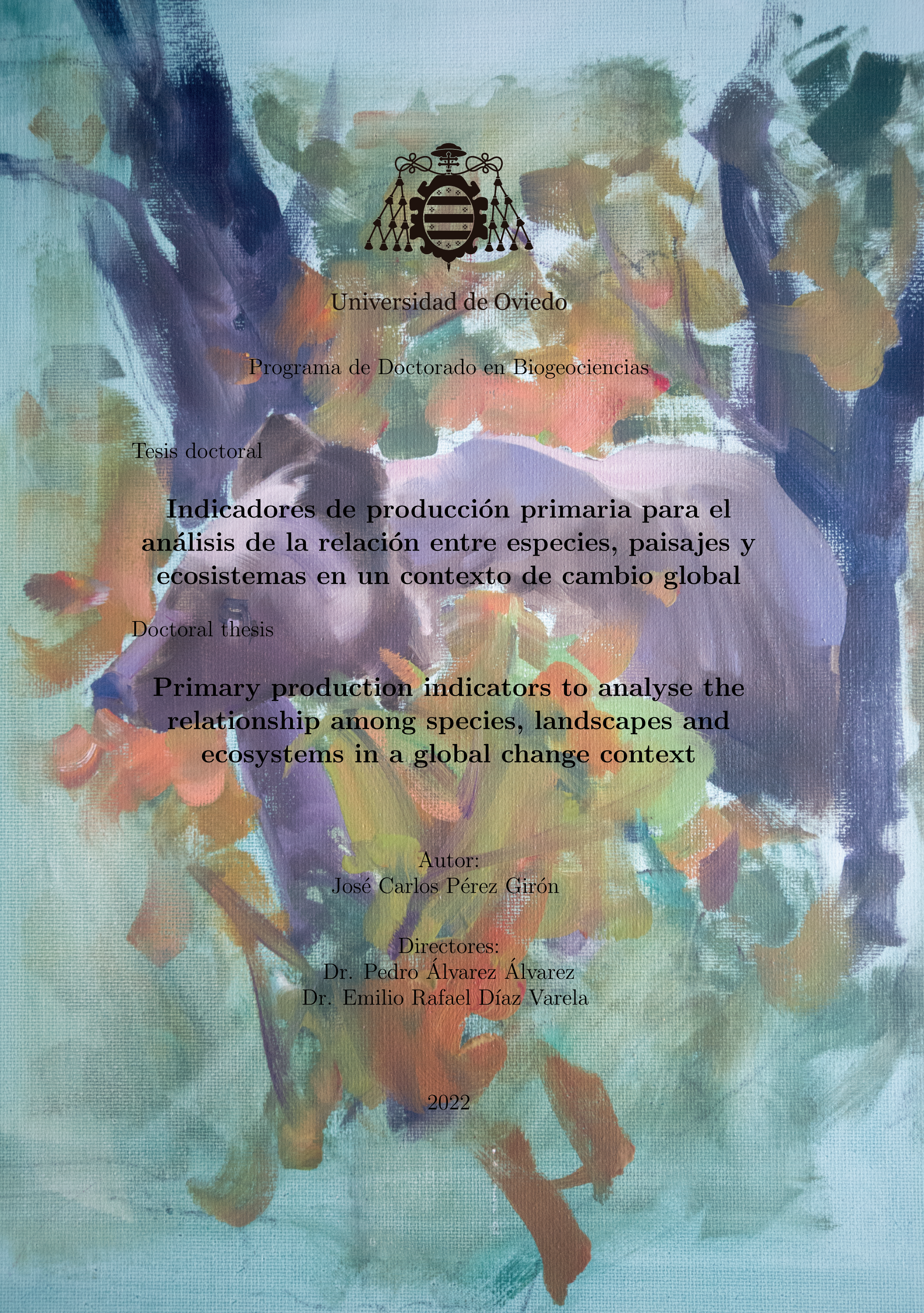

Universidad de Oviedo

Programa de Doctorado en Biogeociencias

Tesis doctoral

Indicadores de producción primaria para el análisis de la relación entre especies, paisajes y ecosistemas en un contexto de cambio global

Doctoral thesis

Primary production indicators to analyse the relationship among species, landscapes and ecosystems in a global change context

Autor:
José Carlos Pérez Girón

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Dr. Pedro Álvarez Álvarez
Dr. Emilio Rafael Díaz Varela

2022

Universidad de Oviedo

RESUMEN DEL CONTENIDO DE TESIS DOCTORAL

1.- Título de la Tesis	
Español/Otro Idioma: Indicadores de producción primaria para el análisis de la relación entre especies, paisajes y ecosistemas en un contexto de cambio global	Inglés: Primary production indicators to analyse the relationship among species, landscapes and ecosystems in a global change context

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RESUMEN (en español)

El cambio climático es considerado una de las principales amenazas para la biodiversidad, los ecosistemas, el desarrollo socioeconómico, el bienestar humano o incluso el futuro de la humanidad. Su efecto es notable tanto a nivel de especie como de ecosistema, así como a las complejas interacciones entre organismos y/o sus hábitats comprometiendo el estado de los ecosistemas, su estructura y función y los servicios ecosistémicos que brindan. La extrema sensibilidad al cambio climático de la Península Ibérica incrementa dicho riesgo en ecosistemas ya amenazados como los sistemas agroforestales de castaño y alcornoque así como para ciertas especies como el oso pardo cantábrico. Por lo tanto, se requieren medidas cuantitativas que representen una función clave del ecosistema e informen sobre el estado del ecosistema como son los indicadores de producción primaria, indicadores ecológicos que permiten cuantificar la asimilación de carbono a través de la fotosíntesis, representando así una de las funciones más importantes del ecosistema. El objetivo general de esta tesis fue analizar los patrones espaciales de la producción primaria, sus cambios y sus factores impulsores del cambio frente al cambio climático en la Península Ibérica para comprender el estado de nuestros ecosistemas, la dinámica vegetal y animal o las estrategias adaptativas de las especies. Para ello, se emplearon diferentes fuentes de datos que permitieron caracterizar el uso del suelo, se utilizaron excrementos de oso para posicionar a los individuos y conocer su dieta, y datos procedentes de sensores remotos y teledetección para caracterizar la producción primaria. Se utilizaron métodos de ajuste paramétricos y no paramétricos para modelar las relaciones con los predictores climáticos, predecir los riesgos para el ecosistema y construir modelos de alimentación. Además, se realizó un análisis de puntos calientes para identificar grupos espaciales significativos de áreas con alta y baja eficiencia de uso de carbono. En general, se encontró que la gestión humana afecta positivamente la productividad de los ecosistemas, mientras que la disponibilidad de agua es más importante que la temperatura. La densidad del rodal juega un papel clave en la adaptación a la variación climática, manteniendo unas condiciones microclimáticas que hacen que ecosistemas sean menos dependientes de las variables ambientales. Se ha observado que el estado de los ecosistemas de castaño es bastante preocupante, mientras que el estado de los ecosistemas de alcornoque refleja sus rasgos ecológicos y las estrategias adaptativas frente a la sequía. Finalmente, con respecto al oso pardo cantábrico, la producción primaria ha sido decisiva para comprender sus patrones de consumo de frutos secos y predecir la distribución espacial relacionada con dicho consumo durante la hiperfagia, pues nuestros modelos destacan las áreas de mayor importancia para la especie o donde se ha producido una expansión reciente.

RESUMEN (en Inglés)

Climate change is considered one of the main threats to biodiversity, ecosystems, socioeconomic development, human well-being, or even the future of humanity. In nature, it affects from individual species to ecosystems, going through the complex interactions among organisms and/or their habitats ,compromising the state of ecosystems, their structure and

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function and the ecosystem services they provide. However, the extreme sensitivity to climate change of the Iberian Peninsula increases the risk for threatened species and ecosystems such as sweet chestnut and cork oak agroforestry systems and Cantabrian brown bears. Therefore, quantitative measures that represent a key ecosystem function and inform about ecosystem state are necessary. Primary production indicators are ecological indicators that allow to quantify the carbon assimilation through photosynthesis, thus representing one of the most important functions of the ecosystem. The general objective of this thesis was to analyse the spatial patterns of primary production, its changes and its drivers of change against climate change in the Iberian Peninsula to understand the state of our ecosystems, plant and animal dynamics or species adaptive strategies. For this purpose, different data sources were employed to characterise land use, bear faeces were used to position individuals and know their diet, and long-term remote sensing data provided primary production. Parametric and non-parametric fitting methods were used to model relationships with climate predictors, predict the risks to ecosystem and construct foraging models. Hotspot analysis was conducted to identify significant spatial clusters of high- and low-efficiency areas. In general, we found that human management positively affects the ecosystems productivity, while water availability is more important than temperature. Tree density plays a key role in the adaptation to climate variation, maintaining microclimatic conditions that make ecosystems less dependent on environmental variables. We observed that the state of the sweet chestnut is quite concerning while the state of cork oak reflects the ecological traits and the adaptive strategies used to survive drought seasons. Finally, regarding Cantabrian brown bears, primary production has been decisive to understand their nut foraging patterns and to predict spatial distribution related to nut consumption during the hyperphagia season, with our models highlighting areas of high importance or where recent expansion has occurred.

SR. PRESIDENTE DE LA COMISIÓN ACADÉMICA DEL PROGRAMA DE DOCTORADO EN BIOGEOCIENCIAS

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GOBIERNO DEL
PRINCIPADO DE ASTURIAS

En tu memoria,
Angelitas

Agradecimientos

> *"Y una vez que la tormenta termine, no recordarás como lo lograste, como sobreviviste. Ni siquiera estarás seguro si la tormenta ha terminado realmente. Aunque una cosa si es segura, cuando salgas de esa tormenta, no serás la misma persona que entró en ella. De eso trataba la tormenta."*
>
> Haruki Murakami

6:48h. 31 de julio del 2018. Jornada intensiva de verano, un día más que comienza en la oficina. Esperas un día tranquilo, pues aunque debes hacer unas entregas, todo está bajo control. Sin embargo, estás nervioso, tienes otros frentes abiertos y hoy... Hoy se avecina tormenta.

15:00h. 31 de julio del 2018. Se termina la jornada laboral, mañana más, y mientras, desde el teléfono y de camino a casa, porque ya no puedes esperar más, confirmas que se ha publicado esa resolución en la que tanto anhelas ver tu nombre entre los seleccionados. Tic, tac, tic, tac... Momentos de incertidumbre mientras se abre el documento, no puedes esperar. !Venga, vamos, vamos! Usas el buscador, porque sí, por que no puedes esperar a leerlo todo y ver donde estás. Al fin, apareces, pero no sabes en que apartado. ¿Seleccionado o excluido? Subes en el documento, hasta ver donde estás. Y ahora sí, hoy es tu día, estás entre los seleccionados. ¡¡Gritas!!, de rabia, de alegría, de saber que lo has conseguido, y que estás dentro. Vas solo por la calle, pero te da igual, lo disfrutas. Y así, es como comienza mi particular tormenta en la que tantos os habéis mojado.

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Y por supuesto, a Ana. Con quien comparto la vida, los momentos, las experiencias, todo... Quien ha sufrido tanto como yo esta tesis, riéndose con mis locuras y escuchando mis cabreos, y en definitiva, aguantándome en las duras y en las maduras. Gracias por tu apoyo. Gracias por estar ahí. Gracias por quererme. Gracias.

Contents

CHAPTER 1

Introduction

1.1 A key function

The energy flow in terrestrial ecosystems is one of the major ecosystem processes and begins with the use of sunlight by autotrophic organisms. An autotrophic organism is the one which is capable to synthesise the nutrients it needs from inorganic compounds, i.e. they are able to make its own food. Specifically, those that capture sunlight energy and build it into organic matter through photosynthesis are called phototrophs. Plants, algae and some bacteria fall into this group. Plants, through photosynthesis, use sunlight, atmospheric CO_2 and water to produce glucose (to be used as energy or food) and release oxygen. The rate at which photosynthesis occurs is called primary production. Henceforth, and for simplicity, primary production will always be referred to as primary production by photosynthetic producers in terrestrial ecosystems.

Primary production constitutes the basis of the carbon cycle in terrestrial ecosystems. It is the first step in the capture, storage, and transfer of energy, providing the organic carbon that supports the basis of the trophic level (including humans), rather, the fundamental process of life (Chapin et al., 2011; Pace et al., 2021). Autotrophs and heterotrophs (consumers) are supported by primary production. On this also depends the reproductive function of plants (Fernández-Martínez et al., 2017; Journé et al., 2021), i.e. the fruit production, which is another fundamental part of the ecosystem functioning, ensuring the continuity of the species itself and constituting an important food source for animal species (or even the only one for such as frugivorous species). Thus, primary production is a key ecosystem function for the structure, functioning and composition of terrestrial ecosystems (Costanza et al., 2007; Falkowski et al., 2000; Sekercioglu, 2010).

However, its importance goes beyond: the Millennium Ecosystems Assessment classified primary production as one of the most important supporting ecosystem services or functions (Millennium Ecosystem Assessment, 2005), which means that it is absolutely necessary for the production of all other ecosystem services. Therefore, understanding that ecosystem services are *"components of nature, directly enjoyed, consumed, or used to yield human well-being"* (Boyd & Banzhaf, 2007), changes in primary production will affect the provision of ecosystem services to society, and these in turn will be reflected in human well-being in the short- and long-term.

1.2 Components of primary production

Primary production is the rate at which photosynthesis occurs, or in other words, the rate at which CO_2 is assimilated (Schulze et al., 2019). From a physiological point of view, photosynthesis is an oxidation-reduction process (Equation 1.1). In the oxidation process the water molecule releases electrons with the production of oxygen and the reduction of CO_2 to form carbohydrates (CH_2O; sucrose and starch) compatible with the needs of the plant cells, and that ultimately will be used by the plant for growth and storage.

$$CO_2 + H_2O + light \longrightarrow (CH_2O) + O_2 \tag{1.1}$$

Gross primary production (GPP) reflect the total amount of carbon stored by plants, which takes into account whole-plant (autotrophic) respiration ($\mathrm{R_a}$). $\mathrm{R_a}$ is the toll that plants must pay for their growth and maintenance (Amthor, 2000; Collalti et al., 2020; Schulze et al., 2019; Van Iersel, 2003), and by which a reduction of C takes place. Therefore, the total amount of energy consumed by $\mathrm{R_a}$ will determine how much energy is available for other uses such as the assimilation processes of vegetative growth and reproduction as well as other non-structural compounds (Collalti & Prentice, 2019; Pace et al., 2021; Pallardy, 2010; Valentini et al., 2000). Subtraction of $\mathrm{R_a}$ gives us the net primary production (NPP), i.e. the net carbon transformed into biomass (leaves, branches, trunks and roots) (Clark et al., 2001; Collalti & Prentice, 2019; Collalti et al., 2020) (Figure 1.1). Both GPP and NPP are expressed as units of C mass per unit area and time (e.g. in g C $\mathrm{m^{-2}}$ $\mathrm{yr^{-1}}$ or kg C $\mathrm{m^{-2}}$ $\mathrm{yr^{-1}}$) and are related as follows (Equation 1.2):

$$NPP = GPP - R_a \tag{1.2}$$

While the GPP values must be greater than zero, otherwise life would not occur, NPP values could reach zero or even negative for limited periods (Collalti & Prentice, 2019; Roxburgh et al., 2005). A zero NPP value implies GPP equal to $\mathrm{R_a}$ which means that the total fixation of energy through photosynthesis is intended to cover the maintenance cost and consequently there is no production of new biomass, i.e, the plant begins a survival phase. But NPP can also be negative for limited periods where $\mathrm{R_a}$ is higher than GPP.

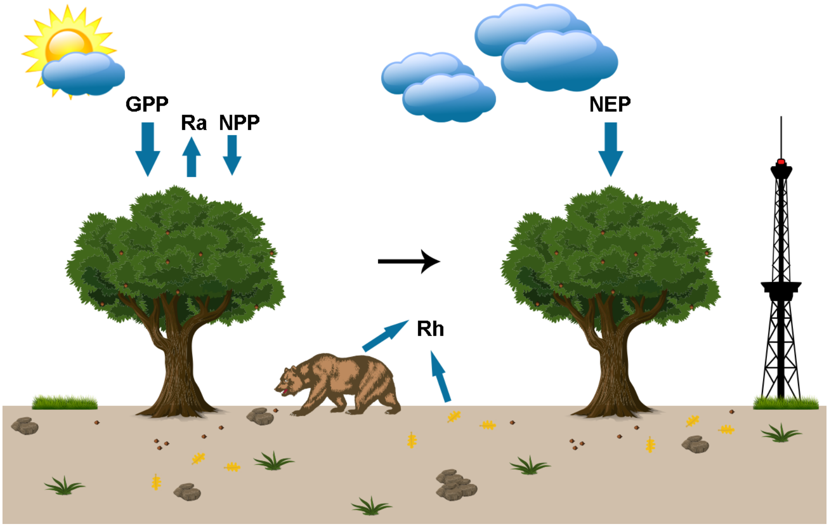

Figure 1.1: Carbon (C) fluxes through an ecosystem estimated or measured by remote sensing and eddy covariance method. Remote sensing usually estimate gross primary production (GPP) and net primary production (NPP). Autotrophic respiration (R_a) is the growth and maintenance cost. Eddy covariance methods measure net ecosystem production (NEP), thus considering R_a and heterotrophic ecosystem respiration (R_h). Inspired by Xiao et al. (2019).

Besides, it is worth mentioning that NPP should always be understood as a temporary element (that is, a rate per unit of time), and therefore should be interpreted as a different concept from standing biomass, which is a measure of a given area at any given point in time (e.g., in kg C m^{-2}) (Pace et al., 2021; Schulze et al., 2019). Also, it should be considered that part of the primary production is allocated to non-structural compounds that are not used for growth, such as sugars, organic acids, or volatile compounds (Collalti & Prentice, 2019). Thus, the total standing biomass of an ecosystem will be the result of the sum of the NPP over time minus biomass losses, and subsequently, over a relatively long period of years, NPP must be equal to or greater than biomass. However, between both concepts there is no direct relationship, so there could be a low rate of primary production at the same time that the biomass is relatively high as a result of accumulation over years, which would be the case of slow-growing species (Field et al., 1995; Lambers & Oliveira, 2019).

Relating the two basic components of primary production, GPP and NPP, it is possible to know the efficiency (or ability) of plants to sequester atmospheric CO_2 through photosynthesis and transform it into new biomass. It is the ratio of NPP to GPP, or better known as carbon use efficiency (CUE) (Gifford, 1995) (Equation 1.3). Values range from 0 to 1, expressing the percentage of assimilated C that is transformed into biomass, where, for example, a rate of

0.4 indicates that 40% of allocated C is transformed into biomass. Thus, the higher the value, the higher the growth per C unit acquired.

$$CUE = \frac{NPP}{GPP} \tag{1.3}$$

Despite the simplicity of the terms, measuring primary production is challenging as there is still great uncertainty about the C allocation by plants. So much so that for a long time two schools of thought have coexisted: one that argued that CUE is constant and universal across forest stands and ecosystems, arguing therefore that NPP-GPP relationship is constant (Gifford, 1995; Waring et al., 1998; Waring et al., 2016) and the second one that emphasised the opposite, CUE varies with environmental conditions (Amthor, 2000; Collalti & Prentice, 2019; DeLucia et al., 2007; Mäkelä & Valentine, 2001). Recently, a new work has been published by those who defended a global and constant CUE across biomes, in which they recognised that there was a misinterpretation of their original publication and that the CUE should be understood as a variable, although on the other hand, they do not discard their original idea of using a constant ratio in global assessments due to the lack of information about NPP allocation (Landsberg et al., 2020).

Either way, it seems to be clear that primary production depends on many factors such as age (Fernández-Martínez et al., 2014; Mäkelä & Valentine, 2001), ecological traits (Madani et al., 2018), stand characteristics and management regime (Campioli et al., 2015), soil characteristics (Ni et al., 2022; Vicca et al., 2012), climate (Gilabert et al., 2015; He et al., 2018; Reichstein et al., 2013; Zhang et al., 2009; Zhang et al., 2014), or disturbances (Kunert et al., 2019), which allow to consider primary production components (GPP, NPP and CUE) as ecological indicators, i.e., quantitative measures able to gather in a single value a set of environmental factors that represents a key ecosystem function, informs about ecosystem state, and gives us interesting information about the risk and resilience of this ecosystem or the species that make it up (Yin et al., 2018). In this regard, the quantification of spatio-temporal variability in NPP and CUE is essential to monitoring how the ecosystem will respond to future changes.

1.3 Measuring primary production

Despite primary production components being theoretically simple, respiration is the most difficult to measure owing to the complexity that gathers (Amthor, 2000; Roxburgh et al., 2005; Waring et al., 1998). In GPP and NPP, some components such as C allocated to non-structural compounds (e.g. sugars, organic acids, or volatile compounds), C losses (e.g. herbivory) or belowground allocation are rather difficult and costly to measure (Field et al., 1995; Knapp et al., 2014). Added to this is the complexity of measurement of primary production in terrestrial ecosystems such as forests, where all layers (tree, shrub and herbaceous) account for and need to be measured (Liang & Wang, 2020). Traditional methods are based on counting biomass directly through harvesting or indirectly using specific allometric equations (Liang & Wang, 2020; Sala & Austin, 2000).

Nowadays, recent technological advances have popularised the use of eddy covariance (EC) flux towers, a micrometeorological direct method based on gas exchange between ecosystems and atmosphere (Baldocchi, 2014; Baldocchi, 2020; Xiao et al., 2019). Specifically, EC towers measure the covariance between a turbulent wind (vertical) and the concentrations of gases it contains (such as CO_2) in a few hundred meters around the tower (Baldocchi, 2014), thus allowing to measure the uptake or emissions of CO_2 by ecosystems. Technically, EC towers measure net ecosystem exchange (NEE), as instantaneous measurement of gas exchange, and net ecosystem production (NEP), as the measurement deals with changes in carbon stocks of the ecosystem. NEP differs slightly from NPP since it considers heterotrophic ecosystem respiration ($\mathrm{R_h}$) relating to GPP and NPP (Equation 1.4) in a direct, precise and continuous way (Figure 1.1). Numerous flux networks have been established across the globe, e.g. the global network of networks, FLUXNET2015 (Pastorello et al., 2020), which comprises multiple regional flux networks, however, the spatial scope is still limited and some ecosystems are under or not represented.

$$NEP = GPP - R_a - R_h = NPP - R_h \tag{1.4}$$

Advances in remote sensing have made it possible to overcome the spatial limitations of EC flux towers providing continuous and freely available spatio-temporal information. Through different approaches such as satellite-derived vegetation indices (VIs)-based models (Huang et al., 2019; Lin et al., 2019), light use efficiency (LUE) models (Hilker et al., 2008; Ryu et al., 2019; Xiao et al., 2019) and process-based models (He et al., 2018) among others, have allowed to quantify GPP and NPP on a regional and global scale. Earlier models like 3-PG (Landsberg & Waring, 1997) or CASA (Potter et al., 1993) (a detailed list can be found on Collalti and Prentice (2019)) assumed a fixed value of CUE to quantify $\mathrm{R_a}$. However, increasing evidence of a variable CUE (DeLucia et al., 2007; Zhang et al., 2009) has led to the development of new models that quantified respiration independently. Among which is the MODerate resolution Imaging Spectroradiometer (MODIS) GPP and NPP product which has become one of the most reliable and popular models (Xiao et al., 2019).

The global MODIS data collection has provided the first operational and spatially continuous GPP and NPP data since 2000 to the present. The algorithm, which relies on the LUE approach (Monteith, 1972), computes GPP as a product of the incident photosynthetically active radiation (PAR), the fraction of absorbed PAR (fAPAR) and the LUE (ε), while NPP is derived from an autotrophic respiration module. Further description of the algorithm can be found on Running et al. (2004) and Zhao et al. (2005). Heinsch et al. (2006) checked the accuracy of MODIS GPP and NPP products arguing that it is consistent with the EC flux tower measures ($r = 0.859$) and that it is capable of capturing spatio-temporal patterns of GPP and NPP across biomes and climate regimes. Turner et al. (2006) pointed out that GPP and NPP tend to be overestimated at low productivity sites and underestimated in high productivity sites, but being responsive to general trends associated with local climate and land use, which agrees with Heinsch et al. (2006). Therefore, MODIS data collection provides a good opportunity to assess spatial patterns of primary production and its climate influence in wide areas and at zero cost, which in turn will form the basis for understanding the state of our ecosystems and their responses in future scenarios of climate change.

1.4 Climate change

From individual species to ecosystems, going through the complex interactions among organisms and/or their habitats are being affected by climate change, compromising the state of ecosystems, their structure and function and the ecosystem services they provide. For that, worldwide and for decades, climate change has been considered one of the main drivers that threaten forest ecosystems and whose trend in the last few years has risen faster than in any other previous period (IPCC, 2021), mainly due to the emissions of greenhouse gases (GHGs) such as CO_2, one of the most important GHGs responsible for global warming. Consequently, at the beginning of the 21^{st} century the Millennium Ecosystems Assessment considered climate change as one of the main drivers of ecosystem change (Millennium Ecosystem Assessment, 2005).

However, despite the warnings, far from improving, the climatic situation has gotten worse. Each decade has been warmer that the previous decade, being the last one the warmest on records while the last six years (2015-2020) registered the warmest records since the pre-industrial period and complying with the expected precipitation reduction (Figure 1.2) (Giorgi & Lionello, 2008; IPCC, 2021; World Meteorological Organization, 2021). All this has meant that in 2019 the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) once again focused on climate change, arguing that it would become an important driver of changes in nature and its contributions to people (IPBES, 2019). But this is not all, the climate change predictions are not promising at all. In addition to the increase of extreme events such as heavy storms, late frosts, heat waves, etc, recent works have argued that droughts will occur more frequently, with greater duration and intensity and with the aggravation that in the Iberian Peninsula they might not be followed by wet winters (Böhnisch et al., 2021).

As said above, climate change is strongly linked with primary production, since it constitutes the basis of the carbon cycle in terrestrial ecosystems, of which atmospheric CO_2 is a key component (Cole et al., 2021; Schulze et al., 2019). Through photosynthesis C is absorbed from the atmosphere while through R_a part of this assimilated C is returned back to the atmosphere,

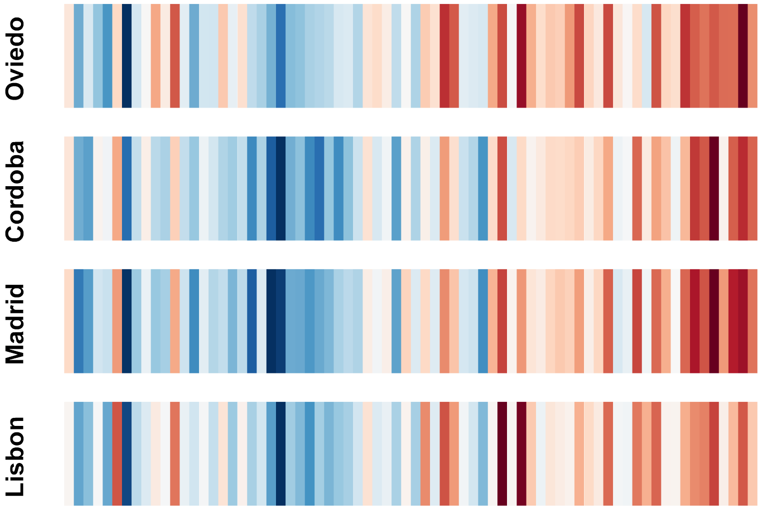

Figure 1.2: Warming stripes from 1950 to the present in some cities of the Iberian Peninsula. Blue bars indicate lower temperatures than average. Higher, it turns red. Data source: ERA5-Land (Muñoz Sabater, 2019)

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controlling the increase in the atmospheric CO_2 concentration, and therefore, having direct impacts on climate (Equation 1.1). Inversely, the processes of photosynthesis and respiration are also affected by climate, thus affecting productivity levels. Therefore, climate change can be considered a two-way process that feeds back. First, it leads to biodiversity losses, compromising the state of ecosystems, which, with a more degraded state, are not capable of mitigating the effect of GHG emissions, so the process is accelerated again. Here lies the importance of conserving high biodiversity ecosystems. However, it should be considered that not all species (or ecosystems) have the same response to climate changes (David-Schwartz et al., 2019; Kumarathunge et al., 2019; Moritz & Agudo, 2013; Radchuk et al., 2019; Vanhove et al., 2021), being necessary to consider different dynamics or adaptive strategies at different levels (species, ecosystem, and their interactions) (Weiskopf et al., 2020).

1.5 Research needs and scope

As it has been pointed out in previous sections, primary production plays a fundamental role in understanding the state of terrestrial ecosystems and their relationship with climate change. This becomes more important when it takes place in regions extremely sensitive to climate change, as is the case of the Iberian Peninsula, where this thesis is focused. But even worse could be the threat to those species and ecosystems located at the limits of their distribution, with declining trends or seriously threatened. Threatened species and ecosystems such as those discussed below were the subject of this thesis.

Sweet chestnut (*Castanea sativa* Mill.) is one of these species with declining trends, due to the land abandonment and degradation process since the middle of the 20th century, originated by changes in socio-economic activities in rural areas (Díaz-Varela et al., 2018; Roces-Díaz et al., 2018a), seriously threatened by some pests and diseases in the last decades, such as ink disease (caused by *Phytophthora cinnamomi* Rands), chestnut blight (*Cryphonectria parasitica* (Murrill) Barr) or asian chestnut gall wasp (*Dryocosmus kuriphilus* Yasumatsu) (Gil-Tapetado et al., 2021; Homs et al., 2001; Lombardero et al., 2021), sensitive to summer droughts (Conedera et al., 2010) and whose state could be aggravated in the near future by climate change, due to its direct and indirect relationships with the former variables. From the socio-economic point of view, it is one of the most important native broadleaved tree species in the Iberian Peninsula (Roces-Díaz et al., 2018b) whose distribution range has been strongly modified by human management (Conedera et al., 2004). It currently occupies the northwest of Spain and northern Portugal, with isolated stands in the south, centre and east of Spain (Figure 1.3), and hence, distributed both in Atlantic and Mediterranean biogeographical regions which in turn constitute two ecotypes differently adapted to climatic conditions (Míguez-Soto et al., 2019). Due to the human management, the chestnut can be found in natural and semi-natural forest stands, as well as human managed stands that traditionally constitute multifunctional agroforestry systems (AFS) such as traditional orchards known in NW Spain as soutos, castañeros or castañeos (in which specific techniques for pruning and grafting are used) and modern plantations for producing wood or chestnut fruit (Míguez-Soto et al., 2019; Roces-Díaz et al., 2018a).

Cork oak (*Quercus suber* L.) is another species with centuries-long management that has given place to AFS known as *montados* in Portugal and *dehesas* in Spain, where the largest populations of this species are found (Figure 1.3) (Díaz-Fernández et al., 1995; Joffre et al., 1999; Pinto-Correia et al., 2011). The land cover patterns of *dehesas* or *montados* are similar to those of savannah, characterised by the presence of scattered trees in varying densities, although it is generally low, with the presence of herbaceous or shrub vegetation in the understory (Correia et al., 2016; Pereira et al., 2007; Piayda et al., 2014; Pinto-Correia et al., 2011). Cork oak AFS state is currently compromised (Costa et al., 2009), so much that it has recently been included as a natural habitat type of community-wide interest within the EU Habitats Directive, and categorised as in serious danger of disappearance. The situation of decline is critical, seriously threatened and affected by various factors (both natural and human-induced) in addition to climate change (Aguilera et al., 2020), such as the proliferation of pests and diseases (Brasier et al., 1993; González et al., 2020), fire recurrence (Guiomar et al., 2015; Silva & Catry, 2006), lack of regeneration, change in land use, and land abandonment (Bugalho et al., 2011; Godinho et al., 2016; Pinto-Correia & Mascarenhas, 1999).

As said above, the species previously mentioned and the ecosystems that

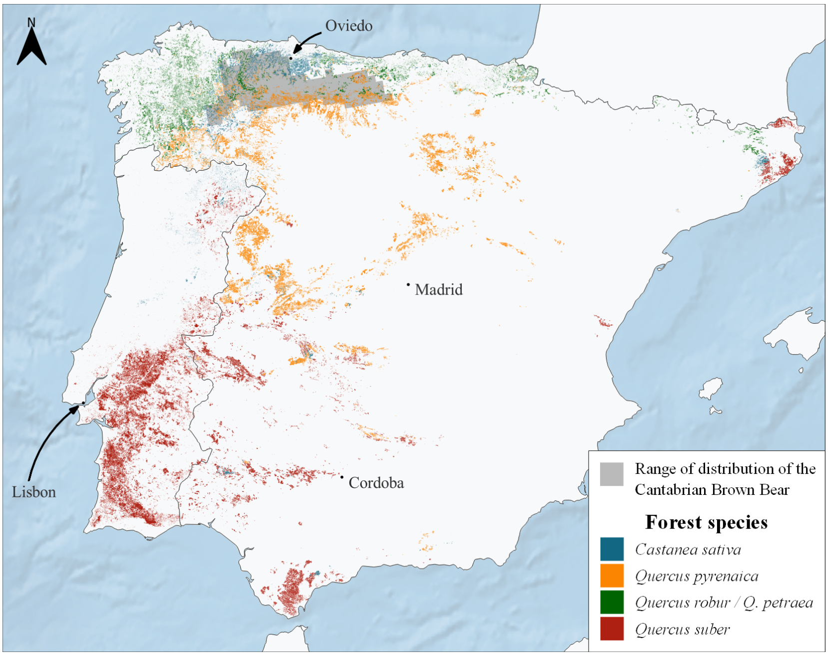

Figure 1.3: Range of distribution of the Cantabrian Brown Bear and presence of forest species. Forest species presence was extracted from the Forest Map of Spain (MFE) and only the predominant species is represented, although co-occurrence of species is possible.

they form constitute socio-ecological AFS that provide valuable contributions to the landscape and environment, fulfilling fundamental functions and processes that ultimately produce a number of types of ecosystem services, such as provision (food, wood and biomass production, etc.), regulation (water quality, erosion control, pollination, disturbance prevention, gene pool, climate regulation, etc.) and cultural services (aesthetic landscape, sense of place, traditional knowledge, etc.). However, there are species whose conservation, due to their consideration of “flagship” and/or “umbrella” species, directly contributes to that of other organisms, habitats or ecological communities (Barua, 2011).

The Cantabrian brown bear (*Ursus arctos* L.) is one of thoset umbrella species, considered as a priority species in the Directive Habitats of the European Union, and as Endangered by the Red List of Threatened Species of the International Union for the Conservation of Nature (IUCN) and the Catalogue of Threatened Species in Spain (Palomero et al., 2021). Despite being still endangered, the Cantabrian brown bear population is growing and expanding in range (Blanco et al., 2020; Gonzalez et al., 2016) implying a challenge in the climate change context. While shorter or absent hibernation periods are expected (Evans et al., 2016; Pigeon et al., 2016), and therefore, more active bears, some tree species related to the brown bear diet during autumn hyper-

Figure 1.4: A brown bear feeding on oak acorns. Source: Navarro et al. (2021)

phagia, such as beech (*Fagus sylvatica* L.) and Atlantic oaks (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) (Figure 1.4) (Bojarska & Selva, 2012; Naves et al., 2006; Rodríguez et al., 2007), may suffer a drastic reduction or fruit failure in the Cantabrian Mountains, (Ballesteros et al., 2018; Clevenger et al., 1992; Dyderski et al., 2018) which could compromise the reproductive capacity of the species (López-Alfaro et al., 2013) or intensify the changes in the bear diet (Navarro et al., 2021). However, climate change could lead to improved productivity of species such as thermophilic oaks (*Q. faginea* Lam., *Q. ilex* L.) and sweet chestnut *C. sativa* Mill. which already form part of the bear diet (Naves et al., 2006; Rodríguez et al., 2007) thus turning them into a key resource, particularly, sweet chestnut whose production is very regular (with relatively few mast years) as a large number of sweet chestnut cultivars undergo asynchronous production.

1.6 Objectives

The general objective of this thesis is to analyse the spatial patterns of primary production, its changes and its drivers of change against climate change in the Iberian Peninsula to understand the state of our ecosystems, plant and animal dynamics or species adaptive strategies.

To do that, the main objective was divided into specific questions that were addressed in the chapters listed below:

- **Chapter 2**. Can climate factors compromise the state and resilience capacity of chestnut ecosystem production?

  In this chapter, I evaluated the influence of climatic variations on chestnut ecosystems in the Iberian Peninsula, as well as their resilience to climate change scenarios. The high constraint imposed on the sample selection led to the selection of practically monospecific stands, and therefore, it allows us to consider it from a species-level perspective.

- **Chapter 3**. Can climate factors compromise the state of cork oak ecosystems? What role does geographical location play?

  In this chapter, I assessed the influence of climate variability on different cork oak in the Iberian Peninsula and the role that the geographical location plays against adverse effects of climate. The human management and species characteristics require an analysis from an ecosystem perspective.

- **Chapter 4**. Can primary production indicators be used to understand the nut foraging patterns and predict the spatial distribution related to nut consumption of an umbrella species like the Cantabrian brown bear during the hyperphagia season?

  In this chapter, I analysed the spatial distribution of brown bears during hyperphagia to understand the nut foraging patterns and modelled nut consumption by using vegetation productivity, topographical variables and landscape metrics. It implies an animal species interacting with different plant species, as well as with the entire ecosystems including humans.

Each one of these chapters corresponds to an original research work written by the author and different colleagues that have been published in the following journals:

- **Chapter 2**. Pérez-Girón, J. C., Álvarez-Álvarez, P., Díaz-Varela, E. R., & 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. Ecological Indicators, 113, 106199. doi: https://doi.org/10.1016/j.ecolind.2020.106199

- **Chapter 3**. Pérez-Girón, J. C., Díaz-Varela, E. R., & Álvarez-Álvarez, P. (2022). Climate-driven variations in productivity reveal adaptive strategies in Iberian cork oak agroforestry systems. Forest Ecosystems, 9, 100008. doi: https://doi.org/10.1016/j.fecs.2022.100008.

- **Chapter 4**. Pérez-Girón, J. C., Díaz-Varela, E. R., Álvarez-Álvarez, P., Palacios, O. H., Ballesteros, F. , & López-Bao, J. V. (2022). Linking landscape structure and vegetation productivity with nut consumption by the Cantabrian brown bear during hyperphagia. Science of The Total

Environment, 813, 152610. doi: https://doi.org/10.1016/j.scitotenv.2021.152610.

Further information about the impact factor can be found on Chapter 7.

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CHAPTER 2

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

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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

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ABSTRACT

Sweet chestnut agroforestry systems make valuable contributions to the landscape and environment, fulfilling fundamental functions and processes. Net primary production (NPP) and carbon use efficiency (CUE) are commonly used as ecological indicators to evaluate the responses of the terrestrial carbon cycle to climate change. Nonetheless, although climate-induced primary production changes have been widely documented at the global scale, few studies have addressed this issue at local scale in relation to sweet chestnut forests. Data from 65 climate maps and MODIS remote-sensed data captured in the Iberian Peninsula between 2000 and 2015 were analysed in this study. Different statistical methods (Linear Regression and Classification and Regression Trees) were used to analyse the potential influence of climate change on sweet chestnut primary production, thus enabling assessment of ecosystem and ecosystem service (ES) supply and of the resilience of these systems in a future scenario of climate change in the Iberian Peninsula. The findings for the whole of the Iberian Peninsula show that NPP and CUE are negatively correlated with temperature variables and positively correlated with latitude. High NPP values mainly corresponded to northern Spain, which is characterised by cold, humid conditions. The CUE values were highest in northern Portugal, mainly in managed, monospecific forest. Overall, the fitted models showed a temporary response in which the monthly variables were particularly important and water availability was more important than temperature. The findings suggest that precipitation is not a limiting factor in Atlantic areas, but that water availability tends to be a limiting factor in Mediterranean areas. However, mean annual temperature (MAT) is also an important driver of sweet chestnut production and may be a limiting factor in a future scenario of climate change. Regions of Provenance (RoP) proved useful for explaining NPP and CUE and classifying the sweet chestnut agroforestry systems. Finally, the study findings also revealed that Iberian sweet chestnut ecosystems and the associated ES supplies are at risk of being seriously affected or even disappearing as a result of climate change, especially in some Mediterranean areas of southern and central Spain.

1. Introduction

Climate is considered one of the main drivers of biodiversity and ecosystem change (IPBES, 2019; Millennium Ecosystem Assessment, 2005), and it is expected to become a major stressor (Bellard et al., 2012; Urban, 2015; Willeit et al., 2019) and a determining factor for ecosystem resilience (Moritz and Agudo, 2013) in the future. Resilience management in social-ecological systems (Berkes and Folke, 1998; Gunderson and Holling, 2002) involves providing the information necessary for activating institutional, adaptive governance (Berkes, 2017; Folke et al., 2005, 2016). In this study we focus on the analysis of the potential influence of climate change on sweet chestnut forests, considered examples of socio-ecological agroforestry systems (Diaz-Varela et al., 2018; Roces-Diaz et al., 2018). Sweet chestnut (*Castanea sativa* Mill.) has a scattered distribution throughout Europe and Western Asia. In Europe, the species covers more than 2.5 million hectares of land (Conedera et al., 2016; Fernández-López and Alía, 2003), with more than 10% located in the Iberian Peninsula: 58,000 ha in Portugal

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(DGT, 2015) and about 239,000 ha in Spain (currently available data, from the III and IV Spanish National Forest Inventories). Sweet chestnut is one of the most important native broadleaved tree species in the Iberian Peninsula, where its distribution is discontinuous. The species mainly occurs in the northwest of Spain and northern Portugal, with isolated stands in the south, centre and east of Spain. It is found at elevations ranging between sea level and 1,800 m and tolerates a wide range of climate conditions, varying from cold, wet conditions in the Atlantic bioclimatic region to hot, dry conditions in the Mediterranean bioclimatic region. Chestnut is generally a temperate deciduous species that prefers temperatures of between 10 °C and 14 °C and minimum annual rainfall of 700 mm (Álvarez Álvarez et al., 2000). It can also be sensitive to summer drought (Conedera et al., 2010).

Sweet chestnut is therefore found in natural and semi-natural forest stands, as well as in managed stands, including both traditional orchards (in which specific techniques for pruning and grafting are used) and modern plantations for producing wood or chestnut fruit (Míguez-Soto et al., 2019; Roces-Diaz et al., 2018). In addition, wild Iberian *C. sativa* populations can be divided into two ecotypes; the Northern Iberian gene pool (mesophytic with higher growth rates), and the Mediterranean Iberian gene pool (more xeric traits and more adaptable to drought) (Míguez-Soto et al., 2019).

C. sativa orchards traditionally constitute multifunctional agroforestry systems (AFS) that can take the form of high-forest, simple coppices, coppices with standards or grafted orchards (Míguez-Soto et al., 2019). These systems provide valuable contributions to the landscape and environment (Díaz Varela et al., 2009; Martín et al., 2012; Roces-Diaz et al., 2018), fulfilling fundamental functions and processes such as primary productivity, soil formation, nutrient cycling, regulation of hydrological flows and biological diversity. This finally produces a number of types of ecosystem services (ES), including provision (food, wood and biomass production, etc.), regulation (water quality, erosion control, pollination, disturbance prevention, gene pool, climate regulation, etc.) and cultural services (aesthetic landscape, sense of place, traditional knowledge, etc.) (Jose, 2009; Roces-Diaz et al., 2018). In addition, sweet chestnut orchards may constitute biodiversity spots with important roles in alternative area-based biodiversity conservation strategies (Diaz-Varela et al., 2018). Consequently, sweet chestnut forests and orchards play a fundamental role in human life and well-being, as well as in wildlife conservation.

Sweet chestnut ecosystems in the Iberian Peninsula are currently threatened by different stressors (both natural and human-induced), including climate change, abandonment of traditional orchards, wildfire and an increased incidence of diseases and pests. As the impact of these factors on ecosystems may involve a risk of loss of ecological processes and properties (Mooney et al., 2009; Schröter et al., 2005, 2019), these in turn may seriously affect the provision of ecosystem services to society, and a reduction in human well-being. Owing to the increase in emissions of greenhouse gases (GGG) such as CO_2 (IPCC, 2007), climate change is one of the most outstanding drivers of ecosystem changes. Anomalies in mean temperatures could affect the Iberian Peninsula, with increments of 1.7 to 4.8 °C, while yearly precipitation could fall by as much as 20% (Christensen et al., 2007; IPCC, 2001, 2013). Consequently, climate change could have serious consequences for chestnut ecosystems in the Iberian Peninsula, possibly leading to significant loss of the goods and services provided. Impacts on the physiological functioning of the plants can be both direct (e.g. by hydric stress) and indirect (via effects on interspecific interactions). Thus, some authors suggest that the increasing temperatures may favour the spread of *Cryphonectria parasitica* (chestnut blight) and reduce the systematically acquired resistance of the host trees (Anderson et al., 2004; Wilhelm et al., 1998). In addition, moisture is considered a key factor for the establishment, spread and longevity of *Phytophthora cinnamomi* (ink disease) (Hardham, 2005).

Indicators are required to enable assessment of the current state of sweet chestnut ecosystems and their related services and of the effects of climate change on development of these ecosystems (Schröter et al., 2005). Specifically, owing to the major role of plants in fixing atmospheric CO_2 via photosynthesis (Falkowski et al., 2000; Sekercioglu, 2010), primary production (i.e. the rate of carbon fixation) is a major ecosystem function that is sensitive to changes in climate (Huang et al., 2019; Stocker et al., 2019; Tang et al., 2019). As a result of the relationship between ecosystem function and the service provision capacity (Costanza et al., 2017, 2007), primary production may thus be considered a useful indicator for climate-induced risks in ecosystems and ecosystem services. Among the indicators of primary production, both net primary production (NPP) and carbon use efficiency (CUE) are widely used to evaluate ecosystems and ES supply (Tang et al., 2019; Zhang et al., 2014), especially regarding the effects of land use and climate change on ecosystems. NPP is the net carbon that is stored after respiration and transformed into biomass. CUE represents the efficiency of plants to sequester carbon from the atmosphere through photosynthesis and is calculated as the ratio of NPP to gross primary production (GPP), i.e. the total amount of carbon stored by plants. Remote sensing techniques enable primary production indicators to be monitored at global or regional scales (Ma et al., 2019; Running et al., 2004). The capture of open data by moderate resolution imaging spectroradiometer (MODIS) provides an opportunity to study the state of ecosystems and the associated risks (He et al., 2018).

The aims of the present study were (i) to evaluate the influence of climate variability on sweet chestnut AFS production in the Iberian Peninsula by using primary production indicators (NPP and CUE) to assess ES supply and associated risks, and (ii) to analyse the resilience of sweet chestnut AFS in a future scenario of climate change.

2. Materials and methods

2.1. Study area and climate data

The study in the Iberian Peninsula focused on mainland Portugal and Spain, and did not include the islands (Fig. 1). The land covers an area of 582,000 km^2, in which forest and other woodland systems comprised about 54.4% and 55.4% in respectively Portugal and Spain in 2015 (Forest Europe, 2015).

In terms of climate, the area is very heterogeneous and broadly

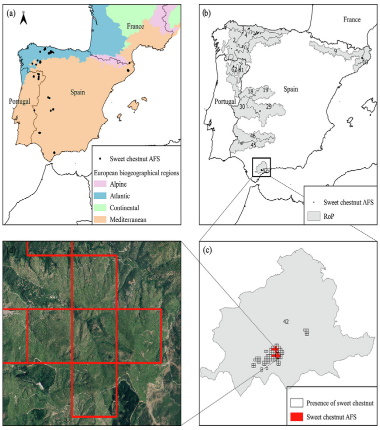

Fig. 1. (a) Study area and location of the sweet chestnut AFS (black dots), (b) distribution of the Region of Provenance (RoP), (c) details of the selected pixels (red squares) within the RoP and (d) close up of selected pixels.

speaking can be divided into three zones: dry climate zones (widespread in the south and southeast); temperate zones with dry, hot summers (most of the Iberian peninsula, i.e. approximately 40% of its surface); and temperate zones with dry, temperate summer climates (most of the northeast of the Peninsula, as well as almost all of the west cost of mainland Portugal) (AEMET, 2011).

The climate data mainly comprise air temperature (minimum, mean and maximum), precipitation and solar radiation. The data set was downloaded from the Digital Climatic Atlas for the Iberian Peninsula (http://opengis.uab.es/wms/iberia/) (Ninyerola et al., 2005), developed by the Autonomous University of Barcelona. The data were included in 65 climate maps (raster maps, resolution 200 m), with climate variables computed monthly and annually from 2285 weather stations between 1951 and 1999. These data were resampled to 1-km resolution, to correspond to the spatial resolution of the MODIS data set, and projected to the ETRS89-UTM zone 30N.

2.2. Modis data

The global MODIS data collection was obtained from the Numerical Terradynamic Simulation Group (NTSG), University of Montana, Public Data Repository. We downloaded the MOD17A3 product, which provides GPP and NPP data (in kg carbon m^{-2}) from 2000 to 2015 at 1-km resolution. The GPP and NPP were computed individually (Running et al., 2004) in raster files in TIF format and assigned to the WGS84 geographic coordinate system. GPP and NPP values of 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 those pixels.

Subsequently, in the QGIS geographic information system (QGIS Development Team, 2019) the MODIS data set was converted into the ETRS89-UTM zone 30N and a data set of points was created using the "pixels to points" tool. The "point sampling tool" complement was then used to extract pixel data for each raster layer, so that each point was the pixel centroid and each point contained the data information of GPP and NPP for all years evaluated. CUE was also calculated as the NPP/GPP ratio.

Validation of MODIS dataset at local scale for sweet chestnut ecosystem is challenging because of the lack of available field data for comparison with MOD17 data (Zhao et al., 2005). Nevertheless, other researchers have reported that the MODIS product is strongly correlated with data from eddy covariance (EC) towers in Spain, although they also observed a slight decrease in the correlation in areas characterised by high precipitation (Northern Spain) and high water stress areas (Southern Spain) (e.g. Gilabert et al., 2015).

2.3. Land use maps

Land use data sources (which are required to identify sweet chestnut agroforestry systems) were different for Portugal and Spain, due to the different approaches used in both countries for data collection and production.

We used the land use map of Portugal developed by the Portuguese Geographic Institute (Carta de Uso e Ocupação do Solo de Portugal Continental – COS) (DGT, 2015), with the aim of characterizing land cover in 2015. In addition, we used the Forest Map of Spain (MFE), at scale 1:25000 (MFE25) or 1:50000 (MFE50) (depending on availability, because it was created with the information captured in national forest inventories carried out in different years: the MFE50 project was completed between 1997 and 2006, and the MF25 was developed after 2007).

In both cases, data were downloaded in vector format and geoprocessed in order to identify sweet chestnut agroforestry systems. For this purpose, we first projected the data to ETRS89-UTM zone 30N and then merged both maps. The Iberian Peninsula is located between UTM zones 29, 30 and 31 (with extreme longitudes spanning from 9° 30′ W to 3° 14′ E), and we considered the geodesic distortion as negligible for the aims of the study. We selected areas designated as "Florestas de castanheiro" from the COS maps as those with sweet chestnut presence and those in which the main species was identified as *Castanea sativa* in MFE (MFE25 where available, and MFE50 for the rest of Spain)

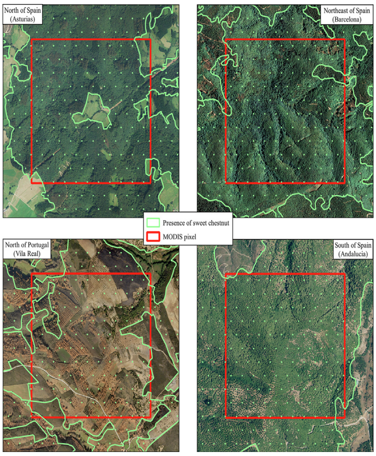

Fig. 2. Pixels randomly selected from those areas selected as sweet chestnut AFS.

To ensure that GPP and NPP values corresponded to sweet chestnut AFS, we only selected these areas if more than 80% of the MODIS pixels were fully occupied by areas in which sweet chestnut was present. Finally, exhaustive visual inspection of the areas corresponding the selected pixels was conducted to confirm the presence of sweet chestnut (Fig. 2).

2.4. Region of Provenance data

The Region of Provenance (RoP) is defined in the EC/1999/105 Directive as "the area or group of areas subject to sufficiently uniform ecological conditions in which stands or seed sources showing similar phenotypic or genetic characters are found, taking into account altitudinal boundaries where appropriate", which should be demarcated by the EU countries following their own criteria. Two classifications are available for the study area. We therefore used RoP to classify and compare sweet chestnut AFS with different ecological traits.

For the Portuguese region, we used the RoPs available from Instituto da Conservação da Natureza e das Florestas (ICNF, 2018) for *C. sativa*. For the Spanish region, we used the divisive RoP method developed by Alía Miranda et al. (2009), in which the territory is divided into ecologically similar zones and it is independent of species because no accumulative RoP system has yet been developed for *C. sativa*.

2.5. Statistical analysis

Several statistical methods can be used in ES supply studies. In this study, two well-defined and complementary parametric and non-parametric fitting methods were used to predict the risks to ecosystem and ecosystem services. Both fitting methods were used for comprehensive analysis of the data and because they provide important complementary information. SPSS software version 23.0 (IBM Corp, 2015) was used for the calculations in the parametric and non-parametric

Table 1
Summary statistics for study variables.

Type	Code	Description of variable	Unit	Mean	Std. Deviation	Min	Max	N
Primary production	NPP	Net primary production	Kg C m^{-2} yr^{-1}	0.8205	0.3710	0.0751	1.6911	94
	GPP	Gross primary production	Kg C m^{-2} yr^{-1}	1.4933	0.5313	0.7677	2.7026	94
	CUE	Carbon use efficiency	Dimensionless	0.5336	0.1422	0.0646	0.6798	94
Precipitation	MAP	Mean annual precipitation	mm	1020.2	171.6	683.0	1762.3	94
Temperature	MAT	Mean annual temperature	°C	12.6	1.4	9.3	15.6	94
	MATmin	Mean minimum annual temperature	°C	7.1	1.5	3.9	10.3	94
	MATmax	Mean maximum annual temperature	°C	18.1	1.6	14.5	20.9	94
Solar radiation	MAPSR	Mean annual solar radiation	kJ m^{-2} day^{-1} μm^{-1}	195.9	12.7	161.2	221.2	94
Topographic	P_CS	Percentage occupied by chestnut stand within the pixel	%	87.6	5.8	80	100	94
	Slope	Terrain slope	%	28.6	11.9	7	54	94
	Elevation	Terrain elevation	m	714.8	175.1	270	1055	94
	LAT	Latitude	Geographic coordinates EPSG:4258	40.799	2.343	36.600	43.464	94
	LON	Longitude		−4.637	3.479	−7.682	2.746	94

methods. R software version 3.5.3 (R Core Team, 2019) was used for descriptive statistics and graphs. Table 1 shows the summary statistics for the structural characteristics of the study areas (for a complete summary, see Supplementary material).

2.5.1. Parametric methods

Multiple linear regression (MLR) was used to model the relationships between primary production indicators (NPP and CUE) and the climatic and topographic variables in order to produce general models and models based on RoP classification.

Candidate predictor variables were required to have an input F-statistic with a significance level of 0.05 or less for inclusion in the model, and no predictor was left in the model with a partial F-statistic with a significance level greater than 0.05.

The model estimates were compared using the adjusted coefficient of determination (R_{fit}^2) and the root mean square error (RMSE). R_{fit}^2 compares the descriptive power of regression models including diverse number of predictors. The RMSE is a quadratic scoring rule that measures the average magnitude of the error (the square root of the average of squared differences between prediction and actual observation) and it was calculated to provide additional information. Finally, residual plots were checked in order to validate the model fit. The variance inflation factor (VIF) was also used to quantify the severity of multicollinearity in the ordinary least squares regression analysis, and it also provided an index that measures the extent to which the variation in an estimated regression coefficient increased due to collinearity. Only models in which all parameters were significant at the 5% level and with $VIF < 10$ were included, thus ensuring that predictions were not highly correlated (Bollinger, 1981; Castaño-Díaz et al., 2017; Mandeville, 2008).

Pearson correlation coefficient was used to determine the strength of the linear relationship between the different variables. A high R value signifies a stronger relationship, while a low R value represents the opposite. Positive R values indicate the same trend, while low R values represent the opposite trend (Benesty et al., 2009). This analysis was conducted with the "corrplot" package (Wei and Simko, 2013) in R software v3.6.1. The remaining graphs were constructed developed with the "ggplot2" package (Wickham, 2009).

Finally, to determine the resilience to climate change of sweet chestnut AFS and their ability to recover, we used simple parametric linear regression to predict when the dependent variable becomes zero and to compare different climate change scenarios. The reference scenarios for the increase in the global mean surface temperature corresponded to the representative concentration pathways (RCP) developed by the IPCC (IPCC, 2013). Specifically, we compared our data with the RCP2.6 scenario, which predicts an increase by up to 1.7 °C by 2100, and with the RCP8.5 scenario, which predicts an increase of as much as 4.8 °C. MAT was the variable selected for simple projections, because it is expected to be correlated with the dependent variables and it is the main variable used in climate change scenarios (IPCC, 2018, 2013).

2.5.2. Non-parametric method

The Classification and Regression Trees (CART) method was selected for use because it provided good fits to the data, with high R^2 values and low RMSE, and it is a good exploratory technique that aims to determine classification and prediction rules.

The main advantages of the CART method can be summarised as follows (Gordon, 2013; Timofeev, 2004): (i) it does not require specification of any functional form; (ii) it does not require variables to be selected in advance; (iii) it can easily handle outliers; (iv) it does not require the assumptions of statistical models and is computationally fast; (v) it is flexible and can deal with missing data; and (vi) the results are easy to interpret.

The objective of CART is usually to classify a data set into several groups by use of a rule that displays the groups in the form of a binary tree (Breiman et al., 2017), which is determined by a procedure known as recursive partitioning, in which each group is the node for the next partition. In this study, the CART method was used to classify the primary production indicators considered (NPP and CUE) in relation to the climate and topographic variables.

Each tree branch is described by the value of one descriptor, chosen so that the values of the response variables for all objects in a daughter group are more similar. The split for continuous variables is defined by $x_i < a_j$, where x_i is the selected descriptor or explanatory variable and a_j is its split value. To choose the most appropriate descriptor x_i and value a_j, CART uses an algorithm in which all descriptors and all split values are considered, selecting those producing the best reduction in impurity between the mother group (t_p) and the daughter groups (t_L and t_R) (Álvarez-Álvarez et al., 2013; Deconinck et al., 2005). This process is repeated for each daughter group until the maximal tree height is reached. Mathematically this is expressed as follows:

$$\Delta i(s, t_p) = i(t_p) - p_L\, i(t_L) - p_R\, i(t_R) \tag{1}$$

where i_t is the impurity, s is the candidate split value, and p_L and p_R are the fractions of the objects in respectively the left and right daughter groups.

The impurity is defined as the total sum of squares of the deviations of the individual responses from the mean response of the group and is expressed as follows:

$$i(t) = \sum_{n=1}^{n} (y_n - \bar{y}(t))^2 \tag{2}$$

where i(t) is the impurity of group t, y_n is the value of the response variable for object x_n and $\bar{y}(t)$ is the mean value of the response variable in group t.

CART methods are not required to conform to probability distribution restrictions, and there is no assumption of linearity or any need to pre-specify a probability distribution for the errors (Bell, 1999).

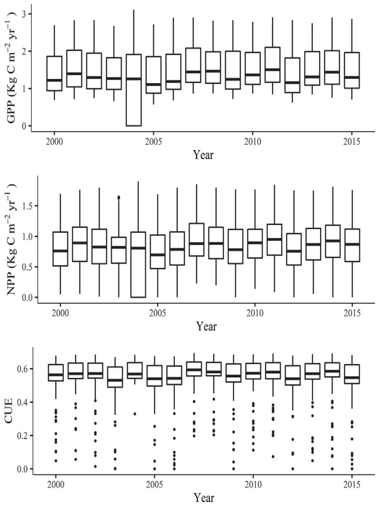

Fig. 3. Box-and-whisker plot showing the mean annual trends in GPP, NPP and CUE. The dots represent outliers.

Complexity and robustness are competing characteristics that must be considered simultaneously during construction of statistical models. The more complex a model is, the less reliable it will be for purposes of prediction. To prevent this from occurring, stopping rules must be applied during elaboration and development of decision trees, to prevent the model from becoming overly complex. Common parameters used in stopping rules include (a) the minimum number of observations in a leaf, (b) the minimum number of observations in a node prior to splitting and (c) the depth (i.e. number of levels) of any leaf from the root node (Song and Lu, 2015). The risk estimate, which is a measure of the within-node variance, was used as an indicator of model performance (IBM Corp, 2015).

3. Results

3.1. Annual trends in NPP and CUE

Mean annual NPP and CUE between 2000 and 2015 (16 years) were calculated using the procedure described above. Fig. 3 shows the dispersion and annual trends in GPP, NPP and CUE in the total sweet chestnut AFS for each year. NPP varied slightly, between 0.66 Kg C m^{-2} yr^{-1} and 0.92 Kg C m^{-2} yr^{-1}, while CUE varied between 0.50 and 0.59, with important within-year variability (see Supplementary material). In 2004, a possible mismatch in the MODIS data led to loss of data and deviations (Fig. 3). The general trend for these three different indicators was homogeneous, with no large variations around the mean values.

When the RoP classification was applied, the homogeneity in the values of the different variables disappeared (Fig. 4). As expected, high values of both NPP and CUE were obtained for sweet chestnut AFS in the north and northwest of Iberian Peninsula (RoP 02, 03, 04, 05, 09 and 10): NPP was greater than 1.04 Kg C m^{-2} yr^{-1} and CUE varied from 0.54 to 0.64. Although NPP was lower in the north of Portugal (RoP 61 and 62) and in RoP 30, CUE values were higher (< 0.66), possibly due to the fact that most of the stands are young fruit plantations. Finally, the lowest values with the maximum deviations corresponded to RoP 29 and 42.

The Atlantic area of Spain and the northern of Portugal may be more strongly influenced by the stand factors or characteristics (fruit plantations, simple coppices, mixture of coppices with standards and abandoned grafted orchards) than by climatic factors, which may partly account for the high values and the variability. By contrast, climate may be the main limiting factor in the Mediterranean area.

3.2. Influence of climate on NPP and CUE

To analyse the responses of vegetation NPP and CUE to the climatic and topographic variables, we used two well-defined and complementary parametric and non-parametric fitting procedures. In general, both NPP and CUE were negatively correlated with mean temperature variables (MAT, MATmin and MATmax) and positively correlated with latitude, and neither were correlated with MAP (Fig. 5). The correlations were always lower for CUE than for NPP. Thus, for NPP values inversely correlated with the mean temperature variables, “r” ranged between -0.62 and -0.70, while despite following the same trend, CUE ranged from -0.41 to -0.52. Furthermore, MAT was highly and positively correlated with MATmin and MATmax (“r” = 0.96 in both cases). As the three variables are highly correlated, they explain the same components of the variance, and we therefore focus the analysis on only one of these.

The main results of both fitting methods are shown in Tables 2 and 3. The parameter estimates and goodness of fit statistics for the parametric models (multiple linear regression) are summarized in Table 2, and non-parametric (CART) models are summarized in Table 3.

For the whole of the Iberian Peninsula, the linear model for NPP provided a good fit, with a high level of variance explained ($R_{fit}^2 = 77.78\%$). The model was only influenced by precipitation variables such as mean precipitation for the months of September, November and December (MP09, MP11 and MP12). Less variance was explained by CUE than by NPP ($R_{fit}^2 = 45.49\%$). In this case, the variables involved were latitude and mean precipitation of July (MP07) (see Table 2 for parameter estimates and model errors).

When we split the sample into Atlantic and Mediterranean bioclimatic regions, we found that the linear model for the Atlantic bioclimatic region did not provide a good fit to the data. The R_{fit}^2 value was 27.86%, for the amount of variance explained by the best model of NPP, including only one variable, mean precipitation of August (MP08). On the contrary, one of the best fits was obtained for the Mediterranean bioclimatic region. With mean precipitation in September (MP09), latitude, and mean temperature in December (MT12), the variance explained in the linear model for NPP yielded $R_{fit}^2 = 81.70\%$. One of the best fits was obtained for CUE, with only latitude and longitude included in the model, yielding $R_{fit}^2 = 48.11\%$.

Table 3 shows the results for the CART models for NPP and CUE, divided into climate variables (upper section) and RoP (lower section). Nodes defining the partitions are hierarchically numbered and show the values for the independent classification variables. Globally, the proportion of variance explained was slightly lower than in the linear models (Table 3), but with satisfactory results. For fitting all variables, the variance explained for NPP yielded a R^2 value of 74.57%, while for CUE, the R^2 value was 25.61%. In both cases, the model included geodetic longitude (LON) together with climatic variables such as mean precipitation in August (MP08) for the NPP fit, and with mean precipitation of December (MP12) and latitude for CUE fit.

Nevertheless, the variability in both NPP and CUE can be explained by RoP only. For NPP, the R^2 value was 69.49% while for CUE, the corresponding value was 40.49%. In this case, the NPP fit was slightly poorer than the previous fit with all variables, but the CUE fit with RoP was better.

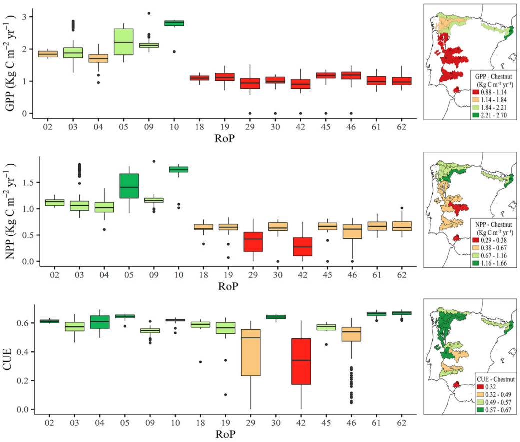

Fig. 4. Mean trends in GPP, NPP and CUE for sweet chestnut AFS grouped by RoP.

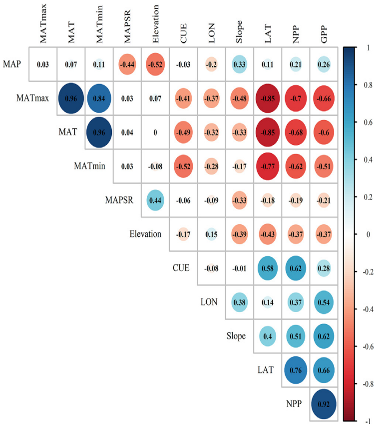

Fig. 5. Correlation matrix for the variables selected in Table 1.

3.3. Resilience capacity

MAT was strongly and inversely correlated with GPP, NPP and CUE (Fig. 5). The adjusted model for NPP provided a better fit with MAT than with CUE (fitting graphs shown in Supplementary material). In both cases a clear trend was observed: as MAT increased the dependent variable decreased until reaching zero. NPP reached zero at 16.6 °C, beginning the survival phase of the ecosystem, while CUE reached zero at 18.4 °C when the chestnut ecosystem and their functions may disappear, or are at risk of disappearing.

In order to assess the resilience capacity, we also examined the range of MAT occupied by RoP and sweet chestnut AFS in these RoP (Fig. 6). Sweet chestnut stands in the south of Iberian Peninsula and at north of the valley of the Guadalquivir (RoP 45 and 46), the hottest location in Europe, preferentially occupied the cold range of MAT in these regions. A similar trend was observed in RoP 10, which also inhabited the highest elevations, ranging from 900 to 1250 m. In the south of the valley of the Guadalquivir with oceanic influence, sweet chestnut AFS occurred in RoP 42, occupying the middle MAT of this region. Portuguese sweet chestnut AFS (RoP 61 and 62) and those in inland areas of Iberian Peninsula (RoP 18, 19, 29, 30) tend to survive at temperatures around the half the range of the RoP. By contrast, those in the northern regions (RoP 02, 03, 04 and 05) tend to occupy the hottest locations, according to the temperature distribution of chestnut within the RoP temperature variability.

As shown in Fig. 6, all sweet chestnut AFS are currently below the survival threshold, with RoP 42 and 45 being closest, at respectively 1 °C and 1.8 °C from exceeding the threshold. The AFS sweet chestnut in northern areas (RoP 02, 03, 04 and 05) ranges between 3.5 °C and 5.1 °C up to edge, and in the Portuguese zones (RoP 61 and 62) and RoP 09 with an average of 4 °C. Finally, those in RoP 10 are furthest from the threshold with a margin of more than 7 °C.

For the most favourable climate change scenario (RCP2.6, MAT increases up to 1.7 °C), only sweet chestnut AFS in RoP 42 will surpass this limit. However, all of the central area of Spain (RoP 18, 19, 29, 30, 45 and 46) is 1 °C below the aforementioned limit. In the worst possible scenario (RCP8.5, MAT increases up to 4.8 °C), almost all sweet chestnut AFS have crossed the survival edge marked by the threshold, while some, mainly those in central Spain (RoP 18, 19, 29, 30, 42, 45 and 46), may even disappear. In this case, only sweet chestnut AFS in RoP 05 and 10, would have a considerable margin, of 2 °C and 4 °C respectively, until reaching the lethal threshold, while the others would have a margin of around 0.5–1.3 °C.

4. Discussion

4.1. Data harmonization

In this work, spatially-explicit data developed and provided by institutions in two different countries was used. In order to detect monospecific chestnut forest patches, the types best suited to this land cover type were selected from both the COS (Portugal) and IFN (Spain) maps. Nevertheless, each map was developed with slightly different objectives: the former is a land cover map, and the latter was created as a support for the national forest inventory. This conditioned our

Table 2
Results of multiple regression showing the best models obtained for NPP and CUE.

Region	Dependent variable	Independent variable	Parameter estimate	Std. Error	RMSE	R^2	R_{fit}^2
Iberian Peninsula	NPP (Kg C m^{-2} yr^{-1})	(Constant)	0.3565	0.1123	0.1749	0.785	0.7778
		MP09	0.0162	0.0010			
		MP11	−0.0081	0.0019			
		MP12	0.0040	0.0013			
	CUE	(Constant)	−1.9133	0.3036	0.105	0.467	0.4549
		LAT	0.0624	0.0079			
		MP07	−0.0031	0.0008			
Mediterranean biogeographical region	NPP (Kg C m^{-2} yr^{-1})	(Constant)	−4.6636	0.8936	0.1582	0.825	0.8170
		MP09	0.0154	0.0017			
		LAT	0.1017	0.0197			
		MT12	0.0904	0.0249			
	CUE	(Constant)	−1.7244	0.2729	0.1146	0.496	0.4811
		LAT	0.0547	0.0067			
		LON	−0.0124	0.0038			
Atlantic biogeographical region	NPP (Kg C m^{-2} yr^{-1})	(Constant)	0.3818	0.2397	0.1767	0.313	0.2786
		MP08	0.0114	0.0038			

methodological approach, which had to solve differences between geodesic reference systems, associated thematic information (i.e. forest data) and typological categories. Specifically, in the absence of similar and coordinated spatial-explicit databases and information, the results of the forest patch selection have been contrasted with orthorectified remote sensed data uniform for both countries to ensure data comparability. This highlights the importance of harmonizing the mapping processes and protocols, especially regarding thematic data developed at intermediate scales.

4.2. Annual NPP and CUE trends

The climate-sensitive parameters vegetation NPP and CUE are widely modelled in carbon cycle-related studies at the global scale (Field et al., 1995). The spatio-temporal response defines the context in which sweet chestnut AFS of the Iberian Peninsula are currently located. In the present study, only minor differences were observed in the general trend for annual mean NPP and CUE between different years, possibly because the stand characteristics have not undergone important changes in most of the AFS during the study period. This may be due to the stability of relatively large and continuous sweet chestnut stands, which should theoretically span more than 80% of the MODIS pixel area, i.e. 100 ha (1 km × 1 km resolution). Consequently, perturbations smaller than the pixel area may be averaged and thus be difficult to detect.

Nevertheless, calculation of NPP and CUE for each RoP revealed a high level of variability. As found by Gilabert et al. (2015), the highest annual NPP and GPP values appeared in the most humid areas in the northern Iberian Peninsula, which are also the coldest regions. However, the highest CUE values did not follow the same pattern. The highest CUE values corresponded to stands in Portugal, where young plantations are destined for fruit production, or areas where sweet chestnut plantations for fruit are traditionally well established (Fernandez-Lopez et al., 2005). These findings confirm that managed

Table 3
Results of the non-parametric fitting (CART) of the models obtained for NPP and CUE. The upper section shows the results for climatic variables, and the lower section shows the results for the RoP.

Variable	R^2	RMSE	Node	Mean	Standard Deviation	Number	Percent	Predicted mean	Parental Node	Independent variable		
										Variable	Improvement	Value
NPP (Kg C m^{-2} yr^{-1})	0.75	0.17	0	0.82	0.37	94	1	0.82				
			1	0.51	0.21	48	0.5	0.51	0	MP08	0.10	< = 21.10
			2	1.14	0.19	46	0.5	1.14				> 21.10
			3	0.64	0.12	28	0.3	0.64	1	LON	0.01	< = −5.66
			4	0.34	0.19	20	0.2	0.34				> −5.66
CUE	0.26	0.14	0	0.53	0.14	94	1	0.53				
			1	0.40	0.18	29	0.3	0.40	0	LAT	0.01	< = 39.48
			2	0.59	0.05	65	0.7	0.59				> 39.48
			3	0.33	0.19	19	0.2	0.33	1	MP12	0.00	< = 182.95
			4	0.53	0.05	10	0.1	0.53				> 182.95
			5	0.65	0.03	23	0.2	0.65	2	LON	0.00	< = −6.63
			6	0.56	0.03	42	0.4	0.56				> −6.63
NPP (Kg C m^{-2} yr^{-1})	0.69	0.17	0	0.82	0.37	94	1	0.82				
			1	1.14	0.19	46	0.5	1.14	0	RoP	0.10	03; 04; 10; 02; 05; 09
			2	0.51	0.21	48	0.5	0.51				62; 61; 18; 19; 29; 30; 46; 45; 42
			3	0.64	0.12	28	0.3	0.64	2	RoP	0.01	62; 61; 18; 19; 30; 46; 45
			4	0.34	0.19	20	0.2	0.34				29; 42
CUE	0.40	0.10	0	0.53	0.14	94	1	0.53				
			1	0.58	0.07	74	0.8	0.58	0	RoP	0.01	03; 04; 10; 02; 05; 09; 62; 61; 18; 19; 30; 46; 45
			2	0.35	0.18	20	0.2	0.35				29; 42
			3	0.64	0.04	31	0.3	0.64	1	RoP	0.00	04; 10; 02; 05; 62; 61; 30
			4	0.54	0.07	43	0.5	0.54				03; 09; 18; 19; 46; 45

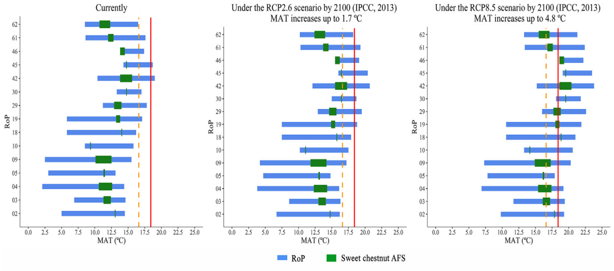

Fig. 6. Current resilience of sweet chestnut AFS, under RCP2.6 scenario and under RCP8.5 scenario by 2100 (IPCC, 2013). Dashed orange line indicates the moment that NPP = 0 (survival begins), and the continuous red line represents CUE = 0 (the chestnut ecosystem and their functions could disappear).

forests (such as fruit plantations, simple coppices, coppices with standards and grafted orchards) have a higher CUE than unmanaged forests (Campioli et al., 2015; Fernández-Martínez et al., 2014), particularly considering monospecific stands (Kunert et al., 2019). Nonetheless, Atlantic regions with highest NPP also have higher CUE values than in Mediterranean regions, owing to the strong influence of climate.

4.3. Responses of NPP and CUE to climate influence

As argued elsewhere (Kato and Tang, 2008), both precipitation and temperature, together with others factors not considered in this study (e.g. extreme climate events, management regime, soil characteristics, ecological traits, age and disturbance), play a fundamental role as drivers of primary production indicators. In general, due to the scale characteristics used in other studies, (mainly global and regional), MAT and MAP have been the main climate-related drivers identified (He et al., 2018; Khalifa et al., 2017; Reichstein et al., 2007; Zhang et al., 2014, 2009). On the other hand, although latitude and longitude are not climatic variables per se, these entail a mixture of factors including temperature and precipitation, among others (Valentini et al., 2000), so that the geographic variations implicitly include an intrinsic change in climatology. In addition, we also used monthly climatic variables, which may provide a better ecological explanation of the influence of climate on sweet chestnut ecosystems in the Iberian Peninsula.

Most climatic variables included in parametric and non-parametric models for NPP are precipitation variables (Tables 2 and 3), as in previous studies indicating that water availability is more important than temperature (Garbulsky et al., 2010; Heimann and Reichstein, 2008; Zhang et al., 2009; Zhao and Running, 2010). In this respect, only MP09 explained 72% of the NPP in the Iberian Peninsula and 75% of NPP for the Mediterranean area. As this was only detected in monthly variables, we can therefore interpret precipitation as a limiting factor only in a short period of the year, specifically when sweet chestnut fruit is ripening or during summer drought months (MP07, MP08 and MP09), and when precipitation at the end of autumn is low (MP11 and MP12) (Gandullo Gutiérrez et al., 2004). In the NPP linear model for the Iberian Peninsula, the monthly precipitation variables explained the model variance and yielded a good fit ($R_{fit}^2 = 77.78\%$). Nevertheless, different responses were found for different areas: precipitation does not appear to be a limiting factor in Atlantic areas, as it is rarely water-limited, while water availability becomes limiting in Mediterranean areas (Reichstein et al., 2007). As argued by Liu et al., (2018), one possible explanation is that precipitation is sufficient for the regular growth of vegetation in relatively humid areas, but that excessive water input may lead to soil erosion. In the present study, precipitation in Atlantic areas was observed to vary within specific limits depending on how vegetation is locally adapted. The average values of MAP and MP09 for Atlantic regions are 1182.6 mm yr^{-1} and 74.5 mm yr^{-1} respectively, while for the Mediterranean region the corresponding values are 970.6 mm yr^{-1} and 49.8 mm yr^{-1}. However, in the central and southern RoP of Mediterranean regions some areas such as RoP 30 or 42 have MP09 values close to 30 mm yr^{-1}, thus confirming this hypothesis.

Regarding temperature, the general model fits only seem to be influenced by one monthly temperature variable (MT12), which explains around 40% of NPP in Mediterranean region, without affecting the Atlantic region (Tables 2 and 3). However, temperature plays a fundamental role, because it affects both the photosynthesis and autotrophic respiration (R_a), the rates of which increase exponentially with temperature by increasing the maintenance cost by plants (Ryan, 1991; Ryan et al., 1994). Respiration rates are lower in the Atlantic region, causing an increase in the CUE, while MAT is higher in the Mediterranean region where the maintenance cost increases and CUE decreases. Although monthly temperature variables do not seem to have a strong influence, the findings revealed that MAT is an important driver of primary production in sweet chestnut stands. MAT explains the variations in NPP and also in CUE (Fig. 6). According to Chen et al., (2019), MAT may explain 50% of the variations in NPP, whereas for CUE, MAT may explain 30% of the variations and both decrease quadratically when MAT increases. Hence, in sweet chestnut AFS in the Iberian Peninsula, CUE is more strongly influenced by MAT than by MAP, indicating a relationship between climate warming and CUE (He et al., 2018).

4.4. Ecosystem and ecosystem services risks

The findings presented above indicate the usefulness of primary production indicators as proxies for assessing ecosystems and the associated risks, given the goodness of fit of the parametric and non-parametric models used in this study. However, primary production indicators may vary among or within ecosystems with climate change and other factors (such as management, ecological traits and age), and the ranges of NPP and CUE that do not entail risks for sweet chestnut are not known. NPP can theoretically be negative ($R_a > GPP$) for limited periods (Collalti and Prentice, 2019; Roxburgh et al., 2005). When NPP reaches zero, the maintenance cost will be therefore be equal to the GPP, and the plant will begin a survival phase. Moreover, several authors have reported a minimum CUE value of 0.2 as the threshold below which the physiological activity of plants cannot be maintained (Amthor, 2000; Keith et al., 2010; Van Iersel, 2003). Our findings show that the NPP values are sometimes equal or close to zero for periods of 1 year in the south of the Mediterranean region (RoP 29, 30, 42, 45 and 46); for chestnut, RoP 29 and 42 are the regions where minimum values of NPP (equal or close to zero) occur in most years and are maintaining the ecosystem. However, our data correspond to regions with low CUE values (such as RoP 29, 42 and 45) close to or below 0.2 (at risk), and we believe that values below 0.3 may also indicate ecosystems at potential risk, considerably increasing the additional respiratory cost, reducing growth and new tissue formation, or even plant collapse. The sustainability of sweet chestnut AFS in the north of Portugal and north of Spain does not depend on current climatic conditions, and therefore ecosystem provision would not be at risk in a hypothetically stable situation. However, and regarding future scenarios of climate change, our projections do not indicate a good future for sweet chestnut. This particularly applies to the Mediterranean regions of the central and southern part of the Iberian Peninsula where the influence of climate drivers is currently high, and the weather is expected to become warmer and drier in the coming years. Our findings suggest that by 2100, under the most favourable scenario (RCP2.6, MAT increases up to 1.7 °C), chestnut ecosystems will begin a survival phase in the south of the Iberian Peninsula, where some CUE values below 0.2 have already been observed. This hypothetical situation may be even worse under the RCP8.5 scenario (when MAT increases up to 4.8 °C), where it is foreseen that all sweet chestnut in the Iberian Peninsula, except in RoP 10 and 05, will surpass the survival threshold ($R_a > GPP$) and some (e.g. those in the most strongly affected regions specified above) may even disappear.

The most recent IPCC Report (IPCC, 2018) indicates temperature increases between 1.5 °C and 2 °C as the most likely scenario, as also suggested by Cox et al., (2018), although neither report dismisses the worst scenario established in the IPCC Report 2013. Bearing this in mind, it is not clear how sweet chestnut AFS will adapt to these conditions. Some authors argue that plant species will adapt to climate change by altering their physical traits (Moritz and Agudo, 2013) with the consequent alteration of plant trait distributions (Madani et al., 2018) or by occupying current ecological niche spaces under new environmental conditions (Dubuis et al., 2013) where local conditions are more favourable. However, recent research suggests an insufficient acclimatization response to climate change by ecosystems during the last 30 years (Huang et al., 2019). While the focus of the present research is not to predict whether these ecosystems will be able to adapt via alteration of physical traits or whether they will occupy new ecological niches, the latter is probably most likely. However, the situation will differ depending on the type of sweet chestnut formations: in the long term, natural or semi-natural chestnut forests may adapt to new and favourable geographical locations (depending on competition with other species and/or land use types). Similarly, chestnut plantations may be established in different locations according to climate tolerance. Nevertheless, the resilience and adaptation of well-established and traditional AFS will ultimately depend on the variations in climatic conditions. Accordingly, provision of ecosystem services will be affected in different ways due to the variations in provision related to the type of formation (see e.g. Roces-Diaz et al., 2018). Considering the multifunctional character of traditional AFS (resulting in a greater capacity to supply bundles of ecosystem services, including provision, regulation and cultural services), climate change may negatively affect the provision of ecosystem services in many regions.

5. Conclusions

In this study, we assessed the influence of climate variations on primary production indicators (NPP and CUE) in sweet chestnut AFS in the Iberian Peninsula and the resilience of these systems in a future scenario of climate change. Overall, the data is robust due to the selection criteria and the use of relatively large and continuous sweet chestnut stands. The annual NPP and CUE show homogenous temporal trends, with no large variations throughout the time frame studied, although the values show high spatial variation for each year considered. However, there are large differences between the mean trends in the different RoP, which were used to represent ecologically homogeneous areas. The highest NPP values corresponded to the north of Spain, associated with the coldest and wettest regions. The highest CUE values corresponded to the north of Portugal, but were very similar to those for some areas of northern and central Spain. Furthermore, the fitted models indicate a close relationship between primary production indicators and climate variables in sweet chestnut, highlighting the importance of including monthly climatic variables, such as summer precipitation, in the models. The findings also revealed that MAT is an important driver of primary production in sweet chestnut AFS, while MAP is not related to any indicator.

Further analysis of the explanatory power of the models, together with the scenarios predicted by the IPCC, revealed that sweet chestnut AFS and the associated ecosystem services supply will be at risk due to the effects of climate change in the Iberian Peninsula. In RCP2.6, the most likely scenario according to the IPCC (IPCC, 2018), important risks of loss of ecosystems and their associated functions will first appear in the south of Iberian Peninsula, while under the RCP8.5 scenario, the risk will be especially high in Mediterranean areas of southern and central Spain. Thus, because of the different ways that the physiological conditions of sweet chestnut may be affected by climate variations (i.e. increases in mean temperature), ecosystems will be affected, and their services reduced. In the worst case, if climate continues to change according to the worse predictions, ecosystems will be lost. In addition, both physical traits and the resilience and adaptation capacity for well-established and traditional AFS will play a fundamental role, always under the influence of final climatic conditions.

CRediT authorship contribution statement

José Carlos Pérez-Girón: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing - original draft, Funding acquisition. **Pedro Álvarez-Álvarez:** Conceptualization, Methodology, Formal analysis, Investigation, Resources, Writing - original draft, Writing - review & editing, Supervision, Funding acquisition. **Emilio Rafael Díaz-Varela:** Conceptualization, Methodology, Investigation, Writing - review & editing, Supervision, Funding acquisition. **Domingos Manuel Mendes Lopes:** Conceptualization, Resources, Writing - review & editing, Supervision, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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CHAPTER 3

Climate-driven variations in productivity reveal adaptive strategies in Iberian cork oak agroforestry systems

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Climate-driven variations in productivity reveal adaptive strategies in Iberian cork oak agroforestry systems

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ABSTRACT

Background: Cork oak agroforestry systems (AFS) have been managed for centuries by humans to produce cork and other goods and services and have recently been recognised as an important reservoir for biodiversity improvement and conservation. However, despite having recently been included as a natural habitat of community-wide interest within the EU Habitats Directive, these systems are in a critical situation of decline. Among other factors, they are strongly threatened by climate change, the effects of which are also expected to be particularly severe in the Mediterranean region. In this study, we aimed to evaluate the influence of climate variability by examining primary production indicators and also to analyse whether the geographical location may have a role in the incidence of the adverse effects of climate.

Methods: Cork oak AFS were identified in the Forest Map of Spain and the Land use map of Portugal and categorized on the basis of canopy cover. Seasonal climate data from 2001 to 2020 were used to model relationships with climate predictors and proximity to the coast. Hotspot analysis was conducted to identify significant spatial clusters of high- and low-efficiency areas.

Results: The responses to the influence of climatic conditions differed among the various cork oak AFS categories, particularly in the forest category, which was less dependent on climate variations. Relative humidity and water availability were the main drivers of net primary production (NPP). Carbon use efficiency (CUE) was limited by relative humidity and spring temperature in open ecosystems. Proximity to the coast proved beneficial, especially in years with adverse weather conditions, but was not a limiting factor for survival of the ecosystem. Finally, the results of the hotspot analysis supported the other findings, highlighting high-efficiency areas close to the coast and cold spots grouped in specific areas or dispersed inland.

Conclusions: Canopy plays a key role in the influence of climatic conditions, particularly in forest categories in which a high density seems to generate microclimate conditions. Water availability, both via the soil and air moisture, is the main driver of primary production, reflecting different adaptive strategies. The oceanic atmosphere may act as a buffer in years of extreme drought.

1. Introduction

Climate is considered one of the main drivers of biodiversity and ecosystem change (Millennium Ecosystem Assessment, 2005; IPBES, 2019) and is expected to become a major stressor (Bellard et al., 2012; Urban, 2015; Willeit et al., 2019). The Mediterranean region has been considered one of the hotspots in future climate change (Giorgi, 2006), and a pronounced increase in temperature (4 °C–5 °C) and a considerable decrease in mean precipitation (of around 25%–30%), mainly in summer, are expected (Giorgi and Lionello, 2008), thus seriously increasing the effects of summer drought in the region. Droughts will occur more frequently, and be of greater duration and intensity, with the added aggravation in the Iberian Peninsula that they might not be followed by wet winters (Böhnisch et al., 2021). Furthermore, this trend has been confirmed by the latest IPCC report, which indicates that the Mediterranean region has been getting warmer and drier in the last few years

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Abbreviations: AFS, agroforestry systems; GPP, gross primary production; NPP, net primary production; CUE, carbon use efficiency; COS, *Carta de Uso e Ocupação do Solo de Portugal Continental* 2018; MFE, Forest Map of Spain; TCD, tree cover density.

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(IPCC, 2021). This may constitute a threat to the future of cork oak ecosystems, which are already in a critical situation of decline (Costa et al., 2009; Pinto-Correia et al., 2011) in the Mediterranean region, where water availability is the main driver of primary production (Reichstein et al., 2007; Garbulsky et al., 2010) and is a major ecosystem function sensitive to changes in climate (Huang et al., 2019; Tang et al., 2019; Stocker et al., 2019).

Cork oak (*Quercus suber* L.) is a typically evergreen Mediterranean tree species, with a range of distribution expanding around the western Mediterranean basin, where the largest populations of this species are found, specifically in the southwest of the Iberian Peninsula (Díaz-Fernández et al., 1995; Pereira, 2007; Navarro Cerrillo et al., 2013). The species is well adapted to mild Mediterranean climates with Atlantic influence, i.e. mild winters and hot and dry summers with high relative humidity (Pereira, 2007; Quero et al., 2008). The presence of the species in continental areas depends on there being some oceanic influence (Navarro Cerrillo et al., 2013). The optimum mean annual temperature ranges between 13 °C and 19 °C, and the species tolerates cold poorly and does not withstand periods of frost, especially below −5 °C (Pereira, 2007; Gil and Varela, 2008; Navarro Cerrillo et al., 2013). The rainfall regime tolerated is within a wide range, mainly greater than 500 mm and reaching up to 2,400 mm (Gil and Varela, 2008), and the species can withstand up to 4 months of summer drought due to its powerful root system. However, cork oak is very sensitive to waterlogging (Pereira, 2007). To deal with summer drought, cork trees have developed deep root systems that enable groundwater uptake (David et al., 2007; Piayda et al., 2014) and physiological mechanisms that prevent water loss, such as efficient stomatal control of transpiration (Nardini et al., 1999; Mediavilla and Escudero, 2004; Pérez et al., 2005; David et al., 2007; Besson et al., 2014).

Centuries-long management of *Q. suber*, frequently associated with holm oak (*Q. ilex* L. and *Q. rotundifolia* Lam.) and to a lesser extent with other oaks (*Q. faginea* Lam. and *Q. pyrenaica* Willd.), has given rise to multifunctional agroforestry systems (AFS) (Joffre et al., 1999; Costa et al., 2009; Pinto-Correia et al., 2011). In these systems, known as *montados* in Portugal and *dehesas* in Spain, cork production prevails together with the production of other goods and services, such as crops and other non-timber productions (mainly grazing and hunting) (Pereira, 2007). For simplicity, we will refer to these systems hereafter as *dehesas*. The land cover patterns of *dehesas* are similar to those of savanna, characterized by the presence of scattered trees in varying densities (Aronson et al., 2009; Fonseca and Pinto-Correia, 2009; Pinto-Correia et al., 2011). However, the tree density is generally low, with the presence of herbaceous or shrub vegetation in the understory (Pereira et al., 2007; Correia et al., 2014, 2016; Piayda et al., 2014). These systems have been key elements of the landscape since time immemorial (Eichhorn et al., 2006; Fonseca and Pinto-Correia, 2009), making valuable contributions to the landscape and the environment, fulfilling fundamental functions and processes such as primary production, soil formation and regulation of nutrient cycles or hydrological flows, in addition to being an important reservoir for biodiversity improvement and conservation (Plieninger and Wlbrand, 2001; Torralba et al., 2016). *Dehesas* have recently been included as a natural habitat type of community-wide interest within the EU Habitats Directive; in view of their conservation status, they have been categorized as in serious danger of disappearance.

Although the problem is not new, already having been reported in the mid-twentieth century, cork oak AFS are in a critical situation of decline (Costa et al., 2009), and their viability has been seriously threatened and affected by various factors (both natural and human-induced) in addition to climate change (Aguilera et al., 2020), such as the proliferation of pests and diseases (Brasier et al., 1993; González et al., 2020), fire recurrence (Silva and Catry, 2006; Guiomar et al., 2015), lack of regeneration, change in land use, and land abandonment (Pinto-Correia and Mascarenhas, 1999; Bugalho et al., 2011; Godinho et al., 2016). Thus, following a cascade reaction (Haines-Young and Potschin, 2010), the loss of ecological functions and processes due to the impact of these factors (Schröter et al., 2005, 2019; Mooney et al., 2009), may trigger a reduction in the capacity to provide ecosystem services, and consequently a risk to human well-being.

The current state of cork oak AFS and the effects of climate on the development of these ecosystems can be assessed using indicators. Primary production indicators, such as gross primary production (GPP) and net primary production (NPP), have been widely modelled in carbon cycle-related studies at the global scale as they are climate-sensitive (Huang et al., 2019; Tang et al., 2019; Stocker et al., 2019). GPP is the total amount of carbon stored by plants, which takes into account autotrophic respiration (Collalti and Prentice, 2019; Collalti et al., 2020). Subtraction of autotrophic respiration gives us the net carbon transformed into biomass (NPP). The NPP/GPP ratio is a measure of carbon use efficiency (CUE), which represents the efficiency of plants to sequester carbon from the atmosphere through photosynthesis. In this type of assessment, the use of open source remote sensing data is very useful as it provides continuous, valuable information on ecosystem productivity over large areas.

The aims of the present study were (i) to evaluate the influence of climate variability on different cork oak AFS in the Iberian Peninsula (categorized by canopy cover) using production indicators (NPP and CUE) and (ii) to analyse whether geographical location may play a role in the incidence of the adverse effects of climate on these ecosystems.

2. Materials and methods

2.1. Study area and climate data

The study focused on mainland Portugal and Spain (Iberian Peninsula) and did not include the islands (Fig. 1). The study region is surrounded by water, mainly by the Atlantic Ocean and the Mediterranean Sea, including 1,793 and 4,964 km of coastline of Portugal and Spain, respectively. The region also comprises 65% of the total distribution range of *Quercus suber* (Caudullo et al., 2019).

The area is very heterogeneous in terms of climate and broadly speaking can be divided into three zones: dry climate zones (widespread in the south and southeast); temperate zones with dry, hot summers (most of the Iberian peninsula, i.e. approximately 40% of its surface); and temperate zones with dry, temperate summer climates (most of the northeast of the Peninsula, as well as almost all of the west coast of mainland Portugal) (AEMET, 2011).

Climate data were obtained by combining ERA5-Land monthly averaged data from 1981 to present (Muñoz Sabater, 2019) and ERA5 monthly averaged data on pressure levels from 1979 to present (Hersbach et al., 2019). We download monthly mean variables from 2001 to 2020, for temperature, precipitation, relative humidity, total evaporation, potential evaporation and volume of soil water at different layers (layer 1: 0–7 cm; layer 2: 7–28 cm; layer 3: 28–100 cm; layer 4: 100–289 cm). All variables were provided at $0.1^\circ \times 0.1^\circ$ spatial resolution (ca. 9 km × 9 km pixel size), except relative humidity, which was distributed at $0.25^\circ \times 0.25^\circ$ spatial resolution (ca. 31 km pixel size). These data were summarized by season, i.e. for winter, spring, summer and autumn months.

Although proximity to the coast is not a climatic variable *per se*, it is a factor that affects climate conditions, with temperatures being higher or lower and coastal areas being wetter than inland areas. Thus, the shortest distance between each *Q. suber* plot and the coast was computed.

2.2. Vegetation productivity data

The global MODIS data collection was 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 gross primary production (GPP) and net primary production (NPP) data (in kg carbon per m^2) respectively, from 2001 to 2020, at 500-m resolution. GPP and NPP

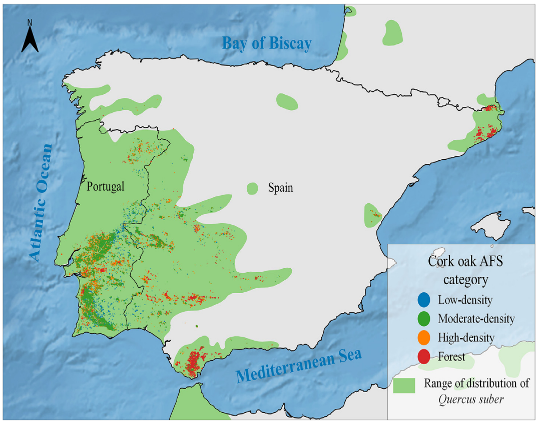

Fig. 1. Range of distribution of *Q. suber* in the Iberian Peninsula and the different types of study plots.

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 those pixels.

The GPP data set (originally one for every 8 days) was used to calculate annual mean values and carbon use efficiency (CUE) (Pérez-Girón et al., 2020). Annual CUE values were calculated as the NPP/GPP ratio, representing the efficiency of plants to sequester carbon from the atmosphere through photosynthesis.

2.3. Plot selection

The digital maps available for Portugal and Spain were different, due to the different purposes of each. For Portugal, we used the *Carta de Uso e Ocupação do Solo de Portugal Continental* 2018 (COS), developed with the aim of characterizing land cover in the country in 2018. In Spain, we used the Forest Map of Spain (MFE), at scale 1:25000 (MFE25) or 1:50000 (MFE50), depending on availability, as the map was created with the information captured in national forest inventories carried out at different times: the MFE50 project was completed between 1997 and 2006, and the MF25 was developed after 2007.

We selected areas designated as “Florestas de sobreiro” y “Superfícies agroflorestais (SAF) de sobreiro” from the COS maps as those with *Q. suber* presence. To harmonize the selection criteria, we reproduced the classification criteria used by COS in MFE, selecting patches classified as “Alcornocales” or “Dehesa”, predominated by *Q. suber* and with a canopy cover greater than 10%, the threshold established in the COS maps.

Finally, to ensure that GPP and NPP values corresponded to *Q. suber* AFS, we only selected the areas if more than 80% of the MODIS pixels were fully occupied by areas in which *Q. suber* AFS was present.

2.4. Categorization

The social, economic and ecological importance of the cork oak has led to its management over centuries, giving rise to different tree densities depending on the aim of the AFS (Aronson et al., 2009; Fonseca and Pinto-Correia, 2009). Tree density seems to control edaphic (Gallardo, 2003) and climatic conditions in this type of ecosystem (Joffre et al., 1999). It has recently been demonstrated that forest canopy has a buffering effect on climatic conditions and their variations, even generating microclimates (De Frenne et al., 2021; Haesen et al., 2021).

Thus, in order to address the different densities in the AFS, we used the Tree Cover Density (TCD) 2018 from the high-resolution products provided by the Copernicus Land Monitoring Service (European Environment Agency) to assign to each previously selected MODIS pixel the average value of the TCD pixels on which the MODIS pixel overlaps. The selected pixels were then classified according to TCD into the following categories (Costa et al., 2006): low-density AFS (<10%), moderate-density AFS (10%–25%), high-density AFS (25%–50%) and forest stands (>50%). According to Costa et al. (2006) the average expected stand densities (in trees per hectare) are 25–35 (±18) for low-density AFS, 36–42 (±17) for moderate-density AFS, 48–55 (±18) for high-density AFS, while the stand density for forest category will be much higher. To check the relationship between TCD and stand density, data from the 3rd National Forest Inventory (IFN3; from its acronym in Spanish) were used to assess whether the stand density (number of trees per hectare) increased with the TCD. Thus, based on TCD, the first three types (low-, moderate- and high-density AFS) can be considered open forest systems, with low tree densities, while the forest category more closely resembles a forest stand structure, with canopy closure expected to create a microclimate.

2.5. Statistical analysis

We used multiple linear regression to determine how cork oak AFS primary production was related to climate predictors and proximity to the coast. Hotspot analysis was used to identify significant spatial clusters of high- and low-efficiency areas.

Multiple linear regression was used to model the relationships between primary production indicators (NPP and CUE) and the climatic variables and proximity to the coast. An exhaustive search for the best predictor subsets was performed using the branch-and-bound algorithm, to test all possible combinations of predictors for final selection of the best model (Narendra and Fukunaga, 1977). As this algorithm returns the best model of each size, we limited the number of predictors to 5. Candidate models were compared using the adjusted coefficient of determination (R^2_{adj}) and the root mean square error (RMSE). To check multicollinearity, we computed the variance inflation factor (VIF) and excluded predictors yielding VIF >10 (Mandeville, 2008).

For proximity to the coast, we used a univariate linear regression approach and applied linear-log models. Spearman correlation coefficient was used to determine the strength of the linear relationship between proximity to the coast and climatic variables. A high R value indicates a stronger relationship, while a low R value indicates the opposite. Positive R values reveal the same trend, while low R values reveal the opposite trend (Spearman, 1904).

Hotspot analysis was conducted by applying the local Getis-Ord Gi* statistic (Getis and Ord, 1992) to identify high and low CUE areas (hotspots and cold spot areas) within the selected pixels. The analysis only included the CUE as this value establishes the threshold to the physiological activity of plants (Amthor, 2000; Van Iersel, 2003; Keith et al., 2010). Local spatial autocorrelation was measured to assess how each data point is surrounded by other data points (neighbourhood) with similarly high or low values. The method returns a Z-score and p-value for each data point assuming a normal distribution. Z-scores greater than 1.96 and less than -1.96 are statistically significant at $p < 0.05$, while larger positive and negative values indicate greater clustering.

The leaps library (Lumley, 2013) implemented in the R software environment (R Core Team, 2020) was used to fit multiple linear regression based on branch-and-bound algorithms. Graphical analyses were conducted with the ggplot2 package (Wickham, 2009). Significant differences were determined using the Wilcoxon-Mann-Whitney test (at $\alpha = 0.01$).

3. Results

3.1. Primary production indicator trends

The 870420 AFS plots were distributed as follows: 11.6% low-density, 28.9% moderate-density, 44.4% high-density and 15.1% forest plots. Tree density differed significantly between the different groups based on forest inventories (Figure S1 in supplementary material), except between the low-density and moderate-density groups. A large difference in tree density between high-density plots (TCD between 25% and 50%) and forest plots (TCD >50%) was noted, and therefore large differences in the influence of climatic conditions were expected.

The trends in GPP and NPP in relation to TCD showed that the indicator value and dispersion increased with canopy cover (Fig. 2). The mean NPP ranged from 0.655 kg $C \cdot m^{-2} \cdot yr^{-1}$ for low-density plots to 0.985 kg $C \cdot m^{-2} \cdot yr^{-1}$ for the forest plots, with maximum values of up to 2.21 kg $C \cdot m^{-2} \cdot yr^{-1}$ reached. Inversely, the CUE value decreased as the canopy cover increased, with mean values ranging from 0.64 in low-density plots to 0.58 in forest plots and maximum values reaching up to 0.72 were reached in each of these types of plots; the minimum value was 0.30 in high-density and forest plots.

Regarding annual trends, the mean values were maintained (Fig. 3a). In general, the dispersion range and average NPP increased with canopy cover, while CUE decreased as canopy cover increased. However, generalized slight decreases in NPP were observed, particularly in 2005, but were not related to CUE. The minimum mean NPP values of the historical series were recorded in 2005, reaching values of 0.474 kg $C \cdot m^{-2} \cdot yr^{-1}$ in the low-density plots, 0.544 kg $C \cdot m^{-2} \cdot yr^{-1}$ in moderate-density plots, 0.611 kg $C \cdot m^{-2} \cdot yr^{-1}$ in the high-density plots and 0.898 kg $C \cdot m^{-2} \cdot yr^{-1}$ in the forest plots. This represents decreases of more than 20% for low-, moderate- and high-density plots, while the decrease in the forest plots was only 11%. The decrease in NPP values was immediately recovered in the following year with increases of the same magnitude as the decreases. The mean CUE values for this period suffered decreases of less than 2% that lasted 2 years, i.e. recovery of the values before the large decrease in NPP occurred in 2007 (not the largest decrease in the historical range). In 2012 and without any precedent, CUE values below 0.3 were observed for a total of 97 samples in the forest category. Similar findings were observed in 2015, 2017 and 2020, in respectively 172, 87 and 201 samples in the forest category. Rather than being an isolated event, this seems to have become a more frequent trend in recent years, first affecting the high-density plots in 2015.

3.2. Influence of climate factors

The parameter estimates and goodness of fit statistics for the multiple linear regression models based on canopy cover are summarized in Table 1. NPP showed a good fit in all categories, with the variance explained increasing with canopy cover (R^2_{adj} ranging from 0.64 to 0.72), except for forest category, which yielded the lowest variance explained ($R^2_{adj} = 0.59$). On the other hand, CUE also showed a good fit in low-, moderate-, and high-density plots, with the variance explained increasing with canopy cover (R^2_{adj} from 0.46 to 0.57) as observed for NPP. The goodness of fit for CUE in forest category was very low, which may indicate that the CUE is influenced by factors other than climate factors.

Relative humidity in the summer months (rhm_Summer) and volume of soil water in the first two layers of soil (swl1 and swl2) in the summer months were the most important predictors for NPP models for low-, moderate- and high-density plots. The influence was similar in models: NPP benefited from an increase in relative humidity and volume of soil water of layer 2, but was negatively influenced by an increase in volume of soil water in layer 1. The most important predictors in the forest plots

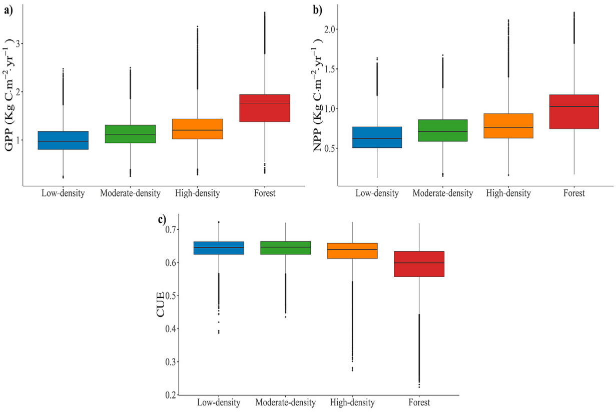

Fig. 2. Box-and-whisker plot showing the mean trends in GPP, NPP and CUE. The dots represent outliers.

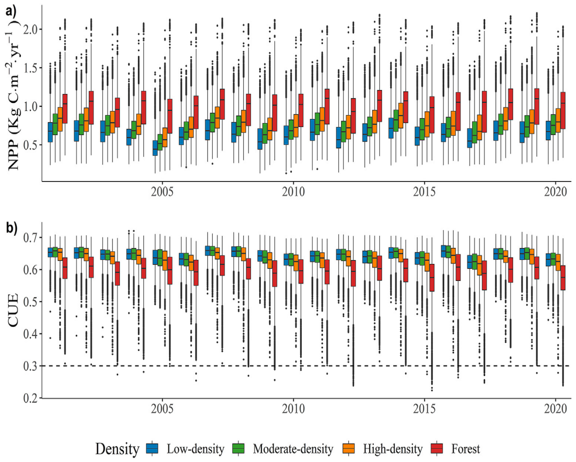

Fig. 3. Box-and-whisker plot showing the annual trends in GPP, NPP and CUE. The dots represent outliers. Dashed black lines indicate the threshold of ecosystems at potential risk (CUE = 0.3).

changed slightly. Relative humidity in the summer months was maintained, but the volume of soil water was replaced by total precipitation in summer (tp_Summer). In addition to changing the predictors, the influence also changed, with the lower rainfall during the summer months leading to higher NPP values.

Regarding CUE, both relative humidity in the summer months (rhm_Summer) and mean temperature of spring months (t2m_Spring) were constant throughout the models, and relative humidity had a positive influence, as occurred with NPP. The mean temperature of spring months negatively affected the CUE. The variables that changed were total evaporation in summer (e_Summer) in the low-density model and volume of soil water in layer 3 in spring (swl3_Spring) in the high-density model.

Table 1
Results of multiple linear regression showing the best models obtained for NPP and CUE.

AFS Category	Dependent variable	Independent variable	Parameter estimate	Std. Error	RMSE	R^2_{fit}
Low-density	**NPP (Kg C·m^{-2}·yr^{-1})**	(Intercept)	0.6889	0.0004	0.1289	0.6438
		rhm_Summer	0.1845	0.0005		
		swvl1_Summer	−0.2162	0.0012		
		swvl2_Summer	0.2119	0.0013		
	CUE	(Intercept)	0.6426	0.0001	0.0239	0.4606
		e_Summer	0.0058	0.0001		
		rhm_Summer	0.0210	0.0001		
		t2m_Spring	−0.0096	0.0001		
Moderate-density	**NPP (Kg C·m^{-2}·yr^{-1})**	(Intercept)	0.7529	0.0002	0.1123	0.6832
		rhm_Summer	0.1702	0.0003		
		swvl1_Summer	−0.1795	0.0007		
		swvl2_Summer	0.1817	0.0007		
	CUE	(Intercept)	0.3065	0.0000	0.4719	0.5039
		rhm_Summer	0.4485	0.0011		
		t2m_Spring	−0.1717	0.0010		
High-density	**NPP (Kg C·m^{-2}·yr^{-1})**	(Intercept)	0.8058	0.0002	0.1152	0.7243
		rhm_Summer	0.1828	0.0002		
		swvl1_Summer	−0.1696	0.0005		
		swvl2_Summer	0.1740	0.0005		
	CUE	(Intercept)	0.6336	0.0000	0.0226	0.5713
		rhm_Summer	0.0206	0.0000		
		swvl3_Spring	−0.0044	0.0000		
		t2m_Spring	−0.0098	0.0000		
Forest	**NPP (Kg C·m^{-2}·yr^{-1})**	(Intercept)	0.9337	0.0005	0.1827	0.5747
		rhm_Summer	0.2047	0.0005		
		tp_Summer	−0.0342	0.0003		
	CUE	(Intercept)	0.5828	0.0002	0.0701	0.1146
		swvl1_Summer	−0.0232	0.0003		
		swvl3_Summer	0.0223	0.0003		
		t2m_Summer	−0.0295	0.0002		

3.3. Proximity to the coast

The relationship between the primary production indicator (NPP and CUE) and the proximity to the coast decreased sharply for short distances, slowing down or becoming asymptotic as the distance increased. Therefore, a linear-log model was constructed: the goodness of fit statistics for NPP and CUE are shown in Fig. 4. In general, the R^2_{adj} values for each indicator and group are similar to the R^2_{adj} values obtained for climatic factors. In the case of NPP, the outcomes were very clear, with the indicator values increasing as the distance to the coast decreased. A weaker relationship was obtained for CUE, although the trend continued to be observed. Finally, forest CUE was not related to the proximity to coast, apparently due to a large number of points near the coast with low CUE values, which may also explain the lack of any relationship between CUE and climatic factors. Annual models (Figures S2, S3, S4 and S5 in Supplementary material) followed the same trends shown here. However, dependency was higher in some years, i.e. 2005 and 2017.

Proximity to the coast was highly and negatively correlated with spring and summer relative humidity ($r = -0.67$ and -0.81, respectively), negatively correlated with average temperature of autumn and winter ($r = -0.52$ and -0.54, respectively) and positively correlated with summer average temperature ($r = 0.48$). The variable was not correlated or only slightly correlated with precipitation and soil water content.

3.4. Hotspot analysis

The Gi* statistics revealed clusters of *Q. suber* AFS with high and low CUE within the study area, respectively corresponding to hotspot and cold spot areas (Fig. 5). In general, the largest hotspot areas occurred in the southwest of Portugal and south and northeast of Spain, always close to the coast, with large clusters in low-, moderate- and high-density plots, mainly in the Alentejo and Algarve regions (Portugal). The cold spot areas were generally located in inland areas, usually sparsely distributed, but forming large clusters in high-density and forest plots. Here we can distinguish three large clusters mainly located in Los Alcornocales natural park (south of Spain), Sierra de Hornachuelos and Sierra Norte de Sevilla natural parks (north of the Guadalquivir valley) and south of Caceres (central Spain). Forest cold spots were almost absent from AFS plots in Portugal.

Comparative box-and-whisker plots indicate significant differences between hotspot and cold spot CUE areas regarding the main independent variables selected in CUE multiple linear regression models (Fig. 6). The trend shown is the same for the different types of AFS, and the differences between hotspots and cold spots were slightly smaller only in the forest category. Hotspots were identified in coastal zones while cold spots were found in inland areas (Fig. 6a). The average distance to the coast was about 10 km for hotspots and more than 120 km for cold spots, except for the forest category, for which the distances were shorter, around 30 km. The dispersion was also remarkable as hotspots varied very little and were grouped very close to the mean, with the inverse observed for in cold spots. Related to the above, relative humidity during the summer months was higher in hotspots (Fig. 6b), with average values around 68%–70%, while for cold spots it was around 47%–48%, except for the forest category, for which the values were slightly higher (61%). Finally, the trends in average spring temperature (Fig. 6c) were very similar, regardless of the canopy cover, with values between 16.5 °C and 18 °C in the hotspots and between 1 °C and 2 °C in the cold spots.

4. Discussion

4.1. Changes with stand density

The multifunctional character of traditionally managed cork oak agroforestry systems has conditioned their structure and composition (Bugalho et al., 2011), mainly characterized by a low tree density with the presence of herbaceous or shrub vegetation in the understory. Consequently, the contribution of each part of the structure to primary production is different. In the dehesa ecosystem, understory species contribute between one third and one half of the total GPP, and consequently, about half or two-thirds of the GPP is contributed by trees (Dubbert et al., 2014; Correia et al., 2016). Therefore, in low-, moderate- and high-density categories the contribution to biomass should be considered in relation to the ecosystem as a whole, rather than in relation to isolated species as e.g. in monospecific *Q. suber* stands. However, in the forest category, trees contribute more than half the value of the primary production indicator and thus establish a relationship with the species.

The results obtained are sensitive to changes in canopy cover, highlighting different trends between the different categories as the canopy cover increases and especially with the forest category, where the effects may be attributed to the species. Both GPP and NPP values increased with canopy cover. The highest GPP and NPP values were associated with the

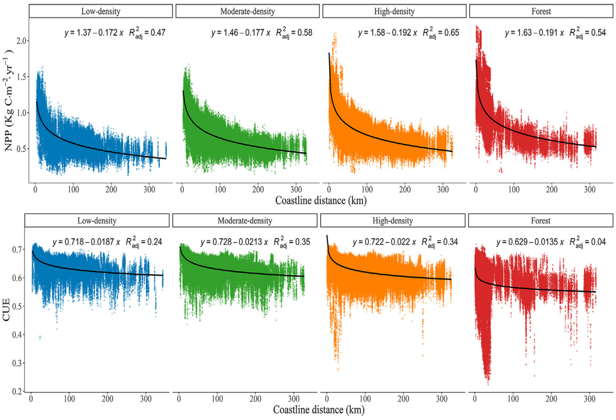

Fig. 4. Linear-log models for NPP and CUE grouped by canopy cover categories. Note that "x" in the model formula indicates $\log(x)$.

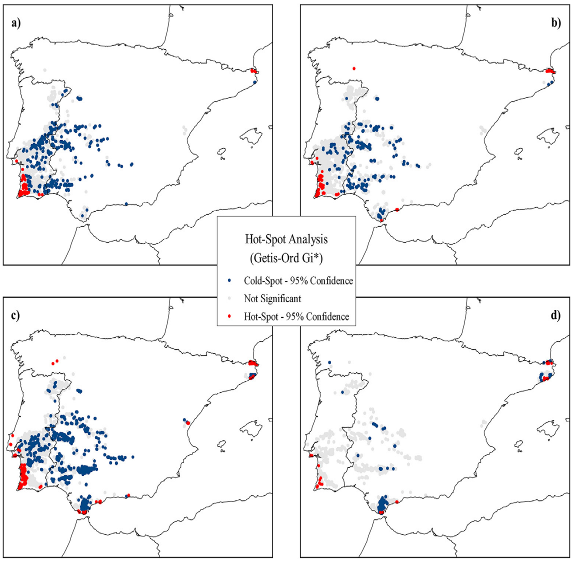

Fig. 5. Location of hotspot (red points) and cold spot (blue points) areas of *Q. suber* AFS based on CUE and grouped by canopy cover categories: a) low-density, b) moderate-density, c) high-density and d) forest. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

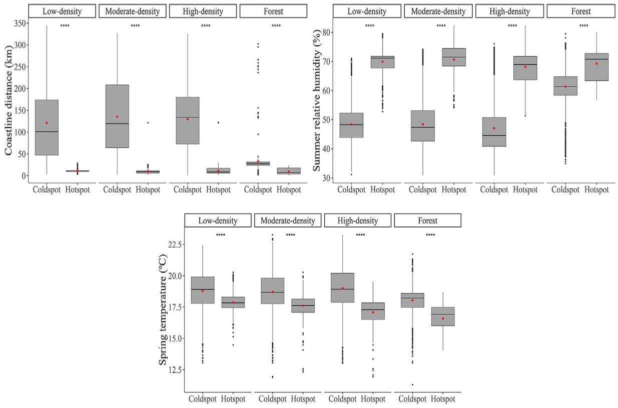

Fig. 6. Box-and-whisker plot comparing a) proximity to the coast, b) summer relative humidity and c) spring temperature in hotspots and cold spot CUE areas. Statistical significance: ns: $p > 0.05$; *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$; ****: $p \leq 0.0001$. The black dots represent outliers. The red dots represent mean values. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

forest category and related to a large number of trees and a greater contribution to the total amount of plant biomass of trees to the indicators than herbaceous or shrub vegetation. By contrast, the opposite effect was observed for influence of the canopy cover on the CUE, with average CUE value decreasing and the total number of low-value outliers increasing as canopy cover increased. These slightly low CUE values, relative to the categories with lower tree canopy density, are consistent with the stand development, as halts in growth are not followed by halted respiration, thus leading to a decrease in CUE (Collalti and Prentice, 2019).

However, the increasingly common very low extreme CUE values in 2012, 2015 and 2020 in high-density AFS and forest categories are of particular concern. These values are very close to the established threshold of 0.2, which may limit the physiological activity of plants (Amthor, 2000; Van Iersel, 2003; Keith et al., 2010) by increasing the additional respiratory cost, reducing growth and new tissue formation, or even leading to plant collapse, thus indicating that ecosystems will potentially be at risk (Pérez-Girón et al., 2020). However, such low values were not observed in the categories with lower canopy cover (low- and moderate-density categories), which may be related to the scarcity of trees. The understorey vegetation in cork oak AFS may mainly comprise annual species or crops, the growth period of which depends on the amount of rainfall and its seasonal distribution, or shrub vegetation well adapted to the Mediterranean summer drought stress (Correia et al., 2016). However, this is not possible with trees, as the weather conditions do not determine whether the trees are alive or dead, as trees can tolerate a range of conditions, with modified maintenance costs affecting carbon assimilation. This difference would therefore explain the absence of low CUE values in the low- and moderate-density categories.

The study findings also highlight the higher CUE of managed ecosystems than of unmanaged ecosystems (Fernández-Martínez et al., 2014; Campioli et al., 2015), suggesting that the conservation and future of these systems - as well as the biodiversity they maintain and the ecosystem services they provide - are strongly dependent on human management (Pereira and da Fonseca, 2003; Bugalho et al., 2011). However, some changes appear to be taking place in these ecosystems as the same pattern was not observed in forest plots and high-density AFS within the historical period considered, indicating that a change in some factor has been accentuated in recent years. Here, different drivers such as economic (e.g. declining profitability of traditional dehesa products or agricultural intensity), socio-cultural (e.g. rural exodus), political (e.g. availability of access to direct payments of EU Common Agricultural Policy (CAP)), technological (e.g. new technics) and natural (e.g. climate change) factors may be affecting these systems in a complex and simultaneous way (Pinto-Correia et al., 2011; Plieninger et al., 2021).

4.2. Responses of NPP and CUE to climate influence

Previous studies have claimed that water is the main driver of primary production in cork oak AFS, mainly linking productivity to the limitations caused by summer droughts (Pereira et al., 2007; Piayda et al., 2014; Ramos et al., 2015; Correia et al., 2016). Our findings also indicate water limitations in summer as the main driver for NPP models in all *dehesa* categories, but to a greater extent in open ecosystems, i.e. categories with low canopy cover (<50%), than in systems with a forest stand type structure. This suggests that summer is a critical season for cork oak AFS, regardless of the canopy cover. Furthermore, although water availability was also a limiting factor in the CUE models in our study, fewer limitations were observed than in the NPP models, as other factors were involved.

The productivity of any plant depends on its ability to maintain photosynthetic tissues with an adequate water level. When water is limiting, water loss in plants is minimized via transpiration, with closure of stomata restricting the entry of CO_2 and thus also limiting photosynthesis (Mediavilla and Escudero, 2004; Rzigui et al., 2018; David-Schwartz et al., 2019; Grossiord et al., 2020). Although this is a typical adaptive mechanism in Mediterranean species, such as *Q. suber* and *Q. ilex*, protecting against summer drought, trees generally display stomatal control over transpiration (Nardini et al., 1999; Pérez et al., 2005; David et al., 2007; Besson et al., 2014); drought also induces leaf senescence in the understorey vegetation, and all of these factors lead to a decrease in primary production levels in the ecosystem (Pereira et al., 2007). Relative humidity plays a key role in this process (closely related to vapor pressure deficit: Grossiord et al., 2020), because the transpiration rate falls as relative humidity increases. This explains why relative humidity in the summer months is the most important variable in all of our models and why it is positively related to NPP. The relationship with CUE is clear, as the maintenance cost increases with the transpiration rate (Amthor, 2000; Van Iersel, 2003), and the maintenance cost will therefore be lower at high relative humidity, and the CUE will increase.

When soil water is available to plants, transpiration rates are mainly controlled by climatic factors. However, when the soil water becomes limiting, the transpiration rate falls (Gardner and Ehlig, 1963). Thus, in the NPP models, in addition to being affected by relative humidity, the low-, moderate- and high-density categories were also positively affected by water volume in the second layer of soil (swl2; between 7 and 28 cm) and negatively by soil water volume in the first 7 cm (swl1). In open ecosystems such as dehesas, the first layer of soil is particularly sensitive to water loss through evaporation, which will form part of the relative humidity of the air; thus, favouring an increase in evaporation would benefit the ecosystem to a greater extent. From the point of view of water absorption by plants, water is more beneficial in deeper layers, where the roots of most trees and of the understory vegetation occur (David et al., 2007; Baldocchi et al., 2010; Correia et al., 2016). This explains the positive relationship with the presence of water in the second layer of soil. Although greater limitation of the amount of water in the third layer of soil was expected due to the location of most roots (from 28 cm to 1 m), we believe that these findings may be explained by daily fluctuations in soil water content due to hydraulic lift processes (David et al., 2007). The water rises to the upper soil layers where it becomes available both to the oak tree roots and understory vegetation (Marañón et al., 2009).

Temperature only appears to influence CUE, especially the average temperature in spring. Temperature plays a fundamental role because it affects both photosynthesis and autotrophic respiration (R_a), the rates of which increase exponentially with temperature, thus increasing the maintenance cost (Ryan, 1991; Ryan et al., 1994). As this only occurs in low-, moderate- and high-density plots, and as *Q. suber* is adapted to Mediterranean climates characterized by high temperatures, this pattern is associated with the vegetative period of the understorey vegetation (Dubbert et al., 2014; Correia et al., 2016). Higher temperatures in early spring may accelerate the activation and germination processes in annual plants, favouring greater photosynthetic activity and therefore greater CUE. However, higher temperatures in late spring are also likely to have the opposite effect, shortening the duration of photosynthetic activity by advancing senescence. Furthermore, temperature affects both the plant part of the ecosystem and also other climatic factors such as relative humidity and soil water content.

Finally, the findings suggest structural and compositional differences between low-, moderate- and high-density AFS and the forest plots. Under forest canopy cover, the amount of photosynthetically active radiation and wind speed are reduced, directly reducing the variations in humidity and temperature and extreme events (De Frenne et al., 2021; Haesen et al., 2021). The effects of canopy throughfall on the soil characteristics are also modified by the contribution of organic matter (Marañón et al., 2009). All of this is translated into differences in primary production and the associated factors. Thus, it was only possible to model the NPP response, and the goodness of fit was lower than that of the previous model; it was not possible to model the CUE, possibly because this variable does not depend on the predictors used. Similarly, the unexpected and negative effect of summer rainfall on NPP may be related to the fact that the basic needs of humidity and water are covered in these stands. Heavy storms occur at the end of the summer, which may cause waterlogging that is damaging to the ecosystem (Pereira, 2007). The storms can also provoke fluctuations ranging from flooding to water deficiency, the latter of which is favoured in periods of high temperatures and can potentiate the spread and infectivity of *Phytophthora* species (González et al., 2020).

4.3. Oceanic influence as a buffer for extreme droughts

The study findings highlighted the influence of oceanic climatic conditions on the NPP of cork oak AFS, with proximity to the coast providing a clear benefit. Similarly, the decrease in NPP with increasing distance from the coast does not seem to be limiting for these ecosystems but rather is asymptotic, either because the tree species is within its distribution range (Gil and Varela, 2008; Caudullo et al., 2019) or because it is adapted to the driest climatic conditions (David et al., 2007; Besson et al., 2014).

The study findings reflect a gradient of change along the dehesa categories. In the low-density category, the highest NPP values, mainly contributed by the understory (Dubbert et al., 2014; Correia et al., 2016), are lower than for the category immediately above the same distance from the coast, up to the highest values found in the forest category. The forest category, coinciding with the ecological response of *Q. suber*, is benefited by a mild oceanic climate with high relative humidity (between 65% and 80%) (Quero et al., 2008), which is also consistent with the observed differences between hotspots and cold spots (Fig. 6). Therefore, under optimal climate conditions a greater number of trees will be more productive. In addition, the high and negative correlation between the distance to the coast and the summer relative humidity again suggests that relative humidity in the summer months is a limiting factor for all cork oak AFS as it is closely linked to stomatal closure (David-Schwartz et al., 2019). A similar but slightly weaker pattern was observed for CUE, the levels of which varied with the proximity to the coast within ranges of distance that generally do not affect the physiological functioning of the ecosystems. In this last case, the microclimate generated by the forest (De Frenne et al., 2021; Haesen et al., 2021) seems to be sufficient to maintain the conditions necessary for adequate carbon assimilation, without depending on the coastal influence.

The findings of the hotspot analysis were consistent with these previous results, highlighting high-efficiency areas near the coastline and cold spots grouped in specific areas or dispersed inland. However, considering the CUE value, some clusters of points suggest some degree of risk to the ecosystem (Pérez-Girón et al., 2020). These CUE values are very low (generally below 0.3) both in high-density and forest categories (Fig. 4) and are particularly notable in the latter at short distances to the coastline, in the south of Spain (Fig. 5), and considering the annual distribution was more pronounced in 2012, 2015, 2016, 2017 and 2020 (Fig. 3). According to the historic drought database for Spain (Vicente-Serrano et al., 2017), droughts were recorded in 2005, 2012, 2015, 2017 and 2019, with those occurring in 2005 and 2017 being the most extreme. For these two years in particular, the goodness-of-fit of our linear-log models increased significantly (Figures S2, S3, S4 and S5 in Supplementary material), which suggests that in extreme drought years, proximity to the coast may buffer cork oak AFS from extreme climate conditions. This further confirms the suggestions of Piayda et al. (2014), who argued that the high vapor pressure deficit (related to temperature and relative humidity (Grossiord et al., 2020) found in cork oak ecosystems in Portugal may be a consequence of the lack of entry of oceanic air masses.

5. Conclusions

The responses of the different TCD-based categories of cork oak AFS to primary production indicators suggest that canopy cover and hence tree density play a key role in the influence of climatic conditions. Forest plots can maintain microclimatic conditions that make them less dependent on environmental conditions, while AFS plots with an open ecosystem (lower densities) depend on macroclimate conditions. Therefore, within the same ecosystem, the response to climate change may vary depending on tree density.

Regarding the influence of climate variability, our findings showed that the responses of the ecosystems reflect the ecological traits and the different adaptive strategies used by the component trees and understory plants to survive drought seasons, where water (soil or air moisture) is the main driver of primary production. Relative humidity is associated with transpiration and water loss through closure of stomata, which will vary depending on the severity of water deficiency, limiting photosynthesis to a greater or lesser extent. At the same time, both the hydraulic lifting processes and the deep roots allow the trees to take advantage of the groundwater from the deeper layers and make it available to understory vegetation with shallow, but not superficial, roots. Temperature only seems to influence CUE in open ecosystems (low-, moderate-, and high-density) in which the understory layer makes a greater contribution to primary production. In particular, an increase in spring temperature could advance the growing season but could also shorten the growth period of annual plants and increase the maintenance cost.

Several factors affect these ecosystems and do so in a complex way, and it is therefore difficult to isolate the individual effects. For example, relative humidity and the proximity to the coast are closely related, thus influencing the carbon balance in cork oak AFS. Our findings show that proximity to the coast improves productivity levels and may also buffer climate conditions in extreme drought years, reducing the associated adverse effects and the risk to the ecosystem. Therefore, in future climate change scenarios, in which the Mediterranean region is expected to be one of the most severely affected and droughts are expected to be more frequent, prolonged, and intense, an important risk of loss of ecosystems and their associated functions will appear. This will affect all ecosystems, although inland ecosystems - where the first disturbances have already been detected - may not be buffered against the oceanic influence and would therefore be particularly affected, while coastal areas, such as southwestern Portugal, may cope better.

Ethics approval and consent to participate

We have no ethical concerns to declare. All authors consented to participate on this manuscript.

Consent for publication

All authors agree with the content of this manuscript and its publication in *Forest Ecosystems*.

Availability of data and material

The datasets analysed during the current study are freely available from the following hosts. ERA5-Land monthly averaged data from 1981 to present and ERA5 monthly averaged data on pressure levels from 1979 to present can be accessed from the Copernicus Climate Change Service (C3S) Climate Data Store (CDS) (https://doi.org/10.24381/cds.68d2bb30 and https://doi.org/10.24381/cds.6860a573). MODIS MOD17A2HGF.006 and MOD17A3HGF.006 products can be accessed from the Land Processes Distributed Active Archive Center (LP DAAC) data pool (https://lpdaac.usgs.gov/products/mod17a2hgfv006/and https://lpdaac.usgs.gov/products/mod17a3hgfv006/). Forest Map of Spain can be accessed from the Ministerio para la Transición Ecológica y el Reto Demográfico webpage (https://www.miteco.gob.es/es/cartografia-y-sig/ide/descargas/biodiversidad/mfe.aspx). Carta de Uso e Ocupação do Solo de Portugal Continental 2018 can be accessed from the Sistema Nacional de Informação Geográfica Of Direção-Geral do Território (https://snig.dgterritorio.gov.pt/rndg/srv/por/catalog.search).

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Authors’ contributions

JCPG, PAA, and EDV together conceived the research idea; JCPG collected and analysed data and wrote the initial draft of the manuscript; all authors contributed to the manuscript review and editing. All authors read and approved the final manuscript.

Declaration of competing interest

The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fecs.2022.100008.

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CHAPTER 4

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

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Research Paper

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

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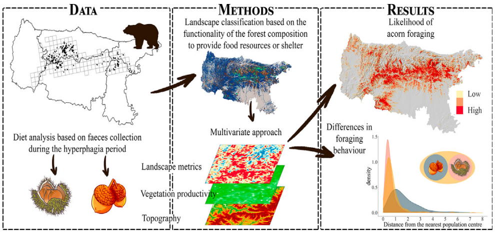
HIGHLIGHTS

- 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

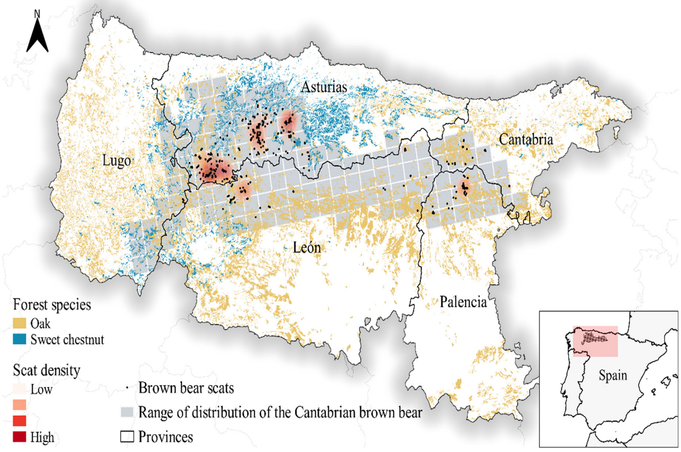

Fig. 1. Location and density of brown bear scats sampled within the study area. Forest species presence was extracted from the Forest Map of Spain (MFE) and only the predominant species is represented, although co-occurrence of species is possible. The oak category comprises *Quercus pyrenaica* Willd., *Quercus faginea* Lam., *Quercus petraea* (Matt.) Liebl., *Quercus robur* L., *Quercus ilex* L. and *Quercus suber* L.. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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	Land use established by the TNFI and the structural forest type in non-wooded areas
Grassland	2	
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

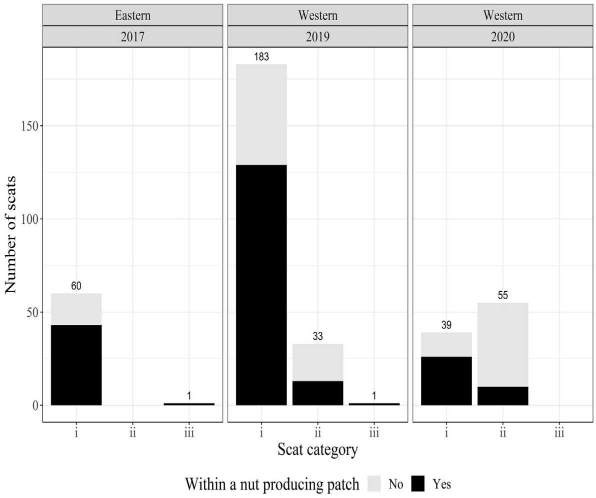

Fig. 2. Scat distribution in year and location categories within a nut-producing patch. The following categories were considered: i) presence of *Quercus* sp. acorn remains, ii) presence of *C. sativa* chestnut remains and iii) presence of both acorn (*Quercus* sp.) and chestnut (*C. sativa*) remains.

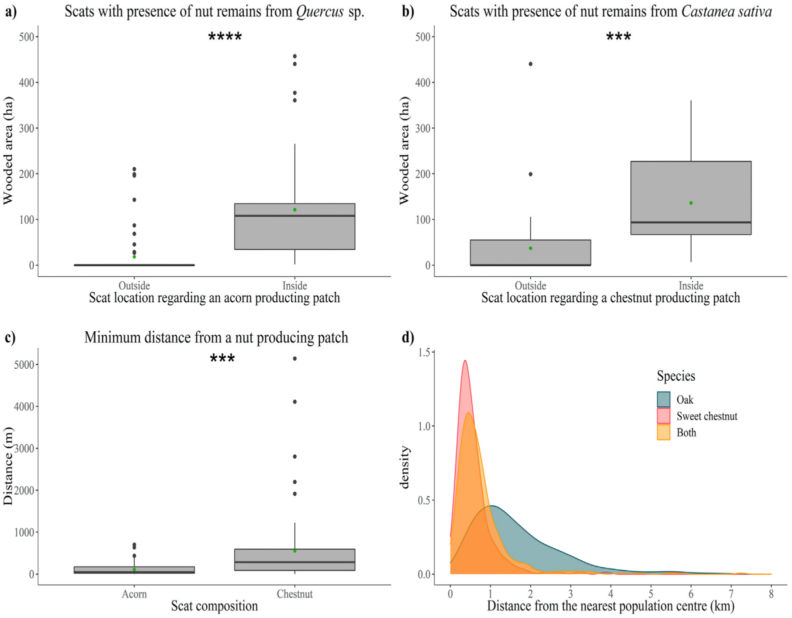

Fig. 3. Box-and-whisker plot comparing the average wooded area of the patch for scats found inside or outside the a) acorn- or b) chestnut-producing patch. c) Box-and-whisker plot comparing the minimum distance between scat containing nut remains and located outside of a forest patch with presence of *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

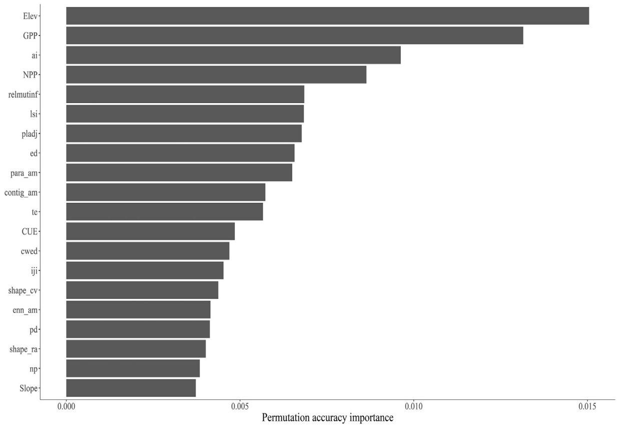

Fig. 4. Top 20 variables in regard to permutation importance for acorn scats, determined using the cforest algorithm.

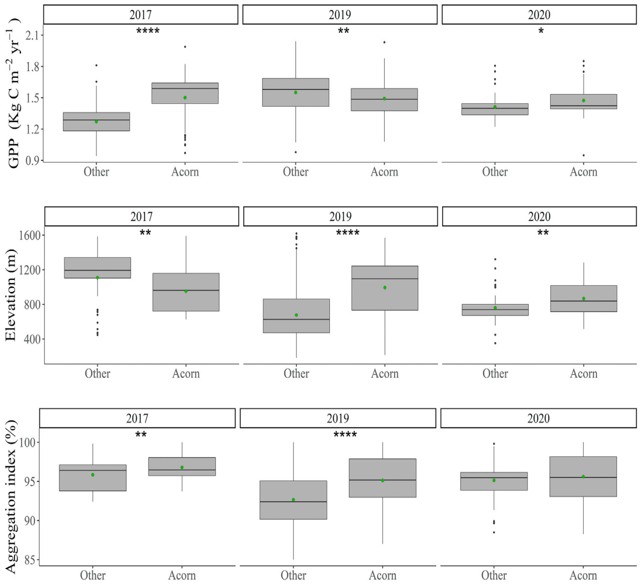

Fig. 5. Box-and-whisker plot comparing the presence and absence of scats containing acorns by years for the most important vegetation productivity, topographical and landscape variables. Statistical significance: *: $p \le 0.05$; **: $p \le 0.01$; ***: $p \le 0.001$; ****: $p \le 0.0001$. The black dots represent outliers. The green dots represent mean values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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.,

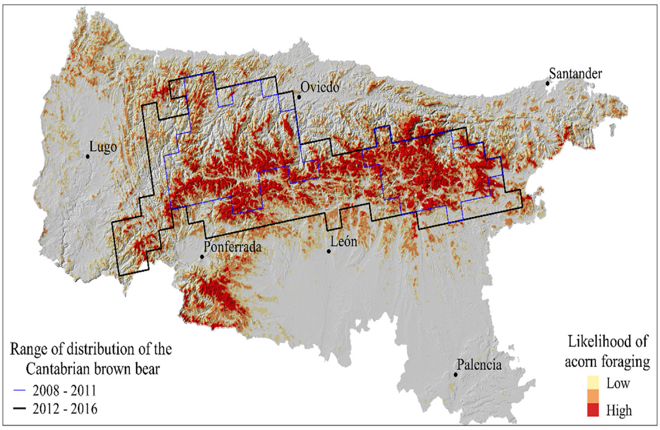

Fig. 6. Maps of probability of acorn foraging by brown bears during the hyperphagia period as determined by the logistic regression model. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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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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CHAPTER 5

Discussion

This thesis has analysed the spatial patterns of primary production, its variability and its drivers of change against climate change in the Iberian Peninsula employing spatially-explicit data developed and provided by different institutions and countries (Spain and Portugal) with slightly different objectives. However, plant and animal species and ecosystems do not understand about administrative borders, but ecological conditions suitable for life. Even more, the human way of life between neighbour regions is not affected by nationality, sharing land-use customs and forestry and agricultural practices, and therefore, giving place to the same agroforestry systems (AFS) embedded in similar social-ecological systems (SES). To capture the spatial character of such systems, relying on their essential characteristics but avoiding the artifacts created by the variability existent between the different data sources, the development of this thesis has been strongly marked by the data harmonisation to solve differences between coordinate reference systems, associated thematic information and typological categories. For that reason it is urgent to highlight in the first place the importance of harmonising the mapping processes and protocols, particularly the National Forest Inventories or Land Use Land Cover (LULC) maps (Nunes et al., 2020; Pérez-Girón et al., 2020).

Currently, these AFS traditionally managed by humans are affected by the phenomenon of the rural exodus, with the consequent land use change or abandonment (Bugalho et al., 2011; Díaz-Varela et al., 2018; Godinho et al., 2016; Pinto-Correia & Mascarenhas, 1999; Roces-Díaz et al., 2018). This compromises their structure, composition and multifunctional character, and with it their ability to provide ecosystem services. Our findings highlight a higher CUE in managed ecosystems compared to unmanaged ecosystems both in the chestnut and cork oak AFS (Pérez-Girón et al., 2020; Pérez-Girón et al., 2022a). Due to the connection between higher levels of CUE and the capacity of ES supply (Costanza et al., 2007), this may suggest a need for these AFS to remain linked to human management. This detachment from human management is undoubtedly a threat to these ecosystems, but also may bring about opportunities for those species that reject closeness to humans, such as Cantabrian brown bears (Pérez-Girón et al., 2022b). Our findings point out a high selectivity by this species for the ecosystem types where to forage nuts and little fruits, especially in periods of hyperfagia, in a compromise between the accessibility to food sources and the avoidance of human presence. That is why, to favour the growth and expansion of the populations of these emblematic and threatened species, initiatives are needed to combine the recovery of traditional management practices in AFS commonly foraged by bears (like e.g. chestnut orchards), with the establishment of new plantations of fruit-production species, especially in locations far from human influence and with an ecological purpose rather than a productive one, such as those promoted by Brown Bear Foundation and to which this thesis has contributed (Project LIFE Bears with future "Improving key food resources and preventing winter conflicts for Cantabrian brown bears under climate change scenarios" – LIFE19 NAT/ES/000913).

As previously mentioned, in addition to human management, there are other factors that influence and modify primary production in terrestrial ecosystems (Section 1.2) but those related with climate are the ones that condition it to a greater extent. In Mediterranean regions where drought is a common event, it is known that water is the main driver of primary production since plant productivity depends on its ability to maintain photosynthetic tissues with an adequate water level (Garbulsky et al., 2010; Pereira et al., 2007; Piayda et al., 2014). Our findings are in accordance with this, reflecting a greater concern for summer droughts rather than for the increases in temperatures. It is true that temperature plays a fundamental role, because it affects both the photosynthesis and R_a. However, the current respiration rates are lower in the Atlantic region for sweet chestnut and chestnut production could benefit from the expected increase in temperatures (Collalti et al., 2020; Pérez-Girón et al., 2020). This fact, together with the confirmed increase in chestnut consumption by Cantabrian brown bears during hyperphagia periods (Navarro et al., 2021; Pérez-Girón et al., 2022b), has led to consider chestnut as a key food source, as is developing the LIFE19 NAT/ES/000913 project.

Nevertheless, there are more reasons to consider primary production as essential to understanding the Cantabrian brown bear nut foraging patterns and spatial distribution during the hyperphagia season. As stated previously (Section 1.5), the population is growing and expanding in range (Blanco et al., 2020; Gonzalez et al., 2016), its presence higher due to short or absent hibernation (Evans et al., 2016; Pigeon et al., 2016), and most important, unlike other brown bear populations further north, Cantabrian brown bears during hyperphagia mainly consume nuts produced by trees such as *Quercus* sp. and *F. sylvatica* L. and *C. sativa* Mill. (Bojarska & Selva, 2012; Naves et al., 2006; Rodríguez et al., 2007). In this sense, ecosystem production is key. It is known that C balance of previous years can limit nut production (Journé et al., 2021) and that allocation of GPP to fruit production by forest species is small; between 0.5 and 10% of the GPP for European Fagaceae species, that can be increased up to 23% in mast years, and between 0.9 and 1.3% of the GPP in *Q. petraea* (Matt.) Liebl. and *Q. robur* L. respectively (Fernández-Martínez et al., 2017; Herbst et al., 2015). This was reflected in our results, as GPP is the most important predictor of brown bear nut foraging patterns, highlighting areas with good conditions for bear feeding during hyperphagia and even revealing those where recent expansion has occurred, such as the interpopulation corridor and towards the southwest of the western subpopulation.

Taking up again the climatic drivers, our work identifies a probable worsening of the physiological and environmental conditions for the sweet chestnut. Particularly, in the Mediterranean regions of the central and southern part of the Iberian Peninsula where very low CUE values have already been observed suggesting a very low carbon assimilation with which the physiological activity of plants cannot be maintained (Amthor, 2000; Van Iersel, 2003). Besides, the expected changes in climate will not favour these conditions, but rather the opposite (Böhnisch et al., 2021), hence our projections indicate the worsening of the conditions for continuity of sweet chestnut formations in these regions (Pérez-Girón et al., 2020). While it is not clear how chestnut will adapt to these conditions and what the resilience and adaptation ability of well-established and traditional AFS will be, previous works have found differentiated ecotypes between Mediterranean and Northern Iberian chestnuts thus revealing adaptive strategies (Míguez-Soto et al., 2019). As we argued in Chapter 2 and Pérez-Girón et al. (2020), ultimately it is possible that plant species will adapt to climate change by altering their physical traits (Moritz & Agudo, 2013) with the consequent alteration of plant trait distributions (Madani et al., 2018) or by occupying current ecological niche spaces under new environmental conditions (Dubuis et al., 2013) where local conditions are more favourable. Despite this, we will have to wait and it will be nature itself that dictates sentence, since each species or ecosystem is unique.

Saving the ecological differences between species, a very different situation is expected for the cork oak, which can be found in Chapter 3 or Pérez-Girón et al. (2022a), where our findings highlighted the adaptive strategies of cork oak AFS that allow them to live successfully in adverse climatic conditions. In this sense, despite the decrease in the ecosystem productivity, it is not seriously affected by climatic factors. Furthermore, the response against climate conditions may also change according to the type of forest structure and composition: under forest canopy cover, climatic drivers are reduced by the stand effect and the microclimate generated by the forest (De Frenne et al., 2021) and primary production will depend on other factors. Besides, it has been observed that the proximity to the coast has a buffer effect against extreme droughts, reducing the associated the risk to the ecosystem.

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CHAPTER 6

Conclusions

The major conclusions of this work are as follows:

- **Chapter 2**. Climate factors that compromise the state and resilience capacity of chestnut ecosystem production.
    - The Atlantic area of Spain and the northern of Portugal is strongly influenced by factors or characteristics related to the stand rather than by climatic factors, while in the Mediterranean area, climate is the main limiting factor.
    - Under the predicted climate change scenarios, the sustainability of sweet chestnut AFS in the Atlantic area of Spain and the northern of Portugal and their ecosystem services provision would not be at risk.
    - The current situation is uncertain in the Mediterranean regions of the central and southern part of the Iberian Peninsula and our future projections point out a severe threaten to the continuity of chestnut ecosystems in any scenario of climate change.
- **Chapter 3**. Climate factors that compromise the state of cork oak ecosystems and role played by geographical location.
    - Tree density plays a key role in the adaptation to climate variation, maintaining microclimatic conditions that make cork oak AFS less dependent on enviromental variables.
    - The response of the cork oak AFS reflects the ecological traits and the different adaptive strategies used by the component trees and understory plants to survive drought seasons, where water (soil or air moisture) is the main driver of primary production.

  - The proximity to the coast improves productivity levels and may also buffer climate conditions in extreme drought years, reducing the associated adverse effects and the risk to the ecosystem.

- **Chapter 4**. Primary production indicators to understand the nut foraging patterns and predict the spatial distribution related to nut consumption of the Cantabrian brown bear during the hyperphagia season.
  - Primary production indicators are good proxies to understand the Cantabrian brown bear nut foraging patterns and spatial distribution during the hyperphagia season, but must be combined with other environmental variables.
  - 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, which will provide refuge areas where bears can remain undetected.
  - The chestnut possibly becomes more important in the bear's diet during hyperphagia, compensating for the variable production of other nuts. After consuming the chestnuts, the bears will tend to move from these stands to quieter refuge areas, while after consuming the acorns, the existence of large, highly aggregated adjacent and complex forest stands may act as refuges where bears can remain undetected.
  - Model prediction highlighted 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) for the Cantabrian brown bear.

CHAPTER 7

Impact factor report

The Journal Impact Factor (JIF), provided by the Clarivate Analytics, and the SCImago Journal Rank (SJR), provided by SCOPUS (Elsevier), are used to measure the impact factor of the published research works in this PhD dissertation.

- Pérez-Girón, J. C., Álvarez-Álvarez, P., Díaz-Varela, E. R., & 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. Ecological Indicators, 113, 106199. https://doi.org/10.1016/j.ecolind.2020.106199
    - JIF 2020: 4.958 (Q2, Environmental Sciences, 72 out of 274).
    - SJR 2020: 1.315 (Q1, Environmental Science, Ecology, 41 out of 392).
- Pérez-Girón, J. C., Díaz-Varela, E. R., & Álvarez-Álvarez, P. (2022). Climate-driven variations in productivity reveal adaptive strategies in Iberian cork oak agroforestry systems. Forest Ecosystems, 9, 100008. doi: https://doi.org/10.1016/j.fecs.2022.100008.
    - JIF 2020: 3.645 (Q1, Forestry, 6 out of 67).
    - SJR 2020: 1.001 (Q1, Agricultural and Biological Sciences, Forestry, 15 out of 162).
- Pérez-Girón, J. C., Díaz-Varela, E. R., Álvarez-Álvarez, P., Palacios, O. H., Ballesteros, F. , & López-Bao, J. V. (2022). Linking landscape structure and vegetation productivity with nut consumption by the Cantabrian brown bear during hyperphagia. Science of The Total Environment, 813, 152610. doi: https://doi.org/10.1016/j.scitotenv.2021.152610.

  - JIF 2020: 7.963 (Q1, Environmental Sciences, 25 out of 274).
  - SJR 2020: 1.795 (Q1, Environmental Science, Environmental Engineering, 7 out of 211).

CHAPTER 8

Resumen en Español

La totalidad de esta tesis doctoral ha sido publicada en lengua inglesa en revistas indexadas de reconocido prestigio y revisadas por pares, asegurando así la rigurosidad de la investigación científica desarrollada. Por ello, para hacer más accesible este documento y cumplir con las normativa de los estudios de doctorado, a continuación, se hará un breve resumen en lengua española.

8.1 Introducción

Uno de los procesos principales y más importantes en los ecosistemas terrestres es el flujo de energía, cuyo punto de partida es el uso de la luz solar por parte de los organismos autótrofos, es decir, aquellos que son aquellos capaces de sintetizar los nutrientes que necesitan a partir de compuestos inorgánicos, o dicho de otro modo, son capaces de fabricar su propio alimento. Concretamente, aquellos que capturan la energía de la luz solar y la transforman en materia orgánica a través de la fotosíntesis se denominan fotótrofos, a cuyo grupo pertenecen las plantas, algas y algunas bacterias. Las plantas, a través de la fotosíntesis, utilizan la luz solar, el CO_2 atmosférico y el agua para producir glucosa (que posteriormente será utilizada como energía o alimento) y liberar oxígeno. Así, a la energía almacenada en forma de materia orgánica como consecuencia de la actividad fotosintética de los productores primarios se le denomina producción primaria, y por simplicidad, de ahora en adelante, se denominará producción primaria a la producción primaria de los productores fotosintéticos en los ecosistemas terrestres.

La producción primaria es el primer paso en la captura, almacenamiento y transferencia de energía, constituyendo la base del ciclo del carbono en los ecosistemas terrestres y proporcionando el carbono orgánico que sustenta los niveles tróficos (incluidos los humanos), por lo que se convierte en un proceso fundamental para la vida (Chapin et al., 2011; Pace et al., 2021). De la producción primaria también depende la función reproductiva de las plantas (Fernández-Martínez et al., 2017; Journé et al., 2021), y por ende, la producción de frutos, que es otra parte fundamental del funcionamiento del ecosistema, asegurando la continuidad de la propia especie y constituyendo una importante fuente de alimento para las especies animales (o incluso la única como en el caso de las especies frugívoras). Así, la producción primaria es una función ecosistémica clave para la estructura, funcionamiento y composición de los ecosistemas terrestres (Costanza et al., 2007; Falkowski et al., 2000; Sekercioglu, 2010).

Pero su importancia va más allá, tanto, que la Evaluación de los ecosistemas del milenio clasificó la producción primaria como un servicio ecosistémico de soporte (Millennium Ecosystem Assessment, 2005), lo que significa que su provisión es condición *sine qua non* la provisión del resto de servicios ecosistémicos no es factible. De tal forma que, entendiendo los servicios ecosistémicos como *"componentes de la naturaleza, que pueden ser disfrutados de forma directa, consumidos o utilizados para generar bienestar humano"* (Boyd & Banzhaf, 2007), los cambios en la producción primaria tendrán su repercusión en las contribuciones que la naturaleza hace a la sociedad, las cuales se verán reflejadas en el bienestar humano a corto y largo plazo.

Entre los componentes de la producción primaria, cabe destacar los siguientes. La producción primaria bruta (GPP) que refleja la cantidad total de carbono almacenado por las plantas teniendo en cuenta la respiración de toda la planta (autótrofa) (R_a) debido a los costes de crecimiento y mantenimiento (Amthor, 2000; Collalti et al., 2020b; Schulze et al., 2019; Van Iersel, 2003). R_a por lo tanto, determinará la energía disponible para otros usos, como los procesos de asimilación del crecimiento vegetativo y la reproducción, así como otros compuestos no estructurales (Collalti & Prentice, 2019; Pace et al., 2021; Pallardy, 2010; Valentini et al., 2000). La diferencia entre R_a y GPP es la producción primaria neta (NPP), es decir, el carbono neto transformado en biomasa (hojas, ramas, troncos y raíces) (Clark et al., 2001; Collalti & Prentice, 2019; Collalti et al., 2020b). Por último, el ratio de NPP entre GPP se conoce como la eficiencia de uso de carbono (CUE) (Gifford, 1995), y expresa la capacidad de las plantas para secuestrar CO_2 atmosférico a través de la fotosíntesis y transformarlo en biomasa.

Una característica muy importante es variabilidad de la producción primaria debido a diversos factores como la edad (Fernández-Martínez et al., 2014; Mäkelä & Valentine, 2001), características ecológicas (Madani et al., 2018), características del rodal y manejo por parte del hombre(Campioli et al., 2015), características del suelo (Ni et al., 2022; Vicca et al., 2012), clima (Gilabert et al., 2015; He et al., 2018; Reichstein et al., 2013; Zhang et al., 2009; Zhang et al., 2014), o perturbaciones (Kunert et al., 2019), lo que permite considerar los componentes de producción primaria (GPP, NPP y CUE) como indicadores ecológicos, y por tanto, emplearlos para informar sobre el estado de los ecosistemas, su riesgo y su capacidad de resiliencia frente a cambios futuros mediante la monitorización de la variabilidad espacio-temporal de sus componentes.

Pero, ¿cómo se cuantifica la producción primaria? Dependiendo de las características del ecosistema que se pretenda cuantificar, son varios los métodos posibles. En ecosistemas terrestres, uno de los sistemas más fiables son las redes de flujo, un método micrometeorológico directo basado en el intercambio de gases entre los ecosistemas y la atmósfera (Baldocchi, 2014; Baldocchi, 2020; Xiao et al., 2019). Sin embargo, además de ofrecer información puntual, su alto coste de instalación limita su alcance espacial, por lo que cuando se necesita información espacio-temporal continua es necesario recurrir a datos procedentes de sensores remotos o teledetección. Un ejemplo, son los datos globales y de libre adquisición capturados por el sensor MODIS que se emplean en esta tesis. MODIS proporciona datos GPP y NPP independientes y espacialmente continuos desde 2000 hasta el presente. Su algoritmo se basa en la eficiencia de uso de la luz (LUE, de sus siglas en inglés) (Monteith, 1972), que calcula la GPP como un producto de la radiación fotosintéticamente activa (PAR) incidente, la fracción de PAR absorbida (fAPAR) y la LUE (ε), mientras que la NPP se deriva de un módulo de respiración autótrofa. Sus datos son consistentes con las medidas de la torre de flujo ($r = 0.859$) y es capaz de capturar patrones espacio-temporales de GPP y NPP en diferentes biomas y regímenes climáticos (Heinsch et al., 2006; Turner et al., 2006). Por lo tanto, MODIS proporciona una excelente oportunidad para evaluar los patrones espaciales de la producción primaria y su influencia climática en áreas extensas y a coste cero, proporcionando información sobre el estado de nuestros ecosistemas y sus respuestas en futuros escenarios de cambio climático.

Y es que, se sabe que tanto especies como ecosistemas, así como las complejas interacciones entre los organismos y/o sus hábitats están siendo afectados por el cambio climático, comprometiendo el estado de los ecosistemas, su estructura y función y los servicios ecosistémicos que brindan. Pero no solo eso, sino que es un proceso bidireccional que se retroalimenta. Primero, conduce a pérdidas de biodiversidad, comprometiendo el estado de los ecosistemas, los cuales, con un estado más degradado, no son capaces de mitigar el efecto de las emisiones de gases de efecto invernadero, por lo que se acelera nuevamente el proceso, lo que pone de manifiesto la importancia de conservar los ecosistemas de alta biodiversidad. Por eso, a nivel mundial y desde hace décadas, el cambio climático ha sido considerado uno de los principales factores que amenazan los ecosistemas forestales y cuya tendencia en los últimos años ha aumentado más rápido que en cualquier otro período anterior (IPCC, 2021), principalmente debido a las emisiones de gases de efecto invernadero como el CO_2. Por ello, a principios del siglo XXI, la Evaluación de los ecosistemas del milenio lo consideró como uno de los principales impulsores del cambio de los ecosistemas (Millennium Ecosystem Assessment, 2005).

A pesar de las advertencias, lejos de mejorar, la situación climática ha empeorado. Cada década ha sido más cálida que la década anterior, siendo la última la más cálida registrada desde que se tienen datos, mientras que los últimos seis años (2015-2020) registraron los registros más cálidos desde el período preindustrial y con la reducción esperada de precipitaciones (Giorgi & Lionello, 2008; IPCC, 2021; World Meteorological Organization, 2021). Pero esto no es todo, pues las predicciones sobre el cambio climático no son nada halagüeñas. Además del incremento de eventos extremos como fuertes tormentas, heladas tardías, olas de calor, etc..., trabajos recientes han argumentado que las sequías se producirán con mayor frecuencia, con mayor duración e intensidad y con el agravante de que en la Península Ibérica podrían no venir seguidas de inviernos lluviosos (Böhnisch et al., 2021).

8.2 Necesidades y alcance de la tesis

Visto el papel fundamental que desempeña la producción primaria para entender el estado de los ecosistemas terrestres y su relación con el cambio climático, cabe pensar que aún mayor es la importancia que cobra cuando el cambio climático afecta regiones extremadamente sensibles, como es el caso de la Península Ibérica, y donde se centra esta tesis. Pero más grave aún es la amenaza para aquellas especies y ecosistemas ubicados en los límites de su distribución, con tendencias en declive o gravemente amenazados, como los analizados en esta tesis.

El castaño (*Castanea sativa* Mill.) es una de estas especies con cuya tendencia es al declive, debido al proceso de abandono y degradación de tierras que desde mediados del siglo XX se originó por cambios en las actividades socioeconómicas en las áreas rurales (Díaz-Varela et al., 2018; Roces-Díaz et al., 2018a), que en las últimas décadas se encuentra además seriamente amenazado por algunas plagas y enfermedades como la enfermedad de la tinta (causada por *Phytophthora cinnamomi* Rands), el cancro (*Cryphonectria parasitica* (Murrill) Barr) o la avispilla del castaño (*Dryocosmus kuriphilus* Yasumatsu) (Gil-Tapetado et al., 2021; Homs et al., 2001; Lombardero et al., 2021), y que por su propia ecología es sensible a las sequías estivales (Conedera et al., 2010) y, por lo tanto, su estado podría agravarse en un futuro próximo por el cambio climático, debido a sus relaciones directas e indirectas con las primeras variables. Desde el punto de vista socioeconómico, es una de las especies de frondosas autóctonas más importantes de la Península Ibérica (Roces-Díaz et al., 2018b) cuyo rango de distribución ha sido fuertemente modificado por la gestión humana (Conedera et al., 2004). Actualmente ocupa el noroeste de España y el norte de Portugal, con rodales aislados en el sur, centro y este de España, y por tanto, distribuidos tanto en regiones biogeográficas atlánticas como mediterráneas que constituyen a su vez dos ecotipos diferentemente adaptados a las condiciones climáticas (Míguez-Soto et al., 2019). El tradicional manejo del hombre hace que el castaño se pueda encontrar tanto en rodales forestales, naturales y seminaturales, así como en rodales antropizados que tradicionalmente constituyen sistemas agroforestales multifuncionales (AFS, de sus siglas en inglés) como los soutos, castañeros o castañeos (en los que se utilizan técnicas específicas de poda e injerto) y modernas plantaciones para la producción de madera o fruto (Míguez-Soto et al., 2019; Roces-Díaz et al., 2018a).

El alcornoque (*Quercus suber* L.) es otra especie con siglos de gestión tras ella que ha dado lugar a AFS conocidas como *montados* en Portugal y *dehesas* en España, y donde se concentran las mayores poblaciones de esta especie (Díaz-Fernández et al., 1995; Joffre et al., 1999; Pinto-Correia et al., 2011). Las *dehesas* o *montados* se caracterizan por la presencia de arbolado disperso en densidad variable, aunque generalmente baja, con presencia de vegetación herbácea o arbustiva en las sotobosque (Correia et al., 2016; Pereira et al., 2007; Piayda et al., 2014; Pinto-Correia et al., 2011). El estado de estos sistemas es actualmente preocupante (Costa et al., 2009), tanto que recientemente ha sido incluido como un tipo de hábitat natural de interés comunitario dentro de la Directiva Hábitats de la UE, y categorizado como en grave peligro de desaparición. Además del cambio climático (Aguilera et al., 2020), son muchos y diversos los factores, tanto naturales como antrópicos, como la proliferación de plagas y enfermedades (Brasier et al., 1993; González et al., 2020), la recurrencia de incendios (Guiomar et al., 2015; Silva & Catry, 2006), la falta de regeneración o el cambio de uso y abandono del suelo (Bugalho et al., 2011; Godinho et al., 2016; Pinto-Correia & Mascarenhas, 1999).

Estos proporcionan valiosas contribuciones al paisaje y al medio ambiente, cumpliendo funciones y procesos fundamentales que finalmente producen una serie de tipos de servicios ecosistémicos, como los de provisión (alimento, producción de madera y biomasa, etc.), regulación (calidad del agua, control de la erosión, polinización, prevención de perturbaciones, acervo genético, regulación del clima, etc.) y culturales (estética, sentido del lugar, conocimiento tradicional, etc.). Sin embargo, existen especies cuya conservación, por su consideración de especie "bandera" y/o "paraguas", contribuye directamente a la de otros organismos, hábitats o comunidades ecológicas (Barua, 2011).

El oso pardo cantábrico (*Ursus arctos* L.) es una de esas especies paraguas, considerada como especie prioritaria en la Directiva Hábitats, y como En Peligro en la Lista Roja de la Unión Internacional para la Conservación de la Naturaleza (UICN) y el Catálogo Español de Especies Amenazadas (Palomero et al., 2021). A pesar de continuar siendo una especie vulnerable, la población de oso pardo cantábrico está creciendo y expandiéndose en su área de distribución (Blanco et al., 2020; Gonzalez et al., 2016) lo que implica un desafío en el contexto del cambio climático, ya que se esperan períodos de hibernación más cortos o completamente ausentes (Evans et al., 2016; Pigeon et al., 2016) y, por lo tanto, un mayor número de osos activos. Por otro lado, algunas especies relacionadas con la dieta del oso pardo durante la hiperfagia, como el haya (*Fagus sylvatica* L.) y los robles atlánticos (*Quercus petraea* (Matt.) Liebl. y *Quercus robur* L.) (Bojarska & Selva, 2012; Naves et al., 2006; Rodríguez et al., 2007), pueden sufrir una reducción drástica o fructificación escasa en la Cordillera Cantábrica (Ballesteros et al., 2018; Clevenger et al., 1992; Dyderski et al., 2018) que podría comprometer la capacidad reproductiva de la especie (López-Alfaro et al., 2013) o intensificar los cambios en la dieta del oso (Navarro et al., 2021). Sin embargo, el cambio climático podría mejorar la productividad de especies como los robles termófilos (*Q. faginea* Lam., *Q. ilex* L.) y castaños *C. sativa* Mill. que ya forman parte de la dieta del oso (Naves et al., 2006; Rodríguez et al., 2007) convirtiéndose así en recursos clave, en particular, el castaño, cuya producción es muy regular (con una vecería relativamente escasa) debido al gran número de variedades cultivares de castaño con una producción asíncrona.

8.3 Objetivos

El objetivo general de esta tesis fue analizar los patrones espaciales de la producción primaria, sus cambios y sus fuerzas motrices del cambio frente al cambio climático en la Península Ibérica para comprender el estado de nuestros ecosistemas, la dinámica vegetal y animal o las estrategias adaptativas de las especies.

Para ello, el objetivo principal se dividió en objetivos específicos que fueron abordados en los capítulos que se detallan a continuación:

- **Capítulo 2**. ¿Pueden los factores climáticos comprometer el estado y la capacidad de resiliencia de los sistemas agroforestales de castaño?

  En este capítulo se evaluó la influencia de las variaciones climáticas en los ecosistemas de castaño de la Península Ibérica, así como su resiliencia ante diversos escenarios de cambio climático. La alta restricción impuesta en la selección condujo a la selección de masas prácticamente monoespecíficas, permitiendo así considerar dicha selección desde una perspectiva a nivel de especie.

- **Capítulo 3**. ¿Pueden los factores climáticos comprometer el estado de los ecosistemas de alcornoque? ¿Qué papel juega la ubicación geográfica?

  En este capítulo se evaluó la influencia de la variabilidad climática en diferentes sistemas agroforestales de alcornoque de la Península Ibérica y el papel que juega la ubicación geográfica frente a los efectos adversos del clima. El manejo humano al que está sometido, así como las características de la especie y los sistemas que forma implican un análisis desde una perspectiva de ecosistema.

- **Capítulo 4**. ¿Se pueden utilizar indicadores de producción primaria para comprender los patrones de búsqueda de frutos secos y predecir la distribución espacial relacionada con su consumo durante la temporada de hiperfagia en una especie paraguas como el oso pardo cantábrico?

  En este capítulo se analizó la distribución espacial de los osos pardos durante la hiperfagia para comprender los patrones de alimentación en frutos secos y se modeló su consumo utilizando la productividad de la vegetación, las variables topográficas y las métricas del paisaje. Esta situación implica una especie animal interactuando con diferentes especies vegetales, así como con los ecosistemas completos, incluidos los humanos.

8.4 Discusión

En esta tesis se han analizado los patrones espaciales de la producción primaria, su variabilidad y sus fuerzas motrices del cambio climático en la Península Ibérica, empleando datos espacialmente explícitos desarrollados y proporcionados por diferentes instituciones y países (España y Portugal) con objetivos ligeramente diferentes. Sin embargo, las especies vegetales y animales y los ecosistemas no entienden de fronteras administrativas, sino de condiciones ecológicas aptas para la vida. Es más, la forma de vida humana entre regiones vecinas no se ve afectada por la nacionalidad, compartiendo costumbres de uso de la tierra y prácticas forestales y agrícolas, y por lo tanto, dando lugar a los mismos sistemas agroforestales (AFS) integrados en sistemas socio-ecológicos similares (SES). Por ello, para captar el carácter espacial de tales sistemas, respetando sus características esenciales pero evitando los artefactos creados por la variabilidad existente entre las diferentes fuentes de datos, el desarrollo de esta tesis ha estado fuertemente marcado por la armonización de datos con el fin de resolver diferencias entre sistemas de referencia de coordenadas, información temática asociada y categorías tipológicas. Por lo tanto, urge resaltar en primer lugar la importancia de armonizar los procesos y protocolos de mapeo, particularmente los inventarios forestales nacionales o mapas de usos y coberturas del suelo (LULC) (Nunes et al., 2020; Pérez-Girón et al., 2020).

En la actualidad, estos sistemas agroforestales manejados tradicionalmente por el hombre se ven afectados por el fenómeno del éxodo rural, con el consiguiente cambio de uso de suelo o abandono de tierras (Bugalho et al., 2011; Díaz-Varela et al., 2018; Godinho et al., 2016; Pinto-Correia & Mascarenhas, 1999; Roces-Díaz et al., 2018a), lo que compromete su estructura, composición y carácter multifuncional, y con ello su capacidad para brindar servicios ecosistémicos. Nuestros hallazgos destacan una mayor CUE en los ecosistemas gestionados en comparación con los ecosistemas no gestionados tanto en los de castaño como en los de alcornoque (Pérez-Girón et al., 2020; Pérez-Girón et al., 2022a). Debido a la relación entre niveles más altos de CUE y la capacidad de provisión de servicios ecosistémicos (Costanza et al., 2007), sugerimos la necesidad de que estos sistemas agroforestales permanezcan vinculados a la gestión humana. De lo contrario, ese desapego de la gestión humana será sin duda una amenaza para estos ecosistemas, pero también una oportunidad para aquellas especies que rechazan la cercanía con los humanos, como el oso pardo cantábrico (Pérez-Girón et al., 2022b). Nuestros resultados apuntan a una alta selectividad de esta especie por los tipos de ecosistemas donde se alimentan de frutos secos, especialmente en períodos de hiperfagia, en un compromiso entre la accesibilidad a las fuentes de alimento y tratar de evitar la presencia humana. Por ello, para favorecer el crecimiento y la expansión de las poblaciones de estas especies emblemáticas y amenazadas, se necesitan iniciativas que combinen la recuperación de las prácticas tradicionales de gestión en sistemas agroforestales comúnmente aprovechados por osos (como por ejemplo, los soutos, castañeros o castañeos), con el establecimiento de nuevas plantaciones en lugares alejados del hombre y con una finalidad más ecológica que productiva, como las que promueve la Fundación Oso Pardo y a las que ha contribuido esta tesis (Proyecto LIFE Osos con Futuro "Mejora de recursos tróficos clave y prevención de conflictos invernales para conservar el oso pardo cantábrico en escenarios de cambio climático" – LIFE19 NAT/ES/000913).

Como se mencionó anteriormente, además de la gestión antrópica, existen otros factores que influyen y modifican la producción primaria en los ecosistemas terrestres siendo los relacionados con el clima los que lo condicionan en mayor medida. En las regiones mediterráneas donde la sequía es un evento común, se sabe que el agua es el principal factor limitante de la producción primaria dependiendo la productividad de las plantas de su capacidad para mantener los tejidos fotosintéticos con un nivel de adecuado agua (Garbulsky et al., 2010; Pereira et al., 2007; Piayda et al., 2014). Nuestros resultados van en esta línea, reflejando una mayor preocupación por las sequías de verano que por los aumentos de temperatura, aunque es cierto que la temperatura juega un papel fundamental, porque afecta tanto a la fotosíntesis como a $\mathrm{R_a}$. Las tasas de respiración actuales parecen ser más bajas en la región atlántica para el castaño y la producción de castaña podría beneficiarse del aumento esperado de las temperaturas por el cambio climático (Collalti et al., 2020a; Pérez-Girón et al., 2020). Este hecho, junto con el aumento constatado del consumo de castañas por parte del oso pardo cantábrico durante los periodos de hiperfagia (Navarro et al., 2021; Pérez-Girón et al., 2022b), ha llevado a considerar la castaña como fuente de alimentación clave para la especie, como así se está teniendo en cuenta en el proyecto LIFE19 NAT/ES/000913.

Sin embargo, hay más razones para considerar que la producción primaria es esencial para comprender los patrones de alimentación en frutos secos y la distribución espacial del oso pardo cantábrico durante la temporada de hiperfagia. La población está creciendo y expandiéndose (Blanco et al., 2020; Gonzalez et al., 2016), su presencia es mayor debido a una hibernación más corta o ausente (Evans et al., 2016; Pigeon et al., 2016), y lo más importante, a diferencia de otras poblaciones de osos pardos más al norte, los osos pardos cantábricos durante la hiperfagia consumen principalmente frutos secos producidos por árboles como *Quercus* sp., *F. sylvatica* L. y *C. sativa* Mill. (Bojarska & Selva, 2012; Naves et al., 2006; Rodríguez et al., 2007). En este sentido, la producción del ecosistema se vuelve un factor clave, pues se sabe que el balance de C de años anteriores puede limitar la producción de fruto (Journé et al., 2021) y que la asignación de GPP a la producción de fruto en especies forestales es pequeña; entre el 0,5 y el 10% de la NPP para las especies europeas de la familia de las fagáceas, que puede incrementarse hasta un 23% en años de vecería, y entre el 0,9 y el 1,3% de la NPP en *Q. petraea* (Mat.) Liebl. y *P. robur* L. respectivamente (Fernández-Martínez et al., 2017; Herbst et al., 2015). Esto se reflejó en nuestros resultados, ya que el GPP es el predictor más importante de los patrones de alimentación de fruto seco del oso pardo, destacando áreas con buenas condiciones para la alimentación del oso durante la hiperfagia e incluso revelando aquellas donde se ha producido una expansión reciente, como el corredor interpoblacional y hacia el suroeste de la subpoblación occidental.

Retomando de nuevo los factores climáticos, nuestro trabajo identifica un probable empeoramiento de las condiciones fisiológicas y ambientales para el castaño, en particular, en las regiones mediterráneas del centro y sur de la Península Ibérica donde ya se han observado valores de CUE muy bajos que sugieren una asimilación de carbono pésima y la mediante cual no sería viable mantener la actividad fisiológica de las plantas (Amthor, 2000; Van Iersel, 2003). Además, la tendencia esperada para el clima no favorecerá estas condiciones, sino todo lo contrario (Böhnisch et al., 2021), por lo que nuestras proyecciones indican el empeoramiento de las condiciones para la continuidad de las formaciones de castaño en estas regiones (Pérez-Girón et al., 2020). Si bien no está claro cómo se adaptará el castaño a estas condiciones y cuál será la resiliencia y la capacidad de adaptación de los sistemas agroforestales bien establecidos, trabajos previos han encontrado ecotipos diferenciados entre castaños mediterráneos e ibéricos, lo que ya revela estrategias adaptativas (Míguez-Soto et al., 2019). En última instancia, es posible que las especies de plantas se adapten al cambio climático alterando sus rasgos funcionales (Moritz & Agudo, 2013) con la consiguiente alteración de su distribución (Madani et al., 2018) o ocupando nuevos nichos ecológicos bajo nuevas condiciones ambientales (Dubuis et al., 2013) donde las condiciones locales sean más favorables. A pesar de ello habrá que esperar y será la propia naturaleza la que dicte sentencia, ya que cada especie o ecosistema es único.

Salvando las diferencias ecológicas entre especies, se espera una situación muy diferente para el alcornoque, pues nuestros resultados destacan las estrategias adaptativas que les permiten vivir con éxito en condiciones climáticas adversas. En este sentido, a pesar de la disminución de la productividad del ecosistema, éste no se ve seriamente afectado por factores climáticos. Además, la respuesta frente a las condiciones climáticas también puede cambiar según el tipo de estructura y composición forestal, pues en masas de tipología forestal con una fracción de cabida cubierta alta, los factores climáticos climáticos se verán reducida su influencia por el efecto de la masa y el microclima generado por esta (De Frenne et al., 2021) y la producción primaria dependerá de otros factores. Además, se ha observado que la proximidad a la costa tiene un efecto amortiguador frente a sequías extremas, reduciendo el riesgo asociado al ecosistema.

8.5 Conclusiones

Las principales conclusiones de este trabajo son las siguientes:

- **Capítulo 2**. Factores climáticos que comprometen el estado y la capacidad de resiliencia de los sistemas agroforestales de castaño.
    - La zona atlántica de España y norte de Portugal está fuertemente influenciada por factores o características propias del rodal más que

  por factores climáticos, mientras que en la zona mediterránea el clima es el principal factor limitante.
  - Bajo los escenarios de cambio climático previstos, la sostenibilidad de los sistemas agroforestales de castaño y su provisión de servicios ecosistémicos en el área atlántica de España y el norte de Portugal no estarían en riesgo.
  - La situación actual es incierta en las regiones mediterráneas del centro y sur de la Península Ibérica y nuestras proyecciones futuras apuntan a una grave amenaza para la continuidad de los ecosistemas de castaño en estas zonas bajo cualquier escenario de cambio climático.

- **Capítulo 3**. Factores climáticos que comprometen el estado de los ecosistemas de alcornoque y papel de la ubicación geográfica.
  - La densidad de la masa juega un papel clave en la adaptación a la variación climática, manteniendo unas condiciones microclimáticas que hacen que los sistemas agroforestales de alcornoque sean menos dependientes de las variables ambientales.
  - La respuesta de los sistemas agroforestales de alcornoque refleja los rasgos ecológicos de la especie y las diferentes estrategias de adaptación utilizadas, tanto por los árboles que lo componen como por las plantas del sotobosque, para sobrevivir a las temporadas de sequía, donde el agua es el principal factor limitante de la producción primaria.
  - La proximidad a la costa mejora los niveles de productividad y amortigua las condiciones climáticas en años de sequía extrema, reduciendo los efectos adversos asociados y el riesgo para el ecosistema.

- **Capítulo 4**. Indicadores de producción primaria para comprender los patrones de alimentación de frutos secos y predecir la distribución espacial relacionada con el consumo de estos durante la temporada de hiperfagia por el oso pardo cantábrico.
  - Los indicadores primarios de producción son buenos indicadores para comprender los patrones de alimentación de frutos secos y la distribución espacial del oso pardo cantábrico durante la temporada de hiperfagia, pero deben combinarse con otras variables ambientales.
  - Los osos prefieren alimentarse de bellotas, específicamente en rodales mixtos de bosques caducifolios relativamente grandes, altamente agregados, con un alto grado de diversidad en el patrón del paisaje, caracterizados por la presencia de rodales adyacentes de diversas clases de cobertura, que proporcionarán áreas de refugio donde los osos pueden pasar desapercibidos.
  - La castaña posiblemente adquiera mayor importancia en la dieta del oso durante la hiperfagia en los próximos años, compensando la producción variable de otros frutos secos. Después de consumir

las castañas, los osos tienden a desplazarse hacia rodales o áreas de refugio más tranquilas, mientras que después de consumir las bellotas, la existencia de grandes rodales adyacentes y complejos, muy agregados, actúan como refugios donde los osos pasan desapercibidos.

– Los modelos de predicción destacaron áreas de gran importancia (p. ej., celdas de distribución permanente) o de reciente expansión (p. ej., el corredor interpoblacional o el suroeste de la subpoblación occidental) para el oso pardo cantábrico.

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APPENDIX A

Supplementary material for Chapter 2

Table A.1: Summary statistics for all study variables.

Type	**Code**	**Description of variable**	**Unit**	**Mean**	**Std. Deviation**	**Min**	**Max**	**N**
Primary production	NPP	Net primary production	Kg C m-2 yr-1	0.8205	0.371	0.0751	1.6911	94
	GPP	Gross primary production	Kg C m-2 yr-1	1.4933	0.5313	0.7677	2.7026	94
	CUE	Carbon use efficiency	Dimensionless	0.5336	0.1422	0.0646	0.6798	94
Precipitation	MP01	Mean precipitation in month 1	mm	112.6	28.6	62.5	177.2	94
	MP02	Mean precipitation in month 2		100.3	25.7	57.9	194.7	94
	MP03	Mean precipitation in month 3		85.1	17.4	63.4	133.4	94
	MP04	Mean precipitation in month 4		90.5	25	53.9	172	94
	MP05	Mean precipitation in month 5		83.1	23.5	44	145.2	94
	MP06	Mean precipitation in month 6		53.2	21.5	19.1	91.8	94
	MP07	Mean precipitation in month 7		31.8	23.5	2.8	77.7	94
	MP08	Mean precipitation in month 8		36.9	27.1	5.4	83.8	94
	MP09	Mean precipitation in month 9		55.6	19.2	27.5	103.7	94
	MP10	Mean precipitation in month 10		101.2	18.9	66.5	174.7	94
	MP11	Mean precipitation in month 11		120.3	28.5	76.3	180.5	94
	MP12	Mean precipitation in month 12		136.3	42.4	63.3	242.7	94
	MAP	Mean annual precipitation		1020.2	171.6	683	1762.3	94
Temperature	MT01	Mean temperature in month 1	°C	5.6	1.4	2.6	8.3	94
	MT02	Mean temperature in month 2		6.7	1.4	3.1	9.1	94
	MT03	Mean temperature in month 3		8.8	1.2	5.3	11.4	94
	MT04	Mean temperature in month 4		10.2	1.1	7	12.4	94
	MT05	Mean temperature in month 5		13.5	1.1	10.8	15.9	94
	MT06	Mean temperature in month 6		17.5	1.5	14.6	20.4	94
	MT07	Mean temperature in month 7		20.9	2.2	17	24.7	94
	MT08	Mean temperature in month 8		20.8	2.2	17.5	24.4	94
	MT09	Mean temperature in month 9		18.1	1.6	14.7	21.1	94
	MT10	Mean temperature in month 10		13.4	1.3	10.2	15.8	94
	MT11	Mean temperature in month 11		9.1	1.4	6.1	12	94
	MT12	Mean temperature in month 12		6.5	1.6	3.4	9.6	94
	MAT	Mean annual temperature		12.6	1.4	9.3	15.6	94
	MTmin01	Mean minimum temperature in month 1		1.4	1.8	-2.4	5.4	94
	MTmin02	Mean minimum temperature in month 2		2.1	1.8	-1.9	6.1	94
	MTmin03	Mean minimum temperature in month 3		3.7	1.7	0.2	7.8	94
	MTmin04	Mean minimum temperature in month 4		4.9	1.5	1.8	8.4	94
	MTmin05	Mean minimum temperature in month 5		8	1.3	5.8	10.8	94
	MTmin06	Mean minimum temperature in month 6		11.4	1.4	8.9	14.4	94
	MTmin07	Mean minimum temperature in month 7		14.2	1.9	11.5	18.1	94
	MTmin08	Mean minimum temperature in month 8		14.1	2	11.3	18.5	94
	MTmin09	Mean minimum temperature in month 9		11.9	1.7	9.3	15.7	94
	MTmin10	Mean minimum temperature in month 10		8.2	1.6	5.5	11.8	94
	MTmin11	Mean minimum temperature in month 11		4.6	1.8	1.5	9	94
	MTmin12	Mean minimum temperature in month 12		2.4	1.9	-1.3	6.7	94
	MATmin	Mean minimum annual temperature		7.1	1.5	3.9	10.3	94
	MTmax01	Mean maximum temperature in month 1		10	1.3	7	12.5	94
	MTmax02	Mean maximum temperature in month 2		11.3	1.2	8	14.2	94
	MTmax03	Mean maximum temperature in month 3		14	1.1	10.4	16.4	94
	MTmax04	Mean maximum temperature in month 4		15.4	1.2	11.9	17.9	94
	MTmax05	Mean maximum temperature in month 5		19	1.4	16	22	94
	MTmax06	Mean maximum temperature in month 6		23.6	2	19.3	27.6	94
	MTmax07	Mean maximum temperature in month 7		27.8	2.9	21.5	33.1	94

Table A.1 continued from previous page

Type	Code	Description of variable	Unit	Mean	Std. Deviation	Min	Max	N
	MTmax08	Mean maximum temperature in month 8		27.6	2.7	21.9	32.9	94
	MTmax09	Mean maximum temperature in month 9		24.3	1.9	19.9	28.5	94
	MTmax10	Mean maximum temperature in month 10		18.6	1.2	15.2	21.5	94
	MTmax11	Mean maximum temperature in month 11		13.6	1.3	10.2	16.2	94
	MTmax12	Mean maximum temperature in month 12		10.7	1.3	7.7	12.9	94
	MATmax	Mean maximum annual temperature		18.1	1.6	14.5	20.9	94
Solar radiation	PSR01	Solar radiation in month 1	kJ m-2 day-1 µm-1	78.7	14.9	42.2	112.7	94
	PSR02	Solar radiation in month 2		121.5	16.7	80.9	158.8	94
	PSR03	Solar radiation in month 3		186.5	16.4	143.6	221.8	94
	PSR04	Solar radiation in month 4		252.9	13	215	277.2	94
	PSR05	Solar radiation in month 5		300.4	8.7	271.3	313.3	94
	PSR06	Solar radiation in month 6		320.8	6.3	297.2	328.4	94
	PSR07	Solar radiation in month 7		308.7	7.4	282.6	318.2	94
	PSR08	Solar radiation in month 8		271.3	11	237.3	290.4	94
	PSR09	Solar radiation in month 9		211.8	15	171.1	242.4	94
	PSR10	Solar radiation in month 10		144.6	16.7	103	181.9	94
	PSR11	Solar radiation in month 11		89.6	15.4	52	125.7	94
	PSR12	Solar radiation in month 12		64.1	13.7	30.3	95.2	94
	MAPSR	Mean annual solar radiation		195.9	12.7	161.2	221.2	94
Topographic	P_CS	Percentage occupied by chestnut stand within the pixel (1km x 1km)	%	87.6	5.8	80	100	94
	Slope	Terrain slope	%	28.6	11.9	7	54	94
	Elevation	Terrain elevation	m	714.8	175.1	270	1055	94
	LAT	Latitude	Geographic coordinates	40.799314	2.343386	36.599908	43.463517	94
	LON	Longitude	EPSG:4258	-4.637072	3.478571	-7.682393	2.746181	94

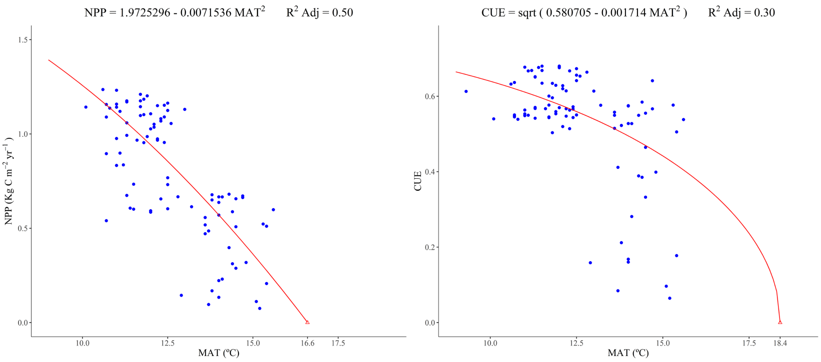

Figure A.1: Supplementary figure. Model fits for NPP and CUE with MAT and sweet chestnut AFS. The blue dots represent the MAT values for each pixel selected (94 in total). The red triangles indicate the points where the fitted curves intersect the x-axes.

APPENDIX B

Supplementary material for Chapter 3

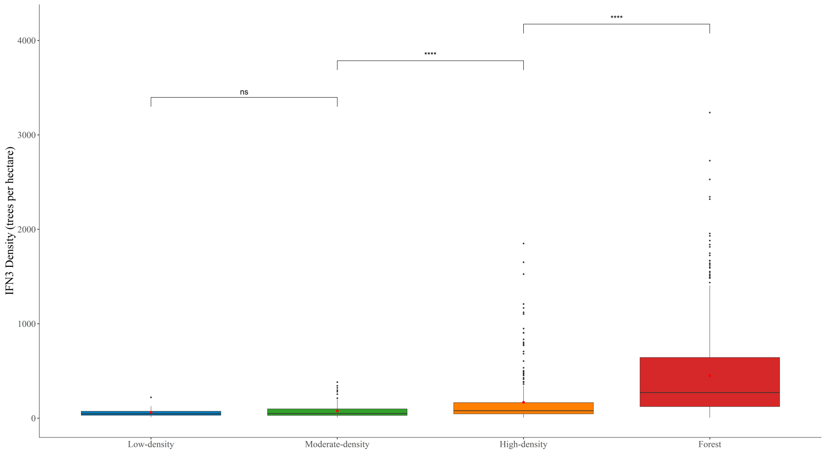

Figure B.1: **Figure S1** in the original publication. Box-and-whisker plot comparing tree density (trees per hectare) based on IFN3 in the different categories of plots under study. Statistical significance: ns: p ¿ 0.05; *: p ¡= 0.05; **: p ¡= 0.01; ***: p ¡= 0.001; ****: p ¡= 0.0001. The black dots represent outliers. The red dots represent mean values.

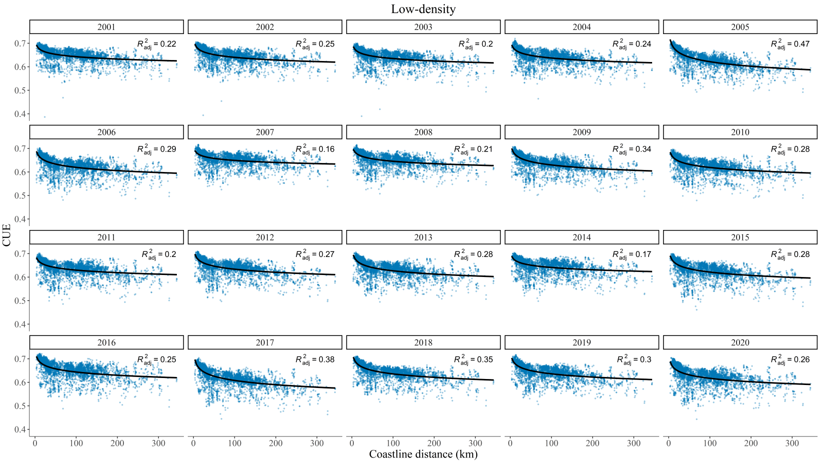

Figure B.2: **Figure S2** in the original publication. Annual linear-log models for CUE in low-density AFS.

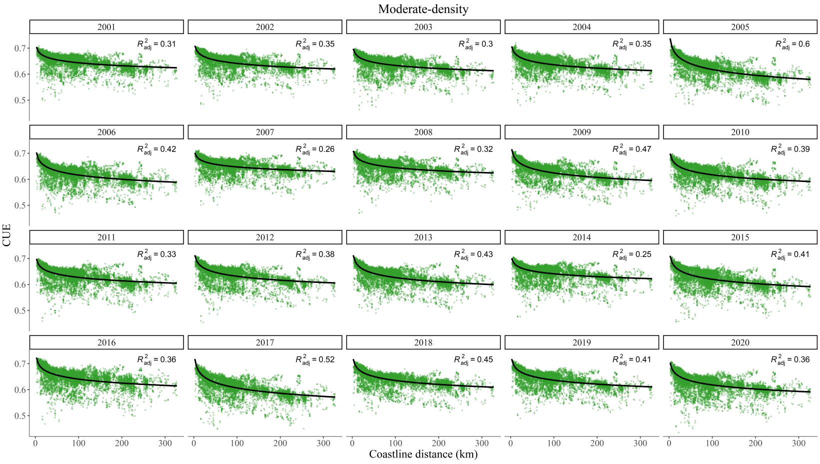

Figure B.3: **Figure S3** in the original publication. Annual linear-log models for CUE in moderate-density AFS.

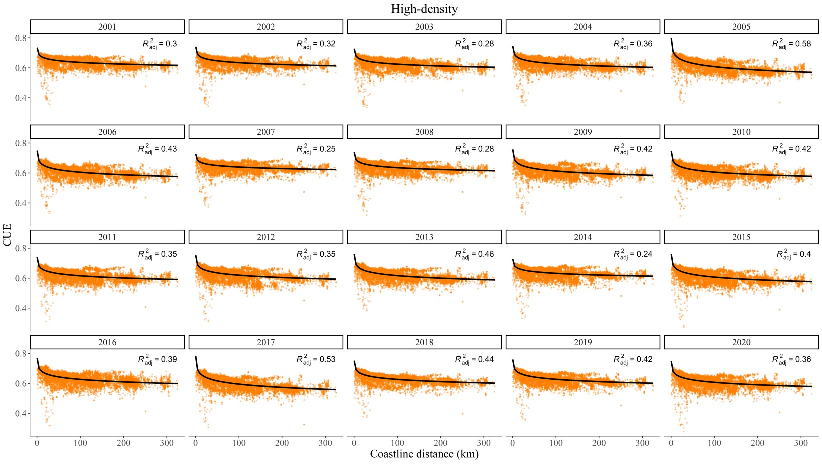

Figure B.4: **Figure S4** in the original publication. Annual linear-log models for CUE in high-density AFS.

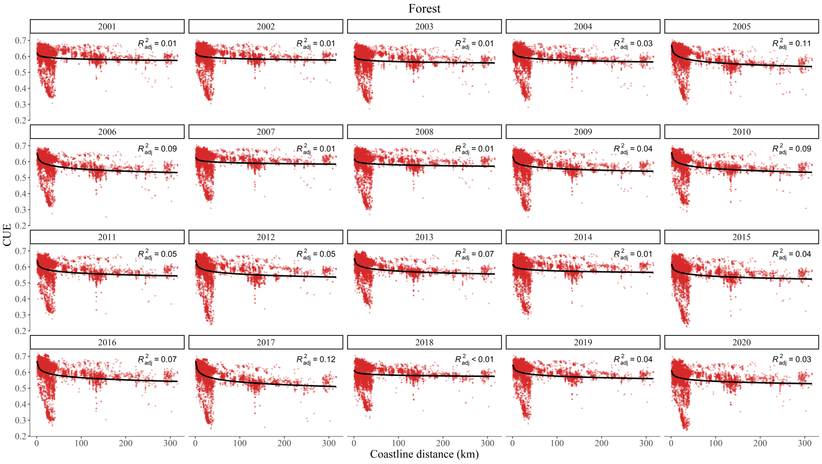

Figure B.5: **Figure S5** in the original publication. Annual linear-log models for CUE in AFS categorized as forest

APPENDIX C

Supplementary material for Chapter 4

Dissimilarity analysis

The 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 x 7 cell window size (side length of 100 m) and ending at 81 x 81 cell window size (side length of 1620 m) in steps of 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 analysed to identify representative scales through the dissimilarity (S) between them. The value of S was calculated as follows (Díaz-Varela et al., 2009; O'Neill et al., 1996; Saura & Martínez-Millán, 2001):

$$S = \frac{M_{max} - M_i}{SD_{max}} x100 \tag{C.1}$$

where M_{max} is the average value of each of the landscape metric generated with a moving window of 81 x 81 pixels, M_i represents the average value of each of the landscape metric generated with a moving window of N x N pixels, and SD_{81} is the standard deviation of the landscape metric generated with a moving window of 81 x 81 pixels. As S shows the differences in percentage relative to the largest moving window, the expected results will gradually converge to zero. In order to examine the characteristic scale domains for the landscape analysed, we will consider the value for the moving window for which the map shows a change in the slope of the curve S as a change in the scale domain. Thus, the variation in the slope of curve S was quantified as p_i, with the following expression (Díaz-Varela et al., 2009):

$$p_i = |\frac{\Delta V_i}{\Delta W_i}| - 1 \tag{C.2}$$

where ΔV_i is the percentage increase in the values of S relative to the maximum value with each change in window size, ΔW_i is the percentual increase in moving-window sizes, and i is each increment in scale. The corresponding maps with positive p_i values will show a high dependence on the scale and will be interpreted as the moving window detecting local effects in the variation of heterogeneity. By contrast, corresponding maps with negative p_i values will be less dependent on scale, thus showing a trend towards self-similarity in the response of heterogeneity across scales (Díaz-Varela et al., 2009).

Thus, from extension of the moving window for which the map shows a change in the sign of p_i, the heterogeneity value will have a low dependence on the scale of the analysis, and it can therefore be considered a representative analytical scale. This makes location of this point a vital methodological process for the correct choice of the window size. A moving window of 61 x 61 pixels (side length of 1220 m) was chosen as the reference window size (see Fig. S1, Figure C.1 in this dissertation).

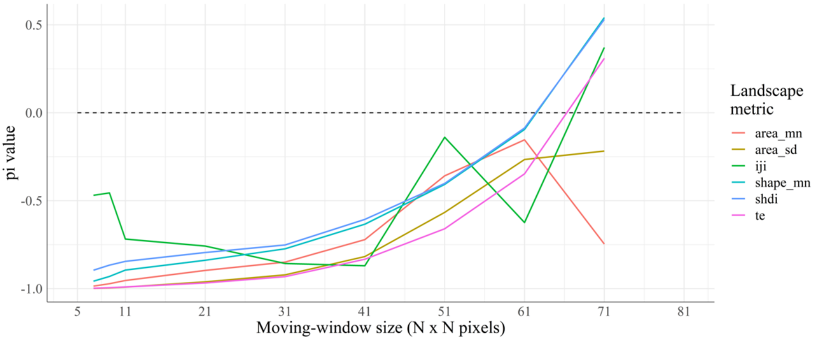

Figure C.1: **Fig. S1** in the original publication. Quantification of (p_i) as the variation in the slope of curve S. The X axis shows the moving window resolution (number of cells).

Table C.1: **Table S1** in the original publication. Summary of the independent variables computed. The following suffixes can also be added to landscape metrics to display the patch distribution statistics: mean (_mn), area-weighted mean (_am), median (_md), range (_ra), standard deviation (_sd), and coefficient of variation (_cv).

Variable type		Variable	Description	Units
Primary production		GPP	Gross primary production	Kg C m-2 yr-1
		NPP	Net primary production	Kg C m-2 yr-1
		CUE	Carbon use efficiency	Dimensionless
		GPPvar	Coefficient of variation of gross primary production	Dimensionless
		GPPmin	Minimum gross primary production	Kg C m-2 yr-1
Topography		Elev	Elevation	Metres
		Aspect	Aspect	North (1), East (2), South (3), West (4)
		GenCur	General curvature	Metres-1
		PlanCur	Plan curvature	Metres-1
		ProfCur	Profile curvature	Metres-1
		Slope	Slope	Percentage
		TPI	Topographic position index	Metres
		TRI	Terrain ruggedness index	Metres
		VRM	Vector ruggedness measure	Metres
Landscape metrics	Aggregation	ai	Aggregation Index	Percent
		cohesion	Patch Cohesion Index	Dimensionless
		contag	Contagion	Percent
		division	Landscape division index	Proportion
		enn	Euclidean Nearest Neighbour Distance Distribution	Metres
		iji	Interspersion & Juxtaposition Index	Percent
		lsi	Landscape Shape Index	Dimensionless
		mesh	Effective mesh size	Hectares
		np	Number of patches	Number
		pd	Patch density	Number per 100 hectares
		pladj	Percentage of like adjacencies	Percent
		split	Splitting index	Dimensionless
	Area-edge	area	Patch area distribution	Hectares
		ed	Edge density	Metres per hectare
		gyrate	Radius of gyration distribution	Metres
		lpi	Largest patch index	Percent
		ta	Total area	Hectares
		te	Total edge	Metres
	Contrast	cwed	Contrast-weighted edge density	Metres per hectare
		econ	Edge contrast index distribution	Percent
		teci	Total edge contrast index	Percent
	Diversity	msidi	Modified Simpson's diversity index	Dimensionless
		msiei	Modified Simpson's Evenness Index	Dimensionless
		pr	Patch richness	Dimensionless
		prd	Patch Richness density	Number per 100 hectares
		rpr	Relative patch richness	Percent
		shdi	Shannon's diversity index	Dimensionless
		shei	Shannon's evenness index	Dimensionless
		sidi	Simpson's diversity index	Dimensionless
		siei	Simpson's evenness index	Dimensionless
	Shape	circle	Related circumscribing circle distribution	Dimensionless
		contig	Contiguity index distribution	Dimensionless
		frac	Fractal index distribution	Dimensionless
		pafrac	Perimeter-area fractal dimension	Dimensionless
		para	Perimeter-area ratio distribution	Dimensionless
		shape	Shape index distribution	Dimensionless
	Entropy	condent	Conditional entropy	Dimensionless
		ent	Marginal entropy	Dimensionless
		joinent	Joint entropy	Dimensionless
		mutinf	Mutual information	Dimensionless
		relmutinf	Relative mutual information	Dimensionless

Table C.2: **Table S2** in the original publication. Significant differences between observed samples and null model approach, randomly redistributing the same number of samples from each category in the study area and replicating the process 100 times. P-value are based on non-parametric one-sample Wilcoxon signed rank test.

Scat category	Nut-fruiting patch	Observed samples	Observed frequency	Average random samples	Average random frequency	p-value
i	Outside	84	0.124	157	0.302	<0.0001
i	Inside	198	0.292	81	0.156	<0.0001
ii	Outside	65	0.096	61	0.117	<0.0001
ii	Inside	23	0.034	5	0.009	<0.0001
iii	Outside	-	-	1	0.003	-
iii	Inside	2	0.003	1	0.002	<0.0001
iv	Outside	305	0.451	215	0.413	<0.0001

Table C.3: **Table S3** in the original publication. The 30 top-performing models obtained with the dredge function of the R package MuMIn.

Model nº	(Int)	ai	CUE	enn_am	enn_sd	Elev	Slope	GPP	df	logLik	AICc	delta	weight
118	-0.3803	0.5432		-0.126		0.7576	0.2171	0.6694	6	-393.945	800	0	0.167
122	-0.3805	0.5211			-0.1264	0.7488	0.2274	0.6688	6	-393.971	800.1	0.05	0.162
114	-0.3848	0.5277				0.7601	0.2196	0.6671	5	-395.088	800.3	0.25	0.147
126	-0.3782	0.5345		-0.09562	-0.09471	0.7495	0.2236	0.67	7	-393.387	800.9	0.93	0.105
120	-0.3831	0.5376	-0.09296	-0.1342		0.7575	0.2003	0.6287	7	-393.473	801.1	1.1	0.096
124	-0.3828	0.5159	-0.07401		-0.1248	0.7495	0.2139	0.6366	7	-393.669	801.5	1.49	0.079
116	-0.3872	0.5217	-0.07749			0.761	0.2058	0.6333	6	-394.755	801.6	1.62	0.074
128	-0.3808	0.5299	-0.08735	-0.1051	-0.08986	0.7497	0.2074	0.6318	8	-392.973	802.2	2.15	0.057
88	-0.3825	0.5565	-0.1354	-0.1418		0.7328		0.6059	6	-396.082	804.3	4.27	0.02
86	-0.3785	0.566		-0.1303		0.729		0.6625	5	-397.142	804.4	4.36	0.019
82	-0.3822	0.5519				0.733		0.6624	4	-398.375	804.8	4.79	0.015
90	-0.3782	0.5467			-0.1144	0.722		0.6636	5	-397.457	805	4.99	0.014
84	-0.3859	0.5414	-0.1203			0.7381		0.6125	5	-397.526	805.1	5.13	0.013
92	-0.3817	0.5371	-0.1189		-0.1132	0.7267		0.6143	6	-396.63	805.4	5.37	0.011
94	-0.3765	0.5597		-0.1048	-0.07927	0.7218		0.6632	6	-396.751	805.6	5.61	0.01
96	-0.3804	0.5511	-0.1322	-0.118	-0.07392	0.726		0.608	7	-395.743	805.7	5.64	0.01
121	-0.3633				-0.144	0.9874	0.2657	0.5947	5	-405.8	821.7	21.67	0
113	-0.3644					1.003	0.2569	0.5942	4	-407.232	822.5	22.51	0
123	-0.3649		-0.102		-0.1398	0.9862	0.248	0.553	6	-405.212	822.5	22.53	0
115	-0.3662		-0.1086			1.002	0.2386	0.5503	5	-406.559	823.2	23.19	0
125	-0.3622			-0.04575	-0.129	0.9905	0.2635	0.5935	6	-405.664	823.5	23.44	0
117	-0.362			-0.08627		1.006	0.2542	0.5925	5	-406.689	823.5	23.45	0
119	-0.3638		-0.119	-0.0961		1.004	0.234	0.5435	6	-405.892	823.9	23.9	0
127	-0.3637		-0.1094	-0.0578	-0.1208	0.9897	0.2441	0.5482	7	-404.997	824.2	24.15	0
91	-0.3623		-0.1516		-0.1249	0.9696		0.5273	5	-409.326	828.7	28.73	0
83	-0.3638		-0.1553			0.9847		0.5267	4	-410.411	828.9	28.87	0
87	-0.3625		-0.1655	-0.1072		0.9859		0.5183	5	-409.574	829.2	29.22	0
89	-0.3604				-0.1291	0.9674		0.5858	4	-410.701	829.5	29.45	0
81	-0.3617					0.9825		0.5862	3	-411.86	829.8	29.74	0
95	-0.3618		-0.1598	-0.07549	-0.09997	0.9731		0.5208	6	-408.957	830	30.03	0

Table C.4: **Table S4** in the original publication. Goodness of fit measures for the candidate acorn model (model nº 114 in Table S3). Confusion matrix statistics values are proportions.

Independent variable	Parameter estimate	Std. Error	AUC	AIC	Omission error	Commission error	Accuracy	Sensitivity
(Intercept)	-0.385	0.087	0.75	800.18	0.29	0.46	0.68	0.54
GPP	0.667	0.110						
Elev	0.760	0.120						
Slope	0.220	0.086						
ai	0.528	0.109						

Table C.5: **Table S5** in the original publication. Goodness of fit measures for interaction acorn model. Confusion matrix statistics values are proportions. ":" indicates interaction between variables.

Interaction model	Parameters	AIC	Omission error	Commission error	Accuracy	Sensitivity
1	Elev + ai:GPP	794.14	0.19	0.48	0.69	0.52
2	GPP + ai:Elev	796.69	0.24	0.43	0.68	0.57
3	ai + GPP:Elev	791.24	0.20	0.49	0.68	0.51

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