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Modelado espacio-temporal de los servicios que proporciona la biodiversidad en los matorrales de la Cordillera Cantábrica (NO España). Efectos de los cambios socioeconómicos a varias escalas.

Spatio-temporal modelling of services provided by the diversity of shrub and heath communities in the Cantabrian Mountains (NW Spain). Effects of socio-economic changes at different scales.

Alejandra Morán Ordóñez

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(Art. 11.3 del R.D. 56/2005)

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CERTIFICAN

que la Tesis doctoral titulada “*Modelado espacio-temporal de los servicios que proporciona la biodiversidad en los matorrales de la Cordillera Cantábrica (NO España). Efectos de los cambios socioeconómicos a varias escalas.*” ha sido realizada por Dña. Alejandra Morán Ordóñez bajo su dirección, y que reúne las condiciones necesarias para su defensa.

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A mi familia

A Stefano

A mis amigos

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The landscape...

... has an important public interest role in the cultural, ecological, environmental and social fields, and constitutes a resource favourable to economic activity and whose protection, management and planning can contribute to job creation;

... contributes to the formation of local cultures and ... is a basic component of the European natural and cultural heritage, contributing to human well-being and consolidation of the European identity;

... is an important part of the quality of life for people everywhere: in urban areas and in the countryside, in degraded areas as well as in areas of high quality, in areas recognised as being of outstanding beauty as well as everyday areas;

... is a key element of individual and social well-being and ... its protection, management and planning entail rights and responsibilities for everyone.

Preamble to the European Landscape Convention 2000

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ABSTRACT

Mountain systems often represent biodiversity hotspots. Due to a combination of their ecological characteristics (strong altitudinal gradients favouring small-scale diversity at short distances) and low intensity management practices (e.g. extensive livestock grazing and small scale agriculture), these areas can sustain a significant diversity of ecosystems and species. Such diversity represents the key factor that allows mountain systems to provide a wide range of ecosystem services, beneficial for both human societies and the species occurring within these landscapes. However, the depopulation of rural areas and the ensuing land abandonment, especially marked since the 1960s, has led to the loss of traditional management, in turn determining loss of semi-natural and natural habitats, homogenization of landscape patterns and loss of biodiversity in the short-medium term. In this Thesis I study land use and land cover changes in the southern slope of the Cantabrian Mountains (NW Spain), at different spatio-temporal scales, identifying the main biophysical and socio-economic factors driving the observed changes. Particular attention is paid to the analysis of the ecosystem services that landscape mosaics of heathlands, shrublands, grasslands and rocks, provide at different institutional scales (ranging from local to international), and to how to raise awareness of their values among the public, stakeholders and managers. This knowledge can represent valuable supporting information when designing current and future management strategies aimed at preserving the conservation values of these landscapes.

Firstly we carried out an assessment of land cover changes at the regional scale between 1991 and 2004, a key period for the implementation of land conservation policies, on the basis of a temporal series of land cover maps created from LANDSAT images through supervised classification methods (accuracy >85%). The main changes were the increase of forest due to secondary succession and the loss of shrub related to shrub-cutting management practices. Spatially explicit models of landscape change were built to predict areas where future land cover changes may occur (i.e. forest recovery). Additionally, we evaluated whether the observed changes in forest and shrub cover and structure may have been determined by land protection status. We determined that in protected areas management measures allowed for decreasing shrub area and connectedness, while these increased in non-protected areas.

As supervised classification outputs (land cover maps) did not prove useful for distinguishing among specific heath and shrub covers, we incorporated LANDSAT channels in distribution

modelling algorithms to determine the current distribution patterns of four heath and shrub formations of high conservation interest, dominated by species with different life traits (specialist vs. generalist). We also evaluated whether including biotic interactions as covariates in distribution modelling approaches would increase the accuracy of predictions, and how the spatial variation of environmental limiting factors of individual species would determine the success of a species under a competition scenario. LANDSAT channels allowed the detection of the specific signal of the dominant species in the canopy of each habitat, improving the accuracy of the models (especially those of the generalist species) and showing some advantages over other remote sensing information traditionally used in species distribution modelling approaches (spectral indices and land cover maps). The most accurate models were those considering abiotic factors, biotic interactions and remote sensing data as predictors. We observed that when two species competed, the dominant species became the main limiting factor for the weakest species, restricting its distribution to competition free areas.

Finally, we characterized the ecosystem services provided by heathlands landscapes (heterogeneous mosaics of heathlands, grasslands and rocks). In particular, we analysed how social changes undergone since the second half of the twentieth century (1950s-2010s) modified both the heathland landscape patterns and the stakeholders' perception of ecosystem services provided by heathlands, at different institutional scales ranging from local to international. We defined the threats currently faced by heathlands and their services across multiple scales and discussed potential management measures. We observed that, in the last sixty years, the demand of provisioning services from heathland landscapes (at local and regional scales) has significantly declined in favour of cultural services, mainly demanded at national and international scales. Finally, we evaluated a practical case study regarding the interaction between ecosystem services (demand of grazing resources and suitability of habitat for breeding bird species).

The results of this Thesis represent a significant improvement of our comprehensive ecological knowledge of the territory, and provide useful information for the implementation of management strategies in the Cantabrian Mountains.

RESUMEN

Los sistemas de montaña constituyen importantes refugios de biodiversidad. Sus características ambientales particulares (fuertes gradientes altitudinales en áreas de reducido tamaño), así como las prácticas de manejo de baja intensidad a que han sido sometidas durante siglos (pastoreo extensivo y agricultura de subsistencia), han favorecido la coexistencia de una amplia diversidad de ecosistemas y especies. Esta biodiversidad es un elemento clave que determina la capacidad de estos sistemas para generar una amplia gama de servicios ecosistémicos de los que se beneficia todo el conjunto de especies que habitan y utilizan esos paisajes, incluyendo las sociedades humanas. Sin embargo, la despoblación de las áreas rurales de montaña y el abandono gradual del territorio, así como de las prácticas de manejo tradicional, especialmente importante desde la década de los 60, ha supuesto, en muchos casos, la pérdida de hábitats naturales y semi-naturales, así como la homogeneización del paisaje, con sustanciales efectos negativos para su biodiversidad a corto-medio plazo. En esta Tesis se analizan los cambios producidos en el paisaje de la vertiente sur de la Cordillera Cantábrica (NO España), a diferentes escalas espacio-temporales, identificando las fuerzas ambientales y socio-económicas que han conducido estos cambios. Se dedica especial atención a la puesta en valor de los mosaicos paisajísticos de matorral, pastizal y roca, tratando de mejorar el conocimiento sobre los servicios ecosistémicos que éstos proveen a diferentes escalas institucionales (de local a internacional). Esta información puede ser de gran valor como apoyo en la toma de decisiones actuales y futuras orientadas a la conservación y/o manejo de estos paisajes.

En primer lugar, se realizó una valoración a escala regional de la dinámica del paisaje para el periodo 1991-2004, crítico para la implementación de las políticas de conservación en esta zona, a partir de mapas de ocupación del suelo derivados de la clasificación supervisada de imágenes LANDSAT (fiabilidad >85%). Los principales cambios detectados fueron el incremento del bosque (asociado a procesos de sucesión secundaria) y la pérdida de matorral (causada por prácticas de manejo tales como los desbroces). En base a esta información, se construyeron modelos espacialmente explícitos que permiten predecir cuáles son las zonas con mayor probabilidad de cambio de ocupación del suelo (ej. recuperación del bosque). De forma complementaria, se evaluó la relación entre las diferentes dinámicas de cambio observadas para estos ecosistemas y el grado de protección del territorio. Se determinó que las medidas de gestión

aplicadas en las zonas protegidas favorecerían una disminución en la extensión y conectividad de los ecosistemas de matorral que, por el contrario, se incrementaban en las zonas no protegidas.

Los mapas de ocupación del suelo derivados de la clasificación supervisada no permitieron discernir específicamente entre diferentes tipos de ecosistemas de matorral. Por ello, en un siguiente paso, se analizó el efecto de incorporar las bandas de las imágenes LANDSAT en modelos de distribución de hábitats que tenían como objeto determinar los patrones de distribución de cuatro tipos de formaciones de matorral con diferentes rasgos vitales (especialistas vs. generalistas). Asimismo, se valoró si la adición de información sobre interacciones bióticas mejoraba las predicciones de los modelos de distribución y/o permitía evaluar si la variación espacial de los factores que limitan la distribución de cada especie podría determinar su éxito bajo condiciones de competencia. La incorporación de las bandas LANDSAT aumentó la exactitud de los modelos (especialmente los de los matorrales dominados por especies generalistas), dado que fue posible detectar la señal específica de la especie dominante. Esto supuso una ventaja frente al uso de otros datos derivados de teledetección tradicionalmente más utilizados en modelos de distribución de especies (mapas supervisados o índices espectrales). Los modelos más exactos fueron aquéllos que consideraron conjuntamente variables bióticas, abióticas y bandas LANDSAT como predictores. Se observó que cuando dos especies compiten, la especie dominante actúa como factor limitante para la otra especie, forzando a ésta a ocupar zonas libres de competencia.

Finalmente, se caracterizaron los servicios ecosistémicos proporcionados por los mosaicos paisajísticos de matorral, pastizal y roca. En concreto, se analizó cómo los cambios sociales devenidos desde la segunda mitad del siglo veinte (1950-2010) han modificado, tanto los patrones espaciales del paisaje, como la percepción y demanda de los servicios que se pueden obtener de éstos (a distintas escalas institucionales desde local a internacional). A continuación se describieron las principales amenazas para la provisión de servicios a diferentes escalas, y se propusieron posibles estrategias de gestión. Se observó que, en los últimos sesenta años, la demanda de servicios de aprovisionamiento de dichos mosaicos (a escalas local y regional) ha disminuido significativamente en favor de la demanda de servicios culturales (a escala nacional e internacional). Finalmente se evaluó, con un caso práctico, la interacción entre la provisión y demanda de distintos servicios (demanda de pastos para ganadería extensiva y disponibilidad de hábitat adecuado para comunidades de aves).

Los resultados de este trabajo permitieron obtener un conocimiento integrado del territorio que puede resultar de gran utilidad para el desarrollo de planes de conservación y gestión en la Cordillera Cantábrica.

INTRODUCTION

1. Importance of mountain systems

Mountain regions occupy approximately one fourth of the Earth's surface, but they provide goods and services to about half of humanity (Becker and Bugmann 2001; MEA 2005). They commonly shelter higher biodiversity than lowlands because altitudinal gradients determine changes in climatic, hydrological and ecological conditions over relatively short distances, allowing small-scale habitat diversity (Becker and Burgmann 2001). At the same time, mountain biota are adapted to relatively narrow ranges of environmental conditions, which make them particularly fragile and vulnerable to global change (Sala et al. 2000).

Pastoralism, forestry and extensive farming systems, highly adapted to restrictive or localized conditions, have been the predominant uses of European mountain systems since the earliest historical times (Beaufoy et al. 1994; MEA 2005). Low intensity traditional management methods (based on grazing, mowing, etc.) have created a wide range of semi-natural habitats, i.e. grasslands, moorlands, heathlands, etc., that now support significant biodiversity (MacDonald et al. 2000).

In the second half of the twenty century, the low profitability of mountain systems compared to high-intensive livestock and agricultural activities in lowlands, has led to their gradual abandonment (MacDonald et al. 2000). When abandonment takes place, secondary succession processes led to the encroachment of vegetation onto old agricultural fields, the replacement of grasslands and clearings by woody cover types with rapidly growing understory (shrub or forest) (MacDonald et al. 2000; Roura-Pascual et al. 2005; Vicente-Serrano et al. 2005; Rey-Benayas et al. 2007; Álvarez-Martínez 2010; Fig. 1). These changes lead to landscape homogenization, loss of cultural heritage (Jongman 2002), increase of fire risk and loss of biodiversity at a short-medium term (Laiolo et al. 2004; Agnoletti 2007; Hawksworth and Bull 2008).

Figure 1 Consequences of land use/cover change in grassland areas (adapted from MacDonald et al. 2000)

2. The study of the landscape

Mountains are heterogeneous and dynamic systems that should ideally be evaluated in the framework of Landscape Ecology. This discipline investigates the relationship between landscape patterns and ecological processes at different scales (Turner 1989). It defines the landscape as a heterogeneous land area composed of a cluster of ecosystems, resulting from the interaction between natural forces and human management (Forman and Gordon 1986; Burel and Baudry 2004). This discipline studies the role played by biophysical and socio-economic drivers in shaping the structure of landscape and its subsequent consequences in ecosystem functions.

Cartography is the basic tool for representing the landscape and analysing its dynamics and function (Burel and Baudry 2004). The technological development of cartography tools in the last decades, with particular improvements in remote sensing and geographic information systems, has allowed a growing number of environmental studies at different scales (land use and land cover change, wildlife and agricultural applications, natural disaster assessment, etc.; see Lillesand et al. 2008 for a review). Remote sensing is a technique allowing the analysis of Earth's surface through images acquired from electromagnetic sensors operating from airborne and spaceborne platforms to assist in inventorying, mapping and monitoring earth resources (Lillesand et al. 2008). It relies on the spectral characteristics of the different surface features of interest (portion of incident energy that one surface feature reflects, measured as a function of wavelength; Fig. 2), providing information about the type of feature and its condition (i.e. water content in case of vegetation).

Remote sensing data have significant advantages compared to other traditional sources of cartography data, such as periodic global cover of the Earth's surface, panoramic vision, multi-scale observation, multi-spectral record and digital output format (Chuvieco 2008; Lillesand et al. 2008).

Figure 2 Spectral reflectance curves envelopes for deciduous and coniferous trees. Each tree type has a range of spectral reflectance values at any wavelength (source: Lillesand et al. 2008)

Remote sensing data have been widely used in landscape studies in two different ways: classification of remote sensing images into different land covers (land cover maps; Schowengerdt 1983; Lawrence et al. 2004; Álvarez-Martínez et al. 2010) and quantitative analyses of continuous variables, mainly vegetation indices (Lozano et al. 2007, 2010). Since the 1990's, remote sensing data and derived products (land cover maps and vegetation indices) have been used to help mapping species habitats or distributions (Suárez-Seoane et al. 2002; Pearson et al. 2004; Newton-Cross et al. 2007; Buermann et al. 2008). In this sense, species distribution models (SDMs) provide a means for exploring the relationship between field observations of species occurrence and environmental predictor variables. There are several statistical modelling methods applied to SDMs (see Franklin 2009 for a review). They can provide ecological and evolutionary

insights and can be used to predict and map species distributions or habitats across landscapes (Elith and Leathwick 2009). These maps are required for many aspects of environmental research, resource management and conservation planning (Franklin 2009).

3. Ecosystem services in management

Landscapes in mountain systems provide a wide range of ecosystem services. Ecosystem services are defined as the conditions and processes through which ecosystems sustain and fulfil human life (Costanza 1997; Daily 1997), either through the direct use or enjoyment of the natural resources, or through the provision of ecosystem functions. They are commonly classified into four groups (MEA 2003): provisioning (grazing, fuel, natural medicines, etc.), cultural (recreation and ecotourism, cultural heritage, etc.) regulating (water purification, carbon sequestration, etc.) and supporting services (i.e. nutrient cycling, biomass production, etc.). Provisioning, cultural and regulating services directly benefit people, while supporting services are needed for production and maintenance of all direct services. Each service is provided by the service provider unit (SPU; Luck et al. 2009), which can correspond to different ecological levels (such as populations, single species, functional groups or even landscapes). Services provided by each SPU may differ when considered across different temporal and spatial scales. Identification and assessment of ecosystem services are decisive tasks for prioritising the protection of ecosystems, that may vary in their capacity for delivering multiple, and sometimes conflicting, services (Harrison et al. 2010). Qualitative and quantitative assessment of the multiple services provided by SPU helps to incorporate ecological knowledge into decision making and can be used as a valuable tool for complementing management planning strategies (Haslett et al. 2010).

4. Heathlands: European trends and current status.

Heathlands are one the main landscapes present in mountain systems. European heathlands are semi-natural habitats, which underwent a large expansion process until the end of the 18th century, as a consequence of centuries of deforestation aimed at creating grazing areas for sheep, goats, cattle and horses (Webb 1998; Pinto-Correia et al. 2005). They are cultural landscapes (*sensu* Fowler 2003), representing the result of the interaction between societies and their natural environment over time, in this case by means of livestock grazing and burning management under physical constraints (e.g. climate, topography, etc.). They have traditionally provided important goods and services to societies (Wessel et al. 2004; Harrison et al. 2010), generally within

subsistence farming systems, where benefits from livestock grazing were complemented with other activities such as fishing, peat extraction, etc. (Webb 1998; Kvamme et al. 2004; Fig. 3). They are considered biodiversity hotspots, especially for their high richness in plants, birds and invertebrates (Usher and Thompson 1993; Thomson et al. 1995; de Bello et al. 2010).

Figure 3 Spatial organization of the traditional agricultural production systems linked to heathlands in southern Europe (Spain and Portugal). Source: Leite (2004).

At the beginning of the 19th century, these areas began to be considered as unproductive wastelands (de Blust 2007). This caused their abandonment and replacement by shrubs or forests through secondary succession (Moen et al. 2006), their degradation and cover by sifting sandy dunes (de Blust 2007), or their gradual conversion to other land covers (e.g. arable fields, urban areas, etc.; Webb 2005) (Fig. 4). However, the main changes occurred since the second part of the twentieth century (Webb 2005; de Bello et al. 2010; Harrison et al 2010). As a consequence, in some European countries, 90% or more of their original heathlands have disappeared (de Blust 2007). The rapid decline of European heathlands raised the alarm of their threatened status which led to their protection under the Habitats Directive of the European Union (in special areas of conservation within the Natura 2000 network; Annex I Habitats Directive, 92/43/EEC; Anon 1992).

Figure 4 a) Traditional heathland management cycle (source: Kvamme et al. 2004); b) Shrub recovery, demarcated by yellow lines, over unmanaged *Calluna vulgaris* heathlands. Cantabrian Mountains, Spain; c) Forest recovery over unmanaged heathlands (scattered trees pointed with yellow arrows). Lüneburger Heide Nature Reserve, Germany.

In Spain, seven heath habitats are protected within the Natura 2000 network (European codes in brackets): Northern Atlantic wet heaths with *Erica tetralix* (4010); Temperate Atlantic wet heaths with *Erica ciliaris* and *Erica tetralix* (4020); European dry heaths (4030); Dry Atlantic coastal heaths with *Erica vagans* (4040); Endemic macaronesian heaths (4050); Alpine and Boreal heaths (4060) and Endemic oro-Mediterranean heaths with gorse (4090). Although Spain has one of the highest diversity of heath habitats in Europe (Calvo and Suárez-Seoane 2011), mainly thanks to the convergence of different biogeographical regions, little is known about their geographical distribution or their current conservation status, which was reported as “unknown” in the last

European assessment of the Habitats Directive for the period 2001-2006 (Article 17; <http://biodiversity.eionet.europa.eu/article17/>). This could be an indicator of the lack of measures aimed at preserving heathlands in Spain, despite of their European protection. Future conservation planning strategies should tackle the assessment and management of heathlands from a regional perspective (to ensure a comprehensive knowledge of their current distributions and status at the main scale for management decisions). This would to guarantee the maintenance of both heathlands and their ecosystem services, which could benefit society at different institutional scales (from local to European).

5. The case studied: The Cantabrian Mountains (León, Spain)

The Cantabrian Mountain range is located in the NW of Spain (Fig. 5). In this Thesis we focus on its southern slope, which is considered a biodiversity hotspot, hosting a wide variety of ecosystems and species, many of them being endemic (Worboys et al. 2010). There are three factors explaining such biodiversity: (i) Its geographical location laying on the boundary between the Atlantic/Eurosiberian and Mediterranean biogeographical regions, where important changes to species diversity are expected to occur on the face of global change (Thuiller et al. 2005); (ii) Its rough topography with elevations ranging from 877 to 2412 m.a.s.l., which in some cases favours microclimatic conditions; (iii) The traditional management carried out for centuries (based on grazing, cutting and burning; Calvo et al. 2002a) which promoted the occurrence of a wide variety of semi-natural habitats (grasslands, heathlands, etc.).

As ecological conditions change over relatively short distances (soil composition, topography, climate, lithology, etc.), it is common to observe Atlantic and Mediterranean ecosystems occupying different slopes within the same mountain (Fig. 6). Atlantic vegetation is generally located on shaded and humid northern slopes. It mainly consists of deciduous forests (*Fagus sylvatica*, *Betula pubescens*, *Quercus petraea*, *Q. robur*) and heathlands of *Calluna vulgaris* and *Vaccinium myrtillus*. Mediterranean vegetation (forests of *Quercus pyrenaica* and *Q. ilex*, and heathlands of *Erica australis*), mostly occurs on its southern areas or in sunny and drier slopes.

The Cantabrian Mountains also represent the southwestern-most and northern-most distribution for a wide variety of Eurosiberian and Mediterranean species, respectively. That makes this area of high relevance for long term conservation of genetic diversity and evolutionary potential (Hampe and Petit 2005).

Figure 5 Location of the study area within the Cantabrian Mountains (NW Spain)

Since the 1990's, different protected natural areas were declared in the Cantabrian Mountains: the regional Park of Picos de Europa and three natural spaces (Valle de San Emiliano, Hoces de Vegacervera, Ancares-Alto Sil). Moreover, from 2000, six *sites of community importance*, sheltering 39 habitats of community interest, and five *special protected areas for birds* were declared within the framework of the Habitats and Birds Directives respectively (Anon 1992; Anon 2009).

Traditional anthropic management has influenced this area for centuries, shaping heterogeneous and complex landscapes. Human settlements mainly occur in valley bottoms and nearby slopes, where forest and shrublands were cleared in order to obtain haymeadows and arable fields for crop cultivation (Calvo et al 2002a; García-Gaona 2002). Forests nearby the villages were managed for a range of purposes, mainly for timber extraction. The highest parts of the mountains were also cleared in order to obtain pastures (or mosaics of pastures and heaths) and maintained through centuries by extensive livestock grazing and burning (Calvo et al. 2005). Some of these pastures, called mountain passes, were rented for summer grazing by transhumant flocks of sheep, representing one of the main sources of income for most municipalities in the Cantabrian Mountains up to the late 1950s (Rodríguez 2004). The decline of the transhumance, due to its low

profitability and competitiveness compared to both lowlands intensive systems and industrial development, favoured a process of rural depopulation, population ageing and emigration to cities (especially since the 1960s; Collantes 2001). This process involved the loss of traditional management and the promotion of new land covers (coniferous plantations, quarries, etc.). These changes have induced deep transformations in the landscape, which could lead to the loss of its biodiversity values.

Figure 6 Pictures from **a** to **c** show how variations in topography and soil conditions allow ecosystems with very different requirements to occur at short distances. a) Beech forest (Atlantic forest) in northern slope (N) vs. forest patch of *Quercus pyrenaica* (Mediterranean) in southern slope (S); b) Small patches of birch forest growing over heathlands dominated by *Calluna vulgaris* (Atlantic) in northern slope (N) vs. heathlands dominated by *Erica australis* subsp. *aragonensis* (Mediterranean) in southern slope (S); c) *Genista hispanica* subsp. *occidentalis* (yellow flowered) require basic soils (limestones) whereas *E.australis* (pink flowered) grows in nutrient-poor acid soils; d) Expansion of *Juniperus thurifera* over terraces previously occupied by crops.

6. Justification of the study

Heathlands have been the aim of study of several research projects developed at small-scale within the Cantabrian Mountains. These studies consisted of field experiments carried out to understand, on the one hand, the dynamics of heathlands when subjected to management disturbances simulating anthropogenic activities, such as grazing, cutting, ploughing and burning (Calvo et al. 1998, 2002a, b, c, 2005; Celaya et al. 2007, 2010; Marcos et al. 2009) and, on the other hand, their responses on the face of global change (mainly consequences of nitrogen depositions: Marcos et al. 2003; Calvo et al. 2007; Cuesta et al. 2008). They all make emphasis on the importance that traditional activities have had in the occurrence of heathlands within this mountain system, arguing about their possible disappearance if management ceases. However to date, little is known about both their current conservation status and their dynamics during the last decades at a regional scale. These dynamics may be determined by processes of land abandonment, which in this area are especially relevant since the 1960s, but also by management strategies, mainly associated to European policies, which have favoured the inclusion of large areas under different land protection status, as natural spaces or natural parks, since the beginning of the 1990s.

Therefore, this Thesis arises from the need of making a spatially explicit assessment of both historical evolution of heathlands and their current distribution patterns in the southern slope of the Cantabrian Mountains. This would require for understanding the overall land use and land cover changes happened in this mountain range, as well as the biophysical and socio-economic drivers behind them. Another key point is the need for revaluation of the conservation value of Cantabrian heathlands, since they are still considered as unproductive lands or wastelands (Calvo et al. 2002b), despite their conservation status (Habitats Directive 92/43/EEC).

7. References

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OBJECTIVES

The general aim of this thesis is to characterize and model land cover changes in the southern slope of the Cantabrian Mountains at different spatio-temporal scales, and to identify the main drivers of change (environmental or socio-economic). Special attention is dedicated to the importance of raising awareness among stakeholders and managers about the value of heathlands, by improving ecological knowledge on the range of ecosystem services they provide across time at different institutional scales (from local to international), which may contribute to current and future management and conservation decisions.

This objective was broken down in the following specific aims:

1. To identify the value of LANDSAT images for assessing land cover changes at a regional scale in the southern slope of the Cantabrian Mountains between 1991 and 2004, a key period for the implementation of land conservation policies. *Chapter 1.*
2. To identify the main biophysical and socio-economic factors driving land cover changes in the southern slope of the Cantabrian Mountains between 1991 and 2004. *Chapter 1.*
3. To develop spatially explicit models to predict areas where land cover change may occur in the future in the southern slope of the Cantabrian Mountains. *Chapter 1.*
4. To evaluate whether the changes in landscape patterns observed at a municipality level in the southern slope of the Cantabrian Mountains between 1991 and 2004 were related to land protection status. *Chapter 2.*
5. To identify and map the current distribution of the most widespread heath and shrub formations with conservation interest in the southern slope of the Cantabrian Mountains, using a habitat distribution modelling approach based on environmental predictors (topography, climate, lithology and human disturbances). These formations are: European dry heaths (dominated by *Erica australis* subsp. *aragonensis*), alpine and boreal heaths (*Calluna vulgaris*), endemic oromediterranean heaths with gorse (*Genista hispanica* subsp. *occidentalis*) and sclerophyllous scrubs dominated by *Cytisus purgans* and *Genista florida*. *Chapter 3.*

6. To assess if the performance of habitat models is affected by the ecological traits of the dominant species (specialist vs. generalist) in these formations. *Chapter 3.*
7. To assess whether the inclusion, as covariates, of data derived from LANDSAT satellite (i.e. reflectance values from channels) improved the accuracy of habitat model predictions obtained using environmental variables only. *Chapter 3.*
8. To explore whether the inclusion of reflectance values in habitat distribution models can improve predictive performance compared to the use of other commonly adopted predictors such as spectral indices or classified land cover maps. *Chapter 3.*
9. To determine the importance of mutual biotic interactions as predictors in modelling the distribution of two heath competitor species with different life traits (*Calluna vulgaris* and *Erica australis*) in the southern slope of the Cantabrian Mountains. *Chapter 4.*
10. To evaluate whether the spatial variation of the limiting factors (biotic and abiotic) for *Calluna vulgaris* and *Erica australis* heathlands can have an influence on the results of their mutual biotic interactions, and hence in their distribution patterns. *Chapter 4.*
11. To identify, characterize and assess the ecosystem services provided by heathland landscapes in the southern slope of the Cantabrian Mountains at different time periods (1950s and 2010s) and institutional scales (from local to international). *Chapter 5.*
12. To assess whether the changes undergone by society in the second half of the twentieth century (socio-ecological systems) have involved changes in the stakeholders' demand of heathlands landscape services (at local, regional, national and international scales). *Chapter 5.*
13. To assess whether landscape changes from 1956 to 2010, at a local scale (mountain passes), can be explained by the demand of provisioning services related to traditional uses (grazing resources by sheep livestock and wild ungulates). *Chapter 6.*
14. To assess whether changes in landscape patterns at a local scale (mountain passes) during the second half of the twentieth century influenced the current provisioning service of suitable habitat for breeding bird species. *Chapter 6.*

THESIS OUTLINE

CHAPTER 1

Using predictive models as a spatially explicit support tool for managing cultural landscapes¹

¹ The content of this chapter was published as:

Morán-Ordóñez, A., Suárez-Seoane, S., Calvo, L. and de Luis E. (2011) Using predictive models as a spatially explicit support tool for managing cultural landscapes. *Applied Geography*, **31**: 839-848.

ABSTRACT

Due to the high sensitivity of mountain landscapes to environmental changes, the study of land cover dynamics has become an essential tool for guiding management policies. Since the second half of the twentieth century, the Cantabrian Mountains (NW Spain) have been substantially altered by the loss of traditional management practices and, more recently, by the new environmental schemes developed by the Regional Government. This area is a biodiversity hotspot, representing the south-western-most distribution limit for a large number of species in Europe. Therefore, small changes in landscape patterns can result in biodiversity losses. In this study, we analyzed land cover changes in the Cantabrian Mountains from 1991 to 2004 by means of remote sensing techniques, identifying the main driving forces and classifying the territory according to its risk of land cover change. Forest expansion and loss of shrublands were the two major trajectories of change apparent during this period. When modelling the occurrence of these land cover changes, we found that performance of models was related to the nature of the change. The most accurate models were associated with processes of secondary succession, i.e. forest expansion (78.6%), while the least accurate models related to changes linked with management decisions, i.e. loss of shrubs (61.8%). The main drivers of change were variations in the number of goats (for the forest expansion model) and changes in the number of head of sheep and cattle (for the loss of shrubs model). Topographic conditions (altitude and slope) were relevant in both models. Our approach proposes an explicit decision support tool for landscape managers, allowing better identification of the areas where they should focus their attention.

1.1. INTRODUCTION

Land cover and land use changes (LCLU) have been widely studied worldwide (Reid et al. 2000; Achard et al. 2006; Seabrook et al. 2007; Izquierdo and Ricardo 2009; Townsend et al. 2009). Understanding the relationships between land cover patterns and their associated processes is extremely important for scientists, landscape managers and policy makers designing nature conservation strategies aimed at preserving some of the unique characteristics of landscapes (Kates et al. 2001). In the European context, there is increasing concern about detecting landscape changes and their ecological consequences in mountain systems (MacDonald et al. 2000; Mottet et al. 2006; Gellrich et al. 2007), since these systems provide important ecosystem services (cultural, provisioning, regulating and supporting) contributing to both highland and lowland economies. Mountain systems constitute important biodiversity hotspots, since their biota is adapted to specific, narrow environmental limits, which makes them extremely sensitive to slight perturbations (Millennium Ecosystem Assessment 2003). Therefore, early detection of changes in land cover patterns has become an important target in these ecological systems since it allows identification of the main landscape drivers and, consequently, the design of realistic management policies.

Through the centuries, human activity has played a decisive role in managing and shaping the landscape of Mediterranean mountain systems (Grove and Rackham 2000). Studies related to land cover trends in these systems have focused mainly on changes resulting from agricultural abandonment. These are widespread, having begun in the early 20th century (Rey-Benayas et al. 2007). In the Iberian Peninsula, additional pressures result from declines in the transhumance system (Molinillo et al. 1997; Gómez and Lorente 2004; Vicente-Serrano et al. 2005), which have been especially noteworthy in the Cantabrian Mountains range. These have involved a gradual loss of traditional management (based on grazing, cutting and burning; Calvo et al. 2007), favouring a process of landscape homogenisation that impacts biodiversity and threatens cultural landscape heritage (Jongman 2002).

Remote sensing techniques have become essential tools for land cover studies at regional scales because of their capacity to provide a temporal series of information on the terrestrial land surfaces and, thus, give an integrated understanding of changing processes in the landscape (see for example Michalski et al. 2008). Predictive models, such as those based on regression, may provide a framework for identifying the driving forces behind land cover changes (Serra et al. 2008). The occurrence of land cover change can be successfully predicted across space by

combining statistical models with spatially explicit data in a geographical information system (GIS) environment (Schneider and Pontius Jr. 2001). This combination of techniques and data represents a powerful tool for defining priority areas in terms of land management and biodiversity conservation (Lehmann et al. 2002).

Within the framework of the European Union (EU) and the Natura 2000 Network requirements (Habitats Directive, 92/43/EEC; Anon 1992), such models can provide important input to the design and application of integrated management strategies. Land use planning in mountain areas, which has traditionally focused on local actions and their short-term consequences, could then be replaced by unified policies addressing the preservation of the natural spaces network as a whole. Furthermore, maps illustrating predicted changes over time could empower land users to understand long-term outcomes of decisions (see for example, Binkley and Duncan 2009), helping to connect people and ecology.

In this study, we evaluated land cover changes in the Cantabrian Mountains during the period 1991 to 2004 using LANDSAT images. We then developed spatially explicit models of land cover change in order to predict where future transitions may occur in the landscape, as well as to define the main forces (biophysical and human) driving the observed changes. The results provide a useful support tool for landscape managers, since it allows the identification of priority areas in terms of conservation.

1.2. METHODS

1.2.1. Study area

The study area is located at the southern slope of the Cantabrian Mountains in the León province (NW Spain). It includes 28 municipalities, covering 3,266 km². Altitude ranges from 877 to 2,412 m.a.s.l. This area lies on the boundary between the Atlantic/Eurosiberian and Mediterranean biogeographical regions, where four bioclimatic belts ranging from supramediterranean to subalpine can be identified (Rivas-Martínez et al. 1987). Average annual rainfall varies from 700 to 1,573 mm. Mean annual temperature varies from 8.2° C to 9.9° C. Atlantic vegetation is generally located on shaded and humid northern slopes. It mainly consists of deciduous forests (*Fagus sylvatica*, *Betula pubescens*, *Quercus petraea*, *Q. robur*) and heathlands of *Calluna vulgaris*. Mediterranean vegetation (*Quercus pyrenaica*, *Q. ilex*) mostly occurs on sunny and drier slopes. The lithology is also diverse, from massive Carboniferous limestones to slate with coal, sandstones, crystal quartzites and conglomerates (Gómez-Sal and Rodríguez 1992). Among the

driving forces that have shaped the landscape of this area over the centuries, transhumance has played an important role. It consists of the movement of flocks of thousands of sheep and goats from the south-Iberian “dehesa” systems to the Cantabrian pastures above the treeline during the summer. This activity has provided an important source of income for most of the municipalities of this area for centuries (Gómez-Sal and Rodríguez 1992). Due to the complex orography, agricultural activities are concentrated on the slopes close to the villages and in valley bottoms. Timber has traditionally been extracted from Atlantic forests for a range of purposes. Since the beginning of the twentieth century, the decline in the transhumance system, the abandonment of agricultural areas due to their lower profitability and the process of population emigration from the countryside to the cities (especially marked since 1960), have resulted in the loss of traditional management practices across the territory. Furthermore, other activities, such as the opening of coal and opencast talc mines, construction of large reservoirs and afforestation of thousands of hectares with conifers, have transformed the landscape.

1.2.2. Data sources

Land cover was mapped using a temporal series of LANDSAT images for the years 1991, 1995, 2000 and 2004 (Table 1.1). We selected images acquired during the summer season in order to obtain the lowest cloud and snow cover (the latter being present sometimes even in late spring).

Table 1.1 LANDSAT images used in the land cover change analyses showing dates of acquirement, type of sensor and sun elevation angle expressed in degrees units (S.E.A.).

Date	Sensor	S. E. A
08-04-1991	TM	54.15
08-15-1995	TM	48.87
09-05-2000	ETM+	49.45
09-24-2004	TM	42.72

LANDSAT images were geometrically corrected following the polynomial method proposed by Palá and Pons (1995), which uses ground control points extracted from aerial photographs as references and a 30 m resolution Digital Elevation Model (DEM) to minimize geometric errors. It was implemented using Miramon software (Pons 2002). Around 60 ground-control points per image were used for geometric correction. Two thirds of these were used to correct the images; the remaining points were used to validate the results. The Root Mean Square Error (RMSE) was lower than the pixel size in all images ($RMSE \pm SD = 16.16 \pm 4.78$). Radiometric correction was

based on the algorithms developed by Markham and Barker (1986) and Morán et al. (1992), while atmospheric correction followed the transmittance model (COST) proposed by Chavez (1996). Down-welling transmittance values for bands five and seven were taken from Gilabert et al. (1994), since atmospheric conditions in their study area were more similar to ours than the area used by Chavez (1996). In order to compensate for differential solar illumination due to the shape of the terrain, a topographic correction was applied following the non-Lambertian C-Correction method (Teillet et al. 1982; Riaño et al. 2003). As each individual image was classified independently, the image series was not normalised.

Other data sources used in this study include a DEM at a 30-meter resolution and several vector layers showing urban areas, water surfaces and coniferous afforestation (see Table 1.2). Since these vector layers are inaccurate because of their coarse scale (1:200,000), they were edited and corrected on screen using high resolution orthophotographies. Socio-economic data accounting for changes in livestock density (number of heads of sheep, cows and goats) and human population density were recorded at the municipality level. All vectorial data were rasterized and resampled to match the LANDSAT 30-m spatial resolution.

1.2.3. LANDSAT image classification

A supervised classification (Maximum Likelihood method; Conese and Maselli 1992; Martin et al. 1998; Shalaby and Tateishi 2007; Schulz et al. 2010) was applied to produce a land cover map per year of study (1991, 1995, 2000, 2004). The variables involved in the process (see Table 1.2) were: (i) LANDSAT bands from 1 to 7 (excluding band 6 because of its coarse resolution). (ii) Two vegetation indices derived from LANDSAT images: the Normalized Differenced Vegetation Index (NDVI) (Rouse et al. 1973) and the standard Greenness Index (GI) of Tasseled Cap Transformation (Kauth and Thomas 1976), as a measure of total photosynthesis and vegetation productivity. (iii) A spatial enhancement variable (texture), calculated as the average of the variance from the third band of each image measured within a mobile window 3x3 pixels. (iv) Topographic variables (altitude and slope) derived from the DEM.

Initially, we defined nine land cover categories: water, rock/bare ground, meadows, climatic pasturelands, heathlands, shrublands dominated by *Genista* spp., coniferous afforestations, forests (including deciduous and evergreen formations) and urban areas. After several preliminary classifications, we identified various conflicting assignments associated with the spatial complexity and heterogeneity of the landscape mosaic in the study area. Particularly relevant were

problems of misclassification when dealing with the category “coniferous afforestations”, since it includes a wide range of development states, from mature to recently planted patches showing confusion with other land cover class as shrublands. This uncertainty was especially relevant in recently disturbed areas (young plantations). For this reason, coniferous afforestations, together with water and urban areas, were masked out and removed from the classification process. The remaining categories were grouped into four final classes: rock/ bare ground, herbaceous vegetation (including meadows and pasturelands), shrublands (including shrublands and heathlands) and forests.

High-resolution orthophotography (years 2000 and 2004) and fieldwork data (2005) were used to define at least 20 training polygons per category with a size of 50 pixels (4.5 ha), which were distributed throughout the study area following a stratified sampling design. Using the same data sources, as well as Spanish Forest Inventories, we created a set of validation layers containing 100 points per category and year.

Classification accuracy was assessed using a confusion matrix, which allowed validation points to be compared with the classified land covers. In order to interpret the matrix, we evaluated persistence and “swaps” (transitions between gains and losses in categories), according to Pontius Jr et al. (2004). Since coniferous plantations, water and urban areas were considered as constant land covers during the study period, we only assessed dynamics within rock/bare ground, herbaceous vegetation, shrubland and forest.

1.2.4. Modelling land cover changes

Principal Components Analysis (PCA) has been widely used in pre-classification change-detection approaches (see examples in Lu et al. 2004; Cakir et al. 2006; Pu et al. 2008; Deng et al. 2008), but less often in post-classification analyses. We applied a PCA on the temporal series of classified LANDSAT images (1991, 1995, 2000 and 2004) to enhance the detection of regions of change under the following assumption: We assigned values of 1 to 4 to the land cover categories, considering them as continuous, incremental stages of a secondary succession process: rock/bare ground (1), herbaceous vegetation (2), shrubland (3) and forest (4). Therefore, higher values will always mean greater complexity of community structure and ecosystem functioning. Consequently, landscape trends involving evolution towards more complex ecosystem structures would imply a shift from 1, 2, or 3 towards 4. On the other hand, land cover changes from 4, 3 or 2 towards 1 would imply a loss in complexity of ecosystem structure backwards in the ecological

succession due to perturbations. Subsequently, an unsupervised classification (ISODATA) was carried out on the first four principal components obtained from the previous step. The resulting cluster classes, corresponding to different categories of land cover change, were used in further analyses. For any given cluster class, a pixel in the landscape will be classified as “1” (present), belonging to their class, or “0” (absent) not belonging.

A sample of 20,000 systematic sample points was then generated throughout the study area to record different trajectories of land cover change (i.e. cluster classes). The sampling size was proportional to the surface corresponding to each change. Topographic and socio-economic data (see Table 1.2) were also assigned to those locations and recorded in a database structured around the cluster category. For each of these trajectories, we selected a prevalent data sample within each presence/absence class but with equal sample numbers in each class. We then applied binary logistic regression (BLR) to model the probability of the occurrence of the main land cover changes as a function of the independent variables.

Before running the regression analysis, we checked for high Spearman correlations among the topographic and socio-economical variables, which would hinder the stepwise selection procedure. Finally, we assessed the significance of each of the independent variables, as a function of “change” or “no change”, using Mann–Whitney *U*-tests. Only significant variables ($p < 0.05$) were retained in the final modelling analysis.

The selection of variables that best fitted into our models was made by means of a backwards stepwise regression. The analysis begins with a full model, where independent variables are removed in an iterative process (Hosmer and Lemeshow 1989) based on a Wald algorithm. The ability of the model’s predictions to discriminate between the response classes was evaluated using Relative Operating Characteristics (ROC) (see Pontius Jr and Schneider 2001; Braimoh and Vlek 2005; Mathew et al. 2009). ROC values range from 0.5 (for a model that assigns the probability at random) to 1 (for a model that perfectly assigns the probability of observing the trajectory in the landscape). The logit function of the probability obtained from the models was converted, through an inverse logistic transformation, into a map showing the probability of change occurrence on a scale of 0 to 1.

GIS analyses were done using ERDAS® IMAGINE 8.5 and IDRISI KILIMANJARO 14.1 and statistic analyses were performed with SPSS 16.0.

1.3. RESULTS

1.3.1. Classification results and accuracy assessment

Table 1.3 shows LANDSAT classification accuracy for the complete temporal series. In all cases, the average accuracy was greater than 85%, which indicates a good level of reliability. The lowest producer's accuracy level corresponded with herbaceous vegetation, which was under-classified (values ranging from 73.91 to 85.22%); while the highest value was for rock/bare ground (values ranging from 87.13 to 97.09 %). The lowest user's accuracy corresponded to shrublands, which were over-classified; while the highest value was for the rock/bare ground category.

1.3.2. Land cover change monitoring

Fig. 1.2 and Table 1.4 show that, at the beginning of the 1990s, the landscape in the study area consisted of a shrubland matrix (42.99% of the total area), with patches of different land cover. Forest patches represented 13.99% of the area and patches directly linked with human activities occupied respectively the 21.46 % (grasslands), 0.77% (water reservoirs) and 1.12% (urban areas). Rock and bare ground occupied 11.91% and coniferous plantations covered 7.77% of the study area.

From 1991 to 2000 the area occupied by shrublands only increased from 42.99% to 43.09% (less than one percent), while rock/bare ground and herbaceous vegetation showed an increase in area by 3.28 % and 5.41 %, respectively. These increases corresponded with forests reduction from 13.99% to 12.34% cover. The most remarkable changes in these vegetation categories occurred during the period 2000-2004, when the cover of both herbaceous vegetation and shrublands decreased (5.31% and 5.93% respectively), while the area of rock/bare ground and forest increased by 13.69% and 16.63%, respectively. For the study period as a whole, shrubland cover decreased a 5.72%, while both rock/bare ground (17.69%) and forests (2.88%) increased. Note that these percentages of change were calculated based on the surface occupied by each land cover in 1991. The area occupied by herbaceous vegetation underwent a slight reduction through the study period.

Table 1.2 Data sources and variables used for LANDSAT image classification and analyses of land cover change.

Type of variable	Data source, scale and spatial resolution	Date	Code	Variable definition
Remote Sensing	LANDSAT images (30m)	1991, 1995, 2000, 2004	Bx	Bands from 1 to 7 (excluding band 6)
			NDVI	Normalized Differenced Vegetation Index (NDVI), calculated as $(NIRC - NR) / (NIRC + NR)$ or $(BAND\ 4 - BAND\ 3) / (BAND\ 4 + BAND\ 3)$
			GI	Greenest Index calculates as $(NIRC / NG - 1)$ or $(BAND\ 4 / BAND\ 2 - 1)$
			TEX	Texture: variable which enhances texture differences between categories. Calculated from the third band of each image
Topographic	Digital Elevation Model (5, 30 m), Junta Castilla y León		DEM	Altitude
			SLO	Slope (degrees)
Land cover	Vectorial layers at 1:200,000 scale, Junta de Castilla y León	2000	URB	Urban areas
			WAT	Reservoirs, lakes and pools
	Spanish Ministry of the Environment (Second and Third National Forest Inventories at 1:200,000 scale)	1996	CON	Patches of conifer plantation established from 1900 to 1996.
		1996	NFI2	Vegetation
		2006	NFI3	Vegetation
Socio-economical	Spanish Statistics Institute, Caja España	1991-2004	POP	Changes in human population density (municipality level) by Ha
	Junta Castilla y León, sanitary campaigns	199-2005	CAT	
			SHE	Change in number of head of cattle, sheep and goats (municipality level) by Ha
			GOA

Figure 1.1 The four categorical land cover maps derived from the LANDSAT scenes used in the analysis (1991, 1995, 2000 and 2004)

The cross-tabulation matrix between 1991 and 2004 (Table 1.4) provides information about systematic transitions between land cover types. For example, herbaceous vegetation, which did not undergo significant net changes (less than 1% decrease), was very dynamic (extensive swapping). In 2004, only 53.26% of herbaceous cover remained invariant from 1991, with 16.90% changing to shrubland, 5.94% to forest and 15.90% to rock/bare ground. Concurrently, 27.06% of the initial shrubland cover, 10.68% forest and 9.00% rock/bare ground shifted to herbaceous vegetation, making the net change of this land cover category almost null.

Table 1.3 Producer's accuracy (P.A.) and user's accuracy (U.A.) values specified per land cover category and year. The percentages of the total study area occupied each year per land cover category are also detailed. NC91/04 represents the percentage of net change for the period 1991-2004 (note that these percentages of change were calculated on the basis of the surface occupied by each land cover in 1991).

	Rock/bare ground			Herbaceous			Shrub			Forests			Overall accuracy
	P.A.	U.A.	%	P.A.	U.A.	%	P.A.	U.A.	%	P.A.	U.A.	%	
1991	96.12	95.19	11.91	84.16	94.44	21.46	93.33	85.22	42.99	94.34	94.34	13.99	92.05
1995	97.09	96.15	13.37	81.25	89.66	21.03	89.42	86.92	42.41	92.38	88.18	13.55	90.20
2000	87.13	97.78	12.30	78.50	88.42	22.63	96.12	77.95	43.09	90.00	90.91	12.34	87.83
2004	93.88	94.74	14.01	79.57	91.85	21.42	93.50	83.60	40.53	91.00	87.03	14.39	89.10
NC91/04			+17.69			-0.19			-5.72			+2.88	

The 2.88% net change in forest cover was mainly associated with a swap from shrubland to forest (33.50%) and from herbaceous vegetation and rock/bare ground to forest (5.94 % and 1.55 % respectively). During the whole study period, forest mainly change towards shrubland (8.73%) and herbaceous vegetation (10.68%).

Table 1.4 Cross-tabulation matrix analyses between the main land covers (values expressed in percentages).

1991	2004			
	Rock/bare ground	Herbaceous vegetation	Shrubs	Forests
Rock/bare ground	67.36	9.00	8.94	1.55
Herbaceous vegetation	15.90	53.26	16.90	5.94
Shrubs	16.00	27.06	65.42	33.50
Forests	0.74	10.68	8.73	59.01

1.3.3. Land cover change modelling

We obtained 12 cluster classes (i.e. possible land cover changes from 1991 to 2004), which were interpreted according to the temporal sequence of land covers detected for the study period. Five cluster classes represented non-change situations, with the remaining seven classes representing different trends of change. Two of these classes of change corresponded with balanced situations between herbaceous-shrublands and shrublands-forests (23.83 and 18.74% of the sample points

respectively). A 9.3% of the points represented areas of random change through time, corresponding with two cluster classes. Another cluster category (5.13%) recorded the processes of perturbation involving the loss of vegetation cover between 1991 and 1995, followed by a later recovery. The two remaining cluster classes corresponded with forest expansion and a consistent loss of shrubland throughout the whole timeframe (4.82% and 4.9% of the sample data respectively). Only the latest two classes were considered in the following statistical analyses.

1.3.4. Forest expansion model

Mann–Whitney *U*-tests on the explanatory variables showed that all of the following variables could significantly explain forest expansion changes: altitude ($p < 0.01$), slope ($p < 0.01$), change in population density ($p < 0.01$) and temporal shifts in number of head of cattle ($p < 0.01$), sheep ($p < 0.02$) and goats ($p < 0.01$). On average, the change “increase of forest cover” predominantly occurred at altitudes of around 1,255 m (ranging from 1,241 to 1,267 m) and slopes of 5.09 degrees (ranging from 5.46 to 7.72). Moreover, this change was associated with sites characterized by larger reductions in both population and number of head of sheep than areas where forest did not increase. The Spearman test did not detect strong correlations among variables ($r < 0.8$). Therefore, all of the independent variables were included in the binary logistic regression analysis (BLR).

Using backwards stepwise regression, only three variables were retained: altitude, slope and number of head of goats. The estimated regression coefficients are shown in Table 1.5. Positive values of the standardized logit coefficients indicate that higher values of the independent variables increase the probability of observing the trajectories. The “odds ratio”, $\text{Exp}(\beta_1)$, measures the likelihood of observing a trajectory if the independent variable is increased by one unit. When $\beta > 0$, $\text{Exp}(\beta) > 1$, indicating that the odds of observing the trajectory increase, and when $\beta < 0$, $\text{Exp}(\beta) < 1$, meaning the likelihood of observing the trajectory decreases. When $\beta = 0$, $\text{Exp}(\beta) = 1$, and the likelihood of observing the trajectory is not affected. The discrimination of the model, estimated through the area under the ROC curve (AUC), was 0.79. The probability map derived from the logistic function is shown in Figure 1.2. The highest probability of forest expansion was mainly found in two locations: the whole southern part of the study area, corresponding with the lower peaks of the Cantabrian mountain range in the province of León, and valley bottoms in the northern part of the study area. In the latter, increasing the distance from valley bottoms reduced the probability of observing this change.

Table 1.5 Main drivers retained in the final BLR models and their estimated coefficients.

	Variable	β_1	SE	Wald	Sig.	Exp (β_1)
Forest expansion	Altitude (<i>DEM</i>)	-0.004	0.000	164.352	0.000	0.996
	Slope (<i>SLO</i>)	-0.099	0.018	29.491	0.000	0.906
	Goat change (<i>GOA</i>)	10.686	5.280	4.096	0.043	43759.825
	Constant	5.787	0.381	230.285	0.000	326.154
Loss of shrub cover	Altitude (<i>DEM</i>)	0.001	0.000	9.704	0.002	1.001
	Slope (<i>SLO</i>)	0.044	0.012	13.104	0.000	1.045
	Cattle change (<i>CAT</i>)	5.332	1.689	9.965	0.002	206.751
	Sheep change (<i>SHE</i>)	-3.781	1.063	12.657	0.000	0.023
	Constant	-1.313	0.311	17.824	0.000	0.269

β_1 : Coefficient, SE: Standard error of estimate, Exp (β_1): Exponential coefficient/odds ratio.

1.3.5. Loss of shrub model

Changes in population density ($p=0.12$) and number of head of goats ($p=0.17$) were excluded from the subsequent analyses according to the Mann–Whitney *U*-test. The remaining variables were taken into account in successive analyses because they were uncorrelated according to the Spearman test ($r<0.8$): altitude ($p<0.01$), slope ($p<0.01$), number of head of cattle ($p<0.01$) and sheep ($p<0.01$). Loss of shrubland cover occurred in areas with a mean slope of 8.5 degrees, characterized by significant losses in the number of head of sheep and, at a lower extent, in the number of head of cattle.

The regression model was fitted as a function of the variables altitude, slope and number of head of both cattle and sheep (Table 1.5). The model discrimination was 0.62, which was lower than the fit of the forest expansion model. The probability map derived from the logistic function is shown in Figure 1.3. In this case, there were no clear patterns of spatial distribution of the change in the study area.

Figure 1.2 Forest expansion model.

Figure 1.3 Probability of loss of shrub cover.

1.4. DISCUSSION

1.4.1. Land cover change monitoring

Land cover changes in the Cantabrian Mountains of León have followed the same trajectories observed in other Mediterranean mountain ranges since the beginning of the 20th century. The loss of traditional management practices (grazing, burning and cutting) have led to abandonment of both pastures and crops, resulting in shrub and forest encroachment (MacDonald et al. 2000; Lasanta-Martínez et al. 2005; Rey-Benayas et al. 2007; Pelorosso et al. 2009; Geri et al. 2010). We observed that, at the beginning of 1990s, almost half of the study area was covered by shrublands as the result of more than one hundred years of decline of the transhumance system (Rodríguez 2004), increasing depopulation and an ageing population in the countryside (Collantes 2001). This process continued in the Cantabrian Mountains until 2000, when the trend started to change. The decrease in shrubland cover from 2000 to 2004 can be directly related to new conservation policies adopted in the study area. Four protected areas have been declared since 1990, covering 38% of the Cantabrian Mountains. In these protected areas, specific silvicultural measures have been introduced since 2000 (Gil and Torre 2007) to favour the regeneration of pastures to support extensive grazing and, at the same time, to create firebreaks to control both the risk and extent of fire. Such measures (particularly shrubland clearance to increase pastureland) have been successfully applied in other regions of Spain (Andalucía, Asturias, Galicia and La Rioja), as well as in other Mediterranean areas (Lasanta et al. 2009). Even in the few years since their introduction, these management strategies have had noticeable effects in the Cantabrian Mountains at regional scale. These include a reduction in arson fires in the study area (Head of Forest Fire Prevention, personal communication). The decrease in the area affected by forest fires can partly explain the 2.88% increase in forest cover recorded throughout the study period. Another key factor was the establishment of restrictive policies in the protected areas, involving a reduction in the incidence of some traditional management practices, such as burning. This is expected to drive secondary succession towards forest stages, as experienced in other protected areas in Spain (Peñuelas and Boada 2003).

At this point, it is necessary to consider the interpretation of change from satellite images when comparing data from different months. Variations in the spectral behavior of the vegetation, due to its leaf water content, may lead to a certain level of confusion between land cover types, particularly in boundary areas, where the uncertainty is higher (Roy 2000). Therefore, pixels on the border between shrublands and forests may be classified as a different land cover type

depending on leaf moisture content. This effect has been detected in the study area, related to the fact that in 2000, the registered rainfall was 1655.1 mm, which represents less than one half of the value recorded in 2004 (3817.4 mm) (Morán-Ordóñez unpublished data). Even considering these sources of error, the trend of increase in forest cover (linked with abandonment) compares well with results reported over the last fifty years in other mountain ranges of northern Spain, including the Pyrenees (Roura-Pascual et al. 2005), as well as other areas of the Cantabrian Mountains (Rescia et al. 2008). Moreover, similar results were obtained by the Third National Forest Inventory 1992-2003 (Ministry of the Environment) for the Province of León.

The amount of herbaceous vegetation remained almost constant during the study period, despite the regional policies applied in the Cantabrian Mountains aimed at increasing pasture areas and enhancing extensive grazing system to economically and ecologically sustainable levels (Celaya et al. 2007). This pattern may result from the compensatory effect of areas where shrub-cutting has been intensive (mainly in the more Atlantic municipalities) and areas where the successional trend linked with the abandonment of agricultural fields is continuing (mainly the most Mediterranean municipalities).

The extent of bare ground also increased over the study period, mainly due to the opening of three large quarries in the area since 1995. Silvicultural measures have also increased the percentage of bare ground in the study area. Shrub clearance has resulted in the affected areas apparently remaining as bare ground before the recovery of pasture species (especially in areas where *Genista* spp. and *Cytisus purgans* have been cleared).

1.4.2. Land cover change modelling

A general goal of ecologists studying patterns of land cover change is to develop useful predictive models from many possible explanatory variables (e.g. Guisan and Zimmerman 2000; Suárez-Seoane et al. 2002) to identify drivers of change. These models can be used as tools allowing managers to develop spatially-explicit environmental policies aimed at managing specific types of land cover to maintain biodiversity and the services they provide. In this sense, the binary logistic regression model successfully identified the drivers that have controlled the two main land cover changes under study (forest expansion and loss of shrubs). This knowledge is essential for defining regional strategies in the Cantabrian Mountains. Nowadays, the management of this area is shared among three administrative sections. Land cover changes, ecological processes and their drivers can differ between sections. Different authorities are responsible for each section, meaning

that management decisions can be designed and performed independently from the others. However, the new challenges for conservation determined by EU policies will require an integrated understanding of the processes in the protected areas (Natura 2000 sites), whose boundaries do not correspond to administrative sections. Therefore, spatial models like the ones developed in this study can help managers to: i) understand what the main land cover processes in the whole mountain range are and where they are taking place; ii) identify the factors driving those changes as well as the extent at which they are acting; iii) integrate local-focused management and regional plans aimed at preserving areas of natural importance as a whole.

Forest expansion was best explained by topographic variables (altitude and slope), together with variations in the number of goats. Negative standardized logit coefficients indicated that the probability of observing the analyzed trajectory decreases at higher altitudes and slopes. This may be due to the fact that forest recovery has occurred mainly in areas at medium altitude and with low slope close to the valley bottoms, where deeper and more fertile soils are found (Gil and Torre 2007). The loss of traditional management, based on timber extraction, and the abandonment of agricultural fields, located close to the villages, have favoured an increase in forest in lower areas. However, the logit coefficient for reductions in the number of goats indicated a positive relationship with the probability of forest expansion. Goats use not only herbaceous vegetation, but also woody species (Papachristou et al. 2005), whereas cattle and sheep only use herbaceous vegetation. This fact should be taken into account to understand the role played by goats in keeping both the forest understory clean of ground fuels and grassland areas clean of shrubs and wooded patches (Verdú et al. 2000; Celaya et al. 2007; Sebastián-López et al. 2008).

In contrast, the model for the loss of shrubland cover had low accuracy ($AUC=0.62$), probably because the change it describes depends not only on biophysical or socio-economic factors, but also on decisions made by managers at a regional level. The opening of pastoral areas by means of shrub clearing has occurred only in municipalities where the neighborhood council demanded them. Shrublands are distributed throughout the study area, across a wide range of environmental conditions. The locations of shrubland clearances are only dependent on the specific place where pastures are required for sheep and cattle grazing and the feasibility of the terrain as a source of short-term pasture. Therefore, even if this land cover change is clearly detected by LANDSAT images, it is difficult to model using logistic regression. The model, in spite of its low accuracy, provides a general description of the main drivers influencing the observed changes. Changes in

cattle numbers were the most important variable in the model, reflecting the increased use of pastures for this kind of livestock, which has become more and more popular in the Cantabrian Mountains of León, as in other areas of the Cantabrian range (Rescia et al. 2008). As a result of the abandonment of the transhumance system, summer pastures have progressively been occupied by cows (even from neighbouring provinces) due to their easier management: farmers can leave the cattle to roam free in the pastures for days, which imply a lower effort than having sheep or goats. Changes in the number of sheep were also important in the model because, as mentioned above, sheep together with cattle are responsible of the demand for shrub cutting.

1.5. CONCLUSIONS

After more than fifty years of rural abandonment and loss of traditional management in León Cantabrian Mountains, important land cover changes can be detected: an increase in bare ground, loss of shrublands and increase in forest cover. These trends have become more significant since 2000, when modification in forestry policies introduced important changes aimed at substituting for the loss of traditional management practices (mainly shrub clearance). LANDSAT images were an important tool for analyzing these changes at a regional scale in mountain areas with high heterogeneity. Binary logistic regression models allowed the main drivers linked with these changes to be identified. In general terms, predictive models such as these could be used as a spatially explicit tool to address management strategies. Based on this information, managers can focus their attention on areas with a high risk of change and declare them as priority areas in terms of conservation and management. Knowledge about the drivers of change can also help in developing particular policies aimed at promoting the maintenance of traditional activities, which could be essential for preserving the cultural landscapes in the Cantabrian Mountains.

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CHAPTER 2

Ecological influence of land protection status on landscape dynamics: a preliminary study in Cantabrian Mountains²

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ABSTRACT

Protected areas constitute central elements for conservation strategies at different organizational levels, from local to international. They play an important role in the protection of threatened species, their habitats and other features of conservation interest. The effectiveness of declaring a protection status would depend on management actions, including restriction of land uses, aimed to ensure conservation targets, even in the face of changing environmental conditions. In this study, we sought to determine whether the patterns of land cover change observed in the Cantabrian Mountains between 1991 and 2004 differed between protected and non-protected areas, and how this could relate to the effectiveness of the protection status. We focused our attention on shrub and forest dynamics. Changes in landscape structure were analyzed with the software FRAGSTATS and GUIDOS, estimating number of patches, patch average mean size, adjacency, shape index, number of patches with inner area, and isolated patches and corridors. We observed that patterns of land cover change differed between protected and non-protected areas, particularly for shrub, although these differences were not significant. In protected areas there was a decrease in the extent and connectedness of shrublands due to the removal of shrub cover to create pastures and reduce the risk of fires; in non-protected areas shrublands increased, due to land abandonment and shrub encroachment associated to secondary succession processes. Trends of change for forests appeared to be influenced more by the proportion of forest cover of each municipality at the beginning of the study period than by their protection status. Further research is needed to accurately measure the effectiveness of protected areas in maintaining land cover stability or in promoting certain types of land cover interest (i.e. forest, heathlands, etc.). It would be needed to increase the number of case studies and also to reduce the uncertainty arising from the land cover maps used as data sources.

2.1. INTRODUCTION

A protected area is defined as an area of land and/or sea especially dedicated to the protection and maintenance of biological diversity, and of natural and associated cultural resources, which is managed through legal or other effective means (IUCN 1994). They constitute central elements for conservation strategies at different organizational levels ranging from local to international (Gaston et al. 2006). Traditionally their establishment has been based on the protection of threatened species and their habitats or of spectacular landscapes, with the aim of ensuring their persistence into the future (Haslet et al. 2010). The designation of protected areas has mainly relied on the representativeness of a given feature of conservation interest (e.g. species, habitat, etc.), often without sufficient consideration given to the quality of the site, its spatial design or its degree of connection to other protected areas (Branquart et al. 2008). This site-isolated system has sometimes affected the effectiveness of conservation measures by forgetting the need of maintaining functional relationships between them (ecological networks; Jongman et al. 2004; Bennett and Mulongoy 2006; Gaston et al. 2006; Kettunen et al. 2007; Haslet et al. 2010). Thus, there is growing demand for structural connectedness and functional connectivity in conservation strategies of protected sites (see Gurrutxaga et al. 2011 for an example application). This includes considering both the physical connectedness within habitats and the permeability of the matrix between protected sites, which can also *per se* shelter high biodiversity values (Pino et al. 2000).

The southern slope of the Cantabrian range (NW Spain) represents a biodiversity hotspot, hosting a wide variety of ecosystems and habitats (Worboys et al. 2010). This is partly due to the fact that it lies at the latitudinal range where two biogeographic regions meet and overlap (Atlantic and Mediterranean), and to the large variety of microclimatic conditions favoured by the rough topography. Due to its high conservation values, more than the half of this area has been protected under different figures since the beginning of the 1990's, including a national park, a regional park, three natural spaces and six biosphere reserves. Moreover, from 2000, six *sites of community importance* sheltering 39 habitats of community interest, and five *special protected areas for birds* were declared within the framework of the Habitats and Birds Directives respectively (Anon 1992; Anon 2009). Temperate heath and scrub, sclerophyllus scrub and forest represent almost 45% of the protected habitats within this area. Most of these Natura 2000 sites physically overlap with the above mentioned protected spaces. According to the precautionary approach proposed by Cooney and Dickson (2005), it should be ensured that human-generated disturbance is limited within these protected areas, allowing the persistence of the same assemblages of species, the

same habitats or the same proportion of features of conservation interest, even in the face of changing environmental conditions. However, this aim is difficult to achieve, especially in protected areas where human activities and local populations are responsible for the protection of biodiversity and, at the same time, active forces of current landscape dynamics. This is the case of the Cantabrian Mountains, where the current landscape and biodiversity patterns are strictly connected to the traditional use of forest resources and the active management of forest, heathlands and shrublands aimed at creating open areas for pasture or cultivation (Morán-Ordóñez et al. 2011).

Management in protected areas promotes conservation, as far as possible, principally through restriction of land uses (grazing regimens, livestock stocking rates, extraction of resources, etc.; Gaston et al. 2006). The effectiveness of land use planning strategies in protected areas should be assessed, to indicate whether management actions are meeting the conservation objectives that have been set (Chape et al. 2005). The tools for analyzing effectiveness would vary depending on the scale of study (from individual site to networks of protected areas). Gaston et al. (2006) suggested that at the regional scale the assessment should focus on the effects of management actions on the overall habitat stability, the viability of the feature of conservation interest, as well as on the effects of disturbances and succession dynamics. It should focus on spatial and temporal interactions between the different habitats, rather than just on their individual characteristics (Saura et al. 2011). Therefore, this assessment would benefit from the use of temporal series of land cover data allowing comparisons of the structural connectedness, from which functional connectivity can be calculated for a specific species or an assemblage of species (Pascual-Hortal and Saura 2006). In non-protected areas land uses are not always reliably controlled, and management is rarely aimed at conservation purposes. These differences between management strategies in protected and non-protected areas would lead to different evolution on the composition and structure of their landscapes.

In a previous study, Morán-Ordóñez et al. (2011) argued that management strategies developed in protected areas may have had noticeable effects in the landscape changes observed at regional scale in the Cantabrian Mountains since the beginning of the nineties. In this study, we aimed to determine whether changes in landscape patterns observed across the southern slope of the Cantabrian Mountains between 1991 and 2004 differed between protected and non-protected areas, and how the difference could be related to the effectiveness of the protection status. In particular, we focused on structural changes at the landscape scale in forest and shrub and heath

land covers (shrub from here on). These were selected as they were the most important habitats under consideration when protected areas were declared (mainly the case of forest), and were widespread at the beginning of the study period (covering 57% of the study area; Morán-Ordóñez et al. 2011). We hypothesized that patterns of change would differ significantly between protected and non-protected areas. Particularly, we would expect an increase in both core areas of forest and their connectedness in protected areas to the detriment of shrub, which would decrease its extent and connectedness due to secondary succession processes towards forest. We also sought to assess if the proportion of forest present at the beginning of the study period had an influence on the changes in landscape structure subsequently observed within the entire study period.

2.2. METHODS

2.2.1. Study sites

The study area is located on the southern slope of the Cantabrian Mountains (NW Spain). Within this area, we selected six municipalities (local administration and management units) as case studies, on the basis of two criteria: (1) their level of protection (protected=P and non-protected=NP) and (2) the percentage of forest cover within each area at the beginning of the 1990s (when protected areas were declared) (Figure 2.1). To classify municipalities on the basis of their forest cover we used a classified land cover map from 1991 derived from supervised classification of LANDSAT images, as described in Morán-Ordóñez et al. (2011). Municipalities were categorized as F1, F2 and F3 if forests occupied, respectively, more than 25%, between 10-25% or less than 10% of their total surface. The final selection was: (i) Municipalities under protection figures: Villablino (P-F1) included in the Natural space of Alto Sil; Puebla de Lillo (P-F2) belonging to the Regional Park of Picos de Europa in Castilla y León and Cabrellanes (P-F3) belonging to the Natural space of “Valles de Babia y Luna”; (ii) Municipalities without any natural protection: Vegaquemada (NP-F1), Soto y Amío (NP-F2) and Sabero (NP-F3).

2.2.2. Land cover analyses

Temporal data on shrublands (including heathlands) and forest cover within the municipalities were extracted from the land cover maps of 1991, 1995 and 2004 obtained through supervised classification of LANDSAT images, as described in Morán-Ordóñez et al. (2011). These land cover maps were reclassified to obtain presence-absence maps (boolean maps) of shrub and forest, which were then clipped with the shape of the municipalities to process each one individually.

Figure 2.1 Location of the study sites within the Cantabrian Mountains. Forest cover of 1991 is based on results of LANDSAT supervised classification of chapter one.

Changes in forest and shrubland structure at landscape level were analyzed with the software FRAGSTATS (McGarigal et al. 2002) and the Morphological Spatial Pattern Analysis tool (MSPA) of the software GUIDOS (Soille and Vogt 2009). FRAGSTATS provides a wide variety of landscape metrics from categorical maps (boolean maps of forest-non forest, shrub and non-shrub in our case) allowing for comparing the landscape structure at the scale of interest (municipality level). GUIDOS software bases its analyses in mathematical morphology theory, leading to the segmentation of arbitrary binary patterns into seven categories: core, islet, loop, bridge, perforation, edge and branch (Soille and Vogt 2009). Compared to FRAGSTATS, GUIDOS is advantageous as it provides information on landscape structure at a pixel-level, with a more directly interpretable graphical output. Final spatial parameters considered in the analyses were: number of patches, patch average mean size, adjacency, shape index, number of patches with inner area, isolated patches and corridors (see Table 2.1 for a more detailed description).

We used FRAGSTATS to analyze trends of land cover change over the complete series of land cover data (1991, 1995 and 2004), whereas GUIDOS was only used to map and compare landscape structure at the beginning and end of the study period to assess the overall dynamics in protected and non-protected areas (1991 and 2004). Finally, we used Mann–Whitney *U*-tests to assess whether the observed changes in the estimated landscape parameters significantly differed between protected and non-protected areas.

Table 2.1 Description of landscape structure parameters analysed at the municipality level for shrublands and forests.

	Parameter	Description
FRAGSTATS	Number of patches (numP)	Number of patches of each land cover type
	Patch size (PS)	Average mean size of each patch (Ha)
	Adjacency (ADY)	Neighbourhoods among patches of the same land cover type
	Shape index (SHI)	Complexity of the patch shape (relation perimeter-area) when compared with a standard shape (an square when working in layer raster format)
GUIDOS	Core patches	Patches with inner area. Inner area correspond to those pixels whose distance to the background/landscape matrix is greater than the border width (considered in this case the pixel size of a LANDSAT image, 30m)
	Isolated patches	Patches without core area which are not connected to any other patch with core area.
	Corridors	Linear elements connecting core patches

2.3. RESULTS

We found opposite trends of change for shrublands according to their land protection status across the study period (Table 2.2). The area covered by shrubs decreased in protected municipalities, with the percentage of change ranging between approximately 8 and 20%. However, in non-protected municipalities shrubland increased by approximately 10%, except for Sabero (NP-F3), where it decreased by 7%. We did not observe clear patterns of change in the area covered by forest with regards to the land protection status. Area covered by forest increased in P-F1, NP-F1 and P-F3, NP-F3 municipalities (values ranging from 6 to 87%) whereas it decreased in P-F2 (29%) and NP-F2 (4.5%).

Temporal changes in landscape structural parameters also differed depending on land protection status (Table 2.2). Protected municipalities showed an increase in the number of both shrubland and forest patches, together with a decrease in the average patch size. However, we did not detect important changes in the shape index (both land covers). There was a decrease in adjacency

values (i.e. connectedness) for both shrubland and forest (ranging from 3 to 12%). In non-protected municipalities, we only observed a common trend of increase in the number of forest patches and a decrease in adjacency of shrub patches (matching the trend in non-protected areas) (Table 2.2). We did not find any other common pattern of change in landscape structure parameters in non-protected areas. None of the observed changes were significantly different between protected and non protected areas (Mann-Whitney U -tests, $p > 0.05$).

Regarding the characterization of the municipalities based only on the proportion of forest cover of each municipality at the beginning of the study period (F1, F2 and F3), we observed a common trend of increase in forest area and also in the number of forest patches in municipalities F1 and F3, independently of their protection status (see values of NPX and $numP$ for forest in Table 2.2). However, in F2 municipalities we observed a common trend of decrease in forest area and increase in the number of forest patches, and decrease in their adjacency.

Figure 2.2 Temporal evolution of shrub structure at a landscape scale in Cabrillanes between 1991 and 2004 (MSPA tool GUIDOS).

Comparing 1991 to 2004, we observed a decrease in the percentage of the total area occupied by shrub core patches, that is, shrub patches of large size (Fig.2.2; Fig. 2.3a). This led to an increase in the number of shrub corridors or union elements between core patches (Fig. 2.2; Fig. 2.3e). This trend was consistent for both protected and non-protected areas. We observed significant differences between protected and non-protected areas with regards the trends of change in the number of shrub isolated patches (Mann-Whitney *U*-tests, $p=0.03$), which increased significantly in protected areas, whereas it remained relatively constant in non-protected areas. We did not observe consistent patterns of change in forests (Figs. 2.3b, 2.3d and 2.3f), although there was a general decrease in the number of core patches except for the non-protected areas classified as F1 and F3 (Fig. 2.3b).

2.4. DISCUSSION

In the southern slope of the Cantabrian Mountains, general trends of evolution of shrublands (including heathlands) at landscape scale seemed to be determined by land conservation status. We observed significant differences between protected and non-protected areas in the degree of isolation of shrub patches. However, we did not find any other significant difference in the evolution of other structural parameters for shrublands. The increase of shrub fragmentation in protected areas (higher number of isolated patches of smaller size), compared with non-protected ones, could be explained by the intensive management carried out in the former since 2000 (Gil and Torre 2007). Shrubs have been removed mainly through mechanic cutting to increase the amount of available pasture for extensive livestock and also to reduce fuel connectivity and hence the risk of arson fires. This kind of management has been mainly promoted in natural spaces, where economic resources are higher thanks to regional, national and European subsidies. The same trend of shrub loss was also observed in one of the non-protected areas (Sabero) where important budgets coming from European subsidies were also invested into shrub clearance for fire prevention (Sánchez 2007). Other causes of shrub fragmentation are associated with the opening of quarries, particularly in the Villablino protected area, where this activity involved the removal of 400 ha of shrub between 1995 and 2004. On the other hand, in non-protected areas the increase in shrub cover and connectedness observed may be due to the shrub encroachment of abandoned crops and meadows linked to secondary succession processes as observed in other mountain ranges of Spain (Vicente-Serrano et al. 2009) and Europe (MacDonald et al. 2000).

The dynamics of forest change were more influenced by the proportion of forest cover at the beginning of the study period than by land protection status (although results were not

conclusive). We observed an increase in forest cover and forest patches in the F1 and F3 municipalities (those with the highest and lowest proportion of forest cover in 1991, respectively). However, the increase in the number of forest patches observed was not related to forest fragmentation, but to recovery processes linked to secondary succession processes. In this sense, we observed new birch forest patches growing widely over shrublands and heathlands (García de Celis et al. 2004). This phenomenon might explain the decrease in the overall size of forest patches (the increase in the number of small forest patches would reduce the average patch size), while the total forest area increased. Particularly, in Vegaquemada (NP-F1), the increase of forest was related to two processes, the expansion of small patches and their connection with associated corridors, establishing larger core patches and the growth of new small forest patches due to secondary succession. Moreover, the cessation of mining activities and the environmental restoration of quarries have favoured the recovery of forest in other non-protected municipalities (Sabero). In F2 municipalities (those with a forest cover between 10-25% at the beginning of the study period), the trends of change were different than in F1 and F2, with decreases in total forest area and in the proportion of core patches. These changes could be associated to fragmentation processes and hence, loss of forest habitat.

Patterns of land cover change differed between protected and non protected areas, mainly in shrub trends but not in forest dynamics. The loss of shrub cover observed within protected areas was lower than could be expected when considering secondary succession processes tending to forest: this could be explained by management actions aimed at reducing fuel continuity and increasing pasture availability. Moreover, we did not find conclusive results for confirming our hypothesis that core areas of forest and their connectedness would increase in protected areas during the study period. This can be due to the uncertainty in the land cover data used as the basis for our analyses.

Landscapes in the Cantabrian Mountains are highly fragmented and heterogeneous due to intensive land use and recurrent disturbances (such as fire events). Fragmentation implies more complex and heterogeneous landscape patterns (Burel and Baudry 2004), with a clear predominance of border areas between forest, shrub and other land covers. Border areas represent a source of uncertainty when classifying LANDSAT images, especially when there are land cover categories with similar spectral behaviour (i.e. forest and shrub; Roy 2000; Díaz et al. 2008). There is inevitably some confusion regarding which category to assign to a given pixel (Lewis et al. 2000; Bradley and Mustard 2005): a pixel representing a mixture of shrub and forest can be

assigned to either category in different years, introducing errors in the classified images, and therefore in the spatial statistics calculated from them (such as the spatial parameters estimated in this study). Thus, our study would benefit from removing uncertainty from the land cover maps derived from hard classified remotely sensed data (Álvarez-Martínez et al. 2010) in order to get more accurate estimates of both shrub and forest landscape trends in protected and non protected areas. Moreover, to obtain more precise assessments of the effectiveness of protected areas in maintaining land cover stability or in promoting certain types of land cover interest (i.e. forest, heathlands, etc.), further research should focus on broadening the extent of this preliminary study either by increasing the number of case studies (protected and non-protected municipalities; F1, F2, F3 classification) or by considering the entire area of protected and non-protected zones. However, since most management is carried out at the local scale (based on municipality or local council decisions) results would be more consistent and easily interpretable from an ecological point of view when increasing the number of replicates.

In conclusion, the evolution of structural parameters of forests and shrublands in the southern slope of the Cantabrian Mountains could not be entirely explained by land protection status. Land protection status influenced shrub cover trends: in protected areas there was a decrease in extent and connectedness of shrublands due to removal of shrub cover to create pastures and reduce the risk of fires; in non protected areas there was an increase of shrublands due to land abandonment and shrub encroachment associated to secondary succession processes. Forest trends seemed to be more influenced by the proportion of forest cover of each municipality at the beginning of the study period than by their land protection status. However, the results of this preliminary study are not conclusive and further research should be aimed at reducing uncertainty arising from the land cover cartography used, while increasing the number of samples of municipalities considered as case studies.

Table 2.2 Temporal evolution of landscape composition and structure within the target municipalities, as estimated with FRAGSTATS: NPX: number of pixels (area); numP: number of patches; PS: average patch size; SHI: shape index and ADY: adjacency. F1, F2 and F3 refer to the proportion of forest cover that the target municipality had at the beginning of the study period (1991): >25% (F1), 10-25% (F2) and <10% (F3).

Protected Municipalities													
		Villablino (P-F1)			%Change	Puebla de Lillo (P-F2)			%Change	Cabrillanes (P-F3)			%Change
		1991	1995	2004	91/04	1991	1995	2004	91/04	1991	1995	2004	91/04
NPX	Shrub	140156	140154	128837	-8.08	92905	91816	82050	-11.68	94123	85592	75364	-19.93
	Forest	54570	53611	57829	5.97	28587	25583	27300	-4.50	3028	2902	5652	86.66
numP	Shrub	1352	1479	1688	24.85	881	1008	1304	48.01	1072	1216	1557	45.24
	Forest	1871	2142	2206	17.90	827	1170	1139	37.73	520	639	1174	125.77
PS	Shrub	9.33	8.53	6.87	-26.37	9.49	8.2	5.71	-39.83	7.9	6.33	4.36	-44.81
	Forest	2.63	2.25	2.36	-10.27	3.11	1.97	2.18	-29.90	0.52	0.41	0.43	-17.31
SHI	Shrub	1.27	1.26	1.27	0.00	1.37	1.34	1.37	0.00	1.31	1.33	1.34	2.29
	Forest	1.27	1.27	1.28	0.79	1.3	1.32	1.3	0.00	1.16	1.17	1.18	1.72
ADY	Shrub	0.79	0.76	0.74	-6.33	0.78	0.74	0.73	-6.41	0.77	0.75	0.74	-3.90
	Forest	0.76	0.72	0.71	-6.58	0.79	0.7	0.72	-8.86	0.55	0.47	0.48	-12.73
Non Protected Municipalities													
		Vegaquemada (NP-F1)			%Change	Soto y Amio (NP-F2)			%Change	Sabero (NP-F3)			%Change
		1991	1995	2004	91/04	1991	1995	2004	91/04	1991	1995	2004	91/04
NPX	Shrub	15075	12624	16573	9.94	25344	23795	28411	12.10	11517	9777	10690	-7.18
	Forest	21200	21161	22436	5.83	10541	10508	7483	-29.01	2652	3139	4334	63.42
numP	Shrub	957	847	881	-7.94	732	801	789	7.79	206	257	255	23.79
	Forest	451	434	585	29.71	378	306	593	56.88	174	174	206	18.39
PS	Shrub	1.42	1.34	1.69	19.01	3.12	2.67	3.24	3.85	5.03	3.42	3.77	-25.05
	Forest	4.23	4.39	3.45	-18.44	2.51	3.09	1.14	-54.58	1.37	1.62	1.89	37.96
SHI	Shrub	1.32	1.33	1.38	4.55	1.36	1.36	1.35	-0.74	1.49	1.44	1.41	-5.37
	Forest	1.3	1.29	1.29	-0.77	1.35	1.36	1.28	-5.19	1.31	1.35	1.31	0.00
ADY	Shrub	0.63	0.63	0.61	-3.17	0.74	0.71	0.7	-5.41	0.69	0.64	0.63	-8.70
	Forest	0.81	0.83	0.81	0.00	0.75	0.77	0.63	-16.00	0.67	0.66	0.69	2.99

Figure 2.3 Temporal change of landscape structure within the target municipalities as estimated with GUIDOS. Figure shows the percentage of the total shrub and forest area that constitute: core patches (patches with inner area; a and b); islets (isolated patches without core area; c and d) and corridors (linear elements connecting different patches of big size: e and f). F1, F2 and F3 refer to the proportion of forest cover that the target municipality had at the beginning of the study period (1991): >25% (F1), 10-25% (F2) and <10% (F3).

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CHAPTER 3

Satellite surface reflectance improves habitat distribution mapping: a case study on heath and shrub formations in the Cantabrian Mountains (NW Spain)³

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ABSTRACT

We aim to map the distribution of four heath and shrub formations constituting habitats of high conservation priority in Europe, whose occurrence is strongly dependent on human activities. Specifically, we assess whether the use of LANDSAT data in habitat distribution modelling may account for land use management, allowing accurate mapping of real distribution patterns. In particular, we explore if reflectance values may be a better alternative to other remote sensing data traditionally used in modelling approaches (i.e. spectral vegetation indices and classified land cover maps). Finally, we test whether modelling performance is affected by the ecological traits of the dominant species of the target formations. We generated maps for the four formations (two specialists vs. two generalists) using MaxEnt. Firstly, we ran the models with environmental predictors only (topography, climate, lithology and human disturbances). Then, we compared the advantages of including, in turn, different data derived from LANDSAT imagery: reflectance values (corresponding to different wavelength channels of the multispectral image), a spectral index and a land cover map. We assessed changes in explanatory power and also in the formation's predicted distribution patterns. Formations dominated by specialist species were accurately mapped on a base of environmental variables only, whereas those dominated by generalists were over-predicted. Average mean temperature, southness and distance to urban areas were the variables contributing most in predictions of environmental models. LANDSAT channels increased the accuracy of all models, but mainly those for formations dominated by generalist species. They showed advantages against other remote sensing data traditionally used in modelling approaches. Habitat distribution models allowed accurate mapping of heath and shrub formations. The use of reflectance values as predictors improved the accuracy of the models, particularly for formations dominated by generalist species, supplying environmental information that was unavailable otherwise.

3.1. INTRODUCTION

Species distribution models (SDMs) provide a means for exploring the relationship between field observations of species occurrence and environmental predictor variables. They can provide ecological and evolutionary insights and can be used to predict distributions across landscapes (Elith and Leathwick 2009). Whilst the response is usually that of a single species, alternatives are possible, including vegetation or habitat types. The latter, Habitat Distribution Models (HDMs), require that the habitat type is clearly distinct and identifiable, and that ecologically the set of species making up that type responds coherently to a suite of predictors. During the last two decades, a broad range of modelling techniques have been developed and tested (see Elith and Leathwick 2009 and Franklin 2009 for reviews). However, model realism and robustness may be influenced not only by techniques but also by other factors, including the nature and ecological meaning of the chosen predictors (Austin, 2002) and the ecological traits of the species under study (McPherson and Jetz 2007; Evangelista et al. 2008).

Among many different predictors that can be used to model species and habitat distribution, those obtained by remote sensing techniques can be very useful (Franklin and Wulder 2002; Kerr and Ostrovsky 2003) since they play an important role in describing land use and land cover, vegetation status or soil moisture at a regional scale. They have been incorporated in models since the 1990's (Franklin 2009), usually as classified land cover maps (Luoto et al. 2002; Pearson et al. 2004; Tuiller et al. 2004; Newton-Cross et al. 2007) or as spectral indices derived from multispectral channels recorded by airborne or satellite-borne sensors (e.g. Osborne et al. 2001; Suárez-Seoane et al. 2002; Zimmermann et al. 2007; Buermann et al. 2008).

However, remote sensing classification outputs (land cover maps) always contain an element of uncertainty (Steele et al. 1998; Metternicht 2003; Shao and Wu 2008). First, it can be difficult to discriminate between vegetation units with similar structure and spectral response (see one example in Díaz et al. 2008 using LANDSAT imagery). Second, at habitat boundaries there is always some confusion regarding which category to assign to a given pixel (Lewis et al. 2000; Bradley and Mustard 2005). This is especially relevant when classifications are performed in heterogeneous landscapes (Álvarez et al. 2010), such as mountain systems (Lasanta et al. 2006; Morán-Ordoñez et al. 2011). As a consequence, the accuracy/quality of the distribution models in these particular areas may be inadequate for ecological applications (e.g. planning conservation strategies).

In comparison, the use of spectral indices may help to avoid these uncertainties. Numerous indices have been calculated and demonstrated to be as efficient as land cover maps in distinguishing between generalized vegetation types, while providing further information on the amount of vegetation and its status. These mainly rely on information provided by visible and near-infrared wavelengths, which are highly correlated with biomass accumulation, leaf chlorophyll levels and photosynthetically active radiation absorbed by the canopy (Lillesand et al. 2008). The indices most commonly used in distribution models are the Normalized Difference Vegetation Index (NDVI; Rouse et al. 1973) and the Green Vegetation Index (GVI; see Zimmerman et al. 2007 for an example application); others include spectral products like the Leaf Area Index (LAI) (e.g., Buermann et al. 2008). However, these indices focus on a narrow window of the electromagnetic spectrum, thereby excluding *a priori* a range of wavelengths that could provide ecologically meaningful information for distribution modelling. Alternative approaches may use either spectral indices integrating all channels of the spectra (i.e. Tasseled Cup transformations; Crist and Cicone 1984; see one example in Stickler and Southworth 2008), or each channel (reflectance values) of a multispectral image independently. The first option informs about general properties such as terrain brightness, vegetation greenness or terrain wetness from a fixed and unbalanced combination of bands defined by the applied algorithm. However, the second option allows any combination of bands, giving freedom to the SDM for selecting and weighting the bands as appropriate for the target species / habitat type. However, to our knowledge, this approach remains unexplored.

Other factors that may influence the accuracy of the final predictions are the ecological traits of the target species (e.g. niche width and range size; McPherson and Jetz 2007). In a study of the effect of the role of species' ecological niche and prevalence on models accuracy, Brotons et al. (2004) observed that it is difficult to get accurate estimates of generalist species, regardless of the modelling approach used. A widespread species is more likely to occur within heterogeneous environments and, therefore, there may be a high number of factors determining its distribution (Osborne and Suárez-Seoane 2002; Suárez-Seoane et al. 2008). Heterogeneity makes it difficult for model algorithms to distinguish suitable environment from the overall area. In contrast, specialist species with narrow ecological niches can be modelled with higher accuracy (McPherson et al. 2004; Tsoar et al. 2007), though that result is admittedly sometimes influenced by the method for evaluating the result, and particularly the chosen extent (Elith et al. 2006).

In mountain systems, ecological conditions often change substantially over relatively short distances, providing a wide range of environments and hence, diversity of habitats and species (Becker and Bugmann 2001). Consequently, mountains supply important ecosystem services (Millennium Ecosystem Assessment 2003) and are valuable areas for biodiversity conservation, especially in the face of impacts from global change (MacDonald et al. 2000; Mottet et al. 2006; Rutherford et al. 2008). The Cantabrian Mountains (NW Spain) are located at the junction of the Mediterranean and Euro-Siberian regions, where important changes to species diversity are expected to occur (Thuiller et al. 2005). Since they represent the south-westernmost distribution limit for many Eurosiberian species, they are an ideal location for long term conservation of genetic diversity and evolutionary potential (Hampe and Petit 2005). Hence more than half the land-surface of this mountain range is now protected under the framework of the Natura 2000 network (Annex I of Habitats Directive, 92/43/EEC; Anon, 1992). These protected areas include several heath and shrub formations, whose occurrence mainly depends on traditional rural practices (Ostermann 1998) including transhumance pastoral systems (i.e. grazing, cutting and burning; Calvo et al. 2005, 2007). Shrub and heath habitats have a low economic value but a high value in terms of conservation because of other services they provide (i.e. prevention of soil erosion, carbon storage, reservoir of genetic biodiversity, etc.; Wessel et al. 2004; Harrison et al. 2010). Even though they are protected at some sites, they still suffer from lack and inadequacy of management, as well as from fragmentation due to different land use practices. Management and conservation programs would benefit from accurate estimates of the spatial distribution of these habitats, as well as knowledge of the environmental drivers behind them.

In this context, we aim to map the current distribution of four dominant heath and shrub formations in the Cantabrian Mountains that are included in Annex I of Habitats Directive 92/43/EEC (Anon 1992) following a habitat modelling approach. Particularly, we assess whether the inclusion, as covariates, of data derived from the LANDSAT satellite improves the accuracy of model predictions over models with only environmental variables. We also explore whether reflectance values (channels) are a better alternative than more traditionally-used remote sensing data (i.e. spectral indices and classified land cover maps). Finally, we investigate whether: (1) remote sensing data provides necessary and otherwise unavailable land use information for predicting the current distribution of our target habitats and, (2) predictive performance of models is affected by the ecological traits of the dominant species (specialist vs. generalist) of the target formations.

3.2. METHODS

3.2.1. Study area

The study area spans the southern slope of the Cantabrian Mountains in León province (NW Spain) (Figure 3.1), covering about 3266 km². Elevation ranges from 877 to 2412 m.a.s.l. This area lies at the limit of two main biogeographic regions: Atlantic/Eurosiberian and Mediterranean, where four bioclimatic belts ranging from supramediterranean to subalpine can be identified (Rivas-Martinez et al. 1987). Annual average rainfall varies from 700 to 1573 mm, while mean temperatures fluctuate from 8.2° C to 9.9° C. Atlantic vegetation consists of deciduous forests (*Fagus sylvatica*, *Betula pubescens*, *Quercus petraea*, *Q. robur*), and heathlands of *Calluna vulgaris* on shadowed and humid northern slopes. Mediterranean vegetation (*Quercus pyrenaica*, *Quercus ilex*) can be found on sunny and drier slopes. The lithology is also diverse, from massive carboniferous limestones to slate with coal grains, sandstones, crystal quartzites and conglomerates (Gómez-Sal and Rodríguez 1992).

Figure 3.1 Location of the study area in the north of León province, Spain.

3.2.2. Ecology of the dominant species in the target habitats and sample collection

Four heath and shrub habitats recorded in Annex I of the Habitats Directive (92/43/EEC; Anon, 1992) were chosen as case studies: European dry heaths (habitat code 4030), alpine and boreal heaths (4060), endemic oro-Mediterranean heaths with gorse (4090) and sclerophyllous scrub

communities represented by *Cytisus purgans* and *Genista florida* formations (5120). These four are the most widespread and common shrub and heath dominated habitats within the study area. Cantabrian heathland formations dominated by *Calluna vulgaris* (a specialist species) represent the southernmost examples of habitat 4060 in Western Europe. They can be found at the highest elevations, growing over acid and poor soils and linked to grazing transhumance systems (Calvo et al. 2007). Another specialist species, *Genista hispanica* subsp. *occidentalis*, dominates shrub formations constituting the habitat 4090 which occur on sunny and dry slopes, growing only over thin base-rich soils mainly linked to limestone rocks. *Erica australis* (a generalist species) dominates habitat 4030 and occurs in acid, dry and thin soils. It covers large areas due to its good regeneration response after burning (Calvo et al. 2002). Fire is one of the main conservation problems in the study area, as well as one of the common management methods used by shepherds to reduce the proliferation of woody species (Calvo et al. 2005). The remaining generalist shrubs, *Cytisus purgans* and *Genista florida*, dominate habitat 5120 and occur in acid, structured and deep soils (rich in nitrogen). *Genista florida* mainly grows in abandoned fields close to valley bottoms, associated to forest soils, while *Cytisus purgans* occurs in deep soils at higher elevations.

Occurrence locations for the four formations were collected through fieldwork in 2005, with random surveys targeting the full environmental variation in the study area and aiming to find at least 100 records of each formation. These resulted in 142 records of *Calluna vulgaris* heathlands, 102 of *Genista hispanica* subsp. *occidentalis* shrub, 177 of *Erica australis* heathland, and 165 of *Genista florida* and *Cytisus purgans* shrub formations.

3.2.3. Predictor variables

Four different groups of ecologically meaningful environmental variables were chosen as predictors: (1) *Topographic*: the primary topographic attributes considered were elevation, slope and southness (as a measure of aspect), all extracted from a 30 m digital elevation model (DEM; Junta de Castilla y León). Secondary terrain attributes were also computed from the 30 m DEM to describe patterns as a function of processes. Firstly, flow accumulation (FWA) and a topographic wetness index (TWI) were calculated as indicators of soil moisture (Moore et al. 1993). Secondly multi-resolution valley-bottom flatness (MrVBF) and multiresolution ridge top flatness index (MrRTF) were computed as measures of flatness in valley bottoms and ridge tops respectively according to the methods in Gallant and Dowling (2003). (2) *Climatic*: annual averaged minimum, mean and maximum temperature, total annual rainfall and total annual radiation were

derived from the Climatic Digital Atlas of the Iberian Peninsula (Ninyerola et al. 2005) at 200 m spatial resolution. (3) *Lithology*: the proportion of limestone in the immediate neighbourhood (based on a 3x3 array) of each pixel was estimated from a lithologic map provided by the Junta of Castilla y León (scale 1:50.000). (4) *Human influence*, quantified as the Euclidean distance to villages. All environmental predictors were resampled to 30 meters (when required) in order to match their pixel size with the LANDSAT spatial resolution. Moreover, urban areas, quarries and reservoirs were masked out from the study area to avoid predictions of the models in known unsuitable areas.

We also used three different types of remote sensing variables in our study: (1) Reflectance values of the channels of a LANDSAT image. (2) The Normalized Difference Water Index (NDWI; Gao 1996). This combines near infrared (NIR; LANDSAT channel 4) and shortwave infrared (SWIR; LANDSAT channel 5) wavelengths, as $(\text{NIR} - \text{SWIR}) / (\text{NIR} + \text{SWIR})$. The reduction of reflectance of SWIR compared to NIR is due to absorption of water in tissues, so that the index value can be used as an estimation of water content in the vegetation. We chose this index after an initial modelling exploration, on the basis that it comprises two informative channels for these heath formations. (3) A land cover map derived from a supervised classification process (Maximum Likelihood algorithm) made on a LANDSAT scene of 2004. The average classification accuracy of the map, based on a confusion matrix, was 90% (Morán-Ordóñez et al. 2011). It consisted of five categories: rock/bare ground, herbaceous vegetation (including meadows and pasturelands), shrublands (including shrublands and heathlands), coniferous afforestations and forests.

Reflectance values corresponded to the corrected digital numbers (DN) of the channels of a LANDSAT TM image from June 2005. Initially we used all channels from one to seven (30 m spatial resolution), except the thermal band (six). Band six follows different protocols for atmospheric and radiometric corrections and would need unavailable field measurements for interpretation and correction. We also already had temperature data for the model so were not concerned at excluding the thermal band. The whole scene was pre-processed in three steps: First, a geometric correction was performed following the polynomial method proposed by Palá and Pons (1995), which uses as reference ground control points extracted from aerial photographs and a 30 m resolution DEM (Junta de Castilla y León) to minimize geometric errors. It was implemented in the software Miramon (Pons 2002). Sixty four ground-control points were used for the geometric correction; two thirds of them were used to correct the image and the rest of the points were used to validate the results. The Root Mean Square Error (RMSE) was lower than the

pixel size (18.23). Then, we applied a radiometric correction based on the algorithms developed by Markham and Barker (1986) and Morán et al. (1992), while the atmospheric correction followed the transmittance model (COST) proposed by Chavez (1996). Down-welling transmittance values for channels five and seven were taken from Gilabert et al. (1994), since their study area had atmospheric conditions more similar to ours than the area used by Chavez (1996). Finally, in order to compensate the different solar illuminations due to the shape of the terrain, a topographic correction was applied following the non-Lambertian C-Correction method (Teillet et al. 1982; Riaño et al. 2003). Corrected reflectance values were included as predictors in the models. Each band provides different information on physical properties of the land surface based on the special absorbance behaviour of each terrestrial feature, which is recorded at the different wavelengths of the spectra.

In order to minimize multi-collinearity problems in subsequent analyses, pairwise correlations between all the predictors were calculated as Pearson's coefficients on a random sample of 10,000 points across the whole study area (see Annex I, Appendix S1 for details in correlations). We selected a subset of variables, with maximum pairwise correlations of 0.71 (Tabachnick and Fidell 1996). For the environmental variables we aimed to keep those variables with a more direct interpretation from the point of view of the ecology of the species (i.e. retaining temperature versus elevation, since the first is an ecological factor directly influencing the growth and distribution of plants, while the second only has indirect effects). Lastly, we ran a descriptive statistical analysis on the final predictors included in the models (Table 3.1) to characterize the environments occupied by each heath-shrub formation.

3.2.4. Modelling framework

The modelling technique selected in this study was the maximum entropy approach (MAXENT; Phillips et al. 2006) due to its reliable performance (Elith et al. 2006) and the nature of the dependent variable. Whilst our surveys provided information on the presence or absence of a formation, we do not interpret the absences as reliable indications of a lack of suitable environments because the Regional Administration manages the vegetation very intensively. Therefore, a method which requires presence-only data seemed most appropriate. MAXENT compares the probability density of covariates across the presence sites with the probability density of covariates across the background (i.e. the selected region), and fits a model that minimises the distance (measured as relative entropy) between the two (Phillips et al. 2006;

Table 3.1 Environmental and remote sensing variables included in models.

	Variable	Description
Environmental variables		
Topographic variables	Slope (SLO)	Slope expressed in degrees
	Southness (STH)	Measure of the aspect normalized to a -1 to 1 scale. Calculated as: $\text{Cos}((\text{aspect} - 180^\circ) \text{ DIV degrees})$
	Topographic wetness index (TWI)	It quantifies the role of topography for redistributing water in the landscape (Moore et al. 1993)
	Multi resolution valley-bottom flatness index (MrVBF)	Measure of the flatness and lowness of the valley bottoms (Gallat and Dowling 2003)
	Multi resolution ridge top flatness index (MrRTF)	Measure of flatness in the ridge top parts of the terrain (Gallat and Dowling 2003)
	Flow accumulation (FWA)	Amount of water available flowing into each cell (Moore et al. 1993)
Climatic variables	Annual rainfall (RAI)	Total annual rainfall (Ninyerola et al. 2005)
	Annual mean temperature (Tmean)	Annual average of mean temperature (Ninyerola et al. 2005)
	Total annual radiation (RAD)	Total solar radiation (Ninyerola et al. 2005)
Lithology	Limestones (LIM)	Proportion of limestone pixels in a 3×3 array. Source: Junta of Castilla y León (scale 1:50.000).
Human disturbances	Distance to urban areas (EDIST)	Euclidean distance from each pixel to the closest urban area (m)
Remote sensing variables		
Band 1 LANDSAT (B1)		Blue band (wavelength= 42-52 μm). It provides information on the increased penetration of light in water bodies, being capable to differentiate soil and rock surfaces from vegetation.
Band 4 LANDSAT (B4)		Near infrared band (NIR; (wavelength = 76-90 μm). It distinguishes among vegetation varieties and conditions.
Band 5 LANDSAT (B5)		Shortwave infrared band (SWIR; wavelength = 1.55-1.75 μm). It is sensitive to the amount of water in both plants and soils.
Normalized Difference Wetness Index (NDWI)		Calculated as $(\text{NIR} - \text{SWIR}) / (\text{NIR} + \text{SWIR})$. It accounts for moisture content in vegetation (Gao, 1996).
Land cover map (COVER)		A 5 category land cover map derived from a supervised classification process (Morán-Ordóñez et al. 2011): rock/bare ground, herbaceous vegetation, shrublands, coniferous afforestations and forests.

Elith et al. 2011). This produces a model that is consistent with the environments across the presence sites and yet as general as possible. See Appendix S2 in Annex I for details of selected settings for MaxEnt.

For each formation we first fitted a control model based only on the environmental variables (ENV). We then fitted three additional models using environmental predictors plus: (1) Reflectance values of the bands (LAND_{ENV} model); (2) NDWI spectral index (NDWI_{ENV}); (3) The classified land cover map (COVER_{ENV}). Each model was run using 70% of the presences (training dataset), retaining the remaining 30% for external evaluation (testing dataset). These are called full models. Ten-fold cross-validation of these full models was used to provide information on the uncertainty of the fitted responses and predictive performance. Predictive performance (cross-validated and on test data) was assessed using the Area Under the ROC-Curve (AUC; Hanley and McNeil 1982), adapted for use with background samples (Phillips et al. 2006).

Continuous outputs (probability from 0 to 1 for the formation to be present) were converted into Boolean maps of suitable-unsuitable areas using two different thresholds or “cut-offs”: (i) “Maximum training sensitivity plus specificity” which maximizes the sum of sensitivity (proportion of actual positives which are correctly identified) plus specificity (proportion of negatives which are correctly identified) and has been considered a useful measure (Liu et al. 2005); (ii) “Equate entropy of thresholded and original distributions” which was introduced by Phillips et al. (2006), and it has not been widely explored. We assessed how the choice of a specific threshold changed the area predicted per formation. We also evaluated how it influenced the fit of the final Boolean maps to the real habitat distributions, by calculating the true positive rate (TPR), i.e. the proportion of test (30%) presence records that were correctly predicted (at both thresholds). We calculated the mean value of this statistic, as well as 95% confidence intervals, over 1,000 bootstrap replicates.

3.3. RESULTS

Tables 3.2 and 3.3 show the performance of both final and cross-validated models for the formations dominated by specialist and generalist species respectively. The AUC values indicate that heath distribution can be successfully predicted. The highest predictive performance corresponded to formations dominated by specialist species ($AUC_{test} \geq 0.9$; *C. vulgaris* and *G. hispanica occidentalis*; Table 3.2). In general terms, models including remote sensing data

(LAND_{ENV}, NDWI_{ENV} and COVER_{ENV}) predicted better than environment-only variables (ENV), particularly for generalist species (Table 3.3). LAND_{ENV} models tended to show the highest predictive performance among models including remote sensing predictors, and with smaller deviations in cross-validated models. However COVER_{ENV} also performed well for *Genista hispanica* subsp. *occidentalis* and all models with remote sensing covariates (LAND_{ENV}, NDWI_{ENV} and COVER_{ENV}) performed similarly for *C.purgans* plus *Genista florida*. The inclusion of remote sensing variables also affected the area predicted by each model, by diminishing it in most cases (Table 3.4). This reduction ranged from 0.2 to 56.71% depending on the kind of model, the contribution of the remote sensing variable within that model, and the threshold applied. LAND_{ENV} models usually produced the largest cuts in the predicted area (Figures 3.2 and 3.3). Maximum training sensitivity plus specificity threshold (MTSPS) was more restrictive than the equate entropy of thresholded and original distributions (ENT). This difference between thresholds was especially marked for models dealing with formations dominated by generalist species (*Erica australis* and *Cytisus purgans* plus *Genista florida*). Figure 3.4 shows the impact of threshold choice on the fit of the final Boolean maps to real habitat distributions. For formations dominated by specialist species, there were no large differences in the TPRs both between type of models and thresholds (95% confidence intervals largely overlapping). However, for those dominated by generalist species, models including remote sensing predictors produced larger TPR than ENV models, and differences between thresholds became more pronounced, especially in ENV models. In general terms, the MTSPS threshold resulted in the lowest true positive rate with values ranging from 50 to 83%, while ENT threshold was less restrictive, increasing percentage of true positive rate predicted by Boolean maps (effect emphasized in models dealing with formations dominated by generalist species). The LAND_{ENV} models produced the highest TPR's for half the model/threshold combinations, with the other two remote sensing methods sharing best TPR for the remaining combinations.

In most models, many variables were relatively unimportant, with only three or four variables usually contributing more than 10% explanation (Tables 3.2 and 3.3; see Appendix S3 in Annex I for the response curves of the main explanatory variables). Topographic wetness index, multiresolution valley-bottom flatness index, multi resolution ridge top flatness index, flow accumulation or total annual radiation always had small contributions to the models. On the other hand, in ENV models some variables contributed strongly in all models: average mean temperature (for all formations), southness (for formations dominated by specialist species) and distance to urban areas (for formations dominated by generalist species). For the LAND_{ENV},

NDWI_{ENV} and COVER_{ENV} models, the importance of the environmental variables was reduced and shifted towards remote sensing parameters. That was specially marked for generalist formations (Table 3.3; *Erica australis* and *Cytisus purgans* plus *Genista florida*). However, remote sensing data were less important for specialist formations (Table 3.2) whose spatial distribution is clearly driven by an environmental factor: temperature (*Calluna vulgaris*) or presence of limestone (*Genista hispanica* subsp. *occidentalis*).

3.3.1. Formations dominated by specialist species

Calluna vulgaris formations are present on northern slopes, with lower mean temperature and higher average rainfall than the other formations (see mean and SD in Table 3.2). Fig. 3.2 shows that there are three main locations where they can be found with higher probability (northeast, northwest and west of the study area). This general pattern is identified by all models, although LAND_{ENV}, NDWI_{ENV} and COVER_{ENV} removed some of the patches predicted at low probability by ENV. Band 4 and NDWI were the second most important contributors to the model explanations in their respective models (LAND_{ENV}, NDWI_{ENV}; Table 3.2). Land cover classes were not important.

Genista hispanica subsp. *occidentalis* formations appear on south facing aspects, growing over limestone substrate, in areas with relatively lower rainfall (see mean and SD in Table 3.2). All models showed a core area of distribution in the north-central part of the study area (Fig. 3.2). Of all remote sensing data, only land cover category contributed significantly to explaining *Genista*'s distribution (20.4%, COVER_{ENV}; Table 3.2), with predictions across all categories but higher probability of occurring on rock/bare ground and pasture land covers (categories 1 and 2 in Annex I, Appendix S3).

3.3.2. Formations dominated by generalist species

Erica australis formations occur over acid substrates, in areas with higher annual mean temperature than the other heath dominated habitat (*Calluna vulgaris*), and at a medium distance from urban areas (see mean and SD in Table 3.3). ENV predicted these formations to be present all around the study area except the south-eastern part (Fig.3.3), while inclusion of remote sensing data predicted a more restricted distribution at the northeast and west of the study area (especially LAND_{ENV}). All remote sensing predictors contributed significantly to the explanation of the models (Table 3.3), although it is mainly remarkable that band 4 in LAND_{ENV} explained 50%

Figure 3.2 Predictions for formations dominated by specialist species (logistic probabilities): (a) Models based on environmental variables (ENV); (b) Models based on environmental variables plus reflectance values of LANDSAT image (LANDENV); (c) Models based on environmental variables plus NDWI (NDWIENV); (d) Models using environmental variables and a land cover map as predictors (COVERENV). Left and right maps correspond to *Calluna vulgaris* and *Genista hispanica* subsp. *occidentalis* predictions, respectively.

Table 3.2 Results of the models using environmental predictors alone (ENV models), and remote sensing data plus environmental predictors (LAND_{ENV}, NDWI_{ENV} and COVER_{ENV} models), for habitats dominated by specialist species. The table shows: (i) the mean and standard deviation of each variable (for presence data); (ii) the contribution of each variable, in percentage, to each model (variables contributing more than 10% are in bold); (iii) AUC values for both full final and cross-validated models, and AUC of the testing data by the full model. See Table 3.1 for the meaning of the variable codes.

	<i>Calluna vulgaris</i>						<i>Genista hispanica</i> subsp. <i>occidentalis</i>					
	Mean	SD	ENV	LAND _{ENV}	NDWI _{ENV}	COVER _{ENV}	Mean	SD	ENV	LAND _{ENV}	NDWI _{ENV}	COVER _{ENV}
SLO	16.60	8.00	7.5	4	6.0	7.3	26.30	9.15	6.3	∞	6.8	3.6
STH	-0.60	0.50	19.6	15.5	16.6	19.0	0.58	0.45	18.6	16.5	18.5	14.6
TWI	9.7	1.36	2.5	1.8	2.7	2.6	8.88	1.84	0	0	0	0.2
MRVBF	0.08	0.26	0.5	0.2	0.6	0.4	0.01	0.12	0.3	0.5	0.1	0.1
MRRTF	0.02	0.17	1.1	0.7	1.0	0.5	0	0	0.8	0.7	0.7	0.3
FWA	11.47	21.14	0.3	0.2	0.5	0.5	68.39	394.43	0.8	0.5	0.6	0.5
RAI	1328	187	12.3	8.9	11.1	9.1	1122	150	3.3	1.4	3.0	2.3
Tmean	5.85	0.76	44.1	30.9	34.6	49.4	6.59	0.74	25.1	21.1	24.9	18.5
RAD	1893	164	3.4	3.6	3.2	1.8	2109	106	3.9	2.3	3.3	4.7
LIM	0.08	0.27	5.2	1.8	3.3	1.1	0.67	0.41	38.9	32.4	39.1	34.0
EDIST	2228	1165	3.5	3.1	3.2	4.9	2172	1187	1.9	1.6	1.2	0.7
B1	0.04	0.01		2.2			0.05	0.01		8.4		
B4	0.22	0.03		22.6			0.31	0.04		9.3		
B5	0.19	0.03		4.6			0.23	0.04		1.4		
NDWI	0.08	0.08			17.1		0.17	0.10			1.7	
COVER	-					3.3	-					20.4
Full model-AUC			0.97	0.99	0.98	0.98			0.94	0.96	0.94	0.96
Cross validated-AUC			0.94 ± 0.04	0.97 ± 0.02	0.95 ± 0.03	0.95 ± 0.04			0.91±0.05	0.93±0.03	0.89±0.07	0.92±0.07
Full model-AUC test			0.93	0.99	0.95	0.95			0.93	0.95	0.93	0.95

Figure 3.3 Predictions for formations dominated by generalist species (logistic probabilities): (a) Models based on environmental variables (ENV); (b) Models based on environmental variables plus reflectance values of LANDSAT image ($LAND_{ENV}$); (c) Models based on environmental variables plus NDWI ($NDWI_{ENV}$); (d) Models using environmental variables and a land cover map as predictors ($COVER_{ENV}$). Left and right maps correspond to *Erica australis* and *Cytisus purgans* plus *Genista florida* predictions, respectively.

Table 3.3 Results of the models using environmental predictors alone (ENV models), and remote sensing data plus environmental predictors (LAND_{ENV}, NDWI_{ENV} and COVER_{ENV} models), for habitats dominated by generalist species. The table shows: (i) the mean and standard deviation of each variable (for presence data); (ii) the contribution of each variable, in percentage, to each model (variables contributing more than 10% are in bold); (iii) AUC values for both full final and cross-validated models, and AUC of the testing data by the full model. See Table 3.1 for the meaning of the variable codes.

	<i>Erica australis</i>						<i>Cytisus purgans plus Genista florida</i>					
	Mean	SD	ENV	LAND _{ENV}	NDWI _{ENV}	COVER _{ENV}	Mean	SD	ENV	LAND _{ENV}	NDWI _{ENV}	COVER _{ENV}
SLO	21.43	7.28	4.0	2.2	2.0	1.3	19.45	7.08	12.2	2.6	8.8	4.5
STH	0.08	0.79	6.8	3.3	5.4	4.6	-0.02	0.77	7.0	4.1	6.7	5.4
TWI	9.32	1.42	0.7	0.5	0.6	0.8	9.3	1.40	4.3	2	4.5	3.9
MRVBF	0	0	4.2	1.5	1.7	1.2	0.02	0.13	5.9	2.8	0.5	0.6
MRRTF	0.02	0.15	2.1	0.7	0.5	1.1	0.03	0.26	6	2.4	2.9	1.7
FWA	32.58	235.62	1.7	0.6	1.5	1.1	44.57	382.13	1.8	0.7	1.8	1.1
RAI	1202	204	3.1	2.3	3.2	4.2	1191	210	5.4	1.2	4.2	3.3
Tmean	6.75	0.74	45.3	22.6	34.9	36.0	7.32	0.82	25.7	12	22.9	16.0
RAD	2033	216	3.1	1	2.2	3.5	2017	174	4.5	2.2	4.1	3.7
LIM	0.06	0.2	17.8	4	16.8	11.4	0.21	0.4	5.4	5.1	9.0	5.6
EDIST	2284	1155	11.2	4.9	8.7	8.0	1297	1025	21.8	14.4	20.0	18.9
B1	0.4	0.001		1.2			0.35	0.04		7.9		
B4	0.22	0.03		50.2			0.26	0.44		10.6		
B5	0.17	0.03		5.1			0.16	0.24		32.1		
NDWI	0.13	0.08			22.5		0.25	0.09			14.8	
COVER						26.8						35.5
Full model-AUC			0.90	0.96	0.93	0.91			0.88	0.94	0.88	0.89
Cross validated-AUC			0.83±0.05	0.92±0.03	0.86±0.06	0.84±0.06			0.78±0.05	0.87±0.05	0.77±0.06	0.80±0.06
Full model-AUC test			0.81	0.91	0.89	0.86			0.70	0.79	0.79	0.81

(relegating temperature to a second place, whereas it was the main explanatory variable for the rest of the models). When land cover types were considered in the model ($COVER_{ENV}$), this formation most commonly occurred on rock/bare ground and shrub categories (land cover categories 1 and 3 in Annex I, Appendix S3).

Cytisus purgans plus *Genista florida* formations occur in areas with a higher average mean temperature than the rest of target habitats, with low-moderate slope and close to the urban areas (see mean and SD in Table 3.3). ENV and $NDWI_{ENV}$ predicted these formations to be present all around the study area but the south-eastern part (Fig. 3.3), while $COVER_{ENV}$ and especially $LAND_{ENV}$ strongly reduced these predictions mainly in the northern central part (Fig 3.3, Table 3.4). All remote sensing predictors contributed significantly to the explanation of the models (Table 3.3), but mainly bands 5 and 4 in $LAND_{ENV}$ (explained 42.7% of the habitat's distribution) and land cover type in $COVER_{ENV}$ (35.5%; higher probability related to shrub cover; land cover category 3 in Annex I, Appendix S3).

3.4. DISCUSSION

Although reflectance data has been widely used in combination with environmental variables for mapping spectrally ambiguous types of vegetation (classification and post-classification methods; Franklin 1996), their implementation in habitat modelling approaches appears unpublished, to our knowledge. In our study we found that inclusion of LANDSAT channels as predictors in HDMs improved the accuracy of models and tended to refine mapped predictions of heath and shrub habitats, compared with environment-only models. The reflectance values provide a direct spectral signal of the heath and shrub formations themselves, distinguishing them from other land covers present within the study area, and providing additional species-specific information. However, it is very important to keep environmental predictors in habitat mapping in order to interpret and understand the ecological factors behind their spatial distribution patterns observed. Reflectance values (channels) are alternatives to other remote sensing data more traditionally-used in modelling (i.e. spectral indices and classified land cover maps). One advantage of reflectance values is they allow the habitat model to identify the most relevant wavelength channel for each formation. This can be particularly valuable when there is a lack of expert knowledge on the optimal combination of bands that best reflects the ecological properties of the species of interest (on the index choice). Moreover, it avoids uncertainties linked to the use of classified land cover maps (as outlined in the introduction). Even though they contribute significantly to most models

(except in *Calluna vulgaris*), landcover did not always provide clear definition between occupied and unoccupied habitats. Specifically, *Genista hispanica* subsp. *occidentalis*, was predicted to occur at least sometimes across all landcover types, while in reality it only grows on limestone rocks and thin pastures.

Figure 3.4 Percentages of testing data predicted as true positives (TPR) when applying two different thresholds: maximum training sensitivity plus specificity (MTSPS; dotted) and equate entropy of thresholded and original distributions (ENT; white). Bars represent average values and whiskers indicate confidence intervals. Results are detailed by habitat and kind of model: ENV (models including only environmental variables), LANDENV (models including also LANDSAT bands), NDWIENV (NDWI plus environmental variables) and COVERENV (classified land cover map plus environmental variables). Habitats dominated by specialist species are marked with an asterisk (*) whereas those dominated by generalist species are indicated by a double dagger (§).

More generally, the performance of the models varied with the ecology and management of the dominant species. Models for formations dominated by specialist species showed a higher accuracy than those of formations dominated by generalists. Similar results were found by McPherson et al. (2004), Hernández et al. (2006) and Guisan et al. (2007). Such results can simply reflect the fact that, with a set extent, models for restricted species only need to be able to successfully predict unsuitable habitat, to gain a high AUC (Elith et al. 2006). However, in this case we have detailed knowledge of this landscape, which confirms that maps of the specialist species are accurate, but the generalists are overpredicted (i.e. the mapped extent is too large). *Calluna vulgaris* and *Genista hispanica* subsp. *occidentalis* have a narrow environmental

tolerance, occurring in areas where they can become dominant due to their high adaptability and competitiveness at those environmental ranges (high elevation and rainfall and low temperatures for *Calluna*; and specific substrate and dry conditions for *Genista*). Although in former times traditional management practices strongly influenced the distribution of *Calluna vulgaris* formations (CVF), these practices have now nearly disappeared (Calvo et al. 2007), favouring secondary succession processes (Calvo et al. 2002). Hence, CVF has now colonised much of its potential distribution (sensu Svenning and Skov 2004). In contrast, *Genista hispanica* subsp. *occidentalis* formations have almost never been subjected to deep perturbations linked with management activities, both because they mainly occur on poor soils in inaccessible areas and because they provide poor quality feed. That is the reason why environmental variables alone tend to accurately map the distribution of both these specialists (their current distribution patterns mostly match up with their potential distribution). Similar results were found by Buermann et al. (2008) for species with restricted range sizes and high habitat sensitivity.

Table 3.4 Area predicted per each habitat by the performed models, regarding to the total study area (expressed as a percentage; “%” columns): ENV (models including only environmental variables), LAND_{ENV} (models including also LANDSAT bands), NDWI_{ENV} (NDWI plus environmental variables) and COVER_{ENV} (classified land cover map plus environmental variables). These percentages were calculated on the basis of two different thresholds: maximum training sensitivity plus specificity (MTSPS) and equate entropy of thresholded and original distributions (ENT). Columns “Change vs ENV” show the variation in the area predicted by models considering remote sensing predictors (LAND_{ENV}, NDWI_{ENV} and COVER_{ENV}) compared with ENV models (e.g.: [NDWI_{ENV}-ENV]*100/ ENV).

		ENV		LAND _{ENV}		NDWI _{ENV}		COVER _{ENV}	
Habitat dominated by		Threshold	%	%	Change vs. ENV	%	Change vs. ENV	%	Change vs. ENV
Specialist	<i>Calluna vulgaris</i>	MTSPS	8.6	5.9	-31.8	7.1	-17.9	7.6	-11.6
		ENT	9.1	5.6	-39.0	7.3	-20.0	8.4	-8.4
	<i>Genista hispanica</i> subsp. <i>occidentalis</i>	MTSPS	15.0	7.4	-51.0	14.0	-6.6	11.8	-21.7
		ENT	17.0	11.9	-29.9	16.9	-0.2	14.5	-14.4
Generalist	<i>Erica australis</i>	MTSPS	19.3	12.6	-35.0	20.5	6.3	17.4	-10.1
		ENT	35.9	15.5	-56.7	26.0	-27.5	28.7	-20.1
	<i>Cytisus purgans</i> plus <i>Genista florida</i>	MTSPS	17.2	16.1	-6.8	16.0	-7.2	21.3	23.3
		ENT	43.5	22.0	-49.4	41.6	-4.4	34.6	-20.4

In contrast, *Erica australis* (EAF) and *Cytisus purgans* plus *Genista florida* formations (CPGFF), dominated by generalist species, can potentially inhabit a wider range of environments than the specialist formations, as far as competition with other species and human activities allow. In the study area, since the year 2000, new silvicultural practices (mainly shrub cutting) have been applied to more than 10,000 ha of these formations (Gil and Torre 2007) to encourage regeneration of pastures for extensive grazing and to create firebreaks for controlling both risk and extent of fire. Since the distribution of these formations is strongly linked with management activities that are poorly documented, inclusion of remote sensing improved predictions of their

current distributions (Bradley and Fleishman 2008). For these generalist formations, remote sensing variables become important predictors in models, with LANDSAT channels (in LAND_{ENV} models) replacing the main environmental explanatory variable of ENV models, and providing the more refined maps. Channel four contributed significantly to the predictions of *Erica australis* (50.2%), *Calluna vulgaris* (22.6%) and *Cytisus purgans* plus *Genista florida* (10.6%).

Reflectance values on the infrared wavelength are related to the internal structure of the leaves, which is highly variable between plant species (Lillesand et al. 2008). However, at the pixel level reflectance values in the NIR depend rather on the canopy structure or plant architecture (Asner 1998). In our case, it allowed detection of the specific signal of the dominant species in the canopy of each habitat and, hence, to map their current distribution. It led to removal of areas where the formations can potentially occur (on a basis of their environmental conditions), but actually are not present due to fire events and shrub cutting practices (hence indirectly informing about land use). It was also useful for differentiating between land cover types in areas where environmental conditions are suitable for more than one formation, that is, areas where their niches would overlap, for instance, *Calluna vulgaris* and *Erica australis*. In the absence of remote sensing information, distance to urban areas could be considered an indirect predictor providing discrimination between these formations. This variable contributed significantly to fit the environmental model of *Erica australis*, which frequently appears as a patchily distributed formation after fire events, as a first stage of secondary succession recovery (Calvo et al. 2002). Since a high percentage of fire events in this area have their origin in livestock activities (fires mainly aimed to regenerate pastures), there is a high probability for this fire-dependent formation to appear close to villages. However this formation requires dry conditions so tends not to appear nearby villages i.e. away from the most humid, deep and structured soils typical of village locations.

Channel five contributed most to the *Cytisus purgans* plus *Genista florida* LAND_{ENV} model, but was not relevant for the other formations. Reflectance in this channel (SWIR) is related to both the moisture content and the thickness of leaves (Lillesand et al. 2008), which indirectly indicates soil moisture content. These formations need deep and structured soils. Although the spectral index NDWI is also a measure of vegetation moisture, it removes those specific variations related to the leaf internal structure (specific of each species) and leaf dry matter content to improve the accuracy in detecting vegetation moisture (Ceccato et al. 2001). In other words, different

vegetation covers with similar water content will have similar NDWI, and this can explain why the predicted extent of the *Cytisus purgans* plus *Genista florida* NDWI_{ENV} map is larger than the LAND_{ENV}. In the absence of remote sensing data, distance to urban areas could act as a proxy for soil characteristics and management. The complex orography of the study area has forced the villages to establish mainly in the scarce flat valleys where the deepest and richest soils can be found. Nowadays, the abandonment of historic agricultural activities has favoured colonization by shrub formations of *Genista florida* (Wessel et al. 2004). Therefore, the probability of this formation (CPGFF) decreases at distances over than 500m from villages (see response curves in Annex I, Appendix S3). In summary, we agree with Pearson et al. (2004) and Zimmerman et al. (2007) that remote sensing information aids definition of the current distribution of target habitats by (1) helping to discriminate between suitable and unsuitable sites that cannot be distinguished from bioclimatic or topographic information alone, by providing missing predictor information (i.e. vegetation and soil moisture; Zimmerman et al. 2007); (2) by providing information on land use (e.g. fires, shrub-cutting practices), for formations whose presence in the landscape is strongly conditioned by land use.

Although continuous predictions provide more information than binary ones (Freeman and Moisen 2008), land managers often require thresholded predictions (Liu et al. 2005). The maximum training sensitivity plus specificity threshold (MTSPST) was one of the best performing thresholds in the presence-absence study of Liu et al. (2005). In our study it always gave a lower true positive rate than MaxEnt's entropy-based one (ENT), though for the specialist-dominated formations the differences were mostly minor (Figure 3.4). MPSPST was particularly restrictive for formations dominated by generalist species modelled with only environmental data. Therefore, it would be advisable for land managers to use ENT threshold when building Boolean maps, in order to get more realistic patterns of heath and shrub habitats' distributions in the Cantabrian Mountains.

Nowadays, the regional administration of Castilla y León is defining management strategies for the sites of Community importance declared within the frame of the Natura 2000 network, their habitats and the species dependent on them. Accurate maps of habitats' current distributions can provide cost-effective information for designing and implementing conservation policies, helping to save resources that can be used for other purposes, including further conservation (Wätzold et al. 2010). For managing Natura 2000 sites, methodologies, such as the one evaluated in this paper,

are practical support tools for both understanding habitat requirements and defining distribution boundaries.

3.5. CONCLUSIONS

Habitat distributions models accurately predicted heath and shrub habitats in the Cantabrian Mountains. However, without remote sensing data, it was more difficult to discriminate between suitable-unsuitable areas for formations dominated by generalist species, which are widespread in the landscape, than for formations dominated by specialists' species. The use of reflectance values as predictors improved the accuracy of the models, providing environmental information that was unavailable otherwise (i.e. habitat status, land use, vegetation and soil moisture content, etc.). The use of reflectance values showed some advantages over other remote sensing data traditionally used in modelling approaches (vegetation spectral indices and classified land cover maps). When Boolean maps are necessary (i.e. conservation plans management or policies design), the equate entropy of thresholded and original distributions provided the most consistently realistic patterns.

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Appendix S1. Correlation matrix.

Pearson's coefficient of correlation between the variables retained for the final models ($r < 0.8$; Tabachnick and Fidell, 1996). Variables: slope (SLO), southness (STH), Multi resolution valley-bottom flatness index (MrVBF), Multi resolution ridge top flatness index (MrRTF), flow accumulation (FWA), annual rainfall (RAI), annual mean temperature (Tmean), total annual radiation (RAD), limestones (LIM), euclidean distance to urban areas (EDIST), band 1 LANDSAT (B1), band 4 LANDSAT (B4), band 5 LANDSAT (B5) and the Normalized Difference Wetness Index (NDWI).

	SLO	STH	MrVBF	MrRTF	TWI	FWA	RAI	Tmean	RAD	LIM	EDIST	B1	B4	B5	NDWI
SLO	1.00	-0.10	-0.45	-0.34	-0.50	-0.12	0.28	-0.38	-0.11	0.20	0.17	0.24	0.05	0.22	-0.12
STH		1.00	0.06	0.01	0.06	0.00	-0.10	0.03	0.60	-0.02	-0.01	-0.08	-0.11	-0.07	-0.03
MrVBF			1.00	0.15	0.53	0.22	-0.10	0.25	0.01	-0.08	-0.14	-0.04	0.12	-0.06	0.13
MrRTF				1.00	0.09	-0.02	-0.16	0.14	0.03	-0.05	-0.03	0.01	-0.04	0.00	-0.03
TWI					1.00	0.42	0.00	0.21	0.03	-0.10	-0.08	-0.15	0.04	-0.18	0.18
FWA						1.00	0.03	0.05	-0.01	-0.02	-0.04	-0.04	0.02	-0.05	0.06
RAI							1.00	-0.30	-0.23	0.04	0.23	-0.09	0.13	-0.06	0.14
Tmean								1.00	0.06	-0.12	-0.55	-0.19	0.11	-0.13	0.20
RAD									1.00	-0.03	-0.01	-0.01	-0.12	0.03	-0.11
LIM										1.00	-0.02	0.31	0.11	0.35	-0.18
EDIST											1.00	0.01	-0.16	-0.03	-0.10
B1												1.00	0.03	0.71	-0.52
B4													1.00	0.20	0.60
B5														1.00	-0.65
NDWI															1.00

The variables excluded from the final models ($r > 0.8$; Tabachnick and Fidell 1996) were: band 2 LANDSAT (B2), band 3 LANDSAT (B3), band 7 LANDSAT (B7), annual averaged minimum and maximum temperature (Tmin and Tmax respectively) and elevation (Elev). They showed high Pearsons' coefficient of correlation as follows: B2 vs B1, r : 0.93; B3 vs B1, r : 0.92; B3vs B2, r : 0.92; B7 vs B3, r : 0.86; B7 vs B5, r : 0.93; Tmin vs Tmean, r : 0.97; Tmin vs Tmax, r : 0.92; Tmax vs Tmean, r : 0.97; Elev vs Tmean, r : -0.95; Elev vs Tmax, r : -0.96; Elev vs Tmin, r : -0.93.

Appendix S2. MaxEnt parametrization

We run all models using MaxEnt version 3.3.1 (Phillips et al. 2006; Phillips and Dudik 2008) with default settings except 10-fold cross-validation. We provided the background to MaxEnt, which consisted on a sample of 10,000 randomly-distributed points avoiding locations at a 90m radius from the presence records, as well as in the masked areas (urban, water surfaces, quarries).

Appendix S3. MaxEnt response curves

Maxent response curves show the effect of each predictor on the logistic response when keeping all other environmental variables at their average sample value (Phillips et al. 2006). Each curve shows the average response (red line) and the standard deviation (blue area), corresponding to the cross-validated models. In this appendix only response curves of variables contributing more than 10% to the explanation of the model are detailed. The models are: ENV (models including only environmental variables), LAND_{ENV} (models including also LANDSAT bands), NDWI_{ENV} (NDWI plus environmental variables) and COVER_{ENV} (classified land cover map plus environmental variables). The variables are: band 4 LANDSAT (band4), band 5 LANDSAT (band 5), southness, total annual rainfall (rainfall), annual mean temperature (tmean), limestones, and distance to urban areas (disteuclid), Normalized Difference Wetness Index (NDWI) and the classified land cover map (landcover). See tables 2 and 3 for contribution of all variables to the models. Numeric categories of the land cover map (landcover) correspond respectively to: (1) Rock/bare ground; (2) Herbaceous vegetation (including meadows and pasturelands; (3) Shrublands (including shrublands and heathlands); (4) Forest; (5) Coniferous afforestations. Habitats dominated by specialist species are marked with an asterisk (*) whereas those dominated by generalist species are indicated by a double dagger (§).

ENV model

LAND_{ENV} model

NDWI_{ENV} model **COVER_{ENV} model**

CHAPTER 4

Biotic interactions as a limiting factor controlling species distribution patterns. The role of species life traits⁴

⁴ The content of this chapter has been submitted for publication consideration to *Journal of Vegetation Science*.

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ABSTRACT

Heathlands represent cultural landscapes of high conservation interest in Europe. Management policies aiming to improve their status may benefit from further knowledge of their current geographic distributions, as well as the factors that influence them. In this study we aim to determine how mutual biotic interactions act as a limiting factor in controlling distribution patterns of two heath competitor species with different life traits in the Cantabrian Mountains (NW Spain): *Calluna vulgaris* and *Erica australis* (specialist vs. generalist). In order to select the best predictors explaining species distribution, we built MaxEnt models which differed in the nature and number of predictors (abiotic, biotic and/or remote sensing variables). We also analysed the geographical variations of the factors limiting species distribution and how they may influence the relative success of species under a competition scenario. Accounting for biotic interactions in distribution models increased the accuracy of predictions compared to models based on abiotic and remote sensing data alone. *Calluna* dominated within the areas where both species could potentially occur, due to its specialized traits being the main limiting factor for *Erica*, which therefore tended to occupy sites outside the potential distribution area of *Calluna*. However, human disturbances can modify this equilibrium by removing the dominant species (since *Erica* has superior regeneration capacity than *Calluna*). Number of limiting factors was significantly different between areas of potential competition and competition-free areas for both species which may also affects the behaviour of a given species under competition scenarios and hence, its occurrence in the landscape.

4.1. INTRODUCTION

Species distribution models (SDMs) aim to predict the distribution of species across landscapes, based on the correlation between the geographical location of species and environmental variables. Since the outputs of SDMs reflect the likelihood of finding the target species throughout a study area, they can help managers developing spatially explicit environmental policies for managing biodiversity and the services provided by it (see Franklin (2009) for a review). Usually, SDMs are interpreted within the conceptual framework of niche theory: this link has been widely discussed, especially over the last two decades, during which SDMs have become a growing field of research (Pulliam 2000; Soberón 2007; Hirtzel and Le Lay 2008; Soberón and Nakamura 2009; Godsoe 2010).

Hutchinson (1957) defined the “fundamental niche” as a n -dimensional hypervolume in which every point corresponds to a state of the environment, which would allow the species to exist indefinitely in the absence of immigration and interspecific competition. Nevertheless, the species will not utilize its entire fundamental niche, but rather a “realized niche” which is much smaller, mainly due to interaction processes with other species. Anderson et al. (2002) described three requirements that should be fulfilled by interacting species when testing the effect of competition processes within the niche framework. These were summarized by Hirzel and Le Lay (2008) as follows: (i) species should not co-occur in broad sympatry, but mostly occupy different areas; (ii) environmental tolerances (niche width) may differ significantly according to life traits (i.e. specialist or generalist species), but show some partial overlap; (iii) species may co-occur in those narrow contact zones, where competitive exclusion can also occur. Furthermore, according to Pulliam (2000), other factors, such as dispersal, have to be considered when assessing the relationship between ecological niche and species distribution. Source-sink dynamics may allow the persistence of a species in “unsuitable areas” because of permanent immigration from source areas. Thus, the realized niche of a species could be larger than its fundamental niche (Pulliam 2000). Conversely, dispersal limitations could prevent a species from reaching “suitable areas” where it could establish viable populations (Svenning and Skov 2004). Thus, the realized niche could be smaller than the fundamental one.

According to the nature of the environmental variables (i.e. resources or conditions) and the spatial scale considered, niches can be classified into two main classes (Soberón 2007): “Grinnellian niches”, defined on abiotic conditions measured at large extent and coarse resolution and relevant for understanding large-scale ecological and geographical properties of species;

“Elthonian niches”, considering variables as consumable resources, strongly related to biotic interactions and competition processes. These should be measured at a local scale (small extent and fine resolution). However, although biotic interactions occur at small scales, they can also influence species distributions, even when analyzed at regional scale (Guisan and Thuiller 2005). Several SDM studies have successfully incorporated biotic interactions from regional to continental scales, increasing the performance and predictive power of models of the target species (Leathwick and Austin 2001; Anderson et al. 2002; Heikkinen et al. 2007; Meier et al. 2010).

Therefore, the occurrence of a species depends on the interaction of three elements, whose equilibrium varies spatially (Soberón and Peterson 2005; Soberón 2007): the existence of suitable abiotic conditions allowing population growth; biotic interactions with other species, such as competition, mutualism or parasitism; and dispersal abilities of the species. In the absence of biotic constraints, the geographic distribution of a species should correspond only to accessible areas with suitable abiotic conditions. However, anthropogenic disturbance can also influence species distributions, although its inclusion in SDMs may be problematic due to its dynamic character and the difficulty of finding spatially explicit data (Zimmermann et al. 2007). Human perturbations can either create dispersal barriers or help establishment in unoccupied suitable areas, as with invasive species (Fitzpatrick et al. 2007) and fire-prone species in Mediterranean ecosystems (Pausas et al. 2006). Moreover, anthropogenic activities can modify environmental conditions and thus produce spatial variations in the distribution of interacting species whose competitive abilities are environment-dependant (Meier et al. 2010).

Heathlands, widely distributed throughout Europe, are cultural landscapes providing important goods and services to societies (Harrison et al. 2010). They are semi-natural habitats, which have coevolved for millennia with human societies (Wessel et al. 2004). Almost 90% of the European heathlands have disappeared during the last 150 years (Webb 2005), mainly since the 1950's. Therefore, they have been included as key habitats to maintain European biodiversity within the Natura 2000 network (Annex I of Habitats Directive; Anon 1992). Maintenance of these anthropogenic habitats depends on specific forms of management, principally traditional agricultural practices, such as grazing, burning, cutting and ploughing (Ostermann 1998). In this paper, we investigated the distribution of two heath species in the Cantabrian Mountains (NW Spain): *Calluna vulgaris* and *Erica australis* (*Calluna* and *Erica* from here on). In this mountain range, formations dominated by these species meet and overlap their European distribution limits

(southernmost for *Calluna* and northernmost for *Erica*; Morán-Ordóñez et al. 2011b). Previous experimental studies have shown the competitive character of *Calluna* and *Erica* in this region and how anthropogenic disturbances (burning, cutting and ploughing) can invert their dominance in a given area due to their different regeneration traits (seeder vs. resprouter respectively; Calvo et al. 2002a,b,c, 2005). It is therefore expected their distribution patterns would depend on historical management and patch regeneration, which in turn varies as a function of both, seed bank and species life strategies (Calvo et al. 2002a,b, 2005).

We sought to determine the best set of predictors for the spatial distribution patterns of *Calluna* and *Erica*, focusing on the role of their mutual biotic interactions. We evaluated whether geographical variations on the limiting factors constraining their distribution influenced the results of their mutual biotic interactions and hence, their occurrence patterns. We hypothesize that *Calluna* is more specialist than *Erica* (Morán-Ordóñez et al. 2011b). Therefore, we would expect a higher dominance of *Calluna* in areas where these species may be in sympatry. However, disturbances could alter the equilibrium between the species modifying the result of their biotic interactions (Meier et al. 2010). Due to the high recurrence of disturbances (mainly fire) to which these species are subjected, we also expected *Erica* to dominate over *Calluna* in areas of potential distribution overlaps (on a basis of their environmental requirements) due to its superior regeneration ability (Calvo et al. 2002a).

4.2. METHODS

4.2.1. Study area and ecology of the target species

The study area is located the southern slope of the Cantabrian Mountains in the León province (NW Spain; Figure 4.1). It represents a biodiversity hotspot, sheltering a wide variety of environments and habitats as a consequence of three main factors: its location at the limit of two biogeographic regions (Atlantic/Eurosiberian and Mediterranean), its uneven topography (which favours microclimatic conditions) and its long history of human perturbations (burning, cutting and grazing).

We chose two heath species as case studies: *Calluna vulgaris* and *Erica australis* subsp. *aragonensis*. Both are dominant species (cover > 70%; Calvo et al. 2002b, c, 2005) in both alpine and boreal heaths (habitat code 4060) and European dry heaths (4030) (Annex I of Habitats Directive; Anon 1992). Formations dominated by *Calluna* are relict in the Cantabrian Mountains, representing the southernmost examples of this habitat in Western Europe. Therefore, they are

highly relevant for the long term conservation of genetic diversity and evolutionary potential (Hampe and Petit 2005). They can be found at highest elevations, growing over acid and nutrient-poor soils. At the same time, the Cantabrian Mountains represent the northern distribution limit of formations dominated by *Erica*, which also occur on acid and thin soils. However, the Mediterranean character of this species allows it to tolerate drier conditions than *Calluna*. The frequent recurrence of fire events in this area has favoured *Erica* formations over large areas, due to its strong regeneration response to burning and cutting (vegetative resprouting; Calvo et al. 2002a).

Figure 4.1 Study area.

4.2.2. Data collection and predictor variables

Presence data for both species were collected through fieldwork in 2005 with random stratified surveys targeting the full environmental variation of the study area. We recorded 142 locations for *Calluna* and 177 for *Erica* at the core of homogeneous patches with a radius of more than 30 m (twice the grain size of the remote sensing data, which constrained the resolution of the modelling analyses).

To build the models we considered three types of predictors (abiotic, remote sensing and biotic variables; Table 4.1) based on our previous knowledge (Morán-Ordóñez et al. 2011b). Abiotic predictors were: (1) topography: slope and southness (as a measure of aspect), both extracted from

a 30 m digital elevation model (DEM; Junta de Castilla y León); (2) climate: mean annual temperature and total annual rainfall, both derived from the Climatic Digital Atlas of the Iberian Peninsula (Ninyerola et al. 2005) at 200 m spatial resolution; (3) lithology: proportion of limestone in the immediate neighbourhood (based on a 3x3 array) of each pixel estimated from a lithological map provided by the Junta of Castilla y León (scale 1:50,000). All of these variables were resampled to 30 m in order to match the spatial resolution of satellite images.

Remote sensing data can improve model predictions by providing important information about key resources and human management that may not otherwise be available (Zimmerman et al. 2007; Morán-Ordóñez et al. 2011b). We chose as predictors the reflectance values of channels 4 and 5 of a LANDSAT TM image (near and shortwave infrared wavelengths respectively; NIR and SWIR) since they successfully accounted for land cover, land use and vegetation status in the study area (Morán-Ordóñez et al. 2011b). Reflectance values on the NIR are related to the internal structure of the leaves, which is highly variable between plant species (Lillesand et al. 2008), whereas those of the SWIR depend on the thickness and the moisture of the leaves, which indirectly reflects soil moisture. LANDSAT channels were derived from an image from June 2005, which was geometrically corrected following the polynomial method proposed by Palá and Pons (1995), incorporating a 30 m DEM (Junta de Castilla y León) to allow close adjustment for topography (average root mean square error of 18.23m). The image was then corrected radiometrically (Markham and Barker 1986; Morán et al. 1992) and atmospherically (Gilabert et al. 1994; Chavez 1996). Finally, topographic correction was applied following the non-Lambertian C-Correction method (Teillet et al. 1982; Riaño et al. 2003) to compensate for different solar illuminations caused by terrain variations. To avoid model predictions in known unsuitable areas, quarries, reservoirs and urban areas were masked out from the study area. Biotic variables were the predictions of presence made for each of the interacting species derived from models based on abiotic predictions. Since multi-collinearity may affect model outputs, we verified that pairwise Pearson correlations among all the predictors were lower than 0.8 (Tabachnick and Fidell 1996).

4.2.3. Modelling framework

We selected the Maximum Entropy algorithm (MaxEnt; Phillips et al. 2006) to model species' distribution, due to its good performance (Elith et al. 2006) and the nature of the dependent variable. Although it is advisable to use presence-absence methods when analyzing biotic interactions within a modelling framework (Leathwick and Austin 2001; Meier et al. 2010),

presence-only methods considering background data may be a more appropriate option in some cases (Elith et al. 2011). In the study area, the intense management of heath formations has favoured their absence in some areas where environmental conditions are suitable for their development (Moran-Ordóñez et al. 2011b). Therefore, using those locations as absences could decrease the reliability of the models. In this case, a sample of 10,000 randomly distributed background points were used as pseudo-absences, avoiding points within a 90 m radius of the presence locations.

In order to establish the best set of predictors explaining species' distribution, we ran four different models per each species (Table 4.1). ABI models were based on abiotic predictors only (topography, climate and lithology). BIO models also accounted for the effect of biotic interactions and they were built (following Soberón 2007) by adding to the ABI model of species A another predictor corresponding to the logistic predictions made for the interacting species B from abiotic predictors. This is a close estimate of the probability that the species is present in the given environment (Elith et al. 2011). LAND models included the reflectance values of LANDSAT NIR and SWIR wavelengths as covariates, in addition to the abiotic variables. BLAND models included abiotic variables, remote sensing predictors and the probability of the presence of the interacting species. To avoid circular analyses, biotic variables were only generated from ABI models, due to the fact that those including LANDSAT channels are already reflecting land cover (Morán-Ordóñez et al. 2011b) and hence the result of historical perturbations, land uses and biotic interactions (Lawler et al. 2006; Heikkinen et al. 2007).

ABI models describe the Grinnellian niche of a particular species on the basis of its abiotic requirements. BIO models help to identify the effect of biotic interactions between species on their predicted geographical distribution (whether the presence of *Calluna* modifies predictions for the spatial niche of *Erica* and vice-versa). LAND models contribute to the modelling approach with land cover information, making the resulting picture more realistic. BLAND models allow inference on whether considering biotic interactions can improve model accuracy regarding models considering either abiotic factors only or abiotic+remote sensing factors.

Each model was built using 70% of the presences (training dataset), retaining the remaining 30% for external evaluation (testing dataset). We called these full models. The uncertainty of the fitted responses was also assessed through 10-fold cross-validation of the training dataset. The predictive performance of both full and cross-validated models was measured using the Area Under the ROC Curve (AUC; Hanley and McNeil 1982), adapted for use with background

samples (presences vs. background data; Phillips et al. 2006). Continuous outputs (probability from 0 to 1 for the formation to be present) were converted into Boolean maps of suitable-unsuitable areas using the *equate entropy of thresholded and original distributions* threshold (Phillips et al. 2006), which provided the most consistently realistic distribution patterns for these species (Morán-Ordóñez et al. 2011b).

Table 4.1 Predictors used to fit MAXENT models. A cross indicates whether a variable is included as a predictor in a model. ABI, BIO, LAND and BLAND refer to the type of model which differs in terms of the predictors used: abiotic variables only (ABI); abiotic variables and variables accounting for biotic interactions with another heath species (BIO); abiotic and remote sensing data predictors (LAND); abiotic predictors, remote sensing data and biotic interactions with the other heath formation (BLAND).

Variable	Description	ABI	BIO	LAND	BLAND
Abiotic variables					
Topography	Slope (SLO)	x	x	x	x
	Southness (SOU)	x	x	x	x
Climate	Temperature (Tmean)	x	x	x	x
	Rainfall (RAI)	x	x	x	x
Lithology	Limestone (LIM)	x	x	x	x
Remote sensing variables					
Band 4 LANDSAT (B4)	Near infrared band (NIR; wavelength = 76-90 μm). It distinguishes among vegetation varieties and conditions.			x	x
Band 5 LANDSAT (B5)	Short middle infrared band (SWIR; wavelength = 1.55-1.75 μm). It is sensitive to the amount of water in both plants and soils.			x	x
“Biotic interaction” variables					
<i>Calluna</i> _{log}	ABI logistic predictions for <i>C. vulgaris</i>		x		x
<i>Erica</i> _{log}	ABI logistic predictions for <i>E. australis</i>		x		x

4.2.4. Characterizing geographical areas of potential biotic interaction

In order to identify geographical areas where competition could occur, Boolean outputs for both *Calluna* (C) and *Erica* (E) were superimposed, as proposed by Anderson et al. (2002). Areas where predictions for both species overlap (CE) represent places of potential sympatry or competitive interactions. This analysis was carried out independently for each model. To assess if there were significant differences among C, E and CE areas on both environmental ranges and

reflectance values, we ran a Kruskal-Wallis test with a subsequent Post Hoc analysis (Siegel and Castellan 1988). Analyses were performed on a random stratified sample of 500 points for each of the three categories using R 2.12.1 (R Development Core Team 2010). If strong competition processes take place in CE locations, the dominant species would consistently cover these areas (Anderson et al. 2002). On the other hand, if there is not a clear competitive process ongoing in CE areas, both formations should be found in paired situations. To explore these relationships, we calculated the percentage of presence records (ground truth dataset) predicted as C, E or CE by each of the four models. We also made a cross-tabulation analysis over the final superimposed maps to assess differences between model predictions.

4.2.5. Geographical variations on limiting factors controlling species distribution patterns

Since the availability and suitability of both environmental conditions and resources varies across geographical space, affecting species potential distribution, we may expect this to have an influence in “outputs” of biotic interactions (competitive dominance, sympatric coexistence, etc.). With the aim of exploring this topic, we applied a modified version of the mapping tool developed by Elith et al. (2010). It originally consists of an algorithm which changes the value of each predictor within a pixel by the average value of that predictor over the species’ occurrence data. It then analyses the effect of that change on species’ predictions (increase/decrease). This calculation is made as many times as predictors are included in the model. The final output is a map which returns, per pixel, the variable producing the largest increase in the species predicted probability of occurrence. Hence, that variable is considered the main limiting factor of the target species in that pixel. However, in each pixel there could be more than one limiting factor. Thus, we also calculated, per pixel, the number of factors increasing the predicted probability over a certain value (we chose 0.1 after an initial modelling exploration). The analysis was run in MaxEnt and R (R Development Core Team 2010). We avoided results in those areas where the probability of presence was under the equate entropy of thresholded and original distributions threshold. Finally, we used Pearson’s Chi squared to test if the number of limiting factors significantly varied among areas where the species is predicted to occur alone (C and E) or in potential interaction with the other species (CE). We only applied this analysis to ABI and BIO models, since there is no straightforward interpretation of remote sensing predictors from the point of view of the ecology of the heath species.

4.3. RESULTS

In all models AUC was greater than 79% indicating good model discrimination (Table 4.2). *Calluna* models showed the highest fit values, which were also more consistent among models. Mean annual temperature was the most frequently selected variable in all models for both species. Southness was also important for *Calluna*. The inclusion of *Erica* logistic output as a variable in *Calluna* BIO and BLAND models contributed less to the final model than vice-versa. When remote sensing data were considered as predictors (LAND and BLAND models), LANDSAT B4 contributed strongly to the explanation of both species occurrence, particularly in the case of *Erica*, where it became the most relevant predictor.

Table 4.2 Modelling results detailed by: (i) Contribution, in percentage, of each variable to final models (variables contributing more than 10% are in bold); (ii) AUC values for both full (training and testing) and cross-validated models (%); See table 4.1 for the meaning of the variable codes and descriptions of the models (ABI, BIO, LAND and BLAND).

	<i>Calluna vulgaris</i>				<i>Erica australis</i> subsp. <i>aragonensis</i>			
	ABI	BIO	LAND	BLAND	ABI	BIO	LAND	BLAND
SLO	10.1	9.8	5.5	5.4	3.3	4.4	2.1	1.8
SOU	22.9	22.8	19.7	19.4	8.3	6.8	2.9	2.9
Tmean	50.3	49.9	34.4	33.5	61.7	54.8	25.2	23.4
RAI	14.3	13.3	9.2	9.2	7.5	6.2	3.4	2.6
LIM	2.3	2.5	0.2	0.3	19.2	17.8	3.5	3.6
B4			24.8	24.7			56.5	54.5
B5			6.2	6.2			6.5	6.3
<i>Calluna</i> log						10.1		4.9
<i>Erica</i> log		1.6		1.1				
Full model AUC train	95.6	95.7	97.4	97.4	85.5	86.2	94.1	94.5
Full model AUC test	93.3	92.9	95.7	95.6	79.6	79.8	91.5	90.7
Cross-validated AUC ($\bar{x} \pm SD$)	94.0 $\pm$ 3.2	93.5 $\pm$ 3.7	95.7 $\pm$ 2.5	95.5 $\pm$ 2.7	80.4 $\pm$ 4.1	81.3 $\pm$ 4.1	91.6 $\pm$ 2.8	92.0 $\pm$ 2.5

4.3.1. Ecological requirements of both species and geographical areas of potential biotic interaction

Calluna appears on northern slopes, in areas with lower mean temperature and higher annual rainfall than *Erica* (Table 4.3). *Erica* establishes on any aspect and prefers steeper slopes than *Calluna*. Although both develop in acid and poor soils, there is a low-medium probability of finding *Calluna* when there is a small proportion of limestone presence in the immediate

neighbourhood of an area, while this chance is almost null for *Erica*. These requirements were consistently found, with slight variations, by all models. Reflectance values for both species differed significantly at both NIR and SWIR wavelengths (being always higher for *Calluna* than for *Erica*).

Spatial distribution patterns of both species varied significantly depending on the model (Fig. 4.2; Table 4.4). The largest suitable area was predicted for both species by ABI models. This area decreased when biotic interactions were summed up as predictors (BIO models). Nevertheless, remote sensing data (LAND and BLAND models) led to the most important reduction in the predicted distribution area: 40% for *Calluna* and 63% for *Erica* with regard to ABI models.

Ecological features characterizing suitable areas for the target species were significantly different in C (*Calluna*-only), E (*Erica*-only) and CE areas (overlapping distributions) according to the Kruskal-Wallis test ($p < 0.001$; Table 4.3). Every post-hoc comparison was significant for temperature and rainfall. For limestone, slope, southness and reflectance values in B4 and B5 bands there were small differences depending on the model. The ranges of the ecological variables in overlapping areas were closer to *Calluna* niche requirements: north facing, on shallow slopes, in areas of higher rainfall and lower temperature. Actually, the percentage of *Calluna* locations predicted to occur in CE areas (ranging from 27.5 to 52.8 % among models) was always much higher than for *Erica* (9.6 to 18.1%). Moreover, the proportion that this contact zone represents regarding to the total predicted area for each formation was always significantly higher for *Calluna* (40.8 to 70.3%) than for *Erica* (14.8 to 20.5%) (Table 4.4).

Table 4.5 summarizes the differences between model predictions based on the superimposed maps. They refer to changes in the area predicted as C, E, CE or N (none of the previous) and help to assess how the inclusion of biotic interactions and remote sensing data contribute to a better fit of the geographic distribution of both species. See AnnexII for descriptive statistics of the variables used to build the models. The main changes that resulted from the inclusion of biotic interactions (BIO) in the abiotic models (ABI) were: 16.89% reduction in CE areas towards C (south facing border areas fulfilling environmental characteristics closest to C), 7.16% lowering of CE predictions towards E (areas with a low rainfall, where the probability of C was very low) and 8.07% decrease in E predictions (locations at the lowest altitudinal boundary of its distribution with a marked Mediterranean character). These transitions (CE-C and CE-E) helped achieve a better fit between the models and real conditions, especially in the case of *Calluna*, where the percentage of locations correctly predicted as C increased from 38.7 to 59.9 % (Table 4.4). The

use of LANDSAT channels as predictors resulted in a large reduction in all C, E and CE predicted areas (BLAND *vs.* BIO and LAND *vs.* ABI; Table 4.5). Locations presenting reflectance values on band 4 of 0.32 ± 0.05 were removed from predictions, since this value is much higher than expected for C, CE and E, and hence, corresponded with areas covered by other land cover. The BLAND model showed the best fit to real conditions, when predictions were compared with known presences of both heath formations (Table 4.4). For both, LAND and BLAND models, we observed that by removing the possible biotic interactions between heath formations, the percentage of *Calluna* known points correctly predicted as C was reduced from 63.4 to 37.2%.

4.3.2. Geographic variation of limiting factors across species' distribution range

According to the ABI models, temperature was the main limiting factor for both species across the study area (Fig. 4.3). In the case of *Calluna* (Fig. 4.3a), where temperature was not a restrictive condition (mainly in the north), southness became the main limiting factor (corresponding with south facing slopes). Rainfall also limited its presence in the southwest of the study area. Similar patterns were found with BIO models. Fig. 4.3b showed that the presence of *Erica* did not constrain the geographic distribution of *Calluna*. *Erica* was limited at a regional scale by slope, limestone presence and temperature (ABI models; Fig. 4.3c). However, when the presence of *Calluna* was considered in *Erica* model (BIO), it constituted the principal constraining factor for *Erica* distribution, corresponding mainly with CE areas (Fig. 4.3d).

The number of factors limiting the distribution of heath formations changed across their predicted geographical ranges. By the case of *Calluna*, this number was significantly higher in CE areas (where its niche may overlap with *Erica*'s niche,) than in those areas where it was predicted to occur alone (C) (ABI: $\chi^2 = 1622$, $df = 3$, $p < 0.001$; BIO: $\chi^2 = 13703$, $df = 4$, $p < 0.01$). For *Erica* we found the opposite trend (ABI: $\chi^2 = 16524$, $df = 4$, $p < 0.001$; BIO $\chi^2 = 31156$, $df = 4$, $p < 0.001$).

Table 4.3 Kruskal Wallis test results and descriptive statistics (mean and standard deviation) for abiotic and remote sensing variables. C and E refer to areas predicted to be occupied exclusively by *Calluna* and *Erica*, respectively, while CE refers to zones where both species are simultaneously predicted (areas of potential sympatry or competitive exclusion). Chi squared statistics of the Kruskal-Wallis test are shown in KW(χ^2) rows while KW Post-hoc shows the results of significant comparisons between C, E and CE predictions on the basis of the variables. See table 4.1 for meaning of variable codes, and descriptions of the models (ABI, BIO, LAND and BLAND).

			SLO	SOU	TMEAN	RAI	LIM	B4	B5
ABI	C		20.6±9.5	-0.6±0.4	5.3±0.7	1215±176	0.5±0.5		
	E		21.9±8.0	0.1±0.8	7.1±0.8	1165±211	0.1±0.2		
	CE		17.2±7.8	-0.5±0.5	6.3±0.5	1309±189	0.0±0.2		
	KW (χ^2)		84	192	697	122	307		
		C-CE	***	n.s.	***	***	***		
	Posthoc	C-E	*	***	***	**	***		
		CE-E	***	***	***	***	n.s.		
BIO	C		19.1±8.7	-0.6±0.5	5.6±0.7	1262±192	0.4±0.5		
	E		21.2±8.2	0.1±0.8	7.0±0.8	1172±204	0.1±0.2		
	CE		17.4±7.7	-0.4±0.6	6.3±0.5	1303±171	0.0±0.2		
	KW (χ^2)		65	185	596	114	307		
		C-CE	*	***	***	***	***		
	Posthoc	C-E	***	***	***	***	***		
		CE-E	***	***	***	***	n.s.		
LAND	C		18.1±8.6	-0.5±0.5	5.6±0.8	124±184	0.3±0.4	0.25±0.03	0.20±0.04
	E		21.6±7.5	0.2±0.7	6.9±0.9	1154±217	0.1±0.2	0.23±0.03	0.17±0.03
	CE		18.0±7.6	-0.5±0.6	6.3±0.6	1294±178	0.1±0.2	0.22±0.03	0.18±0.03
	KW (χ^2)		74	281	473	108	115	316	234
		C-CE	n.s.	n.s.	***	***	***	***	***
	Posthoc	C-E	***	***	***	***	***	***	***
		CE-E	***	***	***	***	n.s.	n.s.	n.s.
BLAND	C		18.1±8.6	-0.6±0.4	5.7±0.7	1269±193	0.2±0.4	0.25±0.03	0.20±0.04
	E		22.2±7.0	0.3±0.7	6.9±0.9	1164±198	0.1±0.2	0.23±0.03	0.17±0.03
	CE		17.8±8.0	-0.4±0.6	6.4±0.7	1302±185	0.0±0.2	0.21±0.02	0.18±0.03
	KW (χ^2)		102	341	403	120	111	297	198
		C-CE	n.s.	***	***	*	***	***	***
	Posthoc	C-E	***	***	***	***	***	***	***
		CE-E	***	***	***	***	n.s.	***	***

All KW chi-squared values are significant at $p < 0.001$ (df=2); Post-hoc significance (df=2): *** < 0.001 , ** $0.001-0.01$, * $= 0.01-0.05$

Table 4.4 Total predicted area after applying the *equate entropy of thresholded and original distributions* threshold (Km^2) and percentage of known localities correctly predicted, detailed by formation and model type. C, E, CE and N refer to predicted suitability areas for *Calluna*-only, *Erica*-only, both heath formations or none, respectively. T_C and T_E describe the total predicted area per formation, calculated as: $T_C = C + CE$ (total *Calluna*); $T_E = E + CE$ (total *Erica*). $CE_{Calluna}$ and CE_{Erica} show the proportion that CE areas represent regarding to T_C and T_E respectively (%). Known localities correspond to presence points used to both train and make external evaluation of models. See table 4.1 for code meaning and description of the models (ABI, BIO, LAND and BLAND).

	Total predicted area (Km^2)				% Presence points <i>Calluna</i> (n=142)				% Presence points <i>Erica</i> (n=177)			
	ABI	BIO	LAND	BLAND	ABI	BIO	LAND	BLAND	ABI	BIO	LAND	BLAND
C	113	165	108	133	38.7	59.9	37.3	63.4	0.6	1.1	0.6	0.6
E	1243	1188	448	469	7.0	7.0	4.2	5.6	81.4	83.1	75.1	76.8
CE	267	207	126	92	52.8	31.7	54.9	27.5	13.6	9.6	18.1	16.4
N	1556	1618	2456	2484	1.4	1.4	3.5	3.5	4.5	6.2	6.2	6.2
$T_C = C + CE$	379	372	234	226								
$T_E = E + CE$	1509	1395	614	561								
$CE_{Calluna}$ (%)	70.3	55.6	53.8	40.8								
CE_{Erica} (%)	17.7	14.8	20.5	16.4								

Table 4.5 Cross tabulation matrices. Each table compares model predictions per pair, on the basis of superimposed Boolean map outputs for *Calluna* and *Erica* heath formations. Numbers in columns reflect the proportion of the total predicted area of a certain category (C, E, CE or N) that is predicted simultaneously in both models, as well as the proportion that changes to a different category. C, E, CE and N refer to predicted suitability areas for *Calluna*-only, *Erica*-only, either heath formations, or none, respectively. ABI, BIO, BLAND and LAND refer to the kind of model (see table 4.1 for code meaning and description of the models).

(a) ABI vs. BIO

		ABI			
		N	C	E	CE
BIO	N	97.2	1.16	8.07	1.49
	C	0.72	96.87	0.01	16.89
	E	2.05	0.03	91.47	7.16
	CE	0.03	1.94	0.46	74.46

(b) BIO vs. BLAND

		BIO			
		N	C	E	CE
BLAND	N	95.88	43.96	64.44	45.36
	C	0.39	53.75	0.08	18.04
	E	3.56	0.11	33.18	8.42
	CE	0.18	2.18	2.30	28.18

(c) BLAND vs. LAND

		BLAND			
		N	C	E	CE
LAND	N	97.63	4.34	5.37	0.19
	C	0.36	72.86	0.08	1.71
	E	1.97	0.24	92.69	4.51
	CE	0.04	22.56	1.86	93.59

(d) ABI vs. LAND

		ABI			
		N	C	E	CE
LAND	N	95.59	47.49	64.86	40.76
	C	0.48	48.78	0.15	16.48
	E	3.73	0.15	32.72	8.81
	CE	0.20	3.58	2.27	33.94

Figure 4.2 Boolean maps showing the predicted areas for *Calluna*-only (C), *Erica* -only (E) and overlapping areas of both species (CE), based on the logistic predictions of MaxEnt models after applying the *equate entropy of thresholded and original distributions* cut-off: (a) ABI models (including abiotic variables); (b) BIO models (include abiotic variables and reciprocal biotic interactions); (c) LAND models (considering abiotic predictors and remote sensing data); (d) BLAND models (abiotic variables, remote sensing predictors and biotic interactions with the another species).

Figure 4.3 Limiting factors maps: (a) Limiting factors for *Calluna* based on abiotic requirements (ABI model); (b) Limiting factors for *Calluna* when the presence of *Erica* is considered as a covariate (BIO model); (c) Limiting factors for *Erica* based on abiotic requirements (ABI model); (d) Limiting factors for *Erica* when the presence of *Calluna* is considered as a covariate (BIO model).

4.4. DISCUSSION AND CONCLUSIONS

The inclusion of biotic interactions as predictors in distribution models at a regional scale improved predictive accuracy, in accordance with other studies (Leathwick and Austin 2001; Heikkinen et al. 2007; Meier et al. 2010). Species life traits were associated to differences in predictive performance, which was consistently higher for the specialist *Calluna*. This species occurred within narrow environmental limits and was easier to predict than the generalist *Erica*, as discussed by Morán-Ordóñez et al. (2011b).

The first group of models, based on abiotic factors (ABI), allowed the identification of the potential geographical space that each heath species could occupy depending on abiotic restrictions (Grinnellian niche; Soberón 2007). Our results confirm observations by Pearson and Dawson (2003), who stated that climatic conditions are the most relevant factors driving species distributions from regional to continental scales (mainly temperature). The geographical distribution of the specialist *Calluna* is limited by high temperature and low rainfall conditions (i.e. Mediterranean climatic conditions found at low altitude), but also by very steep slopes at the top of the mountains, where climatic conditions are harsh and soil availability is scarce. However, the generalist *Erica* can develop under a wider range of abiotic conditions and, consequently, was predicted to occur over larger areas in the Cantabrian Mountains. It is more drought-tolerant and, therefore, it occurs on steeper slopes where soil water retention is low. Similar to *Calluna*, *Erica* was not present on the mountain ridges. Although both grow over acid and poor soils, *Calluna* is predicted to occur in proximity to limestone areas. This reflects that it frequently grows over acid soil deposits accumulated at the pass between limestone ridges. This situation is rarely found for *Erica*.

The second set of models (BIO) highlighted the effect of biotic interactions between the two target species on their geographical distribution patterns. The abundance of a competitor is important to the extent that it affects environmental conditions, such as the availability of nutrients, water, space or light (Pulliam 2000). However, due to the scale of the study, we could only evaluate competition between the two heath species in terms of geographical space, interpreted as an indirect measure of resource competition, due to the fact that species are competing for establishing in a soil that satisfies their nutrient requirements. If one species is dominant, it should have a negative effect on the other. Model results showed that this is mainly the case of *Calluna* dominating *Erica* in overlapping areas. This dominance is explained by the specialist character of *Calluna* (occurring following narrower environmental conditions), whose occurrence resulted in

the main limiting factor for *Erica* in overlapping areas. As a consequence, niche width for *Erica* is constrained by *Calluna*'s presence towards "competition free" areas. More evidence for competitive dominance by *Calluna* was observed in highly patchy and heterogeneous heath mosaics corresponding with ecotones (CE). *Erica* showed lower cover values in formations dominated by *Calluna* than vice versa (Calvo et al. 2002a). However, it is rare to find patches where both species occur in paired situations (mixed formations of *Calluna* and *Erica* at 50% of cover; Calvo L. personal com.). We also observed that a lower proportion of the overlapping areas are dominated by *Erica*. They may correspond with recurrently disturbed areas where *Erica* has a better regeneration capacity than *Calluna* (Calvo et al. 2002a).

Morán-Ordóñez et al. (2011b) observed that the use of radiance values from LANDSAT improved the accuracy of distribution models for the target species, by providing environmental information on land cover, land use or vegetation status that was otherwise unavailable. This effect was especially relevant in the case of generalist species such as *Erica*. In this study, the highest explanatory and predictive accuracy was obtained by BLAND models, including abiotic factors, biotic interactions and land cover information. Similar results were found by Heikkinen et al. (2007). Remote sensing variables helped to remove from BIO predictions those areas where potential occurrence of heath species is not realized for two main reasons: secondary succession processes and human disturbances. *Calluna* and *Erica* require recurrent disturbances (mainly fire) to maintain their formations in a building state (Calvo et al. 2005). However, the loss of traditional practices has increased the cover of heath and shrub communities to almost half of the study area at the beginning of 1990s (Morán-Ordóñez et al. 2011a). As a consequence, *Calluna* has entered a mature to degenerate state (sensu Watt 1955), which may involve its large scale replacement by more competitive grasses. In the case of *Erica*, secondary succession may transform it into scrub or woodlands (Calvo et al. 2007). Regarding to human disturbances, some of the potential areas predicted for *Erica* (by ABI models) are located near to valley-bottoms and villages, where they have been commonly eliminated to create arable fields (Calvo et al. 2002b). Despite the general trend towards the abandonment of traditional farming, this practice persists in some areas of the Cantabrian Mountains (mainly valley-bottoms; Rescia et al. 2008). However, the human intervention contributing most to the reduction of these heath communities is shrub-cutting management carried out by the Regional Administration since 2000, with the removal of 100 km² of shrub and heath between 2000 and 2005 (Morán-Ordóñez et al. 2011a). These conditions are reducing the spatial distribution of both species (mainly *Calluna*, which regenerates worse than *Erica* after cutting; Calvo et al. 2005). On the other hand, remote sensing data allowed the

identification of patches of the target species located outside the envelope defined by ABI models, extending the realized niche to “unsuitable” areas (sensu Pulliam 2000).

In summary, accounting for biotic interactions in distribution models increases the accuracy of predictions compared to models based on abiotic and remote sensing data alone. Analyses of the limiting factors constraining species distributions (abiotic and biotic) and of their spatial variation, allowed a better understanding of current distribution patterns and the species success under competition scenarios. *Calluna* dominated areas of potential sympatry due to its specialized character, limiting the distribution of *Erica* to competition-free areas. However, human disturbances can modify this equilibrium by removing the dominant species. Although we could only evaluate the effect of the main limiting factor in competition outputs, we observed that the number of limiting factors for both species differed between areas of potential competition and competition-free areas. Further research (combining modelling approaches and field observations) should aim to assess if this spatial variation in the number of limiting factors may also affects the behaviour of a given species under competition scenarios.

Management recommendations

In the Cantabrian Mountains, the Regional Administration is currently designing specific plans for managing and preserving heath habitats and species of high conservation interest, within the Natura 2000 network framework (Habitats Directive; Anon 1992). As regards the target species of this study, it is especially important to carefully plan conservation strategies for *Calluna*: these formations are currently in a senescent stage, which means that they do not resprout after cutting, and hence, require fire events to stimulate germination and maintain population viability (Calvo et al. 2002b). Since 2000, shrub-cutting policies aimed at reducing arson fires have had a noticeable effect in the study area (Morán-Ordóñez et al. 2011a). Thus, although *Calluna* is competitively dominant against *Erica*, the lack of appropriate management (fire) can modify the equilibrium between the two species in areas where both niches overlap, favouring the establishment of *Erica* formations in areas currently covered by *Calluna*. The absence of fire may similarly cause the loss of *Calluna* formations in areas where competition occurs, not with *Erica*, but with other species (i.e. grasses; Barker et al. 2004). Due to the difficulty of restoring the traditional practices on which both species depend, their conservation status would improve by burning small patches (prescribed fires) throughout their entire geographic distribution. This would favour a patchy distribution of heterogeneous states of development from young to mature stages, which would guarantee the renewal and maintenance of their formations. Climate change should also be

considered in future management plans. Climatic warming could reduce the availability of suitable conditions for *Calluna* formations, leading to replacement by other Mediterranean communities (as observed in the Pyrenees by Peñuelas and Boada 2003).

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ANNEX II

Descriptive statistics of transition areas among models.

Mean and standard deviation of predictor values corresponding to areas where changes between models were detected in cross-tabulation analyses ($\bar{x} \pm SD$). ABI, BIO, LAND and BLAND refer to the kind of model: ABI models include abiotic variables; BIO models consider abiotic variables and biotic interactions with another species; LAND models are based on abiotic predictors and remote sensing data; and BLAND models include abiotic and remote sensing predictors as well as biotic interactions with another species. The variables are: Slope (SLO), Southness (SOU); mean annual temperature (Tmean); total annual rainfall (RAI); presence of limestone (LIM); reflectance values of near infrared wavelength LANDSAT (B4); reflectance values of shortwave infrared wavelength LANDSAT (B5); *Erica* logistic predictions based on ABI models (*Erica* log); *Calluna* logistic predictions based on ABI models (*Calluna* log). “Change” column refers to the changes between each pair of compared models. C, E, CE and N refer to predicted suitability areas for *Calluna*-only, *Erica*-only, both heath species or none, respectively.

MODEL PREDICTORS										
Cross-tabulation transition	Change	SLO	SOU	Tmean	RAI	LIM	B4	B5	<i>Erica</i> log	<i>Calluna</i> log
ABI-BIO	E-N	22.3±9.7	0.0±0.8	7.8±0.8	1066±206	0.13±0.31			0.21±0.05	0.01±0.02
	CE-C	16.9±7.4	-0.7±0.4	5.9±0.5	1359±180	0.17±0.29			0.35±0.10	0.54±0.18
	CE-E	17.4±7.3	-0.6±0.6	6.5±0.7	1186±183	0.05±0.14			0.55±0.13	0.17±0.02
BIO-BLAND	C-N	19.8±9.7	-0.5±0.5	5.7±0.7	1211±186	0.69±0.43	0.32±0.05	0.24±0.06	0.12±0.13	0.31±0.17
	E-N	20.7±8.2	0.0±0.8	7.2±0.8	1175±203	0.11±0.27	0.32±0.05	0.19±0.04	0.38±0.15	0.02±0.03
	CE-N	17.3±7.6	-0.4±0.6	6.4±0.6	1297±170	0.01±0.04	0.32±0.05	0.19±0.04	0.48±0.11	0.31±0.13
	CE-C	15.7±7.5	-0.5±0.5	6.1±0.6	1296±166	0.00±0.02	0.25±0.02	0.19±0.03	0.44±0.12	0.43±0.15
	CE-E	18.3±6.5	-0.3±0.6	6.3±0.5	1282±169	0.00±0.01	0.23±0.02	0.15±0.02	0.52±0.10	0.24±0.08
BLAND-LAND	C-CE	17.5±7.0	-0.7±0.4	6.0±0.5	1344±178	0.14±0.32	0.22±0.03	0.18±0.03	0.36±0.16	0.52±0.19
ABI-LAND	C-N	19.7±10.1	-0.5±0.5	5.5±0.7	1166±186	0.75±0.42	0.32±0.05	0.25±0.06		
	E-N	21.0±8.3	0.0±0.8	7.3±0.8	1167±204	0.10±0.26	0.32±0.05	0.19±0.04		
	CE-N	17.1±7.9	-0.5±0.6	6.4±0.6	1299±173	0.07±0.21	0.33±0.05	0.19±0.04		
	CE-C	16.1±7.9	-0.5±0.5	6.0±0.6	1313±166	0.04±0.16	0.26±0.02	0.20±0.04		
	CE-E	17.7±6.1	-0.4±0.6	6.4±0.5	1265±170	0.03±0.13	0.23±0.02	0.15±0.01

CHAPTER 5

Temporal changes in socio-ecological systems and their impact on ecosystem services at different institutional scales: a case study of heathlands⁵

⁵ The content of this chapter has been submitted for publication consideration to *Ecosystems*.

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ABSTRACT

Heathlands are cultural landscapes providing a wide range of goods and services to societies. These semi-natural habitats, of high conservation interest, are at risk of degradation and disappearance in most parts of Europe mainly due to land abandonment and other land use changes. In the Cantabrian Mountains (NW Spain), the decline of grazing activities (mainly linked to sheep transhumance systems) in heathland landscapes, open mosaics of heathlands and grasslands, has favoured their expansion in the last decades. In this study we used the Framework for Ecosystem Service Provision to identify and assess the ecosystem services provided by heathlands in the Cantabrian Mountains (provisioning, regulating and cultural services), in order to raise awareness among the public, stakeholders and managers. We analyse how the social changes in the second half of the twentieth century have resulted in changes in both, the landscape patterns and the stakeholders' perception of heathlands' ecosystem services, from local to international scale. We found that although areas covered by heathlands are today larger than in the 1950s, the demand of provisioning services (goods) from these landscapes have significantly declined in favour of cultural services (mainly those related to their conservation values). These landscapes have traditionally depended on a stable local socio-ecological system, which has transformed into the current unstable multi-scale system, in which the demand of services for different stakeholders produces conflicting situations. These in turn can drive the degradation of heathlands and the loss of the biodiversity they support.

5.1. INTRODUCTION

Heathland landscapes (open mosaics of grasslands and heathlands) underwent a large expansion process in Europe until the end of the 18th century, as a consequence of centuries of deforestation aimed at creating grazing areas for sheep, goats, cattle and horses (Pinto-Correia et al. 2005). They constitute cultural landscapes and have traditionally provided important goods and services to societies (Wessel et al. 2004; Harrison et al. 2010). Nevertheless, at the beginning of the 19th century these areas began to be considered as unproductive wastelands (de Blust 2007). This caused either their abandonment and replacement by shrub or forest through secondary succession processes (Moen et al. 2006), or their gradual conversion to other land uses (e.g. arable fields, urban areas, etc.), the greatest changes occurring within the second part of the twentieth century (Webb 2005; de Bello et al. 2010; Harrison et al. 2010). In some European countries only 10% or less of the original heathlands remain (de Blust 2007). Despite this general trend, there are exceptions. In the Cantabrian Mountains (NW Spain), the decline of grazing activities in heathland landscapes, traditionally linked to sheep transhumance, is a relatively recent process which was specially marked since the 1950s (Rodríguez 2004). This decline has favoured a large increase in the area covered by heathlands and shrublands encroaching grasslands (Celaya et al. 2010; Morán-Ordóñez et al. 2011a). Heathlands are semi-natural systems: their maintenance depends mainly on specific traditional rural practices such as grazing (Ostermann 1998), whose recovery in these mountain systems is now unlikely due to their low profitability and competitiveness compared to lowland systems (MacDonald et al. 2000). However, there is a strong interest at the European level in preserving heathlands (Annex I Habitats Directive, 92/43/EEC; Anon 1992). They are considered biodiversity hotspots in Europe due to their high richness in plants, invertebrates and birds (de Bello et al. 2010). Differences in geology, soils and climate have generated a wide diversity of heathlands in Europe, which can only be preserved by safeguarding an equally wide range of local types (Leite 2004). However, if they are to be preserved for their high conservation value, how can they be maintained at their current status, or improved, when they depend on unprofitable activities?

The challenge is to identify all the benefits provided by these habitats which would justify their maintenance, apart from the provisioning of grazing resources, and to raise awareness of their value among stakeholders and managers. In this sense, the relatively novel field of research on Ecosystem Services (ES) can provide a framework for the description and assessment of both current and potential benefits. Its implementation can add value to strategies for species/habitat

conservation in human-dominated regions (Luck et al. 2009; Haslett et al. 2010). ES are the conditions and processes through which ecosystems sustain and fulfil human life (Costanza 1997; Daily 1997). It is an anthropocentric concept because it implies that the supply of a service from a given ecosystem depends on the human demand for it. Each service is provided by the “service provider” unit (Luck et al. 2009), which can correspond to different ecological levels (such as single species, populations, functional groups, ecosystems or even landscapes). Several studies have tried to identify, classify and evaluate the services provided by the main ecosystems worldwide, across all organizational levels and using different methodologies (see Wallace 2007 for a review of classification methods), while detailing information about their conservation status and main threats (drivers of change). These threats are generally common and well known for most ecosystems: mainly land use and climate change (Sala et al. 2000; Schröter et al. 2005). Management actions have been suggested in order to maintain or improve the supply of a given service (favouring adaptation processes of the ecosystems or proposing mitigation actions), mainly at global or continental scales (MEA 2003; EASAC 2009; RUBICODE 2009). Several countries are currently applying those methodologies to adapt the continental results to their particular cases (e.g. United Kingdom: UKNEA 2011; USA: EPA 2009; Spain: EME 2011). However, there is still insufficient information on the dynamics of service provisioning at a local or regional scale (MEA 2003), which often represent the practical scales at which management strategies are designed and implemented. For instance, at a local scale there is limited knowledge of the consequences of land use and vegetation cover change on ecosystem services and human well-being (Reyers et al. 2009), because these consequences have been more widely explored at large scales (Schröter et al. 2005; Metzger et al. 2006). Temporal dynamics should be also an important component of the ecosystem service approach to be considered, since ecosystem responses occur over large periods of time (Rounsevell et al. 2010).

In this study, we sought to identify and characterize the ecosystem services provided by heathland landscapes in the Cantabrian Mountains. In particular, we investigated how social changes in the second half of the twentieth century have changed both the landscape patterns and the stakeholders’ perception of the provision of services by these landscapes (at local, regional, national and international scales). We assessed how this multi-scale analysis (considering temporal and institutional scales) could help the design of management strategies for heathland landscapes.

5.2. APPROACH TO THE STUDY AREA

5.2.1. Study area

The study area is located at the southern slope of the Cantabrian Mountains in the León province (NW Spain). It represents a biodiversity hotspot (Worboys et al. 2010), being located on the boundary between the Mediterranean and Atlantic/Eurosiberian regions, where climate change is expected to determine important changes to species (Thuiller et al. 2005). Due to its high conservation value, since 1998 several *Special Protection Areas* (Birds Directive 2009/147/EC; Anon 2009) and *Sites of Community Importance* were declared in the area within the framework of the Natura 2000 network, including at least 30 habitats of community interest from those listed in the Annex I of the Habitats Directive (92/43/EEC, Anon 1992). It also represents the southwestern distribution limit for many Eurosiberian communities (i.e. *Calluna vulgaris*-dominated heathlands), thus representing a good location for long-term conservation of genetic diversity and evolutionary potential (Hampe and Petit 2005).

Transhumance has been one of the main driving forces shaping the landscape of this area over centuries: it consists of seasonal movements of sheep flocks across the Iberian Peninsula, to take advantage of the availability of complementary grazing resources (south-Iberian “dehesa” systems in winter and north-Iberian mountain pastures in summer mountain passes). For centuries, the rental of mountain passes represented the main source of income for local municipalities (Rodríguez 2004), and for some of those it is still important nowadays. Additionally, the care of herds represented a source of employment for mountain villages (Rodríguez 2004). However, this system has undergone a deep crisis in the twentieth century (especially relevant since 1960; Figure 5.1a), due to its low profitability for both owners and shepherds, and its low competitiveness with industrial systems which favoured a process of rural depopulation and emigration to cities (Fig. 5.1b). This resulted in the loss of sustainable management based on grazing, cutting and burning (Calvo et al. 2007), which in turn has induced large changes in landscape patterns and composition (Molinillo et al. 1997; Gómez-Sal and Llorente 2004; Vicente-Serrano et al. 2005). In our study area, burning was traditionally used to increase the availability and quality of pastures in mountain passes, where the landscape consisted of an open mosaic of heathlands and grasslands. This activity favoured in turn the maintenance of open heathlands at a building state due to their fire-prone character (Calvo et al. 2002a, 2002b, 2005). Thus, the occurrence of some heath-dominated habitats in this area is directly associated to transhumant activities (Bunce et al. 2004) and therefore their current geographic distribution

follows these of the mountain passes (see Fig. 5.2 based on results of Morán-Ordóñez et al. 2011b).

a)

b)

Figure 5.1 (a) Evolution of the transhumance in León, since the second half of the nineteenth century (number of sheep using mountain passes). Source of data: Rodríguez (2004). **(b)** Changes in population of the municipalities of the Cantabrian Mountains of León owning mountains passes, compared with changes in the total Spanish population. Source: INE population census (Spanish National Institute of Statistics).

5.2.2. Socio-ecological systems and landscape change

We analysed ES in the Cantabrian Mountains during two different time periods: 1950s and 2010s. The first period represents a pre-rural abandonment situation. The rural population in mountain areas was organized in nuclei located in valley bottoms with small extensions of land nearby the villages, used as orchards; larger areas in closest slopes were used for subsistence crops (cereals, potatoes, etc), and also for forage crops and natural meadows for the winter subsistence of the villages' livestock (Mayor 2002). Mountain passes, placed in the highest parts of the mountains, were rented to transhumance flocks owned by farmers from lower valleys or the south of Spain. The decades of 1940-60s represented the last peak of the transhumance activity before its final decline (Rodríguez 2004; Fig. 5.1a). The current situation (2010s) shows the result of the

landscape evolution after the transhumance decline and the rural emigration process (see Fig. 5.1). The loss of traditional management in the valley bottoms and closest slopes caused the conversion of crops and meadows into different types of grassland or shrublands (Gómez-Sal et al. 1993; Rescia et al. 2008; Morán-Ordóñez et al. 2011a). A remarkable extent of these “unproductive” areas was planted with coniferous trees (Gómez-Sal et al. 1993; Calvo et al. 2002a). On the mountain passes, secondary succession processes caused the spread of heath and shrub, resulting in a homogenization of the landscape (Rescia et al. 2008; Morán-Ordóñez et al. 2011a). These observed land use and cover changes match the general trends of landscape evolution due to land abandonment that occurred in other mountain ranges in Europe during the same period (MacDonald et al. 2000; Vicente-Serrano et al. 2005; Lasanta et al. 2009).

5.3. IDENTIFICATION OF ES. INSTITUTIONAL AND TEMPORAL SCALES

ES supplied by heathland landscapes were characterized according to the Framework for Ecosystem Service Provision (FESP) proposed by Rounsevell et al. (2010). We classified the services into three groups (Tables 5.1 and 5.2) following the Millennium Ecosystem Assessment: provisioning, regulating and cultural services (MEA 2003). Supporting services, defined as background ecosystem functions allowing the maintenance of other services, were not considered in this study in order to avoid double counting of ES (*sensu* Hein et al. 2006; e.g. pollination and honey production). We identified the different ecosystem services belonging to each group, defining the following aspects for each service: (1) Ecosystem Service Providers (ESPs) or the ecological level (landscape, species, etc.) contributing to the ES provision; (2) Ecosystem Service Beneficiaries (ESBs) or those sections from society (stakeholders) who benefit or would potentially benefit from the ES; (3) profits obtained from the service and their value (when possible); (4) Service Providing Unit (SPU) or the attributes that the ESP should fulfil to guarantee the delivery of a service at the desired level; (5) threats and impacts and (6) current or potential responses aimed at preserving the provision of the service. ESBs and profits (2 and 3) were analyzed separately for each of the socio-ecological systems described above. Gomez-Sal and Rodríguez (1992) and Rodríguez (2004) represented valuable sources of information to identify and analyze the provision of ES of both current and past socio-ecological systems linked to heath-pasture landscapes. Other important data sources were technical reports on the use of mountain passes (Tecnosylva 2004) and historical data basis on livestock and game reserves were provided by the Regional Administration (Junta de Castilla y León).

Figure 5.2 Location of the study area (NW Spain). Mountain passes traditionally used for sheep grazing are shown in dotted areas. Predicted distribution of heath formations dominated by *Calluna vulgaris* and *Erica australis* based on the results of Morán-Ordóñez et al. (2011b) are represented with colours: pink (*C. vulgaris*), yellow (*E. australis*) and green (areas where the distribution of both species overlaps).

Hein et al. (2006) analyzed the relationships among services provided at different ecological scales (species, ecosystem, landscape, etc.) and the different institutional scales at which benefits of ES are valued by stakeholders (local, provincial, global, etc.). They argued that identification of stakeholders at different scales allows the analysis of potential conflicts in environmental management. Following a similar approach, we have identified, for both socio-ecological systems (1950s and 2010s), the institutional scales demanding or valuing the ES supplied by heathland landscapes. We constructed comparative diagrams showing how the ES previously identified within the FESP framework distribute across institutional scales in each socio-ecological system.

5.4. ECOSYSTEM SERVICES ON A TEMPORAL PERSPECTIVE

5.4.1. Provisioning services

There is a wide range of goods potentially provided by heathland landscapes (see Table 5.1). However, the demand for goods in the 1950s was significantly higher than it is today (especially the local demand). This is in accordance with European trends (MEA 2005; Harrison et al. 2010). The subsistence system characterizing the 1950s made use of all local natural resources available: heath wood as fuel (timber), fertilizer (cuttings mixed with manure), livestock bedding and

thatching. The maintenance of an open heath-pasture landscape mosaic ensured the availability of high quality grazing resources in mountain passes, attracting herds of sheep from the south of Spain. They were rented every year, and represented an important income for the municipalities and a source of employment for local inhabitants (Rodríguez 2004). The remaining mountain passes (those not rented) were used for local livestock feeding. Fresh food products (honey, meat, cheese) were sold in local and regional markets. Other products such as wool reached high prices on the national market (Rodríguez 2004). Game represented an additional food source for the local population, although this was a marginal service, limited to small species, mainly partridge and hare. Populations of big preys were scarce due to either persecution as they attacked extensively reared livestock (case of wolves) or competition with the extensive livestock and unavailability of adequate habitat (case of ungulates; Sáenz de Buruaga 1985). Medicinal plants linked to heath-pasture habitats (mainly *Gentiana lutea*) were collected by local people and sold in national markets.

Nowadays most provisioning services are marginal, i.e. fertilizers, fuels (Wessel et al. 2004). Fresh products are mainly sold in regional markets and their prices have significantly decreased. The wool market associated to transhumance flocks has almost disappeared in Spain (Rodríguez 2004). The higher profitability of intensive systems versus extensive systems (transhumance) has reduced the demand for the rental of mountain passes in the last 40 years (with the subsequent decline in income for municipalities): most of them are currently abandoned or grazed by cattle and horses, mainly endangered local breeds subsidized by the Common Agricultural Policy (CAP; Anon 2005). However, cattle and horses make a different use of the heath-pasture mosaic than sheep, leading to higher levels of shrub encroachment (Calvo et al. 2002a). Cattle and horses feed only on herbaceous resources while sheep feed on both herbaceous and woody vegetation such as heath (Osoro et al. 2003; Celaya et al. 2007). The decrease in livestock pressure, particularly sheep, and its consequences in the heath-pasture landscape have also favoured the increase of wild herbivorous populations (i.e. roe deer *Capreolus capreolus*, deer *Cervus elaphus* and chamois *Rupicapra rupicapra*; see Figure 5.3). Two game reserves have been created within the area since 1960 (covering approx. 110,000ha). Thus, game has evolved from its marginal use as a provisioning service to an extensive recreational service, as in other parts of Spain (Wessel et al. 2004). The harvesting of *Gentiana lutea* is nowadays regulated by law (after being banned due to overexploitation) and mostly managed by national companies, paying fees to local councils. There are, however, two provisioning services under increasing demand by the current society, which were not even considered by the socio-ecological system of the 1950s. They are related to the

conservation values of these agro-sylvopastoral systems (natural heritage and ecological values; numbers 9 and 10 in Table 5.1) due to the high proportion of endangered fauna and flora species and interesting plant communities that they shelter (Gómez-Sal and Llorente 2004).

5.4.2. Cultural services

Heritage related to the shepherds' culture (traditions, songs, tales, handicrafts, constructions, etc.) and their traditional management of the heath-pasture mosaic is one of the most important cultural services of these landscapes (see Table 5.2). This culture has been orally transmitted for centuries, with only few written sources documenting it (Gómez-Sal and Rodríguez 1992; Rodríguez 2004). In the 1950s these cultural values were part of the local lifestyle, whereas nowadays they are disappearing. Conversely, other cultural services valued nowadays were ignored in the 1950s, particularly related to aesthetic and conservation values (services 12 and 13 in Table 5.2). The number of tourist visiting natural spaces in León province has increased significantly in the last decade (see Figure 5.4 for an example), together with the number of related business activities such as rural accommodation, restaurants, etc. (Lago and Sevilla 2008). This follows general trends of other Western countries where nature tourism has become a major cultural service (Hein et al. 2006).

5.4.3. Regulating services

The location of heath-pasture landscapes in mountain systems, make them particularly important for the provision of drinking water to populations living downstream, and for controlling erosive processes by maintaining slope stability through the vegetative cover (MEA 2005; Table 5.2). These services can be considered as timeless services since they have been valued during centuries by all societies. In addition, the carbon-sequestration capacity of heath-pastures, ignored in the 1950s, is increasingly valued today for its potential contribution to climate change mitigation (UKNEA 2011). Nowadays, the information about the role of shrub and heath vegetation on carbon storage is scarce and uncertain (RUBICODE *online*): the amount of sequestered carbon will vary as a function of the proportion of grass and woody vegetation (Jackson et al. 2002), which depends on the management of this mosaic. Wessel et al. (2004) and Alonso et al. (2012) also showed that for similar heath-grassland equilibrium mosaics, the amount of sequestered carbon would also vary depending on temperature and rainfall conditions.

5.5. ECOSYSTEM SERVICES ACROSS INSTITUTIONAL SCALES

Figure 5.5 shows, for each socio-ecological system (1950s and currently), how the benefits of the heath-pasture landscape mosaic accumulate at a range of institutional scales (from local to international). Identification of stakeholders at different scales allows identification of potential conflicts in environmental management, in particular between local and regional/national stakeholders (Hein et al. 2006).

Figure 5.3 Evolution of populations of wild herbivores in the game reserve of Mampodre (Cantabrian Mountains) since the second half of the twentieth century (3a), compared to the evolution on the livestock demand on the mountain passes within the same area (3b). Source: Junta de Castilla y León.

Table 5.1 Provisioning services supplied by heathland landscapes. For each service we detail: Ecosystem Service Providers (ESPs); Ecosystem Services Beneficiaries (ESBs) and profits obtained from the service; Service Providing Unit (SPU) and their threats and impacts; current or potential responses aimed to preserve the service provision. * Source: Junta de Castilla y León (Regional Administration).

Service	ESPs	1950s		Present		SPU and impacts	Response
		ESBs	Profits/valuation	ESBs	Profits/valuation		
(1) Direct goods: Honey	Heath (<i>Calluna vulgaris</i> and <i>Erica australis</i>) Flowering plants	Local population	Food supply	Small producers.	Price of the honey in local/regional markets	Heath communities containing plants at pioneer states of development.	
				Tourism		Low profitability and low demand of high quality organic products.	Policies aimed to promote the market of high quality goods produced with environmentally-friendly techniques
(2) Indirect goods: meat, wool, cheese, etc.	Livestock feeding within these landscapes	Owners of sheep herds				Herds of sheep and cattle grazing these areas.	
		Buyers of the products (local and regional market mainly)	Income related to the sale of these products in local, regional and national markets	Owners of cattle and horses.	Benefits related to sale of these products mainly in local and regional markets	Higher profitability of intensive livestock feeding vs. extensive systems.	
		Local population				Low market value of some of these products (i.e. wool).	
(3) Game (hunting and shooting)	Populations of game species <i>Alectoris rufa</i> <i>Perdix perdix</i> subsp. <i>hispaniensis</i> <i>Lepus castroviejo</i> <i>Lepus granatensis</i> <i>Sus scrofa</i> <i>Capreolus capreolus</i> <i>Cervus elaphus</i> <i>Rupicapra rupicapra</i>	Local population	Food supply	(4) Hunters	Two game reserves declared in 1966 covering approx. 110,000 ha.	Populations of hunting and shooting species at a desirable level.	
				Local/regional population (restaurants, rural hostels, etc.)	2010 benefits reported by these game reserves: 335,370€ *	Overexploitation of certain species (i.e. <i>Perdix perdix hispaniensis</i> ; <i>Lepus castroviejo</i>) whose populations are nowadays considered at a vulnerable conservation status.	Control of the demand as a recreational service.
(5) Grazing	Heath-pasture landscape at the highest parts of the mountains	Local councils	Employment for local people.	Local councils	Biodiversity shelter.	Open heath-pasture landscape mosaic.	Shrub cutting management.
		Local population	The rental of mountain passes represented the main annual income for mountain municipalities.		Income for the rental of summer pastures. 2007: 247,500€ *	Decline of the traditional sheep transhumance system, favouring scrub encroachment and homogenization of the landscape.	Control burning of small heath patches
		Owners of herds who rented the summer pastures	Grazing resources.	Owners of herds who rented the summer pastures	Grazing resources		

(6) Fuel (wood)	Heaths (<i>Erica</i> sp. and <i>Calluna vulgaris</i>) and Shrubs (<i>Cytisus</i> sp. and <i>Genista</i> sp.)	Local population	Availability of fuel for cooking and heating.	It is a marginal service	<i>Heath and shrub cover</i>	Promoting the use of heath and shrub biomass removed in shrub-cutting management activities for production of pellets and their sale in local markets
			Branches were also used to thatch houses and for livestock bedding.			
(7) Fertilizers	Heathlands and Livestock	Local population	Low cost fertilizers for application in crops and orchards	It is a marginal service	<i>Heath branches used for livestock bedding mixed with manure.</i>	Rural depopulation and abandonment of the subsistence crops. Development of chemical fertilizers.
(8) Medicines	<i>Gentiana lutea</i>	Local population National companies	Local income for harvesters who sell the product to local companies	Pharmaceutical and cosmetic industry.	Related to the selling of cosmetic products in the national and international market.	<i>Presence Gentiana lutea populations associated to heathlands.</i>
				Local councils who receive money for the exploitation of the resource.	Over-exploitation. Poaching.	Regulatory legislation in relation to the exploitation and management of this natural resource.
(9) Protecting genetic variability of heathland species.	<i>Calluna vulgaris</i> heathlands	-	-	European Union (Natura 2000 network).	<i>Maintenance of healthy communities of Calluna vulgaris heathlands.</i>	
				Natural heritage. National programs of biodiversity conservation.	Senescence and loss of these communities due to the loss of traditional management.	Declaration of Sites of Community Importance including heath and pasture habitats.
(10) Provisioning of Habitat	Heath-pasture landscape mosaic	-	-	Heath specialist specie	Conservation of natural heritage and biodiversity values.	Reforestation with coniferous species.
				Species-dependent of the heath pasture landscape mosaic (some of them present in the Annex I of the Birds Directive; Anon 2009: <i>Luscinia svecica</i> <i>Perdix perdix</i> <i>hispanensis</i>)	Land use change. Shrub encroachment and landscape homogenization.	Specific habitat-oriented management.

The socio-ecological system of the 1950s represented a stable situation, mainly reliant on interdependent local services (Fig. 5.5a). Every stakeholder, at all institutional levels, was interested in the maintenance of such stability. Traditional grazing and burning management ensured the yearly self-maintenance of the open heath-pasture landscape patterns from which it depended. The shepherds' culture had a strong influence on the system, because it represented the style of life of the population of mountain villages associated to the heath-pasture landscape mosaic (in some cases there were entire villages and social groups making seasonal movements between regions following the grazing resources, i.e. social group of "vaqueiros de alzada"; García 2009). Benefits from the rental of mountain passes had direct repercussions in the social welfare state of mountain villages, funding social services such as school and health systems (Rodríguez 2004). Provisioning services were mainly and strongly demanded by the local population, who was interested in their maintenance at a sustainable level, due to the subsistence character of the system. In some cases, the demand of provisioning services, mainly fresh products as meat, was oriented to their sale in local or regional markets, but its effect was always limited to local incomes. The regional and national importance of the provisioning services was related to the fact that transhumance linked León province with other regions of southern Spain, so that both regions benefitted from the system (use of complementary resources yielding meat and wool production). It was an important national activity balancing cost-benefits over all scales (i.e. wool market).

The stable local system of the 1950s has developed into an unstable multi-scale system (Fig. 5.5b). For example, the conservation of biodiversity is a novel ES, demanded by stakeholders at the national and international scale (*sensu* Hein et al. 2006), in this case mainly by the Natura 2000 network commitments. The precautionary approach, as proposed by Haslett et al. (2010), calls for maintenance of intact ecosystems as far as possible (in this case heterogeneous landscape mosaics) to ensure continued service provision of conservation-related ES in the face of changing environmental conditions. Nevertheless, the current traditional management, as explained in previous sections, is insufficient to preserve the *status quo* of these landscape mosaics. This would require the involvement of the local population (scarce when compared to the 1950s) and the recovery of demand for provisioning services (at least to a certain extent). However, for people living in a natural reserve or a National Park, conservation values scarcely contribute to specific improvements in their welfare (employment, culture and economic reactivation, etc.; Rescia et al. 2008), apart from the benefits to those involved in the tourism sector and to farmers (subsidies

related to endangered local breeds). Local populations tend to perceive their necessities as under-represented in the Regional or National administration plans, particularly as opposed to environmental issues. Thus, living within a natural reserve is sometimes considered a handicap because of the management restrictions imposed by the land use planning programs of these natural spaces (Rescia et al. 2008), which sometimes do not consider local population claims.

Figure 5.4 Annual number of visitors in the Picos de Europa National Park, placed in the Cantabrian Mountains. The southern slope of this Park (approx. 40 % of its total area) belongs to the León province. Alpine mosaics of heath and pastures are one of the most important habitats present in this Park and one of its most distinctive traits. Graph also shows the evolution in the number of tourist using rural accommodation in León province. Source: INE (Spanish National Institute of Statistics).

Therefore, there is a gap between national and international demand of ES related to conservation values and their local production. Stakeholders at different scales are demanding different services, potentially leading to an unstable system. One possible solution for bridging this gap would imply the promotion of public policies aimed to stimulate local people for carrying out actions that increase/maintain the levels of a desired ecosystem, through direct payments (i.e. subsidies) or incentive mechanisms (i.e. taxes) (Jack et al. 2008).

Table 5.2 Cultural and regulating services supplied by heathland landscapes. For each service we detail: Ecosystem Service Providers (ESPs); Ecosystem Services Beneficiaries (ESBs) and profits obtained from the service; Service Providing Unit (SPU) and their threats and impacts; current or potential responses aimed to preserve the service provision. * Source: Junta de Castilla y León (Regional Administration).

CULTURAL SERVICES			1950s	Present			
Service	ESPs	ESBs	Profits/valuation	ESBs	Profits/valuation	SPU and impacts	Response
(11) Cultural heritage	Landscape heathland mosaic, which is the result of the management that shepherds have made of these areas for centuries	Local population	Stile of life, traditions, handicrafts, sense of place, shepherds’ culture	Local population	Sense of place	Open heath-pasture landscape mosaic and all the species associated to it.	Policies aimed to protect these landscapes within the framework of the Natura 2000, and to promote the maintenance of traditional management activities.
					Ancestral culture		
				Tourist	Conservation values due to the high biodiversity of these cultural landscapes which are encouraged to protection by EU/National designation		
(12) Ecological values	Heathland landscape mosaic	-	-		They constitute hotspots of biodiversity.	Loss of traditional management (sheep grazing and control burning).	
(13) Recreation and ecotourism	Heathland landscape mosaic	-	-	Tourists	Development of new business in the area.	Reforestation.	Regional strategies to promote tourism within these areas
				Owners of rural business (restaurants, hotels, etc.)	Recreational values for people enjoying these landscapes	Land use change (quarries, sky resorts, etc.)	
REGULATION SERVICES							
(14) Prevention in soil erosion	Heathlands	Popultion, both at local and regional scales	Prevention of problems of erosion because heathlands develop in high slope hills: otherwise the terrain slides.	Population, both at local and regional scales	Same 1950s, although current population is more concerned about the problem of soil erosion	Vegetation cover.	Management practices oriented to reduce biomass continuity (e.g. shrub-cutting, control fires on small patches of heath)
(15) Water purification	Heathlands	Population, both at local and regional scales	Availability of high quality fresh water to human supply.	Population, both at local and regional scales	Availability of high quality fresh water to human supply.	The high shrub and heath biomass accumulated as a consequence of the loss of traditional management which can favour arson fires.	
(16) Carbon sequestration	Heathlands			Earth population	Reduction of the greenhouse effect		

However, this is very controversial, among other reasons, because there is a risk that economic arguments about services will override and outweigh non-economic justifications for conservation (Redford and Adams 2009). Moreover, if these public policies are to reduce, rather than reinforce, the instability of the system, they should not be imposed to local managers from regional, national or international institutions but should arise from a consensus among all institutional levels, taking into account demands from all stakeholders.

There are also conflicting interests between different stakeholders demanding ecosystem services at the same institutional scale (Tacconi 2000). For instance, there is competition between the demand of leisure activities (hunting) and biodiversity conservation targets at both national and international levels (Fig. 5.5b). Recreational hunting is one of the most economically valuable activities taking place nowadays in heathland landscapes at a national and international scale. National game reserves within this area were declared in 1966, although currently their management mainly depends on the Regional Administration. They attract hunters from diverse parts of Spain and even from other countries. Two of the species which have been traditionally hunted in these areas are the grey partridge *Perdix perdix* subsp. *hispaniensis* and the broom hare *Lepus castroviejoi*. They are endemisms of the Iberian Peninsula with very restricted distributions, with the main populations in the Cantabrian Mountains and the Pyrenees for the grey partridge and in the Cantabrian Mountains for the broom hare (Blanco and González *online*). Habitat requirements for both species are similar: semi open pasture-heath/shrub mosaics in uplands, as they are found in the mountain passes (elevation >1000m) (Novoa et al. 2002; Ballesteros and Palacios 2009). The endemic grey partridge is included in the Annex I of the Birds Directive since 1979 (endangered species) (Anon 2009) implying it shall be the subject of special conservation measures concerning their habitat. However, it was hunted in the game reserves of the Cantabrian Mountains until 2001, which has caused a strong decline in their already threatened populations. Similar situation is found with the broom hare which is still hunted nowadays in some parts of the study area, although it is been classified as vulnerable by the UICN (UICN 2011) and therefore considered to be facing a high risk of extinction in the wild. These represent examples of how the demand of an ES (sport hunting) acts as an antagonist (*sensu* Harrington et al., 2010) of the supply of another ES (biodiversity conservation values), constituting an additional factor of instability of the current heathland landscape socio-ecological system.

Figure 5.5 Demand of ES across different institutional scales. Pictures represent the fifties (5a) and the current (5b) socio-ecological systems and the heath-pasture landscapes. Institutional scales are represented in nested boxes placed around the pictures organized from local (inner box) to international scales (outer box). Provisioning, regulating and cultural services are represented respectively in the right-bottom, left-bottom and right-top corners of each diagram. Numbers of the services correspond to those indicated for each service in Tables 5.1 and 5.2.

a)

5.6. CURRENT THREATS AND POSSIBLE ACTIONS

The main threat to ES supply by these landscapes is the abandonment of the traditional management, on which grasslands and heath communities are dependent (Calvo et al. 2002a, 2005, 2007; Bunce et al. 2004). This results in homogenisation processes in the landscape (mainly shrub and heath encroachment and hence, loss of grass patches) involving a reduction in biodiversity at a short-medium term (Garzón-Heydt 2004; Bartolomé et al. 2005) and threatening the cultural landscape heritage (Jongman 2002). Therefore, abandonment mainly affects all services related to their ecological and aesthetic values (services from 8 to 13 in Tables 5.1 and 5.2). For instance, *Calluna vulgaris* is the main component of some heathlands within the mountain passes (4060 *Alpine and Boreal heaths*; Habitats Directive 92/43/EEC, Anon, 1992). The maintenance of these communities at a building state depends exclusively on fire-stimulated germination (Calvo et al. 2002a, 2002b, 2005). The lack of fires, due to land abandonment, have led these communities to enter in a mature to degenerate state (*sensu* Watt 1955), which in the short term will result in their large scale replacement by more competitive grasses or shrubs (Calvo et al. 2002b), eventually leading to the loss of these heath habitats and the biodiversity they support. Another example of how the loss of traditional grazing systems could seriously affect natural and conservation values of these areas is that transhumance is able to influence the top of the ecosystem (scavengers) through the supply of sheep carcasses that are left in the field, contributing to a sustainable management of Egyptian and Griffon vulture populations (Olea and Mateo-Tomás 2009).

Moreover, the loss of traditional management implies the loss of the cultural heritage of the transhumant shepherds, given the influence heathlands had on its development (mainly provisioning services: 1, 2, 5, 6, 7 and 8 in Table 5.1). To compensate for the current low profitability of this system, additional support to the remaining transhumant shepherds would be necessary. Some proposed measures are the direct payment for their ecological contribution to the conservation of ES provision, or the promotion of a market of high quality goods produced with environmentally-friendly techniques (Rescia et al. 2008). Another initiative was the creation of schools for shepherds, aimed at revaluating the profession and ensuring the generational renewal (<http://escueladepastores.es>). Such actions might help prevent the disappearance of one of Europe's ancient and most interesting cultures (Bunce et al. 2004). However, it would be difficult to re-value some of the services in the current socio-ecological system, such as the provisioning of fertilizers due to the high availability of "low-cost" chemical fertilizers (Wessel et al. 2004).

Land abandonment also results in the accumulation of woody above-ground biomass. This in turn may increase the risk of arson fires (Celaya et al. 2010), which affect biodiversity directly, as well as reducing or damaging the supply of regulation services: carbon release, increase of erosion processes and reduction in water quality (services 14, 15 and 16 in Table 5.2). Currently, the Regional Administration (Junta de Castilla y León) is carrying out silvicultural management aimed at facilitating the regeneration of pastures to support extensive grazing, while reducing the connectedness of the fuel and hence, decreasing both the risk and extent of fire. These actions, mainly consisting of shrub-cutting, have yielded successful results in creating grasslands in other regions of Spain (Lasanta et al. 2009). There is however a drawback in the way they are applied in the Cantabrian Mountains, which is related to the recovery response of the type of heath or shrub removed in the process. In the Cantabrian Mountains, cutting *Calluna vulgaris* stands has resulted in a shift in the community species composition (Calvo et al. 2002b; 2002c): cutting practices favour resprouters (such as *Erica australis*) over seeders (*C. vulgaris*) (Calvo et al. 2002b, 2005). This may determine the loss or replacement of the less competitive heath species. However, this factor is rarely considered when designing silvicultural strategies. Controlled fires on patches of *C. vulgaris* would help providing grazing resources in the short term, while preserving *C. vulgaris* dominated habitats at a building state. Between 2000 and 2005, more than 10,000 ha of shrub and heath were cut in the study area (Morán-Ordóñez et al. 2011a). However, biomass removed is left on site, thus increasing the nutrient loads. Looking back to the socio-ecological system of the 1950s, there would be a chance of recovering the service related to provisioning of wood for fuel, currently limited to the production of pellets for local markets, as it has been tried in other countries as Denmark (Gregersen, *personal com.*).

Other threats relate to land use and climate change. The most remarkable land cover/use change within these areas has been the plantation of coniferous trees over large areas of heath (Gómez-Sal et al. 1993; Calvo et al. 2002a). In relation to climate change, some authors have indicated that climate warming could induce an altitudinal shift of Eurosiberian species (e.g. *C. vulgaris*) towards higher altitudes, followed by their replacement by more Mediterranean species (e.g. *Erica australis*) with the consequent change in the landscape composition (Braña et al. 2009). This has already been observed in the Pyrenees where *C. vulgaris* communities are being replaced by the Mediterranean holm oak *Quercus pyrenaica* (Peñuelas and Boada 2003).

5.7. CONCLUSIONS

Heathlands are cultural landscapes and hotspots of biodiversity. However, the conservation status of these habitats is been reported as “unfavourable-bad” in the last European assessment of the Habitats Directive (Article 17; <http://biodiversity.eionet.europa.eu/article17/>). In the same assessment, the conservation status of all heath dominated habitats present in the Cantabrian Mountains was classified as “unknown”. Some of the heathlands from this area (i.e. Alpine and boreal heaths dominated by *Calluna vulgaris*), and hence the landscape mosaics in which they are integrated, are at risk of degradation and loss due to the disappearance of the traditional management activities on which they depend. Land managers responsible for these landscapes are not aware of the whole range of potential services that they could provide, sometimes taking decisions that worsen their conservation status (i.e. cutting over *Calluna vulgaris* heathlands). Therefore, designing conservation strategies for heathlands in this area, where previous management was never specifically aimed at heath habitat preservation, poses a significant challenge.

The ES assessment framework can help achieving conservation targets. The Framework on Ecosystem Service Provision used in this study, and the analysis of ES demand at different institutional and temporal scales, are useful tools to identify and describe the whole range of ES provided by these landscapes, the main threats and stakeholder conflicts on the demands for ES. This information helps incorporating ecological knowledge about multiple ecosystem services of heathlands into decision making. Quantification and economic valuation of ES could be more valuable for policy makers and land managers than qualitative analyses (Johst et al. 2006). However, there is still a gap of knowledge on the importance of different services across heathland landscapes in the Cantabrian Mountains that had to be filled before quantification (sensu Harrison et al. 2010). Moreover, quantification is not always simple, especially for those services with ecological or socio-cultural values, which should also be taken into account when taking decisions on trade-offs between the management of different ES (de Groot 2010). There are also services, which have to be preserved without economic quantification (i.e. conservation values) (Redford and Adams 2010). We are aware that heathland landscapes are an almost endless series of nested mosaic of patches at different spatial scales (Haslett et al. 2010) and hence, there could be many services yet for identifying at some of these scales, which means that further research is needed to have the entire picture of services offered by these valuable landscapes.

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CHAPTER 6

Interactions between ecosystem services: does the demand of grazing services influence the provision of suitable habitat for birds?⁶

⁶ Morán-Ordóñez, A., García, J., Suárez-Seoane, S., de Luis, E. and Calvo, L. (2012) Interactions between ecosystem services: does the demand of grazing services influence the provision of suitable habitat for birds? *Manuscript*.

ABSTRACT

Mountain passes are land management units that have been linked to sheep transhumance for centuries. In these areas, landscape consists of a mosaic dominated by grasslands, heathlands and shrublands, that has traditionally provided multiple ecosystem services to species and human societies. In this study, we assessed the interaction between two services associated to landscapes of mountain passes located in the Cantabrian Mountains (NW Spain). In particular, we analysed whether the demand of grazing services by sheep and wild ungulates have affected landscape patterns during the second half of the twentieth century and how these landscape patterns may have had an influence on the service of provision of habitat for breeding bird species. We used linear mixed effect models to assess the power of stocking rates of sheep and deer in explaining landscape pattern change. We then developed a species distribution modelling approach to evaluate the influence of historical and current landscape patterns on the provision of suitable habitat for birds and also to map those areas where the most suitable habitat is provided (where the highest bird species richness is expected to occur). We found a significant decrease in both patch size and total area occupied by grasslands between 1956 and 2010, as a consequence of shrub encroachment, and also a significant loss of spatial heterogeneity and diversity. However, these landscape patterns were not explained directly by the demand of grazing services, possibly due to the stronger influence of other management activities (i.e. burning). Areas within mountain passes that have historically maintained higher heterogeneity of ecosystems were predicted to provide more suitable habitat for birds, supporting higher species richness. However, changes in land management and land use (i.e. changes in the type of livestock or further abandonment of grazing areas) would favour homogenisation of the landscape, reducing the provision of suitable habitat for supporting high bird species richness within these areas at short-medium term.

6.1. INTRODUCTION

Grasslands, heathlands and shrublands (GHS from here on) use to co-occur in heterogeneous landscape mosaics that have a high conservation interest, as they shelter endemic and/or endangered species, as well as possessing significant aesthetic and cultural values (Wessel et al. 2004; Harrison et al. 2010). Actually, many of these ecosystems are considered as biodiversity hotspots in Europe, since they support a high richness in plants, invertebrates and birds (de Bello et al. 2010). As a consequence, they provide a wide range of services, meaning that species and human societies benefit either from the direct use or enjoyment of their natural resources or from the provision of ecosystem functions (Costanza 1997; Daily 1997). The services provided by these ecosystems have been already identified, at a European level, by Harrison et al. (2010) and can be classified into four groups (MEA 2003): provisioning (grazing, fuel, natural medicines, etc.), cultural (recreation and ecotourism, cultural heritage, etc.), regulating (water purification, carbon sequestration, etc.) and supporting (i.e. soil formation). Provisioning, cultural and regulating services directly benefit people, while supporting services are needed for the maintenance of all direct services (*sensu* Harrinton et al. 2010).

In mountain ranges, the presence of GHS mosaics is being traditionally linked to anthropic land uses, such as grazing and small-scale and low-intensity farming systems (MacDonald et al. 2000; MEA 2005). Services provided by these ecosystems in mountain regions have greater importance, when compared with those located in lowlands, being particularly relevant services related to their ecological values and regulating services (MEA 2005). In mountains, climatic, hydrological and ecological conditions change over short distances due to strong altitudinal gradients. This allows variation in small-scale habitats, which in turn shelter high biodiversity (Becker and Bugmann 2001). Services of regulation of ecological processes are also important, due to the strong influence of mountains systems in downstream processes, for example by limitation of soil erosion, downstream movement of soil nutrients, avoidance/mitigation of damaging impacts of disastrous events such as floods, etc.

The societal demand of services from GHS mosaics in mountain systems has declined in the last decades, mainly due to land abandonment and transformation to other uses (MacDonald et al. 2000; Poschlod et al. 2005; Webb 2005; de Blust et al. 2007). This is due to changes in social needs and preferences (Hein et al. 2006; Rousenvell et al. 2010), which in most European countries have resulted in a decreasing demand on the provision of goods (fuel, grazing, etc.) and

an increasing demand on recreational, cultural and conservation values (Wessel et al. 2004; Harrison et al. 2010). However, stakeholders at different institutional levels (from local to international) may demand different services from these ecosystems, producing conflicting situations (sensu Hein et al. 2006). For example, one species could be demanded for leisure activities (sport shooting), while having high conservation interest for its restricted populations, endemic character, etc. (Morán-Ordóñez et al. unpublished data). Thus, management decisions aimed at enhancing or maintaining the supply of one service can be detrimental to others (see Chan et al. 2006 for an example application). Trade-offs among ecosystem services can lead to the loss of conservation values if some other ecosystem services are prioritized (such as those related to the exploitation of natural goods). Therefore, due to the conservation value of GHS ecosystems (Natura 2000 network; Anon 1992), a comprehensive assessment of trade-offs in both services' supply and management should be used as a complementary tool in conservation strategies. Particular attention should be paid to the intersection between ecological values and other ecosystem services.

In the Cantabrian Mountains (NW Spain), landscapes dominated by GHS are widespread as a consequence of centuries of deforestation and land management aimed at creating grazing areas for sheep, goats, cattle and horses (Pinto-Correia et al. 2005). Within this area, the most interesting examples of landscape mosaics combining these ecosystems are found in mountain passes. Mountain passes are land management units, located in the alpine and subalpine belts, traditionally used by sheep transhumant flocks for summer grazing (Rodríguez 2004). The heterogeneous spatial mosaic currently found in these areas, due to grazing and other management actions such as burning, causes them to support high species diversity (Garzón-Heydt 2004). Generally, heterogeneous landscape patterns have been shown to promote high richness of bird species (Böhning-Gaese 1997; Pino et al. 2000; Ataury and de Lucio 2001; Laiolo et al. 2004; Mitchell et al. 2006; Bacaro et al. 2011). Thus, most mountain passes are currently considered as *sites of community interest* and *special protected areas for birds* declared within the Natura 2000 network (Habitats and Birds Directive: Anon 1992, 2009). However, the traditional management is disappearing, mainly due to the decline on the transhumance system (Rodríguez 2004), which is favouring landscape homogenization at a regional scale through shrub encroachment at a short-medium term (Morán-Ordóñez et al. 2011). This fact may potentially induce loss of biodiversity.

In this study we aim to assess whether changes in landscape patterns in mountain passes in the second half of the twenty century can be explained by the demand of grazing resources by sheep

livestock and wild ungulates. We also analyse if these landscape changes would influence the current provision of suitable habitat for breeding bird species. We suggest that maintaining the demand of grazing services (at sustainable levels) would favour the maintenance of heterogeneous landscape mosaics, which in turn would allow the provision of suitable habitat for sustaining high bird richness.

6.2. STUDY AREA

Mountain passes are located in the southern slope of the Cantabrian Mountains (NW of Spain; Fig. 6.1), where climatic conditions (a mixture of Mediterranean and Atlantic/Eurosiberian influence) favour availability of fresh pastures across the entire summer. In this study we selected 12 mountain passes as case studies, covering a total 4700 ha (the average area of mountain passes was 388 ha). They were equally distributed between the two zones of the Cantabrian Mountains where most mountain passes are located (Babia and Argüellos). Although some are spatially contiguous, they represent independent management units: sheep stocking rates can vary between neighbour mountain passes and movement of flocks between them is not allowed. Moreover, other management actions, such as burning of brooms and heaths are decided and carried out independently in each mountain pass, depending on the needs of individual shepherds. To reduce the variability between the case studies that could result from both environmental conditions and management practices (being able to influence results), we focused on three main aspects when selecting mountain passes: (1) all mountain passes should have been yearly grazed in summer exclusively by sheep flocks, at variable stocking rates, since the 1950s, as changes in the type of livestock (i.e. cattle or horses) would induce different vegetation dynamics due to diverse diet preferences (Celaya et al. 2007; Osoro et al. 2003); (2) wild ungulates should be found in both areas; (3) passes should cover approximately the same altitudinal range in both study zones (ranging from 1470 to 1820m), while capturing as much environmental variation as possible.

6.3. METHODS

6.3.1. Surveys of bird species richness

Surveys were conducted in 2010 and 2011 during the breeding season (from 1st May to 15th June), three hours after sunrise and under fair weather conditions (i.e. without rainfall or strong wind). A point transect sampling method was used to estimate the abundance and detectability of birds (Bibby et al. 2000; Buckland et al. 2001). The number of transects and survey points (sites) in

each mountain pass was proportional to its total area, which resulted in a total of 180 survey sites. After preliminary surveys and analyses on the effective radius of detection of species (DISTANCE 6.0; Buckland et al. 2001), we set a minimum distance of 250 m between survey sites in order to avoid double counting of the same individuals (Buckland 2006). We carried out one visit to each survey site and bird species were recorded during five minutes by both visual and aural contacts (after waiting a minute upon arrival, allowing birds to resume normal behaviour; Bibby et al. 2000).

Figure 6.1. Location of the study area and mountain passes in the Cantabrian Mountains

6.3.2. Data on landscape change and land management

Landscape change was assessed at two different levels: mountain pass and survey site (bird survey point). All analyses were based on a land cover cartography derived from aerial photographs (scale 1:33,000) and high spatial resolution orthophotographs (25 cm), corresponding to 1956 and 2010 respectively. Aerial photos from 1956 were digitalized and orthorectified in ERDAS (2001). The final root mean squared error (RMSE) of orthorectified photos was fitted to less than 2 m and the output pixel size was 2 m. Triangulations were made using the bilinear interpolation resampling method.

Six land cover classes were identified and manually digitalized, at a high spatial detail, for both time steps: rock/bare ground, pastures (grasslands), shrub (including broom and heath), forest, anthropic (roads, forest paths, quarries, buildings, recently burned areas, etc.) and water bodies. Land cover maps of 2010 were validated and improved by visual examination during several field trips to the mountain passes (2010-2011). Finally, this cartography was rasterized to a 5-m spatial resolution for further analysis.

Analyses at the mountain pass level aimed to assess general trends of landscape change between 1956 and 2010 and their relationship with the demand of grazing service. We estimated landscape change on the basis of the following structural parameters, calculated for pasture and shrub land covers: patch density, average patch size, shape index and clumpiness. Moreover, to characterize the complexity of the landscape mosaic, we calculated Shannon's diversity index and landscape heterogeneity on the basis of all land cover classes (Table 6.1). These parameters were chosen since habitat area, isolation and heterogeneity of the surrounding landscape have been demonstrated to have noticeable effects on biodiversity (de Bello et al. 2010). All values were calculated using FRAGSTATS (McGarigal et al. 2002), except heterogeneity which was calculated using the software Chloé (Baudry et al. 1999). Variation in demand of grazing services was estimated by measuring changes in sheep and red deer stocking rates between 1956 and 2010. These data were derived from records of mountain pass auctions (number of sheep assigned to each mountain pass) and ungulate population censuses from game reserves (source: Junta de Castilla y León; Sáenz de Buruaga 1985). Both sheep and red deer make wide use of woody vegetation in their diets (Gebert and Verheyden-Tixier 2001; Celaya et al. 2007) and changes in their stocking rates can induce large land cover changes in the GHS landscape mosaic of the mountain passes. Roe deer and chamois are also abundant on the study sites, however they have a low influence on the shrub-pasture equilibrium due to their strong preference for herbaceous vegetation (García-González and Cuartas 1996; Cornelis et al. 1999). Therefore, they were not considered in our analyses.

Analyses at a survey site level allowed for identifying the relationship between landscape change and the service of habitat provision. We created a set of GIS layers including: data on birds' richness together with topography, landscape structure and composition of each survey site. Topographic variables were: elevation, topographic wetness index (as indicator of soil and water accumulation; Moore et al. 1993) and southness (as a measure of aspect). These variables were derived from a digital elevation model of 5 m spatial resolution (source: Junta de Castilla y León).

Landscape structure was estimated through the index of heterogeneity, while landscape composition included the average percentage of shrubland, pasture and rock. To account for landscape change, we calculated the difference in both heterogeneity and shrubland proportion in the neighbourhood of each survey site for the period 1956-2010 (Table 6.1). All variables were computed in square mobile windows defined at two different scales, according to birds' expected detectability in the landscape mosaic: 50x50 m (the average effective detection radius for the species) and 100x100 m (the maximum detection radius).

6.3.3. Statistical analyses

6.3.3.1. Relationship between grazing services demand and landscape change

We first estimated landscape change between 1956 and 2010 through a cross-tabulation matrix and a cross-classified image. Then, we built linear mixed-effect to assess whether the demand for grazing could explain variations in the structural parameters at the mountain pass level. Individual models were performed for each response variable: patch density, average patch size, shape and clumpiness indices (all of them calculated for pastures and shrublands), heterogeneity and diversity. Each model included average elevation, year, sheep and red deer density as fixed-effect predictors and a random effect, which varied depending on the model, accounting for temporal autocorrelation across repeated measures within the same mountain pass. Pairwise correlations between fixed effects were smaller than 0.7 in all cases (Spearman's test), allowing their inclusion within the same model.

We first selected the most appropriate random effect for each response variable: we used likelihood ratio tests to compare models including all fixed effects and different structures of the random effect term (i.e. mountain pass alone or nested within zone). Models including mountain pass (site) as random effect were selected as most parsimonious for all response variables, except for average pasture patch size, for which mountain pass nested within zone was most supported. Once adjusted the random effect, we selected the fixed terms by removing variables that were not significant ($\alpha=0.05$) through backwards stepwise selection, until adjusting the minimal adequate model. We considered variables with a significant effect ($p<0.05$) to be those that best explained variation in the response variables (Zuur et al. 2009). Finally, residual plots were examined to check on normality assumptions.

Linear mixed-effects models also allowed for assessing significant differences on the stocking rates of sheep and red deers of the mountain passes between 1956 and 2010.

Data analyses were carried out with the R statistical programme, version 2.14.1 (R Development Core Team 2011) using the “lme” function in the “nlme” package (Pinheiro et al. 2011).

6.3.3.2. Relationship between landscape change and the provisioning service of habitat

To analyse how historical and current landscape patterns may determine the provisioning service of habitat for breeding bird species, we chose a species modelling approach (MaxEnt; Phillips et al. 2006; Elith et al. 2006; Phillips and Dudík 2008; Elith 2011). This method would also allow us to map the areas where more suitable habitat is provided to support higher bird species richness. Although MaxEnt does not find causal relationships among dependent and independent variables, it shows preferential conditions of the predictors (i.e. landscape patterns and topography) for the explained variable (bird richness). This method has been successfully used in other studies aimed to estimate species richness (Graham and Hijmans 2006; Pineda and Lobo 2009), although following a different method. These authors created individual distribution models of each species that were afterwards overlapped to obtain a prediction of species richness. In our case, we took advantage of the availability of richness field data collected at the scale of the survey points, reducing the accumulated error involved when overlapping single species models. We converted richness records to one-zero records, being “1” the survey sites where the number of species was higher than the average richness within all mountain passes. Thus, presence data would reflect those sites where the service of provision of habitat for birds is higher than average. We excluded from richness calculation those species observed only in flight, since they do not necessarily depend directly on GHS habitats.

We built two different kinds of models: (i) CURR models, using as predictors: current landscape patterns and composition (heterogeneity and percentage of shrub, pasture and rock/bare for the year 2010) and topography (Topographic Wetness Index, southness and elevation). (ii) HIST models, considering: 2010 landscape patterns and composition, topography and variables accounting for landscape change (change in heterogeneity and shrub for the period 1956-2010) (Table 6.1). Each model was run twice, on a basis of two different spatial resolutions (50x50 m and 100x100 m). Since multi-collinearity may affect model outputs, we verified that pairwise Spearman’s correlations among all predictors were lower than 0.7.

Table 6.1. Variables measured at a mountain pass and survey site level.

Parameter	Description
Mountain pass level	
Landscape structure	
Patch density	Number of pasture or shrub patches, per 100Ha, divided by total landscape area
Average patch size	Mean area of pasture and shrub patches (Ha)
Shape index	Measure of pasture and shrub patch shape complexity: patch perimeter (given in number of cell surfaces) divided by the minimum perimeter (given in number of cell surfaces) possible for a maximally compact patch (in a square raster format) of the corresponding patch area.
Clumpiness	It measures adjacency of patches of the same class, pasture or shrub, by comparing their distribution with a spatially random distribution.
Shannon's diversity index	Number of each land cover type weighted for relative representation
$SDI = \sum_{pi=1}^m pi \ln pi$	Pi= probability of occurrence of the land cover i within the overall landscape m= total number of land covers
Heterogeneity	Measurement of the uneven distribution of land covers within the mountain pass (Baudry et al. 1999)
$Het = \sum_{pij=1}^m pij \ln pij$	Pij= probability of contacts between i and j land covers m= total number of contact combinations among land covers
Grazing demand	
Sheep‡	Density of sheep/ha x 0.15 (source: Junta de Castilla y León)
Deer‡	Density of red deers/ha x 0.25 (source: Junta de Castilla y León)
Survey site level *	
Topographic wetness index	It quantifies the role of topography for redistributing water in the landscape (Moore et al., 1993)
Southness	Measure of the aspect normalized to a -1 to 1 scale. Calculated as: Cos ((aspect -180°) DIV degrees)
Elevation	Average elevation derived from a digital elevation model of 5m of spatial resolution (source: Junta de Castilla y León)
Heterogeneity	Average heterogeneity on the neighbourhood of the survey site (Baudry et al. 1999)
Shrub	Proportion of shrub cover on the neighbourhood of the survey site
Pasture	Proportion of pasture cover on the neighbourhood of the survey site
Rock/bare ground	Proportion of rock cover on the neighbourhood of the survey site
Change in heterogeneity	Heterogeneity of 2010- heterogeneity of 1956
Change in shrub	Shrub cover of 2010- shrub cover of 1956

* All variables relative to survey sites were measured at two different scales through mobile windows representing square neighbourhoods of 50x50 and 100x100m

‡ Densities are multiplied by a factor to obtain stocking rates in livestock units per hectare (LSU/ha) which considers the resource consumption of each species making their densities and stocking rates comparable.

We ran “full” models using 70% of the survey locations (training dataset), retaining the remaining 30% for external evaluation (testing dataset). Ten-fold cross-validation was also applied on the training dataset to estimate errors around fitted responses. The predictive performance of both full and cross-validated models was measured using the Area Under the ROC-Curve (AUC; Hanley and McNeil 1982), adapted for use with background samples (presences vs. background data; Phillips et al. 2006). In order to map areas where the provision of the habitat service for bird species is high or low-null (high/low suitable areas from here on), final outputs were converted into boolean maps using the “maximum training sensitivity plus specificity” threshold (Liu et al. 2005). This threshold maximizes the sum of sensitivity (proportion of actual positives which are correctly identified) plus specificity (proportion of negatives which are correctly identified). Boolean maps were intersected with the cross-classified image (1956-2010) to characterize land cover trends in high/low suitable areas. Specifically, we assessed the effect of increasing rates of shrub encroachment (from 0 to 100%) in the predicted provisioning of habitat for breeding birds as a function of the final shrub cover in 2010.

6.4. RESULTS

6.4.1. Demand for the provision of grazing as a driver of landscape change

The landscape mosaic of mountain passes in 1956 consisted in a shrub matrix (45.7%), with patches of pastures (30.5%) and rock/bare ground (22.6%) (Table 6.2). In 2010, the shrub matrix covered almost 60% of the total area, while the proportion of pasture and rock/bare ground areas decreased (to 22.8 and 16.8% respectively). Forests, anthropic patches and water bodies covered less than 2% of the total area (at both time steps). The largest changes during this period were rock/bare ground to shrub (20.4%) and pasture to shrub (48.5%).

Results of linear mixed effect models suggested significant differences between 1956 and 2010 for some of the structural parameters at the mountain pass level. The variable “year” was consistently selected in the models of shape index of pasture and shrub, average patch size of pasture and shrub, heterogeneity and diversity ($p < 0.05$; Table 6.3). Particularly, models predicted a decrease in average shape index value for both pasture and shrub (from 2.47 to 2.16 and from 2.13 to 1.98 respectively), average size of pasture patches (2.69 to 1.51 ha), heterogeneity and diversity (from 1.32 to 1.22 and from 1.03 to 0.95 respectively). Moreover, models predicted average patch size of shrub to increase from 1.96 to 4.3 ha (Table 6.3). We did not observe any

significant trend for clumpiness and patch density of both shrub and pasture, since models did not explain more variance than a null-model.

We found significant differences in red deer stocking rates between 1956 and 2010 ($p < 0.01$; $\bar{x} \pm \text{SD}_{(1956, 2010)} = 0 \pm 0$ and 0.06 ± 0.05 deers/ha), but this was not the case of sheep stocking rates ($p > 0.05$; $\bar{x} \pm \text{SD}_{(1956, 2010)} = 2.36 \pm 1.36$ and 1.96 ± 0.60 sheep/ha). However, the demand of grazing resources by sheep or red deer within the mountain passes did not contribute significantly to explaining the landscape change ($p > 0.05$ in all models where these variables were selected in the minimal adequate model; Table 6.3).

Table 6.2 Cross tabulation matrix representing land cover change in all mountain passes from 1956 (columns) to 2010 (rows). Values are in percentages.

		Land cover 1956						Total 2010
Land cover 2010		Rock/bare ground	Pasture	Shrub	Forest	Antropic	Water	
	Rock/bare ground	71.65	1.08	0.41	0.55	16.29	0.00	16.82
	Pasture	7.79	49.20	13.15	1.64	8.11	0.67	22.83
	Shrub	20.42	48.48	85.11	10.76	34.21	0.22	58.54
	Forest	0.08	0.62	0.99	85.65	2.06	0.00	1.10
	Antropic	0.06	0.61	0.35	1.41	39.32	0.00	0.55
	Water	0.00	0.00	0.00	0.00	0.00	99.11	0.17
Total 1956		22.64	30.49	45.73	0.50	0.47	0.17	100.00

6.4.2. Service of provision of habitat for breeding bird species

A total of 890 individuals, belonging to 48 species, were contacted in the 180 survey sites (see Annex III of supplementary material for the full list of species). Regarding their observed preferences of habitat within the mountain passes, we found 13 grassland, 10 shrub, 3 woodland and 15 ecotone species. Seven species were unclassified because either they occurred in all habitats (i.e. the black kite *Milvus migrans*; common cuckoo *Cuculus canorus*; common buzzard *Buteo buteo* and the griffon vulture *Gyps fulvus*) or required for specific habitat features as water mass (mallard *Anas platyrhynchos*), cliffs (grag martin *Ptyonoprogne rupestris*) or antropic environments (house sparrow *Passer domesticus*). Nine of the observed species are included in the Annex I of the Birds Directive (Anon 2009): *Perdix perdix hispaniensis* (grey partridge), *Anthus campestris* (tawny pipit), *Emberiza hortulana* (ortolan bunting), *Lullula arborea* (woodlark), *Luscinia svecica* (bluethroat), *Sylvia undata* (dartford warbler), *Pyrrhocorax pyrrhocorax* (red-billed chough), *Circus pygargus* (Montagu's harrier) and *Gyps fulvus* (griffon vulture). The most common species were the hedge accentor *Prunella modularis* (found in 78.89% of the sample point sites), the water pipit (*Anthus spinoletta*; 28.33%), the sky lark

(*Alauda arvensis*; 27.22%) and the common stonechat (*Saxicola torquata*; 25.56%). Richness values did not differ significantly among mountain passes and survey sites.

Table 6.3 Minimal adequate linear mixed-effect models of the structural landscape parameters measured in the mountain passes. Models of landscape parameters which did not explain more variance than a null model are omitted. Year1956 coefficients are the basic intercepts of the models. Predictions of each model, standardized to the mean values of altitude, sheep or deer in each case, and their correspondent standard errors were calculated for both time steps.

Model	Estimate	t	P value
Shape index of pastures			
Intercept	2.67	16.81	0.000
Year2010	-0.27	-2.76	0.020
Sheep	-0.68	-1.58	0.145
Predicted value (1956/2010): 2.47 / 2.16 (SE=0.097)			
Shape index of shrublands			
Intercept	2.13	48.64	0.000
Year2010	-0.15	-2.41	0.035
Predicted value (1956/2010): 2.13/ 1.98 (SE=0.044)			
Average patch size of pastures			
Intercept	15.73	2.83	0.020
Year2010	-1.47	-3.06	0.014
Elevation	-0.01	-2.38	0.041
Sheep	-1.69	-1.13	0.289
Deer	24.69	1.07	0.312
Predicted value (1956/2010): 2.69 / 1.51 (SE= 1.182)			
Average patch size of shrublands			
Intercept	3.82	3.53	0.005
Year2010	2.70	3.78	0.004
Sheep	-6.33	-2.15	0.057
Predicted value (1956/2010): 1.96 / 4.3 (SE=0.6470)			
Heterogeneity			
Intercept	1.32	24.08	0.000
Year2010	-0.11	-2.74	0.019
Predicted value (1956/2010): 1.32 / 1.22 (SE= 0.0549)			
Diversity			
Intercept	1.03	22.04	0.000
Year2010	-0.08	-2.98	0.013
Predicted value (1956/2010): 1.03 / 0.95 (SE= 0.0467)			

The predictive performance of models of habitat suitability was always lower than 75% in both final and cross-validated models (AUC_{test} and $AUC_{cross-validated}$), indicating poor to moderate model discrimination (Table 6.4). There were only marginal differences in predictive performance between both CURR and HIST models and between different spatial resolutions.

For all models, the most important predictors of bird richness in the mountain passes were topographic wetness index, elevation and proportion of pasture and shrubland cover. Sites with high provision of habitat were located below 1800 m, had a high accumulation of soil and water

(high values of TWI), regardless of aspect, and always included a certain area of pastures integrated in heterogeneous mosaics with shrublands and rock/bare ground (high values of shrubland or rock/bare ground decreased the suitability to shelter high bird species richness) (Fig. 6.2 and 6.3). In these areas, the landscape either remained stable during the study period (no change in either heterogeneity or shrub cover), or heterogeneity or shrub percentage increased (Fig. 6.2).

Table 6.4 Modelling results detailed by: (i) Contribution, in percentage, of each variable to final models (these contributing more than 10% are in bold); (ii) AUC values for both full (training and testing) and cross-validated models. CURR models include as predictors current patterns of landscape structure and composition (heterogeneity, shrub, pasture and rock/bare ground), together with topographic variables (topographic wetness index, southness and elevation. HIST models included as covariates current landscape patterns, topography and also variables accounting for landscape evolution within the study period (1956-2010): change in heterogeneity and shrub. Each model was run at two spatial resolutions 50x50m and 100x100m.

Variables/Results	CURR-50m	CURR-100m	HIST-50m	HIST-100m
Topographic Wetness Index	22.4	24.7	20.2	22.7
Southness	6.1	3.7	5	3.2
Elevation	21.3	22.6	19.8	20.8
Heterogeneity 2010	7.2	5.7	5.2	5.2
Pasture 2010	21.6	28.2	20.4	26.6
Shrub 2010	11.2	10.3	9.9	8.6
Rock/Bare ground 2010	10.1	4.8	9.1	5.6
Change in heterogeneity (1956-2010)			5.7	3.7
Change in shrub (1956-2010)			4.7	3.8
Full model AUC train (%)	81.2	81.2	82.4	81.5
Full model AUC test (%)	61.9	61.5	63	61.8
Cross-validated AUC (%; $\bar{x} \pm SD$)	72.9 $\pm$ 8.3	69.1 $\pm$ 5.8	71.6 $\pm$ 7.2	68.7 $\pm$ 7.5

When boolean maps of habitat suitability (50x50 m HIST model) were compared to the cross-classified image (1956-2010), we observed that almost 65% of the areas highly suitable for birds maintained the same land cover during the study period (30.5 % of them being grasslands), 21% showed shrub encroachment (change from rock/bare ground or grassland to shrub) and 11.7% increased the amount of grasslands (shrub to grassland or bare ground to grassland). Areas of low suitability corresponded to areas of no change (total 74%: 66 % of them were shrub and rock/bare ground), to areas where shrub increased (19%) and to areas where grasslands increased (6%). Similar results were found for 100x100 m HIST predictions.

Effects of shrub encroachment in habitat provisioning service for bird species differed depending on both the increase in shrubland between 1956 and 2010 and its initial and final percentage in the neighbourhood of a considered area (Table 6.5). Although there was a slight increase/decrease in values with increasing neighbourhood area considered (50x50 or 100x100 m), in general we

observed that approximately 70% of the areas where shrub increased had low suitability for supporting high bird richness, whereas 30% had high suitability (Table 6.5). Areas where the shrub percentage in the neighbourhood of a pixel was higher than 80% in 2010 were mainly classified as low suitable for supporting high bird richness. Areas where the increase of shrubland (from 0 to 80%) implied a shrub percentage in 2010 between 40 and 80% were mainly classified as highly suitable.

Table 6.5 Shrub encroachment effect on model predictions of low/high habitat suitability for bird species (measured as percentages). Calculations were made on a basis of 10,000 random stratified points (regarding the percentage of increase of shrub) over the predictions for HIST model (model considering topographic variables and current and historical data on land cover) First column refers to the percentage of increase on shrub within the period 1956/2010. Second column refers to the final percentage shrub cover found in 2010. Values reflect percentage of sampling points that occurred in low or high suitable areas within each increase of shrub percentage.

		Predicted habitat suitability for birds (HIST model)			
		50x50m resolution		100x100m resolution	
Increase of shrub	Shub cover 2010	Low	High	Low	High
0-20%	<40%	17.90	14.55	18.35	10.64
	40-80%	9.15	15.16	15.78	18.72
	>80%	35.18	8.06	31.33	5.18
20-40%	<40%	9.20	8.93	4.06	4.72
	40-80%	8.62	19.08	17.20	22.51
	>80%	44.35	9.83	42.00	9.50
40-60%	40-80%	12.40	21.47	16.39	12.17
	>80%	58.19	7.95	64.18	7.26
60-80%	40-80%	11.24	14.74	9.53	8.64
	>80%	66.29	7.74	71.67	10.15
80-100%	>80%	67.05	32.95	82.77	17.23
Total		68.36	31.64	72.63	27.37

6.5. DISCUSSION

One of the main changes in traditional management in the Cantabrian mountain passes during the last 60 years has been the reduction in grazing demand by transhumant sheep flocks (Rodríguez 2004). On the other hand, populations of wild ungulates have significantly grown in the area in the last decades following to reintroduction programs and decreasing competition with domestic livestock (Sáenz de Buruaga 1985). Thus, we expected the demand of grazing services by sheep or wild ungulates to explain changes in landscape structural patterns. Nevertheless, we did not find such results. This may reflect that landscape changes would not respond in our case study to the direct demand for grazing, but to other management activities (such as burning) aimed at improving grazing resources, for which spatially explicit data were lacking. At the end of the grazing season (end of September - beginning of October), shepherds used to burn patches of

heath and broom in order to maintain open areas, avoid shrub encroachment and ensure availability of high nutritional quality grasslands for the following summer (Calvo et al. 2002a, Rodríguez 2004). However, by the beginning of the 1990's most of mountain passes were included under different categories of land protection status, being banned the use of fire as a management tool. Thus, the use of fire by shepherds ceased, allowing rapid post-fire recovery and expansion of shrublands and heathlands (Calvo et al. 2002a, b). The reduction in fires also allowed the growth of small patches of forest from scattered trees that had been confined to margins of streams due to the intensive management.

Figure 6.2 Maxent response curves. Each curve shows the effect of each predictor on the logistic response when keeping all other environmental variables at their average sample value. The average response of the variable is indicated with a red line and the standard deviation with a blue area. The figure shows as an example response curves corresponding to the cross-validated model of 50m that includes predictors accounting for landscape evolution (HIST model).

The Cantabrian Mountains are considered a biodiversity hotspot due to the high variety of species they support (Worboys et al. 2010). However, changes in landscape patterns due to cessation of traditional management could alter the provision of habitat for bird species in the area. Model predictions showed that areas providing higher suitable habitat for breeding bird species (i.e. supporting higher species richness) corresponded to the less homogenous zones within each mountain pass. This is in concordance with other studies in which heterogeneity of landscape

patterns was one of the most important explanatory factors for bird richness (Böhning-Gaese 1997; Pino et al. 2000; Ataury and de Lucio 2001; Mitchell et al. 2006; Bacaro et al. 2011). Generally, landscapes with many different habitat types are able to support more species than those dominated by one or a few habitat types (Böhning-Gaese 1997). In the mountain passes, areas providing more suitable habitat mainly corresponded to zones where open grasslands have historically been maintained in combination with other land covers, mainly shrubs, heaths, rocks and water resources (high values of the Topographic Wetness Index corresponded to small streams, gullies or flat areas where water accumulated, such as peat soils and small lakes). They also included areas where grassland cover percentage has been increased by shrub-cutting (Morán-Ordóñez et al. 2011). Highly suitable habitat for bird species was also predicted in areas where there was an increase of less than 80% in shrub cover during the study period. This is due to the fact that pastoral abandonment of grasslands temporally increases habitat heterogeneity thanks to shrub encroachment (Suárez-Seoane et al. 2002; Laiolo et al. 2004), favouring new conditions for more bird species, especially those dependent on shrub or ecotone habitats. However, when shrub became highly dominant (>80%), areas were predicted as providing low suitable habitat for high bird species richness, since species adapted to open spaces decline (Laiolo et al. 2004; Zozaya et al. 2012). Therefore, our results support the hypothesis of intermediate disturbance, whereby maximum diversity will be attained with an intermediate level of disturbance (Connell, 1978; Huston 1979; Pineda et al. 2002). The recovery of small forest patches due to secondary succession also created new conditions and resources, which may explain the presence of forest bird species (i.e the European nuthatch *Sitta europaea*), increasing overall species richness. Areas of low suitability were mainly rocky crests (due to harsh conditions and low availability of food resources for birds) and areas covered by shrub throughout the entire period (large homogeneous shrub patches).

Although causality relations cannot be inferred from MaxEnt models, response's variable and output maps provided clues about the landscape patterns and topographic conditions more related to bird richness patterns, also allowing for identifying areas offering the most suitable habitat for breeding bird species. The low performance of the models could be related to several factors. On one hand, we found that richness patterns did not differ significantly among mountain passes and survey sites: this may result from our site selection, specifically aimed at reducing variability among mountain passes in terms of environmental conditions and management practices. This in turn reduced the discriminative power of the models because similar richness values were found

for the entire range of each environmental predictor (land cover, topography and historical land cover). On the other hand, the land cover cartography used as a basis for the analyses may also have influenced model performance. Shrub was considered as a unique land cover, without distinguishing among types of shrub or heath, in order to allow for comparison between 1956 and 2010 landscape patterns. However, the presence of a species at this scale may not respond to general shrub cover, but rather to the cover of a certain type of shrub or heath providing microhabitat (e.g. the bluethroat *Luscinia svecica* occurs in mountain passes only associated to shrub patches of *Cytisus purgans*; García unpublished data). Thus, although our approach gave us clues about the historical evolution of landscape in the mountain passes and its influence on current availability of suitable habitat for bird species, our study would benefit from a further evaluation considering different types of heath and shrub habitats.

Interactions between services. Conservation implications

Traditional management has allowed the maintenance of GHS landscape mosaics in the mountain passes for centuries. Intermediate levels of disturbance associated to the demand of grazing services (mainly grazing and burning) have led to heterogeneous semi-open mosaics determining the provision of suitable habitat for many bird species. However, the decline on the sheep grazing system that has traditionally exploited mountain passes for centuries has led to changes in the livestock (mainly horses and cows), loss of traditional management (burning) and, in some cases, the complete abandonment of mountain passes. Cattle and horses make a different use of the shrub-grassland mosaic (feeding only on herbaceous resources compared to sheep which make larger consumption of woody vegetation; Osoro et al. 2003; Celaya et al. 2007), leading to higher levels of shrub encroachment (Calvo et al. 2002a). These situations can represent a future scenario to be considered when planning conservation strategies for maintaining the provisioning service of habitat, at a desirable level, for bird species, as well as for other species of high conservation interest (i.e. carabid beetles; Taboada et al. 2011). Most of the species we detected in this study directly depend on open grasslands or ecotones and may, therefore, be negatively affected by the homogenization of landscape patterns caused by long term abandonment of GHS landscape mosaics followed by shrub or forest replacement (sensu Suárez-Seoane et al. 2002 and Laiolo et al. 2004). It would also affect other species which do not directly depend on the GHS mosaic, but on the resources linked to grazing systems and transhumance flocks (as observed for the Griffon vulture *Gyps fulvus* and its dependence on livestock carcasses; Olea and Mateo-Tomas 2009). Moreover, shrub homogenization would increase the accumulation of woody above-ground

biomass and lead to higher risk of arson fires (Pausas et al. 2008), which would affect directly biodiversity at both short and medium term. Despite the high resilience of heath and shrub communities, at the elevation of our study area, they require between 9 and 20 years to recover the original vegetation structure (Calvo et al. 2002b, 2005). Since land management associated to grazing systems in mountain passes has played a decisive role in shaping current patterns of bird diversity, it would be decisive to integrate socio-economic aspects linked to grazing activities in bird management strategies, in order to avoid negative interactions between these two important services provided by these landscapes: provision of grazing resources and of suitable habitat for bird species.

6.6. CONCLUSIONS

Mountain passes of the Cantabrian Mountains have experienced deep changes in landscape over the last 60 years. The main change has been the decrease of grasslands as a consequence of shrub encroachment, mainly due to the abandonment of traditional management linked to grazing systems. However, we found these changes were not directly explained by the demand of grazing services (stocking rates of sheep and wild ungulates). Zones within mountain passes that have historically maintained higher heterogeneity of habitats (with a combination of grasslands, shrublands, rocks and water resources) were predicted to provide more suitable habitat for breeding bird species. The loss of semi-open GHS mosaics due to land abandonment or changes in the demand of grazing services (cattle and horses instead sheep) can lead to landscape homogenization with negative consequences for the provisioning service of habitat for birds. Levels of intermediate disturbance would allow the maintenance of heterogeneous mosaics, highly suitable for supporting high species richness of breeding birds.

Figure 6.3. Figure shows the land cover evolution of two mountain passes ("El Prado" and "Lagüezos" in left and right columns respectively), and the areas where the service "provisioning of habitat" for bird species is higher on a basis of MaxEnt models' results of HIST model at 50*50m spatial resolution ("Richness row").

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ANNEX III

List of the bird species recorded in the 180 survey sites of the mountain passes surveys of 2010-2011. Column “Habitat” classifies the species regarding their ecological preferences: grassland, shrub, woodland or ecotone. Abundance, percentage of detection (percentage of sampling point sites where the species was recorded) and conservation status are also indicated. SPEC = Species of European Conservation Concern (BirdLife Internacional. 2004). Species used in the modelling analyses are indicated with an asterisk. Source: García, *unpublished data*.

Common name	Scientific name	Habitat	Abundance	Detection %	Conservation status	Directive Birds
Hedge accentor	<i>Prunella modularis</i> *	Shrub	226	78,89%		
Water pipit	<i>Anthus spinoletta</i> *	Grassland	64	28,33%		
Sky lark	<i>Alauda arvensis</i> *	Grassland	53	27,22%	SPEC 3	
Linnet	<i>Carduelis cannabina</i> *	Ecotone	48	15,00%	SPEC 2	
Common stonechat	<i>Saxicola torquata</i> *	Ecotone	46	25,56%		
Ortolan bunting	<i>Emberiza hortulana</i> *	Ecotone	43	18,89%	SPEC 2	Annex I
Blackbird	<i>Turdus merula</i> *	Ecotone	40	22,22%		
Bluethroat	<i>Luscinia svecica</i> *	Shrub	36	19,44%		Annex I
Yellow-billed chough	<i>Pyrrhocorax graculus</i>	Grassland	32	6,67%		
Common whitethroat	<i>Sylvia communis</i> *	Ecotone	32	17,22%		
Northern wheatear	<i>Oenanthe oenanthe</i> *	Grassland	30	15,56%	SPEC 3	
Wren	<i>Troglodytes troglodytes</i> *	Shrub	26	13,89%		
Red-billed chough	<i>Pyrrhocorax pyrrhocorax</i>	Grassland	24	8,33%	SPEC 3	Annex I
Red-legged partridge	<i>Alectoris rufa</i> *	Ecotone	19	7,22%	SPEC 2	
Black redstart	<i>Phoenicurus ochruros</i> *	Grassland	18	10,00%		
Rock bunting	<i>Emberiza cia</i> *	Shrub	13	6,67%	SPEC 3	
Yellowhammer	<i>Emberiza citronella</i> *	Ecotone	13	6,11%		
Robin	<i>Erithacus rubecula</i> *	Shrub	13	6,67%		
Whinchat	<i>Saxicola rubetra</i> *	Ecotone	11	3,89%		
Tawny pipit	<i>Anthus campestris</i> *	Ecotone	10	5,56%	SPEC 3	Annex I
Montagu’s harrier	<i>Circus pygargus</i>	Ecotone	9	3,33%		Annex I
Garden warbler	<i>Sylvia borin</i> *	Shrub	9	5,00%		
Blackcap	<i>Sylvia atricapilla</i> *	Shrub	8	4,44%		
Common wood pigeon	<i>Columba palumbus</i>	Woodland	7	1,67%		
Pied wagtail	<i>Motacilla alba</i>	Grassland	7	3,89%		
Grey partridge	<i>Perdix perdix hispaniensis</i> *	Ecotone	7	2,22%	SPEC 3	Annex I
Common cuckoo	<i>Cuculus canorus</i>		6	3,33%		
Rock Thrush	<i>Monticola saxatilis</i> *	Grassland	6	3,33%	SPEC 3	

Annex III (Continued).

Common name	Scientific name	Habitat	Abundance	Detection %	Conservation status	Directive Birds
Rock Thrush	<i>Monticola saxatilis</i> *	Grassland	6	3,33%	SPEC 3	
Common quail	<i>Coturnix coturnix</i>	Grassland	5	2,78%	SPEC 3	
Magpie	<i>Pica pica</i>	Ecotone	3	0,56%		
Dartford warbler	<i>Sylvia undata</i> *	Shrub	3	1,67%	SPEC 2	Annex I
Common kestrel	<i>Falco tinnunculus</i>	Grassland	2	1,11%	SPEC 3	
Eurasian Jay	<i>Garrulus glandarius</i>	Woodland	2	1,11%		
Corn bunting	<i>Miliaria calandra</i> *	Grassland	2	1,11%	SPEC 2	
Common chiffchaff	<i>Phylloscopus collybita</i> *	Shrub	2	1,11%		
Grag martin	<i>Ptyonoprogne rupestris</i>		2	1,11%		
European serin	<i>Serinus serinus</i> *	Ecotone	2	1,11%		
Mallard	<i>Anas platyrhynchos</i>		1	0,56%		
Tree pipit	<i>Anthus trivialis</i> *	Ecotone	1	0,56%		
Common buzzard	<i>Buteo buteo</i>		1	0,56%		
Common raven	<i>Corvus corax</i>	Grassland	1	0,56%		
Carriion crow	<i>Corvus corone</i>	Grassland	1	0,56%		
Common chaffinch	<i>Fringilla coelebs</i> *	Shrub	1	0,56%		
Griffon vulture	<i>Gyps fulvus</i>		1	0,56%		Annex I
Wood lark	<i>Lullula arborea</i> *	Ecotone	1	0,56%	SPEC 2	Annex I
Black kite	<i>Milvus migrans</i>		1	0,56%	SPEC 3	
House sparrow	<i>Passer domesticus</i>		1	0,56%	SPEC 3	
European nuthatch	<i>Sitta europaea</i>	Woodland	1	0,56%		

GENERAL DISCUSSION

1. Main land cover trends

Land cover changes in the Cantabrian Mountains during the last decades have been coincident with those accomplished in other Mountain ranges in Europe: heath and shrub encroachment in abandoned fields and grasslands, forest expansion and homogenization of landscape patterns (MacDonald et al. 2000; Jongman 2002; Roura-Pascual et al. 2005; Vicente-Serrano et al. 2005; Agnoletti 2007; Rey-Benayas et al. 2007; Álvarez-Martínez 2010). These landscape dynamics have been detected at both regional and local scales and also at different temporal time spans (from 1991 to 2004 in Chapters 1 and 2, and from 1956 to 2010 in Chapter 6), being mainly linked to changes in traditional extensive livestock farming and agricultural systems.

In the southern slope of the Cantabrian Mountains, the decline of the transhumance system, based on sheep grazing, has been a driver of special relevance for explaining these land cover changes (mainly marked since 1960s). This decline has involved the loss of traditional management based on grazing, cutting and burning (Calvo et al. 2002a), which had allowed the maintenance during centuries of large areas of open-mixed mosaics of semi-natural grasslands, heathlands and shrublands (at a building state). This gradual loss of management have lead to higher levels of shrub encroachment in the landscape (Calvo et al. 2002a) and to the appearance of new land covers, as open mining and coniferous plantations (Gómez-Sal 1993) (Chapter 1). Moreover, sheep have been substituted, in some cases, for cattle or horses, which make a different use of the open-mixed mosaics, feeding only on herbaceous resources, while sheep make larger consumption of woody vegetation (Osoro et al. 2003; Celaya et al. 2007). Additionally, the decline on the transhumance system has favoured depopulation of mountain areas, since it was the most important source of incomes for both municipalities and families for centuries (Rodríguez 2004). Rural abandonment involved the encroachment of small agricultural subsistence fields by *Rosa canina* and *Cytisus* shrub (as observed in similar mountain ranges; Suárez-Seoane 1998; Bartolomé et al. 2005). However, since 2000, new management policies aimed at both creating pasture areas and reducing the risk of fire have resulted in a reduction of both shrubland and heathland areas and their connectedness in the last years (mainly shrub-cutting since 2000; Gil and Torre 2007) (Fig. 1). This was especially relevant in protected areas, due to the higher availability of economical resources aimed at managing natural resources (Chapter 2).

Puerto de Vegarada (Lugueros)

Figure 1. Effects of shrub cutting practices on heath and shrub extension and connectedness: a) Heathland of *Calluna vulgaris* and *Vaccinium myrtillus* dominated the landscape before 2011. Only a few patches of pasture and broom (yellow flowered) can be observed; b) In 2011 patches of *Calluna vulgaris* were cut and biomass was removed. Only some isolated patches of broom remained in cut areas.

2. Contribution of remote sensing data to our study

The combination of historical and recent sources of geographical data allowed for understanding medium-long term ecological processes as secondary succession (Carmel and Kadmo 1998). Particularly, remote sensing images were a key source of environmental data when analyzing land cover patterns and dynamics at a regional scale (Roughgarden et al. 1991; Rogan et al. 2002; Franklin and Wulder 2002; Lozano 2007; Lillesand et al. 2008; Álvarez-Martínez et al. 2010) (Chapter 1 and 2). Complementarily, the use of historical and current aerial photographs allowed for analysed long term changes at a local scale (Chapter 6).

Analyses of temporal series of Landsat images through hard classification methods (MaxLike) have been widely used for obtaining land cover maps and explaining general landscape dynamics within a given area (i.e. Shalaby and Tateishi 2007; Schulz et al. 2010). However, the land cover classified maps obtained in our study (Chapter 1) contained an element of uncertainty related to the difficulty of distinguishing between classes of vegetation with similar structure and spectral response (Steele et al. 1998; Metternicht 2003; Shao and Wu 2008). Uncertainty especially occurs at habitat boundaries, where there is always some confusion regarding which category to assign to a given pixel (Lewis et al. 2000; Bradley and Mustard 2005). This problem is particularly relevant when classifications are performed in heterogeneous landscapes (Álvarez-Martínez et al. 2010) such as the Cantabrian Mountains (Chapter 1). In our study, confusion between land cover categories mainly occurred when trying to distinguish between heathlands and shrublands (which had to be grouped within the same class) and classes of forests. This reduced the accuracy of subsequent analyses made on a basis of the temporal series of land cover maps (i.e. effects of land cover status on changes in landscape structural patterns; Chapter 2).

However, when individual channels were combined with other environmental variables (topography, climate) in species/habitats distribution modelling techniques, they allowed for successfully building accurate spatially explicit maps of the current distribution of different formations dominated by heath or shrub species (Chapter 3). Landsat channels aided definition of the spatial outputs by providing missing predictor information (i.e. land cover vegetation and soil moisture; Pearson et al. 2004; Zimmerman et al. 2007). They allowed for detecting of the specific signal of the dominant species of each heath formation, helping to discriminate between suitable and unsuitable sites that could not be distinguished from bioclimatic or topographic information alone. Improvement of map accuracy by Landsat channels was especially relevant when modelling formations dominated by generalist species, which were otherwise over-predicted. This

approach showed advantages versus the traditional implementation of remote sensing data in species distribution modelling as land cover maps or spectral indices (Suárez-Seoane et al. 2002; Pearson et al. 2004; Newton-Cross et al. 2007; Buermann et al. 2008). It allowed the model to identify the most relevant wavelength channel for each formation without need of pre-selection of a spectral index, avoiding also incorporating the uncertainties linked to the implementation of classified land cover maps.

Nevertheless, when modelling and mapping the current distribution of two competitor species (i.e. *Calluna vulgaris* and *Erica australis*) the highest explanatory and predictive accuracy of models was obtained by models including biotic interactions, abiotic factors and remote sensing data as predictors, as observed in other studies (Heikkinen et al. 2007) (Chapter 4). Although biotic interactions occur at small scales, they can also influence species distributions at a regional scale (Guisan and Thuiller 2005). Their inclusion in modelling approaches increased the performance and predictive power of models of the target species (Leathwick and Austin 2001; Anderson et al. 2002; Heikkinen et al. 2007; Meier et al. 2010). Presence of a dominant competitor in a given area (i.e. *Calluna vulgaris* due to its specialist character) will be the main limiting factor for the weakest competitor (i.e. *Erica australis*). As a consequence, distribution of the weakest competitor will be constrained to “competition free” areas. Moreover, significant differences in the number of limiting factors affecting species distribution between areas of potential competition and competition-free areas would influence competition “outputs” of biotic interactions (competitive dominance, sympatric coexistence, etc.). However, further research is needed to support this observation.

3. Management implications

Heathlands and shrublands occur across the Cantabrian Mountains under a range of abiotic and abiotic constraints, as described in chapters 1 to 4. Despite their abundance, heathlands have been traditionally considered wastelands or marginal lands, and still do, (Calvo et al. 2002b), being converted to other land covers, when possible (pine plantations; Gómez-Sal et al. 1993), due to its low productivity. Loss of traditional management is putting at a risk of degradation and disappearance these formations of high conservation interest (Habitats directive; Anon 1992) (Chapters 1 to 4), as well as the biodiversity they support (Chapters 5 and 6). In the Cantabrian Mountains, active management specifically aimed at heathlands conservation is still lacking. The first step to develop effective conservation policies should be to raise awareness regarding the

value of heathlands among stakeholders and managers at different institutional scales. In this Thesis, these values were assessed by examining the ecosystem services that heathlands provide, which can help achieving conservation targets.

The Framework on Ecosystem Service Provision proposed by Rounsevell et al. (2010), allowed for successfully identifying a wide range of ecosystem services provided by heathlands on a temporal scale, as well as their beneficiaries, main threats and potential management responses to preserve the provision of each service (Chapter 5). Ecosystem services belonged to three groups (MEA 2003): provisioning (heath and shrub wood as fuel, fertilizer, for livestock breeding and thatching houses, medicinal plants, game, grazing resources, etc.), cultural (cultural heritage, sport hunting, conservation values) and regulating services (prevention in soil erosion, carbon storage, etc.). Heathlands were traditionally associated to subsistence systems up to the 1950s (dependent on interdependent local services), which mainly demanded provisioning services (at local and regional scales). However, nowadays the demand of provisioning services has significantly declined in favour of cultural services (mainly those related to conservation values demanded at national and international scales). Currently, the demand of ecosystem services for stakeholders at different institutional scales (from local to international) produces conflicting situations (*sensu* Hein et al. 2006; i.e. conservation of threatened species vs. sport hunting), that could induce to the loss of degradation of heathlands and their biodiversity values.

The analyses on heathlands distribution patterns and drivers of change, together to the ecosystem services assessment, introduced in this Thesis, provides ecological knowledge about heathlands in the Cantabrian Mountains that should be incorporated into current decision making and management planning at different scales (mainly local and regional). This has already been done in other European countries, where heathlands are subjected to specific management aimed at their conservation (e.g. England or Norway). By the case of Castilla y León, this information could be of especial interest when designing management plans within the Natura 2000 network (which are currently under development).

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CONCLUSIONS

1. LANDSAT images proved a useful tool for evaluating land cover changes which occurred, at a regional scale, in the southern slope of the Cantabrian Mountains during the period 1991-2004. The most relevant changes detected were an increase in bare ground areas, a loss of shrublands and heathlands and an increase in forest cover. *Chapter 1.*
2. The main drivers of land cover change identified at a regional scale in the Cantabrian Mountains between 1991 and 2004 were: (i) Mining (opening of quarries); (ii) Variation in livestock stoking rates; (iii) Shrub and heath cutting practices aimed at favouring the regeneration of pastures to support extensive grazing and to create firebreaks for controlling both risk and extent of wildfires and (iv) Secondary succession processes towards forest stages, favoured by land abandonment and the decrease in forest fires. *Chapter 1.*
3. Forest cover is expected to increase mainly in valley bottoms and neighbouring slopes. This change is mostly controlled by topographic factors (altitude and slope) and variations in goat stocking rates. Shrubland and heathland loss will depend on decisions made by managers at a regional level, on the basis of the demand of pastures by cattle and sheep grazing. Spatially explicit outputs of land cover change models provided relevant ecological knowledge to define management actions in this area. *Chapter 1.*
4. The changes in landscape patterns observed at the municipality level in the southern slope of the Cantabrian Mountains between 1991 and 2004 were partially related to land protection status. The extent and connectedness of shrublands and heathlands decreased in protected areas and increased in non-protected areas. Forest trends were more influenced by the proportion of forest cover present at the beginning of the study period (1991) than by land protection status. *Chapter 2.*
5. Habitat models based on environmental predictors accurately predicted the distribution of four heath and shrub formations of high conservation interest in the southern slope of the Cantabrian Mountains. *Chapter 3.*

6. The ecological traits of species influenced the performance of habitat models. Models of formations dominated by specialist species (*Calluna vulgaris* and *Genista hispanica* subsp. *occidentalis*) showed higher accuracy than those of formations dominated by generalists (*Cytisus purgans* plus *Genista florida* and *Erica australis* subsp. *aragonensis*), the distributions of which were over-predicted. *Chapter 3.*

7. The inclusion of LANDSAT channels as predictors in habitat distribution models of heathlands and shrublands improved model accuracy and helped to obtain more realistic spatial predictions, when compared with models including environmental variables only. They allowed the detection of the specific signal of each formation and provided environmental information that was otherwise unavailable (mainly regarding land cover and moisture content of both vegetation and soil). *Chapter 3.*

8. The use of reflectance values in habitat distribution models showed some advantages over other remote sensing data previously used in modelling approaches. They allowed the model to identify the most relevant wavelength channel for each formation, instead of selecting a priori a given spectral index, avoiding uncertainties arising from the use of classified land cover maps. *Chapter 3.*

9. Model predictions for *Calluna vulgaris* and *Erica australis* benefited from including their mutual biotic interactions as covariates when modelling their current distributions. More specifically, the highest explanatory power and predictive accuracy was obtained by including biotic interactions as predictors in the models, together with abiotic factors and remote sensing data (LANDSAT channels). *Chapter 4.*

10. The spatial variation of the limiting factors (biotic and abiotic) for *Calluna vulgaris* and *Erica australis* heathlands had a strong influence in determining their current distribution patterns. Particularly, *Calluna vulgaris* constituted the main limiting factor for *Erica australis* in areas of potential sympatry, where the former dominated due to its specialized character, limiting the distribution of *Erica australis* to competition-free areas. However, human disturbances can modify this equilibrium, based on limiting factors, by removing the dominant species. *Chapter 4.*

11. The number of factors limiting the distribution of heath formations changed across their predicted geographical ranges. In the case of *Calluna vulgaris*, this number was significantly higher in areas where its niche might overlap with *Erica australis*' niche (areas of potential sympatry) than in those areas where it was predicted to occur alone (competition-free areas). For *Erica australis* we found the opposite trend (a smaller number of limiting factors in areas of potential sympatry). These differences may affect the behaviour of these species under competition scenarios. However, our results are not conclusive and further research (combining modelling approaches and field observations) is needed to assess the effect of the number of limiting factors in competition studies. *Chapter 4.*

12. The ecosystem service provision framework proved a useful tool for describing the whole range of ecosystem services provided by heathlands in the southern slope of the Cantabrian Mountains. These included provisioning (heath and shrub wood as fuel and fertilizer or for livestock breeding and thatching houses, medicinal plants, habitat, grazing resources, etc.), cultural (cultural heritage, sport hunting, conservation values) and regulating services (prevention in soil erosion, carbon storage, etc.). In the last sixty years, the demand of provisioning services from heathlands (at local and regional scales) has significantly declined in favour of cultural services, mainly demanded at national and international scales. *Chapter 5.*

13. The socio-ecological system of the 1950s was mainly dependent on interdependent local services (most heathland services were demanded at a local scale and benefited the local population). The socio-ecological system of the 2010s is an unstable multi-scale system in which services are demanded by stakeholders at different institutional scales producing conflicting situations (i.e. conservation of threatened species vs. recreational hunting). *Chapter 5.*

14. The main landscape change observed in mountain passes between 1956 and 2010 was an increase in shrublands (including heathlands) to the detriment of rock/bare ground and grasslands. This modified the landscape structure, as shrub patch expansion resulted in more rounded edges between shrub and pasture patches and the average size of pasture patches decreased. These changes also determined a decrease in spatial heterogeneity and diversity. However, landscape patterns within mountain passes were not explained by the demand of grazing services by sheep or wild ungulates, possibly due to the stronger influence of other management activities on landscape dynamics (i.e. burning). *Chapter 6.*

15. Comparison of historical and recent sources of geographical data (aerial photos of 1956 and orthophotos of 2010) helped understanding medium- and long-term ecological processes at a local scale in mountain passes. Changes in landscape patterns influenced the current service of provisioning suitable habitat for breeding bird species. Particularly, zones that have historically maintained higher heterogeneity of habitats (mosaic of grasslands, shrublands and rocks) supported a higher richness of species. *Chapter 6.*

CONCLUSIONES

1. Las imágenes de satélite LANDSAT fueron herramientas clave en la evaluación temporal de los cambios de ocupación ocurridos a escala regional en la vertiente sur de la Cordillera Cantábrica durante el periodo 1991-2004. Los principales cambios detectados fueron: incremento del suelo descubierto, pérdida de matorral y aumento del bosque. *Capítulo 1.*

2. Los principales *drivers* o agentes de cambio observados a escala regional en la Cordillera Cantábrica fueron: (i) las actividades mineras a cielo abierto; (ii) la variación en la carga y presión ganaderas; (iii) los desbroces de matorral realizados con la doble finalidad de incrementar la disponibilidad de pasto para ganado extensivo y crear cortafuegos para controlar, tanto el riesgo, como la intensidad de incendios y (iv) los procesos de sucesión secundaria favorecidos por el abandono del territorio y el descenso en el número incendios. *Capítulo 1.*

3. El incremento del bosque se producirá principalmente en los fondos de valle y las laderas próximas a éstos. Este cambio está controlado principalmente por factores topográficos (altitud y pendiente), así como por la carga de ganado caprino. La pérdida de matorral estará asociada a decisiones de manejo tomadas por los gestores a escala regional basadas, principalmente, en la demanda de pastos para ganado ovino y vacuno. Los mapas resultantes de los modelos de cambios de ocupación del suelo proporcionaron un conocimiento ecológico que puede resultar de gran utilidad en el desarrollo de planes de gestión y manejo en esta zona. *Capítulo 1.*

4. La dinámica estructural del paisaje en los municipios estudiados en la vertiente sur de la Cordillera Cantábrica durante el periodo 1991-2004 no pudo asociarse completamente al grado de protección del territorio. La extensión y la conectividad espacial de los matorrales se redujeron en zonas protegidas, mientras que aumentaron en zonas no protegidas. Sin embargo, la proporción de bosque presente en cada municipio al inicio del periodo de estudio (1991) jugó un papel más importante en la evolución del bosque que el estado de protección del territorio. *Capítulo 2.*

5. Los modelos de hábitat basados en variables ambientales predijeron con exactitud la distribución de las cuatro formaciones de matorral de elevado interés de conservación en la vertiente sur de la Cordillera Cantábrica. *Chapter 3.*

6. Las estrategias vitales de la especie dominante de cada formación de matorral condicionaron los resultados de los modelos. Así, los modelos de las formaciones dominadas por especies especialistas (*Calluna vulgaris* y *Genista hispanica* subsp. *occidentalis*) fueron más realistas que aquellos de las formaciones dominadas por generalistas (*Cytisus purgans* junto con *Genista florida* y *Erica australis* subsp. *aragonensis*). En este último caso, las predicciones sobreestimaron la distribución de dichas formaciones. *Capítulo 3.*

7. La inclusión de las bandas de las imágenes LANDSAT incrementó el ajuste de los modelos de distribución de formaciones de matorral y contribuyó a obtener predicciones espaciales más realistas en comparación con los modelos basados sólo en predictores ambientales. Las bandas permitieron detectar la señal de reflectancia específica de cada formación, incorporando al modelo información no disponible de otro modo: ocupación del territorio y contenido en humedad del suelo y de la vegetación. *Capítulo 3.*

8. El uso de los valores de reflectancia de las bandas LANDSAT como predictores en los modelos de hábitat mostró ventajas frente al uso de índices espectrales y mapas derivados de procesos de clasificación de imágenes satélite. Esta aproximación permitió al modelo seleccionar la banda más relevante para cada formación, evitando reducir la información espectral a un único índice, así como la incertidumbre asociada al uso de mapas de ocupación. *Capítulo 3.*

9. El ajuste y realismo de los modelos de *Calluna vulgaris* y *Erica australis* se incrementó cuando se consideró como variable explicativa la interacción biótica entre ambas especies. En concreto, los modelos que mostraron mayor exactitud y poder predictivo fueron aquellos basados en variables bióticas junto con abióticas y derivadas de la teledetección (bandas del LANDSAT). *Capítulo 4.*

10. La variación espacial de los factores (bióticos y abióticos) que limitan la distribución de los brezales de *Calluna vulgaris* y *Erica australis* ejerció una fuerte influencia en sus patrones de distribución. En concreto, *Calluna vulgaris* resultó ser el principal factor limitante para *Erica australis* allí donde potencialmente podrían ocurrir en simpatría. En estas zonas, *Calluna vulgaris* dominó, dado su carácter especialista, forzando la exclusión competitiva de *Erica australis*, que sólo podría aparecer en áreas libres de competencia. Sin embargo, las perturbaciones antrópicas pueden alterar este equilibrio basado en factores limitantes, mediante la eliminación de la especie dominante. *Capítulo 4.*

11. El número de factores que limitaron la distribución de las especies de brezal estudiadas varió a lo largo de su área de distribución. Para el caso de *Calluna vulgaris*, éste número fue significativamente mayor en aquellas zonas donde su nicho se superpondría con el nicho de *Erica australis* (áreas donde potencialmente podrían ocurrir en simpatría) que en aquellas zonas libres de competencia. En el caso de *Erica australis* se observó la tendencia contraria (menor número de factores limitantes en zonas de potencial simpatría). Estas diferencias en el número de factores limitantes podrían condicionar el comportamiento de ambas especies bajo situaciones de competencia. Sin embargo, nuestros resultados no son concluyentes y se requiere de una investigación más profunda, combinando modelos teóricos y trabajo de campo, para valorar si esta variación en el número de factores limitantes puede tener un efecto real en la dominancia competitiva de una especie. *Capítulo 4.*

12. El marco teórico de valoración de los servicios de los ecosistemas resultó ser una herramienta de gran utilidad para identificar y describir el amplio rango de servicios proporcionados por los brezales en la vertiente sur de la Cordillera Cantábrica. Dichos servicios fueron: aprovisionamiento (ej. uso de madera de brezo y escoba como combustible y fertilizante o para techar y encamar al ganado, extracción de plantas medicinales, provisión de hábitat, etc.), culturales (patrimonio cultural, caza deportiva, valores de conservación) y regulación (prevención de la erosión del suelo, fijación de carbono, etc.). En los últimos sesenta años, la demanda de servicios de aprovisionamiento de los brezales (a escalas local y regional) ha disminuido significativamente en favor de la demanda de servicios culturales. *Capítulo 5.*

13. El sistema socio-ecológico de la década de los cincuenta dependía principalmente de servicios locales interdependientes (la mayoría de los servicios proporcionados por los brezales de demandaban a escala local y beneficiaban a la población local). Este sistema se ha transformado en la actualidad, en un sistema multi-escalar inestable en el que la demanda de servicios de los brezales por parte de sectores pertenecientes a diferentes escalas institucionales produce situaciones conflictivas (ej. demanda de servicios de conservación de especies amenazadas vs. demanda de permisos para cazar esas mismas especies). *Capítulo 5.*

14. El principal cambio en el paisaje observado en los puertos pirenaicos para el periodo 1956-2010 fue la expansión del matorral, en detrimento de zonas ocupadas por roca/suelo descubierto y pastizal. Estos cambios de ocupación repercutieron en la estructura del paisaje: la expansión del matorral produjo bordes más redondeados entre matorral y pastizal y se redujo el tamaño medio de las manchas de pastizal. Estos cambios supusieron un descenso de la diversidad y heterogeneidad espacial. Sin embargo, los patrones estructurales del paisaje de los puertos pirenaicos no pudieron relacionarse con la demanda de pasto por parte de las ovejas ni de los ungulados salvajes, posiblemente debido a la mayor influencia en las dinámicas de cambio de otras actividades de manejo tradicional, tales como el cese de las quemas. *Capítulo 6.*

15. La comparación de cartografía actual e histórica (ortofotografías del 2010 y fotos aéreas de 1956) a escala local permitió comprender los procesos ecológicos que operan a medio-largo plazo en los puertos pirenaicos. Los cambios producidos en los patrones paisajísticos determinaron la importancia del servicio de aprovisionamiento de hábitat para las aves nidificantes. Concretamente, aquellas zonas donde el manejo tradicional permitió el mantenimiento de mosaicos heterogéneos de pastizal, matorral y roca constituyen zonas de elevada idoneidad para albergar gran riqueza ornítica. *Capítulo 6.*

CARTOGRAPHIC MATERIAL

Mountain pass “Lagüezos”. La Cueta, Cabrillanes. León.

Maps guide

Top left: aerial photo 1956

Top right: land cover 1956

Bottom left: orthophotography 2010

Bottom right: land cover 2010

Land cover legend

Water	Shrub
Antropic	Pasture
Forest	Rock/bare ground

Photo by Javier García (2011)

Mountain Pass “Vega Redonda”. La Cueta, Babia. León.

Maps guide

Top left: aerial photo 1956

Top right: land cover 1956

Bottom left: orthophotography 2010

Bottom right: land cover 2010

Land cover legend

Water	Shrub
Antropic	Pasture
Forest	Rock/bare ground

Photo by Javier García (2011)

Mountain Pass “El Prado”. Vega de Viejos y Meroy, Cabrillanes. León.

Maps guide

Top left: aerial photo 1956
 Top right: land cover 1956
 Bottom left: orthophotography 2010
 Bottom right: land cover 2010

Land cover legend

Water		Shrub
Antropic		Pasture
Forest		Rock/bare ground

Mountain pass “Rañadoiro”. La Cueta, Cabrillanes. León.

Maps guide

Top left: aerial photo 1956

Top right: land cover 1956

Bottom left: orthophotography 2010

Bottom right: land cover 2010

Land cover legend

Water		Shrub
Antropic		Pasture
Forest		Rock/bare ground

Photo by Angela Taboada (2009)

Mountain pass “Cuevalancho”. Torre de Babia, Cabrillanes. León.

Maps guide

Top left: aerial photo 1956

Top right: land cover 1956

Bottom left: orthophotography 2010

Bottom right: land cover 2010

Land cover legend

Water		Shrub
Antropic		Pasture
Forest		Rock/bare ground

Photo by Alejandra Morán (2011)

Mountain pass “Vallina Luenga”. La Cueta, Cabrillanes. León.

Maps guide

Top left: aerial photo 1956

Top right: land cover 1956

Bottom left: orthophotography 2010

Bottom right: land cover 2010

Land cover legend

Water		Shrub
Antropic		Pasture
Forest		Rock/bare ground

Mountain pass “Tiendas y Fontanilla”. Valdelugeros. León.

Maps guide

Top left: aerial photo 1956

Top right: land cover 1956

Bottom left: orthophotography 2010

Bottom right: land cover 2010

Land cover legend

Water		Shrub
Antropic		Pasture
Forest		Rock/bare ground

Photo by Javier García (2011)

Mountain pass “Solana y Carba”. Valdelugueros. León.

Maps guide

Top left: aerial photo 1956

Top right: land cover 1956

Bottom left: orthophotography 2010

Bottom right: land cover 2010

Land cover legend

Water		Shrub
Antropic		Pasture
Forest		Rock/bare ground

Photo by Javier García (2011)

Mountain pass “Pozos y Peñavare”. Cerulleda y Redipueñas, Valdelugeros. León.

Mountain pass “La Llana y Monte”. Villaverde de la Cuerna, Valdelugueros. León.

Maps guide

Top left: aerial photo 1956

Top right: land cover 1956

Bottom left: orthophotography 2010

Bottom right: land cover 2010

Land cover legend

Water	Shrub
Antropic	Pasture
Forest	Rock/bare ground

Photo by Javier García (2011)

Mountain pass “Cácabo”. Puebla de Lillo e Isoba. León.

Maps guide

Top left: aerial photo 1956

Top right: land cover 1956

Bottom left: orthophotography 2010

Bottom right: land cover 2010

Land cover legend

Water		Shrub
Antropic		Pasture
Forest		Rock/bare ground

Photo by Alejandra Morán (2010)

Mountain pass “Peña”. Puebla de Lillo e Isoba. León.

Maps guide

Top left: aerial photo 1956

Top right: land cover 1956

Bottom left: orthophotography 2010

Bottom right: land cover 2010

Land cover legend

Water	Shrub
Antropic	Pasture
Forest	Rock/bare ground

Photo by Leonor Calvo (2011)