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# Indicators for the evaluation of the conservation value of mountain landscapes in the framework of the Pan-European Biological and Landscape Diversity Strategy

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Departamento de Biodiversidad y Gestión Ambiental  
Área de Ecología

INDICADORES PARA LA EVALUACIÓN DEL VALOR DE CONSERVACIÓN  
DE LOS PAISAJES DE MONTAÑA EN EL MARCO DE LA ESTRATEGIA PAN-  
EUROPEA DE LA DIVERSIDAD BIOLÓGICA Y DEL PAISAJE

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INDICATORS FOR THE EVALUATION OF THE CONSERVATION VALUE OF  
MOUNTAIN LANDSCAPES IN THE FRAMEWORK OF THE PAN-EUROPEAN  
BIOLOGICAL AND LANDSCAPE DIVERSITY STRATEGY

**Paula García Llamas**  
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**A mi familia**

**A mis amigos y compañeros**



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# Table of contents

Abstract.....	17
1. Introduction .....	21
2. Objectives.....	31
3. Thesis outline .....	32
4. The case study .....	33
Chapter 1. Using remote sensing products to classify landscape. A multi-spatial resolution approach.....	37
Chapter 2. Landscape heterogeneity as a surrogate of biodiversity in mountain systems: what is the most appropriate spatial analytical unit?.....	77
Chapter 3. Linking species functional traits of terrestrial vertebrates and environmental filters: a case study in temperate mountain systems .....	115
Chapter 4. Impact of land cover change on ecosystem service supply in mountain systems .....	149
GENERAL DISCUSSION .....	183
GENERAL CONCLUSIONS.....	18391



# Índice

Resumen.....	19
1. Introducción.....	21
2. Objetivos.....	31
3. Esquema de la Tesis .....	32
4. El caso de estudio.....	33
Capítulo 1. Uso de productos de teledetección para la clasificación del paisaje. Una aproximación multi-escalar.....	37
Capítulo 2. La heterogeneidad del paisaje como indicador de la biodiversidad en sistemas de montaña: cual es la unidad espacial de análisis más adecuada? .....	77
Capítulo 3. Relación entre los rasgos funcionales de vertebrados terrestres y los filtros ambientales: un caso de estudio en sistemas montañosos templados.....	115
Capítulo 4. Impacto de los cambios en la cobertura terrestre sobre la provisión de servicios ecosistémicos en sistemas de montaña .....	149
DISCUSIÓN GENERAL.....	183
CONCLUSIONES GENERALES.....	193



## Abstract

Mountain landscapes are highly heterogeneous mosaics of great conservation concern that have resulted from the interaction among climatic variability, altitudinal gradients, uneven topography, and long-term human intervention history. Such heterogeneity constitutes a key factor allowing mountains to become biodiversity hotspots, as well as suppliers of a wide range of ecosystem services which are beneficial for human well-being. This Doctoral Thesis aims to identify spatial variations in landscape heterogeneity on the basis of remote sensing data across a range of mountain systems in Spain (i.e. the Cantabrian Mountains, the Central System and the Spanish Pyrenees), to assess its relationship with biological diversity patterns and ecosystem services supply at different temporal and spatial scales.

As a basis to identify spatial variations in landscape heterogeneity, the landscapes of the three mountain systems were classified and characterized by using data on land cover, topography and human influence that were combined by running a Principal Component Analysis (PCA) followed by a cluster analyses. For the specific case of the Cantabrian Mountains, we evaluated the applicability of two of the most readily available open remote sensing products informing on land cover (the categorical map CORINE at 30 m resolution and the continuous NDVI spectral index derived from NOAA-AVHRR satellite imagery at 1 km resolution), to be used in landscape classifications across different spatial resolutions (30 m, 90 m, 180 m and 1 km). These remote sensing products allowed for successfully developing meaningful landscape classifications across different spatial resolutions.

The relationship between landscape heterogeneity and terrestrial vertebrate species richness in the three mountain systems was assessed using two spatial analytical unit approaches: eco-geographic (watersheds) vs arbitrary (square windows of different sizes). The effect of the landscape heterogeneity on vertebrate species richness was closely dependent on the spatial analytical unit approach and the spatial analytical unit size. We claimed for further consideration of eco-geographic approaches in biodiversity studies, since traditional arbitrary

approaches might show limitations for detecting relationships between landscape heterogeneity and biodiversity patterns.

We evaluated the role of landscape heterogeneity, among other environmental filters, on structuring functional trait (feeding guild, habitat use type and daily activity) assembly of terrestrial vertebrate species in the Cantabrian Mountains. We detected a major role of climate, topography and human influence variables as environmental filters of functional traits, compared to the role of landscape heterogeneity.

Finally, we explored how land cover changes, undergone during the last two decades (1990-2012) in the Cantabrian Mountains, have modified the potential supply capacity of ecosystem services (regulating, provisioning and cultural services) at regional and local scales. We also compared trends in the use of ecosystem services with estimates of their potential supply at local scale. We observed landscape homogenization, which favored regulating and provisioning services associated to woody vegetation expansion, while decreasing the potential supply of services associated to traditionally managed landscapes, such as livestock. These changes in ecosystem service potential supply matched trends in ecosystem service use.

The results of this Thesis have improved existing knowledge on the role of landscape heterogeneity for explaining and preserving biodiversity patterns and ecosystem service supply, which are beneficial for human well-being, in mountain systems.

## Resumen

Los paisajes de montaña son considerados como mosaicos altamente heterogéneos de gran interés desde el punto de vista de la conservación, los cuales son resultado de la interacción entre la variabilidad climática y topográfica, los gradientes altitudinales y la influencia antrópica. Esta heterogeneidad constituye un factor clave para explicar el papel de los sistemas de montaña como centros de biodiversidad y como sistemas proveedores de una gran variedad de servicios ecosistémicos, que contribuyen al bienestar humano. Esta Tesis Doctoral tiene como objetivo identificar las variaciones espaciales en la heterogeneidad del paisaje, a partir de datos de teledetección, en una serie de sistemas montañosos de España (la Cordillera Cantábrica, el Sistema Central y los Pirineos españoles), con el fin de evaluar su relación con los patrones de diversidad biológica y la provisión de servicios ecosistémicos a distintas escalas espaciales y temporales.

Como base para identificar las variaciones espaciales en la heterogeneidad de paisaje, se clasificaron y se caracterizaron los paisajes de los tres sistemas de montaña mediante el uso de datos relativos a la cobertura terrestre, topografía e influencia humana, que se combinaron mediante la aplicación de un Análisis de Componentes Principales (PCA) seguido de un análisis cluster. En el caso específico de la Cordillera Cantábrica, se evaluó la aplicabilidad de dos de los productos de teledetección de libre acceso, relativos a la cobertura terrestre, más comúnmente utilizados (el mapa categórico CORINE Land Cover a 30 m de resolución y el índice espectral NDVI derivado de las imágenes de satélite NOAA-AVHRR a 1 km de resolución espacial); para el desarrollo de clasificaciones de paisaje a diferentes resoluciones espaciales (30 m, 90 m, 180 m y 1 km). Estos productos de teledetección permitieron elaborar con éxito clasificaciones de paisaje con sentido ecológico a través de distintas resoluciones espaciales..

La relación entre la heterogeneidad del paisaje y la riqueza de especies de vertebrados terrestres, en los tres sistemas de montaña, fue analizada utilizando dos unidades espaciales de análisis diferentes: unidades eco-geográficas (cuencas) vs unidades arbitrarias (ventanas cuadrangulares de diferente tamaño). El efecto de la heterogeneidad del paisaje sobre la riqueza de especies de vertebrados

terrestres dependió, en gran medida, del tipo de unidad espacial de análisis y del tamaño de la misma. Es necesario de una mayor consideración de los enfoques de análisis eco-geográficos en los estudios de biodiversidad, ya que los enfoques de análisis arbitrarios, tradicionalmente utilizados, podrían mostrar limitaciones para detectar las relaciones entre la heterogeneidad de paisaje y los patrones de biodiversidad.

Por otra parte, se evaluó el papel de la heterogeneidad del paisaje, entre otros filtro ambientales, en la estructuración de los rasgos funcionales (tipo de alimentación, tipo de uso del hábitat y periodo de actividad) de las especies de vertebrados terrestres en la Cordillera Cantábrica. Se detectó una mayor influencia del clima, la topografía y las variables de influencia humana como filtros ambientales de los rasgos funcionales de las especies de vertebrados terrestres, en comparación con el papel de la heterogeneidad del paisaje.

Por último, se exploró la influencia de los cambios en la cobertura terrestre, experimentados durante las dos últimas décadas (1990-2012) en la Cordillera Cantábrica, sobre los cambios en la capacidad potencial de provisión de servicios ecosistémicos (servicios de regulación, provisión y culturales), a escala regional y local. De igual forma, se compararon las tendencias en el uso de los servicios ecosistémicos con las estimaciones de su provisión potencial a escala local. Se detectaron tendencias hacia la homegenización del paisaje, las cuales favorecieron la provisión potencial de servicios de regulación y de provisión ligados a las expansion de la vegetación leñosa, mientras que la provisión potencial de servicios asociados a paisajes tradicionales, como la capacidad ganadera, se vio reducida. Estos cambios en la provisión potencial de servicios ecosistémicos se correspondió con las tendencias de cambio en el uso de los mismos.

Los resultados de esta Tesis permiten mejorar el conocimiento existente sobre el papel que desempeña la heterogeneidad del paisaje en la explicación y preservación de los patrones de biodiversidad y la provisión de servicios ecosistémicos que contribuyen al bienestar humano, en los sistemas de montaña.

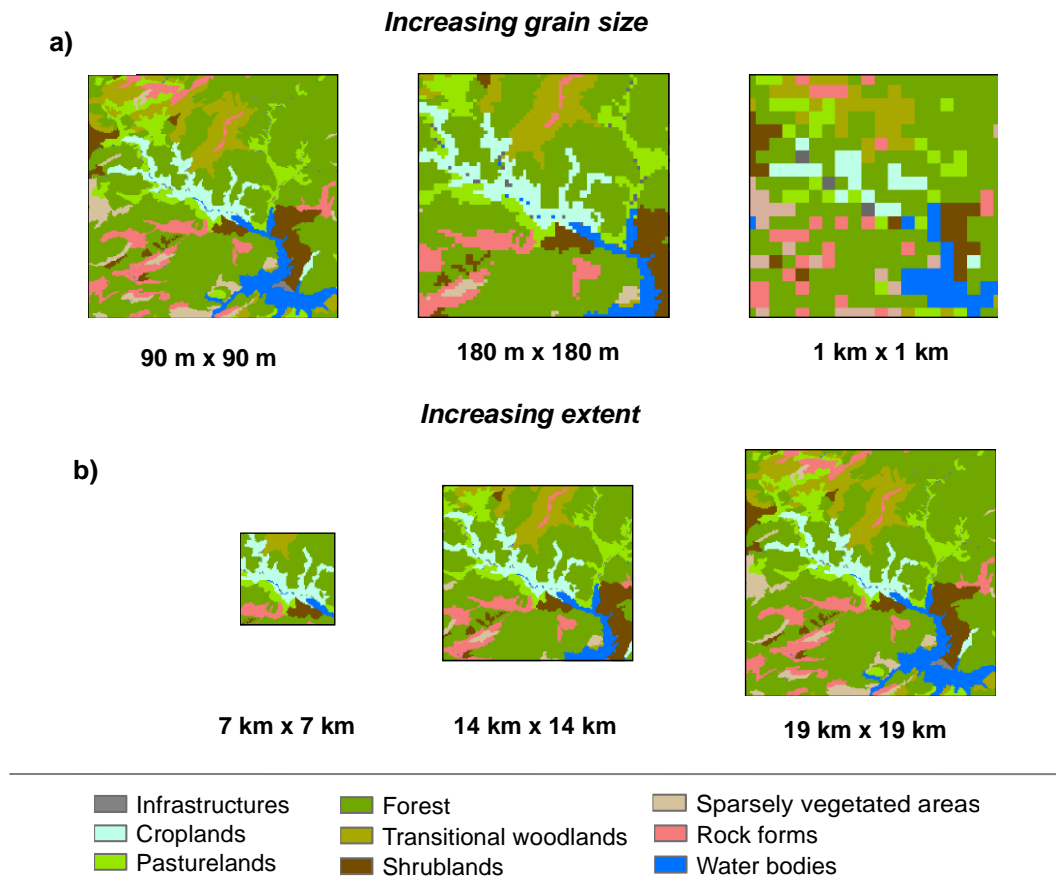


# 1. Introduction

## 1.1. The landscape as a framework of study: the importance of landscape heterogeneity

Historically, the analysis of ecological systems has been addressed considering homogeneous fragments of communities and ecosystems, regardless of their spatial context (Cushman *et al.*, 2010). However, the emergence of landscape ecology in the mid-1980s, allowed for recognizing the importance of spatial heterogeneity in ecological studies and the need to study patterns and processes over large regions (Turner *et al.*, 2001). From the perspective of landscape ecology, landscape is understood to be a spatially heterogeneous mosaic composed of clusters of ecosystems, each cluster representing areas of fairly homogeneous environmental conditions, resulting from the interaction among physical, ecological, socioeconomic and cultural factors and processes (Wu & Hobbs, 2002). In this way, landscape ecology looks into the composition and configuration of landscape elements or patches and the role played by landscape structure in a wide range of ecological patterns and processes (Wiens & Milne, 1989), which operates at different spatial and temporal scales (Turner *et al.*, 2001).

Ecological patterns and processes have a characteristic scale (or range of scales) at which they operate and at which they can be most effectively studied (Wu & Li, 2006). Scale generally refers to the spatial (grain and extent) and temporal dimension of a phenomenon (Figure 1). As landscapes are spatially heterogeneous areas, structure, dynamics and functions of landscape are scale-dependent, hence these landscapes being hierarchical and scale-dependent systems (Turner, 1989). The perception of landscape spatial patterns depends on the scale at which observations are made (Schooley, 2006). For example, a landscape that is heterogeneous from the perspective of a small mammal could be perceived as homogeneous from the perspective of a larger one. Likewise, landscape might show a stable mosaic at one temporal scale but could change at another, depending on the moment when the study has been conducted.



**Figure 1.** Schematic representation of components of spatial scale, grain and extent. a) Effect of increasing grain size from 90 m x 90 m to 180 m x 180 m and 1 km x 1 km grain size and b) effect of changing the extent (from 7 km x 7 km window size to 14 km x 14 km and 19 km x 19 km) of a landscape map based on the CORINE Land Cover dataset.

This scale-dependence is related to the hierarchy theory that distinguishes levels of organization and levels of observation and conceives the scale as a constraint of the observer, rather than an intrinsic property of a system (Uuemaa *et al.*, 2005). As a result of scale multiplicity within spatial patterns and ecological processes, scale becomes a keystone concept in landscape ecology, core to understand the pattern-process interactions (Wu & Qi, 2000) and the dynamics of territory (Álvarez-Martínez, 2010).

Cartography is the basic tool for characterizing and analyzing the landscape and its spatial heterogeneity (Burel & Baudry, 2004). The development and improvement of remote sensing techniques and Geographic Information Systems (GIS) have provided powerful instruments for landscape mapping. Further, the

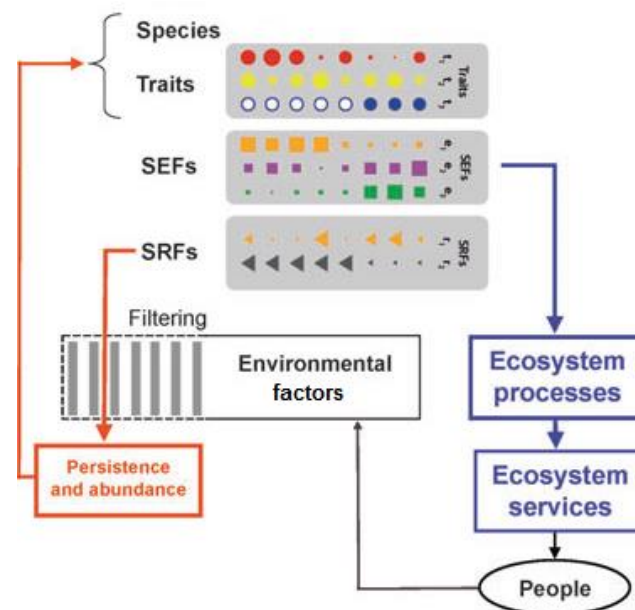
application of GIS has made it possible to handle and operate with important amounts of spatial data, while remote sensing provides considerable multiscale data useful for characterizing the spatial structure and mosaic of landscape (Lioubimtseva & Defourny, 1999). The utilization of remote sensing in landscape studies has largely focused on two different aspects: classification analyses to identify land cover classes (Lawrence *et al.*, 2004; Álvarez Martínez, 2010; Morán-Ordóñez, 2012) and quantitative analyses of vegetation (e.g. phenology, primary productivity; Gamon *et al.*, 2013 or aboveground biomass Zhu & Liu, 2015) based on continuous variables, mainly spectral indexes (Lozano *et al.*, 2010). Using additionally complementary spatial data (e.g. topography or urban influence data), detailed landscape maps can be developed from derived remote sensing products.

All remote-sensing based classifications are however subject to a certain degree of error and uncertainty (Shao & Wu, 2008). Therefore, it would be necessary to carry out a verification process that estimates the quality of the mapping product and its operational applicability (Álvarez-Martínez *et al.*, 2010). Quantitative statistical accuracy assessment techniques, such as confusion matrixes and derived error metrics (Foody, 2002), provide a powerful mechanism for a reliable evaluation of thematic maps (Congalton, 2001; Shao & Wu, 2008). Likewise, uncertainty associated with the existence of mixed pixels, representing areas that contain more than one class, in the definition of crisp mutually exclusive classes can be analyzed on the bases of fuzzy logic (Foody, 2002; Bolliger & Mladenoff, 2005).

The landscape approach is gaining recognition in the context of biological diversity conservation, prompting that policies, at national and international level, include landscape subject in their agendas (Calvo-Iglesias *et al.*, 2009). The Pan European Biological and Landscape Diversity Strategy intends to stop and reverse the degradation of biological and landscape diversity values in Europe (Council of Europe, 1996). Likewise, the European Landscape Convention encourages the identification of landscapes and their values and the analysis of landscape characteristics, with the aim of conservation, management and planning (Council of Europe, 2000). In this context, biotic processes and biological diversity are influenced by the spatial heterogeneity of the landscape mosaic, thus evidencing the relevance of landscape diversity for the expression of biological diversity

(Walz, 2011). Landscape metrics, usually derived from categorical maps, are often used to describe the compositional and spatial configuration of the landscape (Schindler *et al.*, 2013). Accordingly, they have become popular biodiversity surrogates for estimating and modelling biodiversity (Katayama *et al.*, 2014; Plexida *et al.*, 2016) in a cost-effective way, within conservation policy strategies (Gimona *et al.*, 2009).

The response of species to landscape heterogeneity is conditioned by species' functional traits (Barbaro & van Halder, 2009; Concepción *et al.*, 2016), through specific effect-response functions (Díaz *et al.*, 2013). The specific response function is associated with species' response to environmental factors, which might act as ecological filters, and the specific effect function determines species' potential to deliver functions (Díaz *et al.*, 2013), based on particular traits.



**Figure 2.** Functional trait evolution, ecosystem function and environmental factors (source: modification by Díaz *et al.*, 2013). Species have certain functional traits ( $t_1$ ,  $t_2$ ,  $t_3$ ; where size of symbols is functional groups within each trait) that determine the functional effects of species on ecosystems (SEFs;  $e_1$  to  $e_3$ ) and their response to environmental factors (SRFs;  $r_1$ ,  $r_2$ ). SEFs and SRFs colours indicate which trait determines their value (e.g. orange is the result of  $t_1$  and  $t_2$ ). SEFs might affect ecosystem properties which are the basis of ecosystem benefits contributing to human well-being, which along with socio-economic drivers, influence environmental factors. These environmental factors might exert a filtering effect on the species pool according to the SRFs, thus affecting the local persistence and abundance of species.

Consequently, landscape heterogeneity, among other biotic and abiotic factors, could be seen as an ecological filter that restricts or excludes species according to their functional attributes (i.e. functional traits; Duflot *et al.*, 2014). Thereby, it might influence functional community composition (Gámez-Virués *et al.*, 2015) and potentially, ultimately ecosystem properties (i.e. process and functioning) which are the basis of many ecosystem benefits (Balvanera *et al.*, 2006) (Figure 2). Accordingly, landscape heterogeneity might affect ecosystem services by directly influencing ecosystem processes and function or indirectly through its effect of biodiversity (Turner *et al.*, 2012).

Ecosystem services are defined as conditions and processes of ecosystems that provide benefits for fulfilling human well-being (Fisher *et al.*, 2009). Interest in multifunctional landscapes, able to deliver multiple ecosystem services, is increasing nowadays (Jones *et al.*, 2013). Spatial heterogeneity is thought to affect the multifunctional character of landscapes (Verhagen *et al.*, 2016), as it can enhance one bundle of ecosystem services while undermining others (Turner *et al.*, 2012). At the same time, the flow of ecosystem services might vary across different spatial and temporal scales (García-Llorente *et al.*, 2016), generally as a consequence of human activities that modify land use and cover (Locatelli *et al.*, 2017) and hence, ultimately affect landscape heterogeneity. Changes in ecosystem services supplied by landscapes are not just a consequence of land cover changes but also an important driving force of future land cover dynamics as well (Verburg *et al.*, 2009). Therefore, understanding interactions between ecosystem services and land cover dynamics might provide information on the relative influence of socio-ecological drivers on ecosystem services (Bennett *et al.*, 2009), which might be helpful for the future continuity of multiple benefits to human well-being.

## **1.2. Overview: importance of mountain systems**

Mountains are singular systems covering 25% of the Earth's surface along all latitudinal belts and climatic zones (Diaz *et al.*, 2003). Landscape heterogeneity in mountains is associated to high levels of environmental and habitat heterogeneity, due to rapid changes in environmental conditions (i.e. temperature or humidity) with elevation gradient (Nunes *et al.*, 2016). This is a major cause of the high biodiversity that mountains support (Morán-Ordóñez *et al.*, 2011). In fact, they are

centres of endemisms and endangered species and ecosystems (Martinelli, 2007). Notwithstanding, nowadays mountains are considered as high vulnerable systems, since they are subjected to different human and natural pressures which are drivers of change (Nogués-Bravo *et al.*, 2007).

Mountains have been recognized not just as centers of biodiversity, but also as multifunctional socio-ecological landscapes providing regulation, provisioning and cultural services for human well-being (Foggin *et al.*, 2016). Approximately 20% of the world's human population inhabit mountains and much more in nearby lowlands, which directly or indirectly benefit from mountain resources and services (i.e. water, flood control, livestock or timber, among others) (Marston, 2008).

Mountain areas in Europe constituted fundamental agro-ecosystems in the pre-industrial society, being established and maintained through a long-term land-use and human intervention history (Vos & Meeke, 1999). The result has been the creation of highly valuable cultural landscapes that are still present today (Schuler *et al.*, 2004). However from the mid-twenties, European mountains have gone through a process of socio-economic marginalization associated to farming and agricultural decline and rural depopulation (Conti & Fagarazzi, 2005). As a consequence, mountains have experienced major changes in composition and configuration of the landscape mosaic, with important effects on ecosystem service flows (Schirpke *et al.*, 2013; Locatelli *et al.*, 2017) and biodiversity (Regos *et al.*, 2016).

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## 2. Objectives

The general aim of this Doctoral Thesis is to identify spatial variations in landscape heterogeneity on the basis of remote sensing data, across a range of mountain systems, to assess its relationship with biological diversity patterns and ecosystem service supply at different scales.

In particular, the specific objectives of the Thesis are:

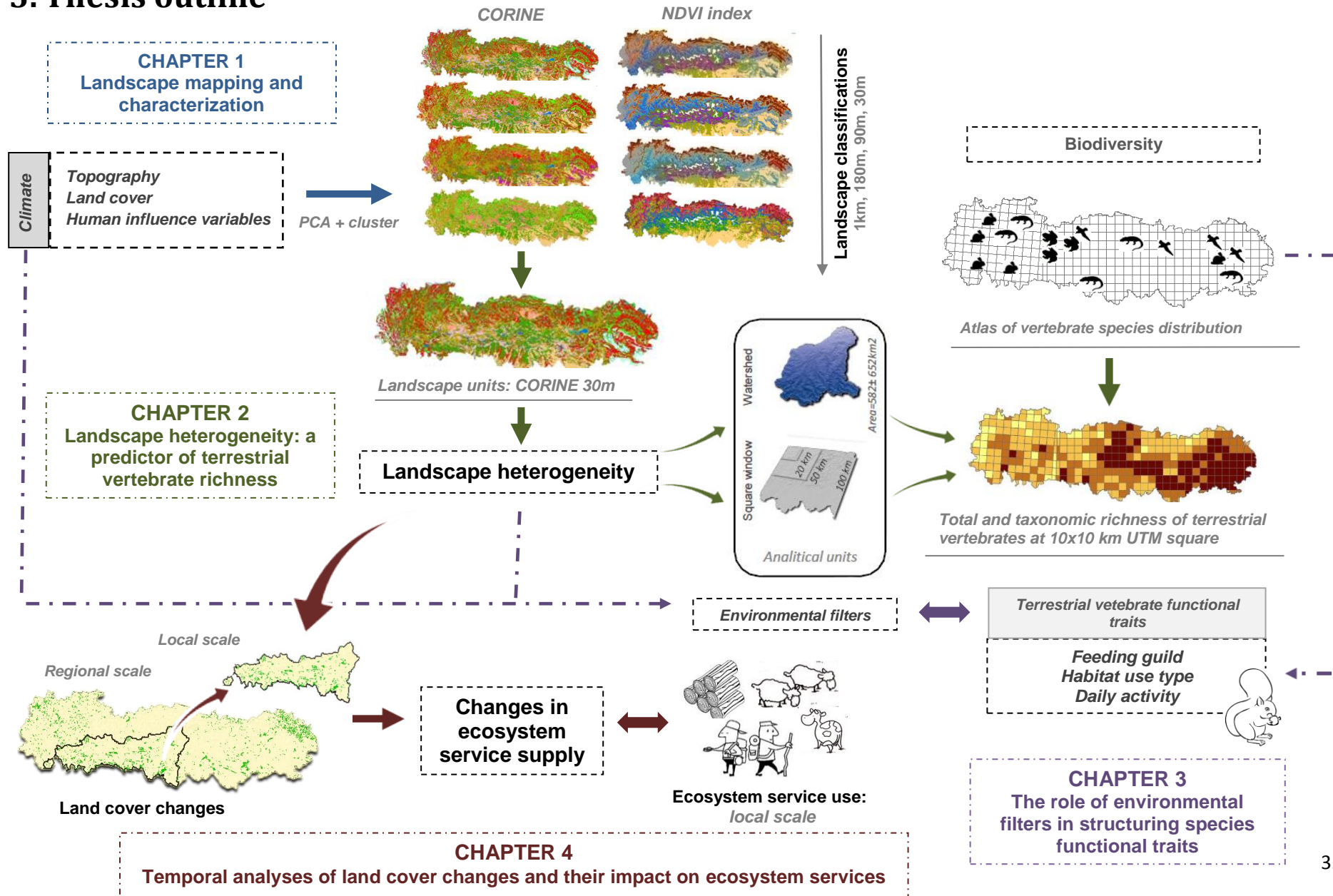
1. To classify the landscape of different mountainous systems, exploring (1) the usefulness of two of the most readily available open remote sensing products accounting for land cover (the CORINE land cover classification from Landsat at 30 m resolution and the NDVI spectral index from NOAA-AVHRR at 1 km) and (2) the applicability of the achieved classifications across different spatial resolutions. *Chapter 1.*

2. To quantify and identify spatial variations in landscape heterogeneity, as well as its role as an indicator of terrestrial vertebrate species richness in mountain systems, using different landscape analytical unit approaches (ecogeographical *versus* arbitrary). *Chapter 2.*

3. To assess the role of landscape heterogeneity as an environmental filter structuring the functional trait assembly of terrestrial vertebrate species in mountain systems. *Chapter 3.*

4. To analyze the impacts of land cover change on the supply/use of ecosystem services (regulating, provisioning and cultural) provided by mountain landscapes during the last two decades at different scales, discussing the relevance of landscape heterogeneity in the provision of ecosystem services. *Chapter 4.*

### 3. Thesis outline

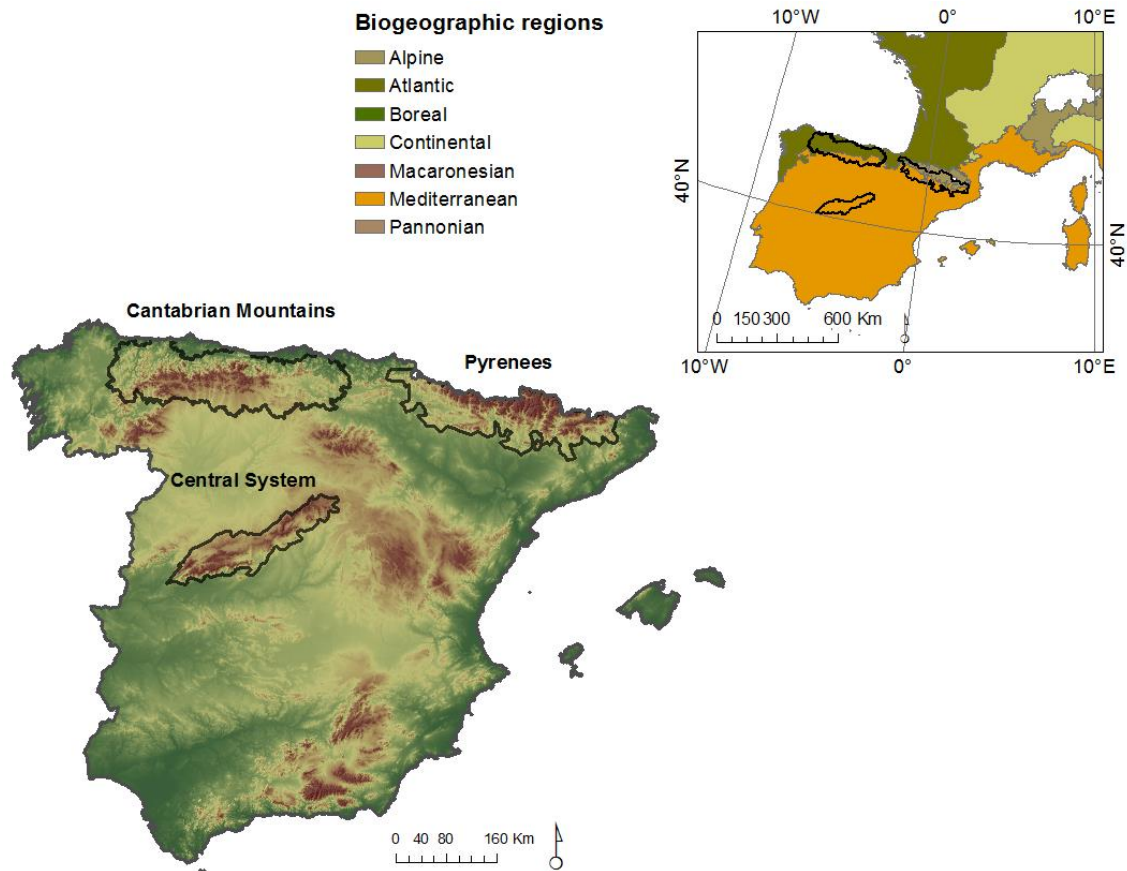


## 4. The case study

In this Thesis, we mainly focus on three mountain systems located across the Iberian Peninsula: the Cantabrian Mountains (NW Spain), the Spanish Pyrenees (NE Spain) and the Central System (Central-W Spain) (Figure 3). The interest of these mountains lies in their condition as biodiversity centers. They are totally or partially included in the Mediterranean Basin, which is recognized as an ecoregion with high diversity levels (Devictor *et al.*, 2010) and a biodiversity hotspot (Maiorano *et al.*, 2013). Furthermore, the Cantabrian Mountains and the Spanish Pyrenees represent the southernmost distribution of a wide range of species of Eurosiberian origin and the northernmost distribution of species of Iberian and Iberoafrikan origin (Martínez-Rica & Recoder, 1990; Morán-Ordóñez, 2012). Infact, the Cantabrian Mountains constitutes a transition between the Atlantic and Mediterranean regions and the Spanish Pyrenees between the Mediterranean, Atlantic and Alpine regions (Rivas-Martínez *et al.*, 1987). Consequently, these mountains are highly significant areas for the long term conservation of genetic diversity, phylogenetic history and evolutionary potential (Hampe & Petit, 2005). The Central System is within the Mediterranean biogeographic region and has been identified as a migratory route and a speciation centre (López-Sáez *et al.*, 2014). As a consequence, it harbors many flora (Médail & Diadema, 2009) and fauna (López-López *et al.*, 2011) endemisms of high conservation concern.

In the Cantabrian Mountains, altitude ranges from sea level up to 2650 m.a.s.l. The composition and structure of the landscape indicate a long history of anthropogenic influence, through forestry and extensive livestock rearing (Morán-Ordóñez *et al.*, 2013). This human intervention gave rise to a wide variety of semi-natural habitats and a complex landscape mosaic, with elements of high cultural value. Thus, landscape is dominated by very anthropised valley bottoms and low areas. At upslopes, vegetation consists on heathlands, shrublands and forest formations, which are influenced by the transitional character between Temperate-Oceanic (in northern slope) and Mediterranean (in southern slope) climate (Rivas-Martínez *et al.*, 2004) of this mountain system. Forests of *Fagus sylvatica*, *Betula pubescens*, *Quercus petraea* and *Q. robur* appear on shaded and humid northern slopes, and *Q. pyrenaica* and *Q. rotundifolia* are present on sunny

and dry southern ones. Montane grasslands and rock formations cover the highest altitudes.



**Figure 3.** Location of the study area: The Cantabrian Mountains (NW Spain), the Spanish Pyrenees (NE Spain) and the Central System (Central-W Spain).

Industrial development in Spain has had important repercussions for rural areas since the mid-twenties (Rescia *et al.*, 2010). Particularly, in the Cantabrian Mountains, it has had important negative demographic effects (Collantes, 2001). At the same time, similarly to other mountain areas in Spain, the low profitability and competitiveness of traditional agro-silvopastoral systems have given rise to a decrease in livestock and farm numbers and to a specialization in livestock production (Corbera, 2006). The immediate consequences of these socio-economic changes have been land abandonment and loss of traditional management practices, thus prompting large landscape changes and a decrease in diversity in the landscape mosaic.

Similarly to the Cantabrian Mountains, the landscape mosaic of the Spanish Pyrenees and the Central System has also been conditioned by anthropogenic activities, linked to forestry, and traditional agricultural and livestock traditional management (Gómez-Limón & de Lucio, 1999; Poyatos *et al.*, 2003; Mottet *et al.*, 2006). In the Spanish Pyrenees, the altitudinal gradient ranges from 100 to 3404 m.a.s.l. Climate also varies between both slopes (northern to southern) from Temperate-Oceanic to Mediterranean (Rivas-Martínez *et al.*, 2004), which is expected to influence vegetation. Natural formations, such as forests of *Q. pubescens* and *Q. ilex* cover sunny slopes and *Fagus sylvatica*, *P. sylvestris*, and *P. uncinata* forests appear on shaded ones. Pasturelands constitutes the subalpine community (Lasanta-Martínez *et al.*, 2005), while crop fields can be found in valley bottoms.

In the Central System, the altitudinal gradient is 280-2592 m.a.s.l. The climate is Mediterranean, characterized by long summer drought periods. Vegetation is dominated by forests of *Q. pyrenaica*, *Q. ilex subsp. ballota* and *Q. suber* (especially in the western sector) and *P. sylvestris* and *P. nigra* eastwards (López-Sáez *et al.*, 2014). At altitudes over 1600 m.a.s.l. shrublands of *Cytisus oromediterraneus*, *Echinopartum ibericum*, *E. barnadesii* or *Erica australis* appear (Rivas-Martínez *et al.*, 1987), and open montane grasslands at the highest altitudes.

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## Chapter 1

# Using remote sensing products to classify landscape. A multi-spatial resolution approach<sup>1</sup>

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## Abstract

The European Landscape Convention encourages the inventory and characterization of landscapes for environmental management and planning actions. Among the range of data sources available for landscape classification, remote sensing has substantial applicability, although difficulties might arise when available data are not at the spatial resolution of operational interest. We evaluated the applicability of two remote sensing products informing on land cover (the categorical CORINE map at 30m resolution and the continuous NDVI spectral index at 1km resolution) in landscape classification across a range of spatial resolutions (30m, 90m, 180m, 1km), using the Cantabrian Mountains (NW Spain) as study case. Separate landscape classifications (using topography, urban influence and land cover as inputs) were accomplished, one per each land cover dataset and spatial resolution. Classification accuracy was estimated through confusion matrixes and uncertainty in terms of both membership probability and confusion indices. Regarding landscape classifications based on CORINE, both typology and number of landscape classes varied across spatial resolutions. Classification accuracy increased from 30m (the original resolution of CORINE) to 90m, decreasing towards coarser resolutions. Uncertainty followed the opposite pattern. In the case of landscape classifications based on NDVI, the identified landscape patterns were geographically structured and showed little sensitivity to changes across spatial resolutions. Only the change from 1km (the original resolution of NDVI) to 180m improved classification accuracy. The value of confusion indices increased with resolution. We highlight the need for greater effort in selecting data sources at the suitable spatial resolution, matching regional peculiarities and minimizing error and uncertainty.

**Keywords:** CORINE, Land Cover, NDVI, NOAA, uncertainty

## 1. Introduction

Different policies have been developed in Europe aiming to regulate landscape conservation, such as the Pan-European Biological and Landscape Diversity Strategy (Council of Europe, 1996), the Action Plan for European Landscapes (ECNC, 1997) and the European Landscape Convention (Council of Europe, 2000). Specifically, the European Landscape Convention encourages Contracting Parties to identify and classify their landscapes for protection, management and planning. In this way, a wide range of initiatives has been implemented at continental, national and regional scales in Europe, attempting to accomplish this recommendation. Examples are the European Landscape Map (LANMAP2) (Mücher *et al.*, 2010), the Spanish Landscape Atlas (Mata Olmo & Sanz Herráiz, 2003) and the German Typology of Landscapes (Gharadjedaghi *et al.*, 2004). However, despite efforts, the European Landscape Character Initiative (ELCAI) (Wascher, 2005) highlighted discrepancies in these landscape classifications in terms of methodology, data sources, spatial resolution and nomenclature (Mücher *et al.*, 2010), which make them incompatible and largely incomparable (Van Eetvelde & Antrop, 2008). Thus, the development of consistent methodologies for landscape classification, able to identify with realism, basic spatial units for use in environmental applications at a large scale, is necessary to fulfil policy and operational requirements (Blasi *et al.*, 2000).

Numerical landscape classifications allocate patches of territory with similar characteristics (e.g., geology, topography, hydrology, land cover, socio-economy) into homogeneous landscape units. Among all landscape components, land cover is probably the most relevant, as it represents the interface between natural conditions and human influences, both across space and time. There is a wide range of data sources that can be used to describe land cover in environmental applications (Tomaselli *et al.*, 2013), mainly consisting of categorical land cover maps derived from remote sensing data, as the International Geosphere-Biosphere Programme (Belward, 1996), the FAO land cover classification system (Di Gregorio & Jansen, 1998, 2004) or the CORINE Land Cover Programme (Bossard *et al.*, 2000). Currently, most of these data can be found freely available, which can be useful for landscape managers, mainly when funding is limited (Nagendra *et al.*,

2013). However, the matching between the spatial resolution of these products, with that at which landscape is intended to be characterized it is not always achievable (Garrigues *et al.*, 2006; Shao & Wu, 2008). A lack of appropriate information can result in a gap between both, desired and hard-headed spatial resolution at which patterns and process can be represented (McCabe & Wood, 2006), generating spatial discrepancies between reality and analysis resolution.

Within the European context, CORINE is probably the data source most used to generate integrative landscape classifications in combination with other thematic data (Mücher *et al.*, 2003, 2006, 2010; Van Eetvelde & Antrop, 2008; Cullotta & Barbera, 2011). However, despite its wide application, CORINE is a classification product derived from Landsat TM imagery that shows important problems of uncertainty (Regan *et al.*, 2002), which can be propagated in subsequent analyses (Shao & Wu, 2008). Therefore, it should be carefully evaluated prior use to guaranty its applicability in management (Foody & Atkinson, 2002; Rae *et al.*, 2007; Kennedy *et al.*, 2009; Hou *et al.*, 2013). This issue become especially relevant in mountain systems, where topographic and microclimatic patterns (Oke & Thompson, 2015) make ecological conditions to change substantially over relatively short distances, providing a wide range of environments and hence, a great diversity of habitats and species (Becker & Bugmann, 2001). Because of this environmental heterogeneity, classifying land cover in mountain areas is especially challenging due to the existence of mixed pixels that can mislead the final classifications (Álvarez-Martínez *et al.*, 2010). Considering these constraints inherent to categorical maps, a good alternative could be the use of continuous variables as the spectral indices derived from remote sensing imagery (Suárez-Seoane *et al.*, 2002; Morán-Ordóñez *et al.*, 2012; Álvarez-Martínez *et al.*, 2015; Rocas-Díaz *et al.*, 2015). The spectral index most commonly used in environmental research is the Normalized Vegetation Index (NDVI) (Rouse *et al.*, 1973; Tucker, 1979). This index has been related to functional attributes of ecosystems like aboveground net primary production (Paruelo *et al.*, 2001), vegetation functional characteristics such as phenology or primary productivity (Gamon *et al.*, 2013) and vegetation structure such as aboveground biomass (Zhu & Liu, 2014). Many authors have applied this index to produce categorical land cover maps which are

then used in subsequent analysis (Muniaty & Ratshibvumo, 2010; Tchuenté *et al.*, 2011; Pervez *et al.*, 2014). Nevertheless, we found no studies using this product as a direct input in integrative landscape classifications. The reason could be that NDVI provides an indication of the “greenness” of vegetation but does not inform directly on land cover, which may hamper the interpretation of final maps (Wang & Tenhunen, 2004).

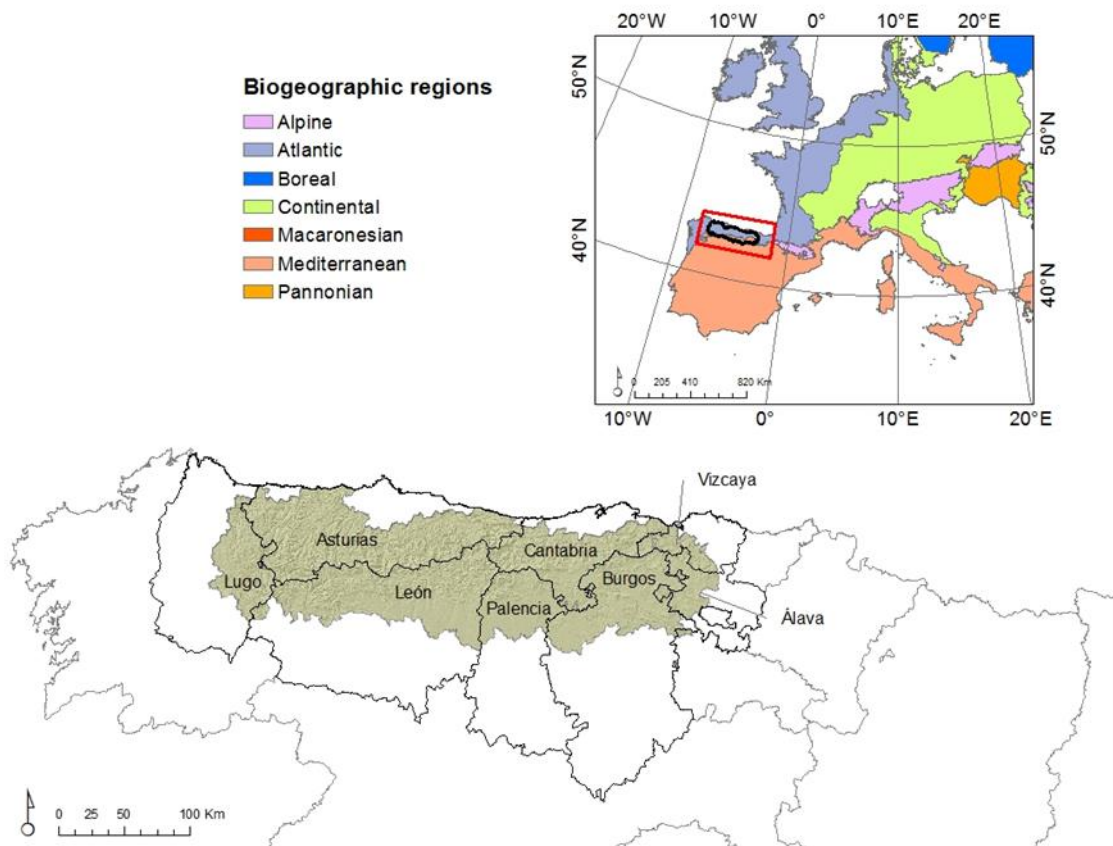
This study aims to explore the applicability of two of the most readily available open remote sensing products accounting for land cover (the CORINE land cover classification from Landsat at 30m resolution and the spectral index NDVI from NOAA-AVHRR at a 1km) for integrative landscape classification across spatial resolutions. In particular, we explore: (i) how classification typology and landscape pattern change across spatial resolution; (ii) how the error and uncertainty associated with data source, spatial resolution and landscape classification process could influence results in a complex mountain system.

## **2. Material and methods**

### **2.1. Study area**

The study area lies in the Cantabrian Mountains (northwest Spain) located at the transition between Eurosiberian and Mediterranean biogeographical regions (Rivas-Martínez *et al.*, 1987) (Figure 1.1). This is an area of 31494 km<sup>2</sup> with altitudes ranging from sea level to 2650 m.a.s.l. Average annual rainfall varies from 700 to 2400 mm and mean annual temperature from 4°C to 22°C. Landscape pattern is heterogeneous and is driven by climatic and topographic conditions, as well as human activities. Land cover types vary from crop fields (in lowlands) to natural vegetation (in mid-highlands), including heathlands scrublands and deciduous forests dominated by *Fagus sylvatica*, *Betula pubescens*, *Quercus petraea* and *Q. robur* on northern slopes and *Q. pyrenaica* and *Q. rotundifolia* on southern slopes. In addition, plantations of *Pinus pinaster*, *P. radiata* and *Eucalyptus globulus* can be found in the study area, covering medium-to-low slopes previously occupied by shrubs and heathers. The Cantabrian Mountains have been widely recognized as a hot spot of biodiversity hosting a wide variety of ecosystems

habitats and endemic species (Worboys *et al.*, 2010; Álvarez-Martínez *et al.*, 2011; Morán-Ordóñez *et al.*, 2011).



**Figure 1.1.** Study area: The Cantabrian Mountains (NW Spain). Information on biogeographic regions was obtained from the Spanish Ministry of Agriculture Food and Environment(<http://www.magrama.gob.es/>).

## **2.2. Input environmental variables: topography, urban influence and land cover**

We derived a set of environmental variables informing on topography, urban influence and land cover at four spatial resolutions (30 m, 90 m, 180 m and 1 km) (Table 1.1). Pixel sizes of 30 m and 1 km correspond to the original resolution of the remote sensing data accounting for land cover, while 90 m and 180 m are intermediate resolutions chosen according to data availability on topography and urban influence.

**Table 1.1.** Variables used for landscape classification. Variables accounting for topography and urban influence were calculated independently at 30 m, 90 m, 180 m and 1 km of spatial resolution from different data sources, while those accounting for land cover (CORINE and NDVI) were derived at each target spatial resolution by pixel aggregation or pixel resampling from the original data source.

Family	Code	Description	Original data set
Topography	DEM	Elevation (m)	Digital Elevation Models (DEM) at 25m, 90m, 200m and 1km of spatial resolution
	SLO	Slope (%)	
	SOLR	Solar radiation (*10 <sup>6</sup> W/h)	
Urban influence	AC	Urban influence across the territory measured as Euclidian distance to settlements (m)	Vector layers at 1:25000, 1:100000, 1:200000 and 1:500000.
Land cover (CORINE)	INFRA	Human infrastructures (%)	CORINE Land Cover 2006 at 30m spatial resolution
	MIN	Mineral extraction sites (%)	
	HERC	Herbaceous crop lands (%)	
	WOOC	Woody crop land coverage (%)	
	PAS	Pasturelands (%)	
	FOR	Forest coverage (%)	
	TWOOD	Transitional woodland-shrublands (%)	
	SCRUB	Mosaic of sclerophyllous-herbaceous vegetation (%)	
	SPAR	Sparsely vegetated areas (%)	
	BARE	Bare areas (%)	
	WET	Wetlands (%)	
	WAT	Water (%)	
Land cover (NDVI)	NDVI	Annual average NDVI index (no units ranging from -1 to +1)	NDVI from NOAA-AVHRR at 1km of spatial resolution for years 1983, 1985, 1990, 1993 and 1996

Topographic variables consisted on elevation solar radiation and slope. They were calculated separately from four Digital Elevation Models (DEM) proximal to the above-mentioned spatial resolutions and obtained from the Spanish Geographic Institute ([www.ign.es](http://www.ign.es)), and the U.S. Geological Survey ([www.usgs.gov](http://www.usgs.gov)). Urban influence was estimated as the Euclidian distance to urban settlements, independently for the target spatial resolutions, using data from the Spanish Geographic Institute ([www.ign.es](http://www.ign.es)). Land cover variables were generated from two datasets: (i) the CORINE categorical map for the year 2006 at 30 m of spatial resolution; and (ii) a mean annual NDVI spectral index at 1 km, derived from a temporal monthly series for years 1983, 1985, 1990, 1993, 1996 and 1999. The CORINE Land Cover classification (<http://www.eea.europa.eu/publications/COR0->

[landcover](#)) comprises 44 land cover classes at the most detailed of the three available levels (Bossard *et al.*, 2000). But, in the study area, only 38 out of the 44 classes were present. These classes were reclassified into 12 main categories with the purpose of simplifying the original dataset (Annex I, Table S1.1). With the aim of improving map reliability, the resulting product was merged with an extra dataset of rivers and infrastructures (roads, railways and settlements) downloaded from the Spanish Geographic Institute site ([www.ign.es](http://www.ign.es)), at 1:200000 spatial resolution. To account for the accuracy of this new CORINE map, we carried out a visual validation based on coetaneous orthophotographs (years 2006 to 2009, at 1:5000 to 1:10000 spatial resolution) and field surveys (Bossard *et al.*, 2000; Vogiatzakis *et al.*, 2006; Kienast *et al.*, 2009) on a dataset of 320 sampling points. We followed a stratified random sampling design by municipality and land cover class, being, therefore, the sampling size proportional to the extent of the municipalities and land cover classes. Accumulative adjustment curves were created to identify a representative number of points. The overall accuracy of the new CORINE was 82.5%, ranging across land cover classes from 66.67 to 100%. The map was resampled at the four target spatial resolutions by using the majority rule, which is one of the most common approaches to aggregate categorical data (Wu, 2004). The 12 classes of the new CORINE were subsequently turned into independent continuous variables by calculating the proportion covered by class at each pixel of 30 m, 90 m, 180 m and 1 km. NDVI original data were captured by an Advanced Very High Resolution Radiometer (AVHRR) on board the NOAA satellite, received by the Natural Environment Research Council Satellite Receiving Station at Dundee (UK) and processed by the Remote Sensing Group at the Plymouth Marine Laboratory (UK). See Suárez-Seoane *et al.* (2002) and Osborne *et al.* (2007) for technical details on these data. The original NDVI dataset had a pixel size of 1 km and was resampled to the above-mentioned spatial resolutions using a nearest algorithm.

Prior to landscape classification analysis we standardized all continuous environmental variables (Table 1.1) to set them to the same range, by applying the equation 1 (Eq. 1).



$$Z = \frac{(X - oldmin) * (newmax - newmin)}{(oldmax - oldmin)} + newmin \quad (\text{Eq. 1})$$

Where  $Z$  is the output raster with new data ranges,  $X$  is the input raster,  $oldmin$  is the minimum value of the input raster,  $oldmax$  is the maximum value of the input raster,  $newmin$  is the desired minimum value for the output raster and  $newmax$  is the desired maximum value for the output raster.

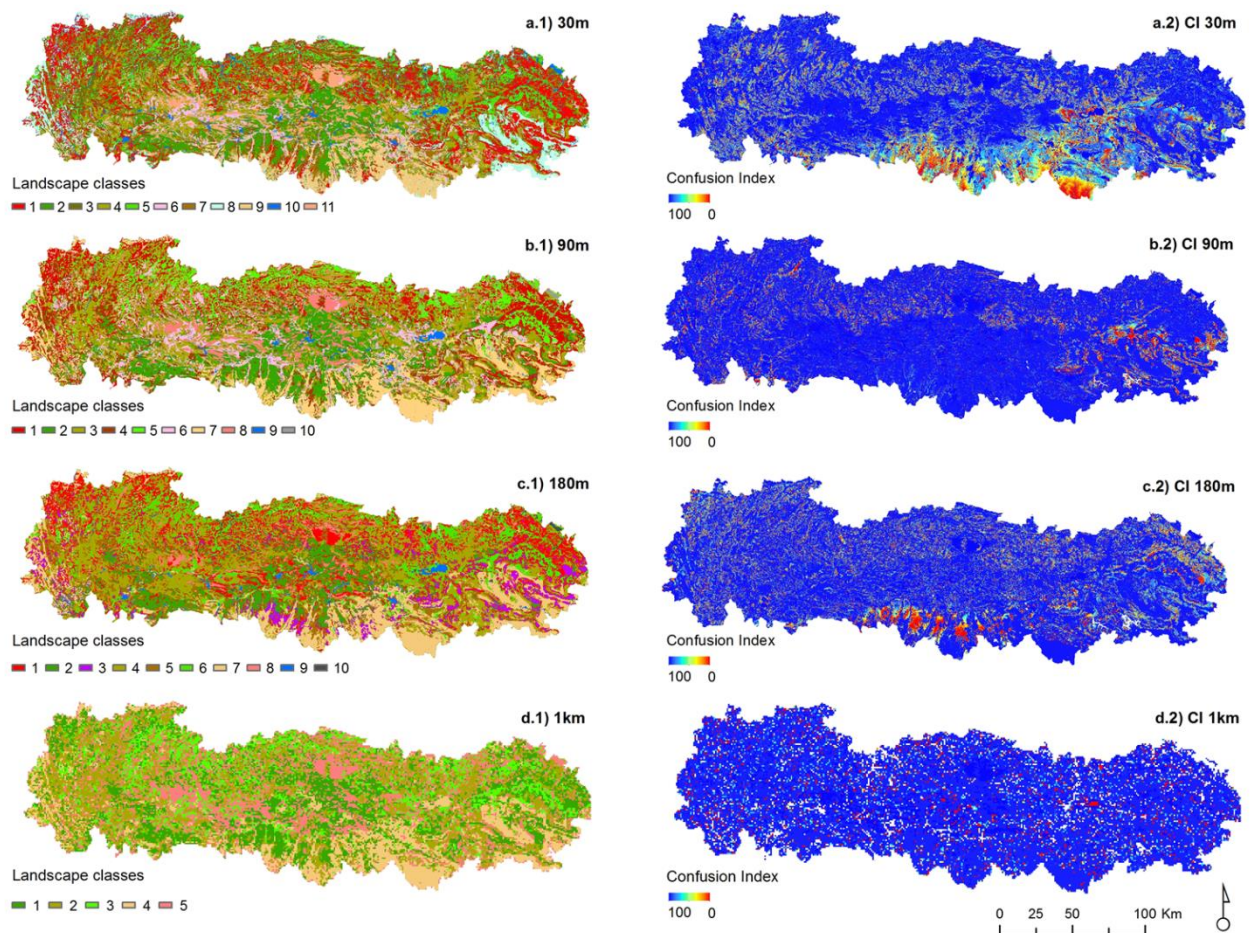
### ***2.3. Landscape classification across spatial resolutions: accuracy and uncertainty***

We accomplished eight landscape classification analyses for the Cantabrian Mountains based on topography, urban influence and land cover (Table 1.1). We carried out an independent analysis for each land cover dataset (CORINE and NDVI) and spatial resolution (30 m, 90 m, 180 m and 1 km). First, we ran a Principal Components Analysis (PCA) over the standardized variables. We then clustered similar pixels into comprehensive landscape classes, by applying an unsupervised classification with the maximum likelihood algorithm on the PCA components (Schowengerdt, 1983; Conese & Maselli, 1992). A similar methodological approach to classify landscape has been used by other authors such as Owen *et al.* (2006); Morán-Ordóñez *et al.* (2011) and Gan *et al.* (2012).

The error of each landscape classification was measured in terms of accuracy, which was quantified by using thematic information related to topography, urban influence and land cover and ortho-photographs (years 2006-2009, scale 1:5000-1:10000), (Bossard *et al.*, 2000; Vogiatzakis *et al.*, 2006; Kienast *et al.*, 2009). Each landscape map was evaluated using independent datasets of 300 points each that were collected across the study area by applying a random sampling design stratified by class. This sampling size guaranteed an adequate representativeness of all landscape classes and was defined according to accumulative adjustment curves (Annex I, Figure S1.1), which allowed for identifying the appropriated number of validation points for each landscape classification. We avoided the use of a unique testing dataset for validating all landscape classifications because any selection of points would be biased towards a particular spatial resolution and/or

original data source. We created a confusion matrix for each classification obtaining the overall percentage of points correctly allocated to landscape classes and the user's and producer's accuracy per class.

The maximum likelihood rule allocates pixels to classes according to their maximum membership probability. However, a pixel may have a certain degree of similarity to more than one class and therefore, almost equal probability of membership to all of them. In these cases, pixel allocation can be erroneous (Lewis *et al.*, 2000). This problem is considered a main source of uncertainty in classification processes (Foody, 2000; Owen *et al.*, 2006).



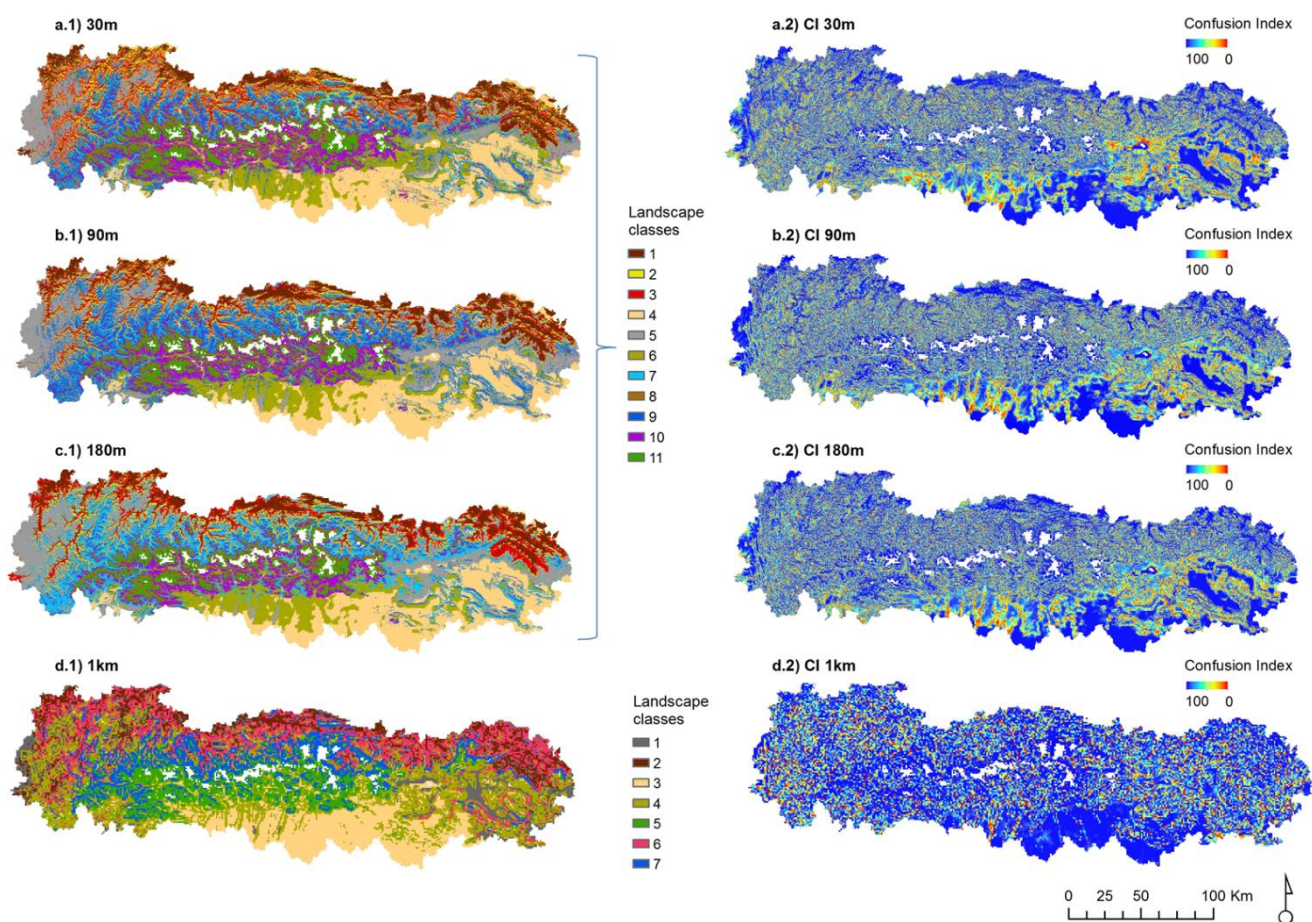
**Figure 1.2.** On the left (a.1-d.1), landscape patterns achieved from classifications based on topography, urban influence and land cover (CORINE) and on the right (a.2-d.2) the associated Confusion Index maps (*CI*) at various spatial resolutions: (a) 30 m, (b) 90 m, (c) 180 m and (d) 1km. See Table 1.2 and Annex I, Tables S1.2-S1.6 for explanation and statistical characterization of landscape classes.

To assess the uncertainty derived from erroneous allocations for each pixel in each class, we applied the methodology of Álvarez-Martínez *et al.* (2010), which is based on fuzzy membership to all landscape classifications. We distinguished between two aspects of classification uncertainty: (i) the uncertainty of pixel allocation to a particular class (probability of membership); and (ii) the confusion associated with the classification of a pixel among classes accepting that one pixel can belong to more than one class (expressed by the Confusion Index). Membership is a measure of the similarity between the characteristics of a particular pixel and the representative vector of a class (Bollinger & Mladenoff, 2005). It was estimated by calculating the Euclidian distance between each pixel value and the characteristic vector of the class. A large Euclidian distance indicates large differences between the pixel attributes and the typical case of the target class. In this case, membership probability will be low and uncertainty high. Membership values were then used to create a Confusion Index (*CI*) map. We calculated the difference between the highest membership probability to a class and the second-largest membership probability for the same pixel to another class. When a class dominates, differences between the highest and the second highest class membership probability is large. In this situation, *CI* tends towards “1” and there is little confusion in class allocation. Otherwise, when membership is similar to more than one class, confusion among classes is high and *CI* tends towards “0”. All analyses were done in ArcGIS 10.2 (Esri, 2014).

### **3. Results**

#### ***3.1. Landscape patterns and classification typologies***

Landscape patterns derived from landscape classifications based on CORINE, as a proxy of land cover, showed a weak geographic structure (Figure 1.2, cases a.1-d.1). The number of landscape classes decreased when pixel size became coarser: eleven classes at 30 m, ten at 90 m and 180 m and five at a 1 km spatial resolution. The typology of the classes also varied among these spatial resolutions.



**Figure 1.3.** On the left (a.1-d.1), landscape patterns achieved from classifications based on topography, urban influence and land cover (NDVI) and on the right (a.2-d.2) the associated Confusion Index maps (*CI*) at various spatial resolutions: (a) 30 m, (b) 90 m, (c) 180 m and (d) 1 km. See Table 1.3 and Annex I, S1.2, S1.7 and S1.8 for explanation and statistical characterization of landscape classes.

When using NDVI as land cover data source in landscape classification, the resulting landscape mosaic was strongly structured across a gradient North to South, being this geographic pattern consistent across spatial resolutions (Figure 1.3, cases a.1-d.1, Annex I, Figure S1.2). Thus, classification typology showed little sensitivity to changes across spatial resolutions. See Tables 1.2 and 1.3 and Annex I Tables S1.2-S1.8 for a detailed characterization of landscape classes.

**Table 1.2.** Description of landscape classes obtained from a set of variables accounting for topography, urban influence and land cover (CORINE). See Supplementary material S1.2-S1.6 for further explanations.

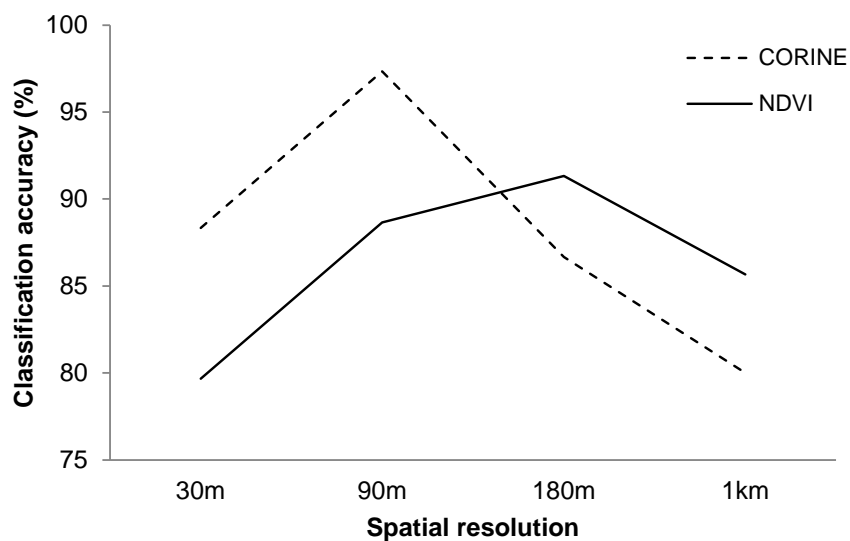
Class	Description
30m resolution	
1	Forests covering coastal and middle-mountain areas under 1000 m.a.s.l.
2	Forests covering central mountains and piedmont areas at altitudes above 1000 m.a.s.l.
3	Transitional to woodlands with relatively low urban influence covering mainly Atlantic and Sub-Atlantic mountains, in areas with mid-low altitudes (600 m.a.s.l.)
4	Transitional woodlands from central and southern areas of the Cantabrian Mountains, with altitudes from 1500 to 900 m.a.s.l.
5	Pastures in mid-low (under 800 m.a.s.l.) Atlantic mountains and coastal areas
6	Pastures covering bottom valleys and hillsides of central Cantabrian Mountains, with altitudes ranging from 1500 to 1000 m.a.s.l.
7	Shrub-herbaceous associations lying at altitudes between 1200 to 500 m.a.s.l.
8	Croplands from depressions and coastal areas at low altitude close to settlements
9	Croplands (non-irrigated arable lands) from paramos and countrysides under 1000 m.a.s.l., being the closest class to settlements
10	Water surfaces and artificial surfaces in areas of wide altitudinal ranges
11	Rocks and areas with little or no vegetation covering wide altitudinal ranges
90m resolution	
1	Forests covering coastal and middle-mountain areas mainly from Atlantic and Sub-Atlantic mountains, under 850 m.a.s.l. and relatively close to settlements
2	Forests covering central mountains and piedmont areas with low urban influence at altitudes above 900 m.a.s.l., with low urban influence
3	Transitional to woodland areas across a wide altitudinal range
4	Shrub-herbaceous associations lying at altitudes between 1200 to 500 m.a.s.l.
5	Pastures in mid-low Atlantic mountains and coastal areas under 600 m.a.s.l.
6	Pastures covering bottom valleys and hillsides of central Cantabrian Mountains with altitudes ranging from 1400 to 700 m.a.s.l.
7	Croplands from coastal areas depressions, paramos and country sides under 1000 m.a.s.l.
8	Rocks and areas with little or no vegetation covering a wide altitudinal range
9	Water surfaces covering a wide altitudinal range
10	Settlements, roads, railways or mines at very low altitude
180m resolution	
1	Areas with little vegetation and forests, covering coastal and middle-mountain areas mainly from Atlantic and Sub-Atlantic mountains, situated at a wide altitude range
2	Forests covering high central mountains and piedmont areas with relative urban influence, at altitudes above 1000 m.a.s.l.
3	Forests covering depressions paramos and countrysides in altitudes under 1000 m.a.s.l.
4	Transitional to woodland areas at wide altitudinal ranges and relative high urban influence
5	Shrub-herbaceous associations lying at altitudes between 1200 to 500 m.a.s.l.
6	Pastures covering areas with wide altitudinal and solar radiation range at middle to slight slope
7	Croplands from coastal areas, depressions, paramos and country sides under 1000 m.a.s.l.
8	Rocks and areas with no vegetation covering a wide altitudinal range
9	Water surfaces covering a wide altitudinal range
10	Settlements, roads, railways or mines at very low altitude
1km resolution	
1	Forests lying at wide altitude range
2	Transitional woodland and shrub areas with fairly urban influence at wide altitudinal ranges.
3	Pastures covering areas with relative urban influence and wide altitudinal
4	Croplands from coastal areas, depressions, paramos and countryside along with water surfaces under 1000 m.a.s.l.
5	Rocks areas with no vegetation and artificial surfaces covering a wide altitudinal range

**Table 1.3.** Description of landscape classes obtained from a set of variables accounting for topography, urban influence and land cover (NDVI). See supplementary material S1.2, S1.7 and S1.8 for further explanations.

Class	Description
30m 90m and 180m resolution	
1	Sea inlets, coastal plains and sub-coastal valleys, located at the lowest altitude dominated by a mosaic of crops and pastures with a high presence of natural vegetation
2	Hillsides under 650 m.a.s.l. with a northern exposure and mid-high slope from Atlantic and Sub-Atlantic mountains, covered by a mosaic of scrubs and forests mixed with pastures in coastal areas
3	Hillsides under 650 m.a.s.l., with a southern exposure and mid-high slope from Atlantic and Sub-Atlantic mountains, covering by a mosaic of scrubs and forests mixed with pastures in coastal areas
4	Complex cultivation patterns (crops and pasture mosaic) with high presence of natural vegetation in areas, with moderate slope at low altitude
5	Woody and scrub vegetation with rock formations covering northern faces of the upper part of Atlantic mountains
6	Woody and scrub vegetation with rock formations covering southern faces of the upper part of Atlantic mountains
7	Hillsides in the central area of the Cantabrian Mountains above 1400 m.a.s.l., with northern exposure and dominated by rock formations with moors and high mountain forests
8	Hillsides and mid-hillsides under 1400 m.a.s.l. and valleys above 1300 m.a.s.l. in the central area of the Cantabrian Mountains, with sun-facing exposure and dominated by broadleaf forest mixed with pastures and heathlands
9	Peaks and mountainsides above 1400 m.a.s.l. with southern western and eastern exposures in the central areas of the Cantabrian Mountains and dominated by rock formations pastures moors heathlands and forests
10	Valley bottoms from high central areas of the Cantabrian Mountains extending to piedmont areas, dominated by pastures in the valley bottoms and mosaics of forests scrubs and crops in piedmont areas
11	Paramos, countryside and depressions at low altitude, with moderate to high solar radiation rates and dominated by intensive crops
1km resolution	
1	Sea inlets, coastal plains and sub-coastal valleys, located at the lowest altitude and dominated by a mosaic of crops and pastures with a high presence of natural vegetation.
2	Coastal hills under 800m, with moderate solar radiation and slope dominated by pastures with natural vegetation areas
3	Depressions mainly covered by complex cultivation patterns in areas with an average altitude of 600 m.a.s.l., slight slope and moderate to high solar radiation rates
4	Middle mountain areas under 1400 m.a.s.l. with moderate solar radiation and slope rates, dominated by forests scrub and transitional woodland formations
5	High central mountains with an average altitude around 1400 m.a.s.l. with moderate slope, high solar radiation rates and dominated by forests, scrubs and bare and semi-bared areas
6	Valley bottoms from high central areas of the Cantabrian Mountains extending to piedmont areas and Sub-Atlantic mountains, with gentle slope and dominated by pastures in valley bottoms and forest formations accompanied by scrubs and mosaic of crops fields in piedmont areas
7	Paramos, countryside and depressions with moderate to high solar radiation rates and dominated by crops

### 3.2. Landscape classification accuracy

Landscape classifications based in CORINE land cover data reached an overall accuracy higher than 80% at all spatial resolutions, with user's and producer's accuracy per class higher than 50% and 68%, respectively (Table 1.4). When the spatial resolution of analysis decreased from 30 m (the original pixel size of CORINE) to 90 m, classification accuracy improved. However, when the spatial resolution was coarser than 90 m, classification accuracy diminished.



**Figure 1.4.** Landscape classification accuracy across spatial resolutions.

Landscape classifications based on NDVI grasped an overall accuracy higher than 79% at all spatial resolutions, with user's and producer's accuracy per class higher than 57% and 65% respectively (Table 1.5). When the spatial resolution of analysis increased from 1km (the original pixel size of NDVI) to 180 m, classification accuracy improved.

**Table 1.4.** User's, producer's and overall accuracy of landscape classification based on topography, urban influence and CORINE (as a proxy of land cover) at different spatial resolutions. The table also shows the probability of membership (i.e., the Euclidian distance from pixel values to the characteristic vector of each class; mean  $\pm$  SD).

	Code	User's accuracy (%)	Producer's accuracy (%)	Euclidean distance
30 m	1	93.33	88.89	3.46 $\pm$ 3.28
	2	85.29	78.38	5.93 $\pm$ 5.63
	3	83.33	68.97	2.93 $\pm$ 3.01
	4	86.49	96.97	2.82 $\pm$ 4.23
	5	100.00	91.18	2.95 $\pm$ 3.09
	6	94.12	94.12	2.82 $\pm$ 2.52
	7	96.15	100.00	2.66 $\pm$ 2.52
	8	89.47	85.00	2.62 $\pm$ 2.04
	9	85.00	89.47	2.69 $\pm$ 4.08
	10	50.00	100.00	3.87 $\pm$ 1.71
	11	93.33	100.00	3.46 $\pm$ 3.28
	<b>Overall</b>		<b>88.33</b>	<b>3.21 <math>\pm</math> 0.98</b>
90 m	1	93.33	93.33	2.90 $\pm$ 2.37
	2	96.08	92.45	2.86 $\pm$ 2.41
	3	95.23	100.00	3.01 $\pm$ 2.22
	4	86.67	89.66	3.06 $\pm$ 2.16
	5	100.00	100.00	2.86 $\pm$ 2.21
	6	100.00	100.00	3.14 $\pm$ 2.27
	7	100.00	100.00	2.74 $\pm$ 1.87
	8	100.00	100.00	3.20 $\pm$ 1.95
	9	100.00	75.00	3.15 $\pm$ 2.01
	10	100.00	100.00	3.32 $\pm$ 1.73
		<b>Overall</b>		<b>97.33</b>
180 m	1	83.64	82.14	3.15 $\pm$ 1.75
	2	93.75	90.91	2.98 $\pm$ 2.84
	3	53.33	72.73	2.38 $\pm$ 1.84
	4	88.89	98.46	3.23 $\pm$ 2.23
	5	100.00	93.75	3.32 $\pm$ 2.08
	6	92.31	83.72	3.04 $\pm$ 2.09
	7	100.00	100.00	2.94 $\pm$ 1.89
	8	100.00	83.33	3.26 $\pm$ 1.88
	9	75.00	75.00	3.43 $\pm$ 1.42
	10	100.00	80.00	3.68 $\pm$ 1.69
		<b>Overall</b>		<b>86.66</b>
1km	1	95.52	75.29	3.47 $\pm$ 2.21
	2	75.32	74.36	3.30 $\pm$ 2.07
	3	92.86	78.00	3.56 $\pm$ 2.58
	4	84.44	88.37	3.42 $\pm$ 2.63
	5	59.42	93.18	3.56 $\pm$ 2.18
		<b>Overall</b>		<b>80.00</b>



Nevertheless, when the spatial resolution was higher than this, classification accuracy decreased. In none of the cases, classification accuracy was maximal at the original spatial resolution of NDVI and CORINE land cover datasets (i.e., 30 m and 1km pixel size respectively) (Figure 1.4).

### ***3.3. Landscape classification uncertainty***

Regarding CORINE-based landscape classifications, membership probability was dependent on the spatial resolution, as Euclidean distances between pixel attributes and the characteristic vector of the class decreased when pixel size increased from 30 m to 90 m. However, they consistently increased when pixel size became coarser than 90 m (Table 1.4). The higher differences in Euclidean distances among classes were detected at 30 m resolution. Additionally, the confusion associated with the classification of a pixel among classes was also dependent on the spatial resolution of analysis (Figures 1.2; cases a.2-d.2). Classes were represented with lower confusion at 1 km and 90 m pixel size. In contrast, the highest confusion was found at the original (30 m) and intermediate (180 m) spatial resolutions.

Considering NDVI-based classifications, membership probability almost did not vary across spatial resolutions (Table 1.5). There were no clear differences in Euclidean distances among classes at any spatial resolution. The use of NDVI in landscape classification produced high confusion among classes ( $CI$  values closer to 0) (Figures 1.3; cases a.2-d.2). We did not find consistent differences in  $CI$  values among 30 m, 90 m and 180 m spatial resolutions, with  $CI$  increasing only at 1 km grain size.

**Table 1.5.** User's, producer's and overall accuracy of landscape classifications based on topography, urban influence and NDVI (as a proxy of land cover) at different spatial resolutions. The table also shows the probability of membership (i.e., the Euclidian distance from pixel values to the characteristic vector of each class; mean  $\pm$  SD).

	Code	User's accuracy (%)	Producer's accuracy (%)	Euclidean distance
30 m	1	96.43	65.85	2.02 $\pm$ 0.66
	2	57.14	100.00	2.14 $\pm$ 0.67
	3	64.00	88.89	2.19 $\pm$ 0.54
	4	87.50	63.64	2.10 $\pm$ 0.59
	5	81.25	86.67	2.13 $\pm$ 0.84
	6	64.29	90.00	2.14 $\pm$ 0.52
	7	88.89	100.00	2.11 $\pm$ 0.82
	8	88.00	88.00	2.05 $\pm$ 0.64
	9	100.00	94.74	2.38 $\pm$ 0.61
	10	83.78	65.96	2.01 $\pm$ 0.75
	11	74.51	90.48	2.02 $\pm$ 0.92
	<b>Overall</b>		<b>79.67</b>	<b>2.12 <math>\pm</math> 0.10</b>
90 m	1	100.00	68.57	2.20 $\pm$ 0.58
	2	72.22	100.00	2.09 $\pm$ 0.78
	3	73.33	100.00	2.12 $\pm$ 0.69
	4	85.19	92.00	2.15 $\pm$ 0.61
	5	83.33	100.00	2.03 $\pm$ 0.90
	6	82.22	94.87	2.14 $\pm$ 0.63
	7	100.00	88.24	2.07 $\pm$ 0.96
	8	100.00	95.45	2.14 $\pm$ 0.66
	9	100.00	100.00	2.12 $\pm$ 0.73
	10	96.97	71.11	2.14 $\pm$ 0.64
	11	87.50	97.67	2.03 $\pm$ 0.94
	<b>Overall</b>		<b>88.66</b>	<b>2.11 <math>\pm</math> 0.05</b>
180 m	1	100.00	84.00	2.08 $\pm$ 0.82
	2	83.33	90.91	2.13 $\pm$ 0.67
	3	77.78	82.35	2.06 $\pm$ 0.87
	4	92.16	87.04	2.15 $\pm$ 0.63
	5	100.00	93.75	2.09 $\pm$ 0.80
	6	93.75	97.83	2.11 $\pm$ 0.76
	7	91.67	100.00	2.07 $\pm$ 0.84
	8	100.00	95.45	2.13 $\pm$ 0.68
	9	100.00	100.00	2.07 $\pm$ 0.81
	10	100.00	83.33	2.14 $\pm$ 0.67
	11	77.78	97.22	2.03 $\pm$ 0.93
	<b>Overall</b>		<b>91.33</b>	<b>2.10 <math>\pm</math> 0.03</b>
1km	1	83.33	83.33	1.96 $\pm$ 1.21
	2	72.73	84.21	2.08 $\pm$ 0.86
	3	87.50	75.68	1.88 $\pm$ 1.13
	4	86.84	80.49	2.03 $\pm$ 0.78
	5	91.43	91.43	2.15 $\pm$ 0.76
	6	85.53	86.67	1.99 $\pm$ 1.00
	7	93.33	95.45	1.76 $\pm$ 1.28
	<b>Overall</b>		<b>85.67</b>	<b>1.98 <math>\pm</math> 0.13</b>

## 4. Discussion

We have demonstrated the value of two of the most readily available remote sensing products accounting for land cover (the CORINE land cover map from Landsat TM at a 30 m pixel size and the spectral index NDVI from NOAA-AVHRR at 1 km) in landscape classification at different spatial resolutions. The consistency of classifications across spatial resolutions is a key concern for landscape managers, because information achieved at a particular level should be reproducible ideally at other decision-making levels (Rocchini & Ricotta, 2007). Nevertheless, although this consistency might be desirable, caution is urged, as landscape is hierarchically structured and most ecological processes and patterns are scale-dependent (Schröder & Seppelt, 2006). Thus, ecological patterns and processes should be evaluated only when the spatial resolution of available data matches the target phenomenon; otherwise, we could miss it (Jelinski & Wu, 1996). Information that can be relevant at low hierarchical levels might become irrelevant over a given threshold of aggregation or *vice versa* (Karl & Maurer, 2010). In this sense, our multi-spatial resolution approach showed how the perception of landscape patterns can be affected by using input data collected at a spatial resolution different to that of the landscape classification analyses.

When using CORINE 30 m as an input in landscape classification analysis, the number and typology of classes differed across spatial resolutions. From a practical perspective, this fact is relevant as it could limit the implementation of this approach for management purposes (Rocchini & Ricotta, 2007). It is well known that thematic resolution (number and typology of classes) of landscape maps may constrain results of further landscape analyses (Suárez-Seoane & Baudry, 2002; Gimona *et al.*, 2009), leading to different ecological findings. Nevertheless, the use of CORINE in landscape classification was advantageous, since landscape classes were easily characterized and interpreted, as CORINE account directly for land cover. Regarding the error and uncertainty of CORINE-based classifications, we found the original data to be a main source of error for further classification process, being the generalization and simplification of reality into a limited set of classes (Hou *et al.*, 2013), as well as the existence of spectral interferences, mixed pixels, system errors or conceptual mistakes (Bossard *et al.*,

2000) the possible causes behind this error. Addressing specifically landscape classification process, transferring information from one resolution to another generally involves generalization and loss of accuracy and reliability (Hou *et al.*, 2013). Nevertheless, according to some authors (Ju *et al.*, 2005; Dronova *et al.*, 2012), this transfer of information does not always imply a loss of accuracy. In heterogeneous landscapes, such as mountain systems, high local variability might lead to high landscape complexity on the ground and noise in the remote sensing, making class allocation process difficult and partially erroneous (Kennedy *et al.*, 2009; Rocchini *et al.*, 2013; Nagendra *et al.*, 2013). Therefore, coarsening the spatial resolution of data (from 30 m to 90 m) could help to reduce the perception of this local variability, improving then the accuracy of classification (Ju *et al.*, 2005). Nevertheless, with further coarsening (beyond 90 m), boundaries between patches could be poorly represented due to a loss of resolution and distortion in land cover information (Shao & Wu, 2008), causing a new error. The loss of the capacity to detect local variability could be also suggested as an explanation of the overall increase of membership probability (and consequent decrease of uncertainty) associated to data coarsening. In this sense, beyond 90 m spatial resolution, the existence of some classes constituted by rather disparate landscape features resulted in large differences between some pixels and the characteristic vector of the class, increasing uncertainty. Additionally, our study suggested that the use of discrete maps, such as CORINE, in landscape classification might reduce partially confusion, allowing landscape classes to be depicted with high certainty. It is reasonable to expect that a reduction of mutually-exclusive classes would decrease confusion among classes (i.e., CI values close to 1) (Strand, 2011). Consistent with this statement, the reduction of classes shearing very similar landscape attributes (classes 8 and 9 were reduced to class 7) when spatial resolution changed from 30 m to 90 m could explain the decrease in confusion. On the contrary, at 180 m resolution, the definition of rather similar classes (like classes 2 and 3) implied an increase in confusion. The reduction in the number of classes at 1 km resolution was probably related to the decrease in CI, due to the lower probability of definition of classes with some degree of overlap. The dependence of CI on spatial resolution could be related to the modifiable areal unit

problem (MAUP), since changes in spatial resolution provided different landscape spatial configuration (Wong, 2009).

Accounting for NDVI-based landscape classifications, we found that the number and typology of landscape classes was only sensitive to change from coarse (1 km) to middle and high spatial resolution (180 m, 90 m and 30 m). This lack in classification consistency from 1 km to the more detailed resolutions could be explained by the role of input variables used in combination with NDVI, especially topography, which is of key relevance to describe landscape in mountain systems. The more detailed information on topography and urban influence included in landscape classifications at middle and high spatial resolution, as a consequence of the real change of resolution, let depict regional peculiarities that could not be addressed at 1 km (Hou *et al.*, 2013). Consequently, the number of classes represented increased. The consistency of NDVI-based landscape classifications across middle and high spatial resolution suggested the adequacy of using spectral indexes, in combination with other variables, in landscape classification processes from a practical point of view. However, the use of NDVI could hamper the description and interpretation of landscape classes, since it informs on biophysical parameters related to vegetation activity, not accounting for land cover directly (Wang & Tenhunen, 2004). Furthermore, some additional considerations should be taken in account concerning the error and uncertainty associated to this data source (Hoy *et al.*, 2013). Atmospheric influences and aerosols tend to decrease NDVI values (Carlson & Ripley, 1997) and fluctuations in soil brightness might also lead to large variations in NDVI signal among images (Liu & Huete, 1995). NDVI signal is sensitive to canopy background and could be saturated at high leaf area index (LAI) values (Pettorelli *et al.*, 2005). Looking at the error of NDVI-based landscape classifications, we found that landscape maps developed at 1 km (the original resolution of NDVI) showed less accuracy than those developed at intermediate resolutions. Maps at the coarsest pixel size might result overly non-specific to be useful (Ju *et al.*, 2005) affecting, therefore, the correct characterization of spatial details of the landscape, due to the vagueness of information (Hou *et al.*, 2013). The decrease in classification accuracy from 90 m to 30m was suggested to be associated with local landscape complexity and variability, making class allocation processes difficult and partially erroneous

(Kennedy *et al.*, 2009; Rocchini *et al.*, 2013; Nagendra *et al.*, 2013). Addressing membership probability, the poor influence of spatial resolution change on results might suggest that NDVI index facilitates the definition of homogeneous classes providing accurate pixel allocation, with independence of spatial resolution. Additionally, the increase in confusion among classes at higher spatial resolution than the original one could be associated with both, the increase in the number of classes and the inherent properties of NDVI as a continuous variable. Assumptions for classification methods include that classes are crisp and mutually exclusive, setting boundaries in sites where classes slightly differ (Foody, 2002; Bollinger & Mladenoff, 2005). This might be a problem when working with continuous data in heterogeneous mountain systems, where classes can be inter-grade and co-exist spatially (Foody, 2002; Morán-Ordóñez *et al.*, 2012), resulting in high confusion in regards to which class a pixel should belong (Álvarez-Martínez *et al.*, 2010). This problem would be reduced in more homogeneous systems, where classes are very different and with clear dominance of one of them across space (Bollinger & Mladenoff, 2005).

## **5. Conclusions**

Remote sensing products informing on land cover, such as the CORINE Land Cover map at 30 m or the NDVI spectral index from NOAA at 1 km, are valuable tools that, used in combination with other thematic information, allow for producing landscape classifications useful for practical applications. The multi-spatial resolution approach here developed provided a relevant framework for landscape managers, particularly when funding is limited and data source at an appropriated spatial resolution are not available. Efforts should be made to select data at suitable resolutions, matching regional peculiarities and minimizing error and uncertainty in results.

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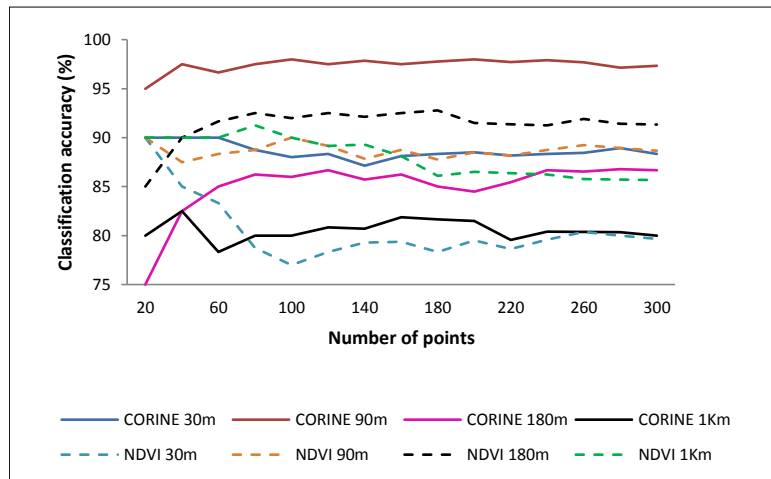
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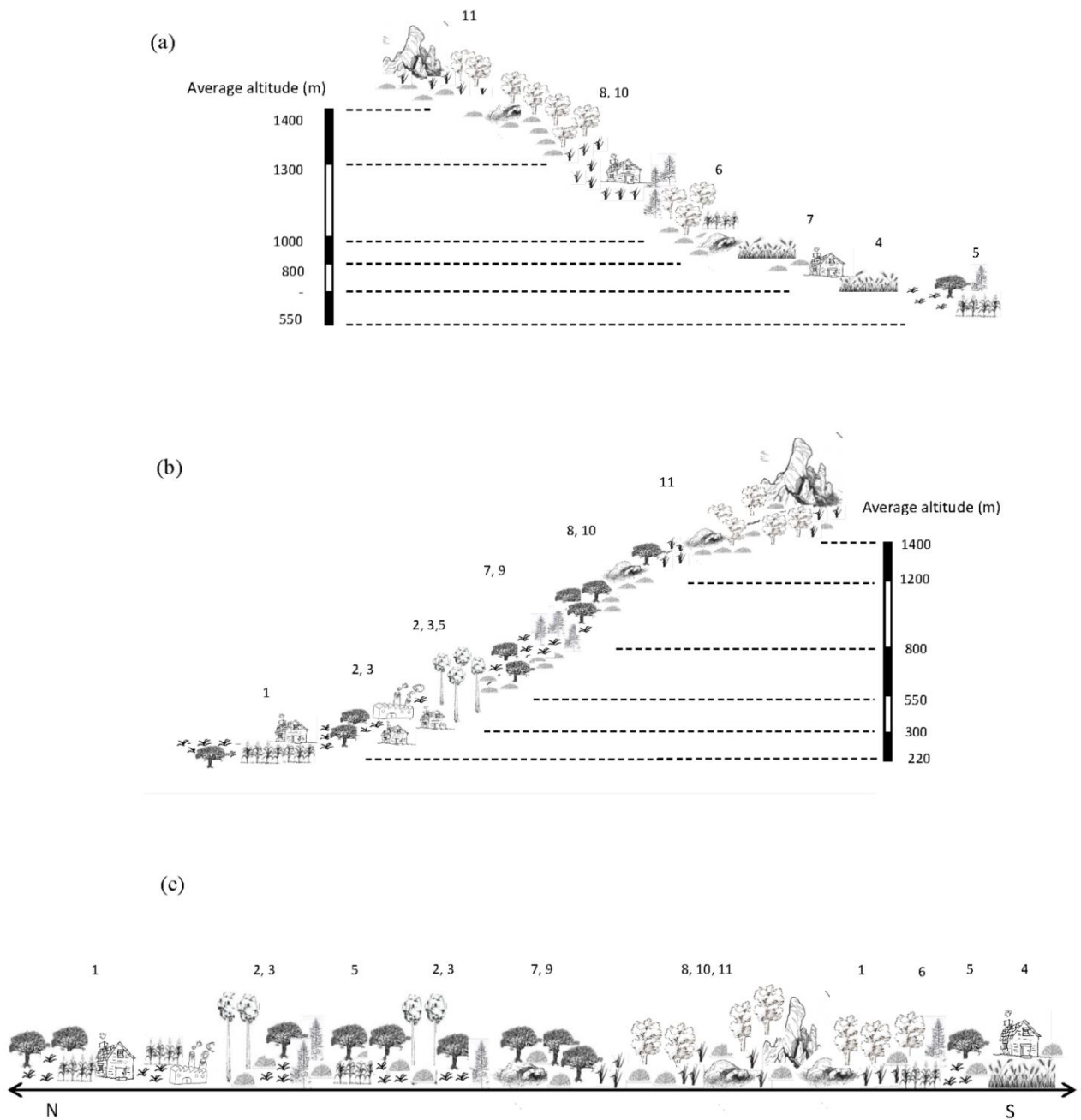
# ANNEX I

**Table S1.1.** Equivalence between classes of the original and new CORINE classifications.

Original CORINE	New CORINE	Accuracy (%)
Continuous urban fabrics	Human infrastructures	Not validated
Discontinuous urban fabrics		
Industrial or commercial units		
Road and rail networks and associated land		
Port areas		
Airports		
Dump sites		
Construction sites		
Green urban areas		
Sport and leisure facilities		
Mineral extraction sites	Mineral extractions sites	100.00
Non-irrigated arable lands	Herbaceous crop lands	75.00
Permanently irrigated lands		
Complex cultivation patterns		
Vineyards	Woody crop lands	66.67
Fruit trees and berry plantations		
Olive groves		
Agro-forestry areas		
Pastures	Pasturelands (including "bocage" type formations)	89.06
Natural grasslands		
Agricultural lands with natural vegetation		
Broad-leaved forests	Forests	78.68
Mixed forests		
Coniferous forests		
Transitional woodland-shrub	Transitional woodland-shrublands	86.11
Moors and heathlands	Shrub, sclerophyllous and herbaceous associations	84.52
Sclerophyllous vegetation		
Peat bogs		
Sparsely vegetated areas	Sparsely vegetated areas	83.33
Beaches dunes sands	Bare areas	100.00
Bare rocks		
Burnt areas		
Inland marshes	Wetlands	Not validated
Salt marshes		
Water courses	Water	100.00
Water bodies		
Sea and ocean		
Estuaries		
Total		82.50



**Figure S1.1.** Cumulative adjustment curves showing the optimal number of points needed for landscape classification validation.



**Figure S1.2.** Example of geographic gradient of landscape classes. Data corresponds to landscape classification made at 90 m of spatial resolution, integrating topography, urban influence and land cover (NDVI). a) Altitudinal gradient of southern slope, b) altitudinal gradient of northern slope and c) North-South gradient. See class legend in Table 1.3.

**Table S1.2.** Statistical characterization of landscape classes (mean  $\pm$  standard deviation) from a set of variables accounting for topography, urban influence and land cover. Table shows the results obtained at 90 m of spatial resolution, as an example: a) CORINE, b) NDVI. See Table 1.1 for code meaning.












a)	Landscape classes based on CORINE									
	1	2	3	4	5	6	7	8	9	10
DEM ( $\times 10^3$ )	0.59 $\pm$ 0.27	1.18 $\pm$ 0.25	1.00 $\pm$ 0.38	0.84 $\pm$ 0.37	0.39 $\pm$ 0.19	1.06 $\pm$ 0.31	0.80 $\pm$ 0.25	1.38 $\pm$ 0.47	0.89 $\pm$ 0.26	0.47 $\pm$ 0.40
SLO	34.00 $\pm$ 19.90	26.71 $\pm$ 17.74	31.98 $\pm$ 19.80	28.82 $\pm$ 19.50	22.64 $\pm$ 14.16	22.92 $\pm$ 17.28	9.14 $\pm$ 9.41	44.17 $\pm$ 25.94	10.15 $\pm$ 12.91	13.88 $\pm$ 13.62
SOLR ( $\times 10^6$ )	1.07 $\pm$ 0.16	1.23 $\pm$ 0.15	1.20 $\pm$ 0.17	1.19 $\pm$ 0.16	1.14 $\pm$ 0.11	1.25 $\pm$ 0.13	1.24 $\pm$ 0.07	1.25 $\pm$ 0.21	1.23 $\pm$ 0.10	1.15 $\pm$ 0.11
AC ( $\times 10^3$ )	1.56 $\pm$ 1.04	2.19 $\pm$ 1.20	2.01 $\pm$ 1.20	1.80 $\pm$ 1.01	0.97 $\pm$ 0.83	1.55 $\pm$ 1.17	1.25 $\pm$ 0.86	2.45 $\pm$ 1.32	1.45 $\pm$ 0.91	0.78 $\pm$ 0.69
INFRA	0.51 $\pm$ 3.07	0.10 $\pm$ 1.12	0.12 $\pm$ 1.16	0.27 $\pm$ 1.96	2.79 $\pm$ 8.44	1.65 $\pm$ 6.54	0.70 $\pm$ 3.20	0.10 $\pm$ 1.13	1.13 $\pm$ 4.69	51.84 $\pm$ 37.18
MIN	0.01 $\pm$ 0.63	0.01 $\pm$ 0.30	0.02 $\pm$ 0.62	0.02 $\pm$ 0.53	0.00 $\pm$ 0.00	2.65 $\pm$ 14.55	0.00 $\pm$ 0.00	0.01 $\pm$ 0.39	0.09 $\pm$ 2.04	0.24 $\pm$ 3.02
HERC	1.82 $\pm$ 7.40	1.53 $\pm$ 7.46	1.05 $\pm$ 5.72	2.71 $\pm$ 9.81	0.33 $\pm$ 2.77	0.28 $\pm$ 2.96	90.95 $\pm$ 14.98	0.14 $\pm$ 1.84	14.20 $\pm$ 17.28	24.99 $\pm$ 28.72
WOOC	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.87 $\pm$ 7.78	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
PAS	3.22 $\pm$ 9.14	0.78 $\pm$ 4.12	2.60 $\pm$ 8.57	2.40 $\pm$ 8.19	76.19 $\pm$ 25.98	77.72 $\pm$ 27.93	1.35 $\pm$ 6.38	2.37 $\pm$ 8.80	30.20 $\pm$ 31.29	4.80 $\pm$ 11.01
FOR	87.92 $\pm$ 17.82	93.86 $\pm$ 12.22	6.55 $\pm$ 14.17	7.11 $\pm$ 14.27	16.56 $\pm$ 22.55	7.76 $\pm$ 16.01	4.32 $\pm$ 11.29	7.48 $\pm$ 16.80	6.25 $\pm$ 16.77	7.74 $\pm$ 15.93
TWOOD	3.97 $\pm$ 10.82	1.84 $\pm$ 6.62	86.24 $\pm$ 19.41	2.62 $\pm$ 8.26	1.36 $\pm$ 5.87	6.74 $\pm$ 14.91	1.78 $\pm$ 7.33	6.92 $\pm$ 15.59	2.93 $\pm$ 11.10	1.19 $\pm$ 5.55
SCRUB	1.69 $\pm$ 6.88	1.39 $\pm$ 6.49	2.53 $\pm$ 9.94	84.57 $\pm$ 18.31	1.99 $\pm$ 8.00	1.39 $\pm$ 6.60	0.80 $\pm$ 4.46	1.08 $\pm$ 5.90	0.83 $\pm$ 5.11	1.88 $\pm$ 8.55
SPAR	0.01 $\pm$ 0.49	0.10 $\pm$ 1.33	0.13 $\pm$ 1.80	0.02 $\pm$ 0.46	0.00 $\pm$ 0.04	0.26 $\pm$ 2.76	0.00 $\pm$ 0.00	28.13 $\pm$ 40.23	0.06 $\pm$ 0.95	0.90 $\pm$ 6.23
BARE	0.09 $\pm$ 1.38	0.39 $\pm$ 3.09	0.67 $\pm$ 4.34	0.13 $\pm$ 1.58	0.02 $\pm$ 0.41	0.62 $\pm$ 4.32	0.00 $\pm$ 0.00	53.67 $\pm$ 41.12	0.04 $\pm$ 0.84	2.00 $\pm$ 9.45
WET	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.16 $\pm$ 3.26	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
WAT	0.27 $\pm$ 1.99	0.01 $\pm$ 0.37	0.09 $\pm$ 1.07	0.16 $\pm$ 1.40	0.60 $\pm$ 2.95	0.06 $\pm$ 0.82	0.10 $\pm$ 1.04	0.09 $\pm$ 1.03	44.27 $\pm$ 42.36	4.43 $\pm$ 11.10





b)	Landscape classes based on NDVI										
	1	2	3	4	5	6	7	8	9	10	11
DEM ( $\times 10^3$ )	0.23 $\pm$ 0.10	0.48 $\pm$ 0.15	0.43 $\pm$ 0.12	0.72 $\pm$ 0.16	0.96 $\pm$ 0.16	0.96 $\pm$ 0.18	1.47 $\pm$ 0.16	1.37 $\pm$ 0.09	1.69 $\pm$ 0.14	1.07 $\pm$ 0.08	0.84 $\pm$ 0.21
SLO	17.73 $\pm$ 9.43	47.91 $\pm$ 13.69	42.26 $\pm$ 12.92	16.07 $\pm$ 8.22	64.71 $\pm$ 21.80	38.09 $\pm$ 11.65	54.73 $\pm$ 17.66	27.03 $\pm$ 12.27	36.07 $\pm$ 17.00	10.64 $\pm$ 6.34	8.37 $\pm$ 7.20
SOLR ( $\times 10^6$ )	1.11 $\pm$ 0.08	0.90 $\pm$ 0.10	1.23 $\pm$ 0.07	1.21 $\pm$ 0.08	0.89 $\pm$ 0.15	1.19 $\pm$ 0.14	1.02 $\pm$ 0.14	1.33 $\pm$ 0.10	1.37 $\pm$ 0.13	1.29 $\pm$ 0.05	1.24 $\pm$ 0.06
AC ( $\times 10^3$ )	1.05 $\pm$ 0.81	1.45 $\pm$ 0.94	1.37 $\pm$ 0.92	1.51 $\pm$ 1.02	1.90 $\pm$ 1.17	1.80 $\pm$ 1.16	2.51 $\pm$ 1.24	2.08 $\pm$ 1.18	142.87 $\pm$ 15.66	1.89 $\pm$ 1.27	1.42 $\pm$ 0.90
NVI	169.43 $\pm$ 11.39	167.57 $\pm$ 9.84	167.45 $\pm$ 9.27	168.84 $\pm$ 9.88	158.38 $\pm$ 13.28	160.49 $\pm$ 10.96	148.84 $\pm$ 15.39	147.75 $\pm$ 12.52	2.98 $\pm$ 1.02	151.02 $\pm$ 8.09	131.38 $\pm$ 13.08





**Table S1.3.** Description of landscape classes obtained at 30 m spatial resolution from a set of variables accounting for topography, urban influence and land cover (CORINE).

Class		Class description
1		Forests covering coastal and middle-mountain areas, mainly from Atlantic and Sub-Atlantic zones of the Cantabrian Mountains. These areas are situated under 1000 m.a.s.l. with middle to slight slope, relatively high urban influence and wide solar radiation ranges.
2		Forests covering central mountains and piedmont areas with low urban influence, at altitudes above 1000 m.a.s.l., middle slope and wide solar radiation range.
3		Transitional to woodlands with relatively low urban influence covering mainly Atlantic and Sub-Atlantic zones of the Cantabrian Mountains. This class is situated in areas with mid-low altitudes (600 m.a.s.l. on average) but middle to high slope.
4		Transitional woodlands from central and southern areas of the Cantabrian Mountains. This class is situated in areas with wide altitude ranges (between 1500-900 m.a.s.l. from high central mountains to piedmont areas), moderate to steep slope and relatively low urban influence.
5		Pastures in mid-low Atlantic mountains and coastal areas under 800 m.a.s.l. with moderate to very slight slope. This is a class with high urban influence and moderate solar radiation values.
6		Pastures covering bottom valleys and hillsides of central Cantabrian Mountains with altitudes ranging from 1500 to 1000 m.a.s.l. and middle solar radiation and slope rates.
7		Shrub-herbaceous associations lying at altitudes between 1200-500 m.a.s.l. in areas of relatively high urban influence with slight to moderate slope and moderate to mid solar radiation rates.
8		Croplands from depressions and coastal areas. It is the class with the lowest altitude values (under 800 m.a.s.l.) covering plains or slight-slope areas which are close to settlements.
9		Croplands (mainly non irrigated arable lands in intensive use) from paramos and countrysides from the southern slopes of the Cantabrian Mountains. It is the class with the highest urban influence, situated under 1000 m.a.s.l. in plains or areas with very slight slope.
10		Water surfaces and artificial surfaces such as settlements, roads, railways or mines in areas of wide altitudinal ranges and slight to moderate slope with low to moderate solar radiation rates.
11		Rocks and areas with little or no vegetation, covering wide altitudinal ranges (between 1400-500 m.a.s.l.) in areas of moderate to high slope and radiation rates.






**Table S1.4.** Description of landscape classes obtained at 90 m spatial resolution from a set of variables accounting for topography, urban influence and land cover (CORINE).

Class		Class description
1		This class comprises areas with little vegetation and forests covering coastal and middle-mountain areas, mainly from Atlantic and Sub-Atlantic zones of the Cantabrian Mountains. These areas are situated at a wide altitude range, with middle to slight slope, relatively high urban influence and also wide solar radiation ranges.
2		Forests covering high central mountains and piedmont areas with relative urban influence, at altitudes above 1000 m.a.s.l., middle to high slope and wide solar radiation range.
3		Forests covering depressions, paramos and countrysides with relative high urban influence. This class is situated under 1000 m.a.s.l., in areas of slight slope and wide solar radiation range.
4		Transitional to woodland areas with relative high urban influence, at middle to high slope and wide altitudinal and solar radiation range.
5		Shrub-herbaceous associations lying at altitudes between 1200-500 m.a.s.l., in areas of high urban influence with slight to rough slope and moderate to mid solar radiation rates.
6		Pastures covering areas with wide altitudinal and solar radiation range, at middle to slight slope. It is the class with the highest urban influence along with class 7.
7		Croplands from coastal areas, depressions, paramos and countrysides situated under 1000 m.a.s.l. in areas of slight slope, wide solar radiation rate and high urban influence.
8		Rocks and areas with no vegetation, covering a wide altitudinal range (between 1700-700 m.a.s.l.) in areas of moderate to high slope and low solar radiation rates.
9		Water surfaces.
10		Settlements, roads, railways or mines in areas of very low altitude and slight to moderate slope with low to moderate solar radiation rates.



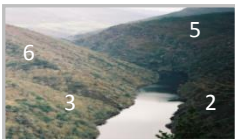



**Table S1.5.** Description of landscape classes obtained at 180 m spatial resolution from a set of variables accounting for topography, urban influence and land cover (CORINE).

Class		Class description
1		This class comprises areas with little vegetation and forests covering coastal and middle-mountain areas, mainly from Atlantic and Sub-Atlantic zones of the Cantabrian Mountains. These areas are situated at a wide altitude range, with middle to slight slope, relatively high urban influence and also wide solar radiation ranges.
2		Forests covering high central mountains and piedmont areas with relative urban influence, at altitudes above 1000 m.a.s.l., middle to high slope and wide solar radiation range.
3		Forests covering depressions, paramos and countrysides with relative high urban influence. This class is situated under 1000 m.a.s.l., in areas of slight slope and wide solar radiation range.
4		Transitional to woodland areas with relative high urban influence, at middle to high slope and wide altitudinal and solar radiation range.
5		Shrub-herbaceous associations lying at altitudes between 1200-500 m.a.s.l., in areas of high urban influence with slight to rough slope and moderate to mid solar radiation rates.
6		Pastures covering areas with wide altitudinal and solar radiation range, at middle to slight slope. It is the class with the highest urban influence along with class 7.
7		Croplands from coastal areas, depressions, paramos and country sides situated under 1000 m.a.s.l. in areas of slight slope, wide solar radiation rate and high urban influence.
8		Rocks and areas with no vegetation, covering a wide altitudinal range (between 1700-700 m.a.s.l.) in areas of moderate to high slope and low solar radiation rates.
9		Water surfaces.
10		Settlements, roads, railways or mines in areas of very low altitude and slight to moderate slope with low to moderate solar radiation rates.






**Table S1.6.** Description of landscape classes obtained at 1 km spatial resolution from a set of variables accounting for topography, urban influence and land cover (CORINE).

Class	Class description	
1		Forests lying at wide altitude range (between 1350-400 m.a.s.l.), in areas of relative urban influence, middle to slight slope and moderated to high solar radiation values.
2		Transitional to woodland and shrub areas with relatively high urban influence, at middle to low slope and wide altitudinal and solar radiation range.
3		Pastures covering areas with relative urban influence, at middle to low slope and wide altitudinal and solar radiation range.
4		Croplands from coastal areas, depressions, paramos and countryside along with water surfaces situated under 1000 m.a.s.l., in areas of very slight slope, wide solar radiation rate and high urban influence.
5		Rocks, areas with no vegetation and artificial surfaces covering a wide altitudinal range (between 1400-500 m.a.s.l.), in areas of moderated to low slope and moderated solar radiation rates.








**Table S1.7.** Landscape classes obtained at 30 m, 90 m and 180 m of spatial resolution from a set of variables accounting for topography, urban influence and land cover (NDVI).

Classes	Class description
1 	Sea inlets, coastal plains and sub-coastal valleys located at the lowest altitude of the study area, with moderate to low solar radiation rates. This is a class with high urban influence and high NDVI values, as it is dominated by a mosaic of crops and pastures with a high presence of natural vegetation (woodlots and hedgerows) and coniferous forests.
2 	This class appears in the Atlantic and Sub-Atlantic part of the Cantabrian Mountains. It mainly covers hillsides under 650 m.a.s.l. with a northern exposure and mid-high slope. This is a class with low urban influence and relatively high NDVI values, which consists of a mosaic of moors, scrubs and forests mixed with pastures in coastal areas.
3 	This class appears in the Atlantic and Sub-Atlantic part of the Cantabrian Mountains. It mainly covers hillsides under 650 m.a.s.l. with a southern exposure and mid-high slope. This is a class with low urban influence and relatively high NDVI values, which consists of a mosaic of moors, scrubs and forests mixed with pastures in coastal areas.
4 	Class similar to class 11, however this class covers areas with higher slope values and higher NDVI rates, since land cover is dominated by complex cultivation patterns (crops and pasture mosaic) with a high presence of natural vegetation.
5 	This class appears in the Atlantic and Sub-Atlantic part of the Cantabrian Mountains, from mid-mountainside to peaks. It shows the highest slope rates of the study area, but low altitude, such as canyons or gorges. It is mainly situated with a northern exposure and has a low urban influence. It has middle NDVI values, since it is dominated by woody and scrub vegetation, with rock formations.
6 	This class appears in the Atlantic and Sub-Atlantic part of the Cantabrian Mountains, from mid-hillsides to the top. It might also appear on southern mountainsides with southern exposure above class 10. It shows slightly higher altitudes and gentler slopes than class 5, on sunny faces. It is a class dominated by moors, scrubs and forests, with low urban influence.

**Table S1.7. (Cont.)**

Classes	Class description	
7		Hillsides in the central area of the Cantabrian Mountains above an average altitude of 1400 m.a.s.l., with northern exposure. It might also appear in peak areas with very low solar radiation rates. This class covers steep slopes, with land cover composed of rock formations with moors and high mountain forests, which explains the middle NDVI values.
8		Hillsides and mid-hillsides under 1400 m.a.s.l. and valleys above 1300 m.a.s.l. in the central area of the Cantabrian Mountains. It might also cover peaks in transitional areas between central and inner Atlantic and Sub-Atlantic mountains. This is on the sun-facing side, although it might also appear in northern exposures below class 7. This is a class with relatively high urban influence and moderate slope. Principal land covers are broadleaf forest mixed with mid-hillside pastures, moors and heathlands.
9		Peaks and mountainsides above 1400 m.a.s.l., with southern, western and eastern exposures in the central areas of the Cantabrian Mountains, high solar radiation values and moderate to rough slopes. This class is dominated by rock formations, along with high-mountain pastures, moors, heathlands and forests, and has a relatively low urban influence.
10		Valley bottoms from high central areas of the Cantabrian Mountains, extending to piedmont areas. This has an average altitude of around 1000 m.a.s.l., with gentle slopes and moderate solar radiation rates. Urban influence is high and land cover consists of pastures in the valley bottoms and mosaics of forests, scrubs and crops in piedmont areas.
11		Paramos, countryside and depressions. This class is the closest to settlements covering flat areas above 600 m.a.s.l., with mid-high solar radiation rates. It has the lowest NDVI values since it is dominated by intensive crops; mainly non-irrigated crops.

**Table S1.8.** Landscape classes obtained at 1 km spatial resolution from variables accounting for topography, urban influence and land cover (NDVI)

Classes		Class description
1		Sea inlets, coastal plains and sub-coastal valleys located at the lowest altitude of the study area, with moderate to low solar radiation rates. This is a class with high urban influence and high NDVI values, as it is dominated by a mosaic of crops and pastures with a high presence of natural vegetation (woodlots and hedgerows) and coniferous forests.
2		Coastal hills under 800 m.a.s.l. with moderate solar radiation and slope values. It is the class with the highest NDVI values since it is dominated by pastures with natural vegetation areas.
3		This class covers areas with an average altitude of 600 m.a.s.l., slight slope and moderate to high solar radiation rates, which are mainly close to settlements. It mainly covers depressions of Lugo and some Northern areas of Burgos and Alava. Land cover is characterized by complex cultivation patterns (mosaic of crops and pasture) with high presence of natural vegetation. This class is similar to class 7 however, it has slightly lower altitude rates and higher NDVI values which is explained by the increase of natural vegetation presence.
4		Middle mountain areas under 1400 m.a.s.l. with moderate solar radiation and slope rates. It is the farthest class to settlements with moderate NDVI values because it is mainly dominated by forests, scrub and transitional woodland formations.
5		High central mountains with an average altitude around 1400 m.a.s.l., with moderate slope and high solar radiation rates. This class is relatively far from settlements with moderate values of NDVI, as it is dominated by forests formations, scrub and bare and semi-bared areas.
6		Valley bottoms from high central areas of the Cantabrian Mountains, extending to piedmont areas and Sub-Atlantic mountains from Lugo. It has an average altitude around 900 m.a.s.l., with gentle slopes and it is relatively close to settlements. It is a class dominated by pastures in valley bottoms, while piedmont areas are covered by broadleaf forest formation and coniferous repopulations, accompanied by scrubs and mosaic of crops fields.
7		Paramos, countryside and depressions. This is the closest class to settlements covering flat areas above 850 m.a.s.l., with mid-high solar radiation rates. It has the lowest NDVI values as it is dominated by intensive crops; mainly non-irrigated crops.







Picture's author: Héctor Astiárraga

## **Chapter 2:**

# **Landscape heterogeneity as a surrogate of biodiversity in mountain systems: what is the most appropriate spatial analytical unit?<sup>2</sup>**

<sup>2</sup>The content of this chapter is under second review in *Ecological Indicators*.

García-Llamas, P., Calvo, L., De la Cruz, M., & Suárez-Seoane, S. (2017) Landscape heterogeneity as a surrogate of biodiversity in mountain systems: what is the most appropriate spatial analytical unit?

## Abstract

The estimated potential of landscape metrics as a surrogate for biodiversity is strongly dependent on the spatial analytical unit used for evaluation. We assessed the relationship between terrestrial vertebrate species richness (total and taxonomic) and structural landscape heterogeneity, testing the impact of using different spatial analytical units in three mountain systems in Spain. Landscape heterogeneity was quantified through an additive partitioning of the Shannon diversity index of landscape classes. Both landscape heterogeneity and species richness were calculated using two spatial analytical unit approaches: eco-geographic vs. arbitrary (i.e., watersheds vs. square windows of different sizes 20 km x 20 km, 50 km x 50 km, 100 km x 100km). We predicted species richness on the basis of landscape heterogeneity by fitting separate linear models for each spatial analytical unit approach. The main results obtained showed that landscape heterogeneity influenced terrestrial vertebrate species richness. However, the emerging relationships were dependent on the spatial analytical unit approach. The eco-geographic approach showed significant relationships between landscape heterogeneity and total and taxonomic species richness in almost all cases (except mammals). Considering the arbitrary approach, landscape heterogeneity appeared as a predictor of species richness only for mammals and breeding birds and at the coarsest spatial scales. Our results claim for further consideration of eco-geographical spatial analytical unit approaches in biodiversity studies and show that the methods of this study offer a valuable cost-effective framework for biodiversity management and spatial modeling, with potential to be adapted to national and global applications.

**Keywords:** habitat diversity; mammals; birds; reptiles; terrestrial vertebrates; watersheds.

## 1. Introduction

Loss of biodiversity is one of the main impacts of land use change, and is associated with landscape fragmentation and habitat loss over recent decades (Lindenmayer *et al.*, 2002; Herrando *et al.*, 2014). Knowledge of the factors driving biodiversity patterns has become a priority for researchers and conservation practitioners (Morelli *et al.*, 2013). Considerable efforts have been made to develop and improve methods for evaluating components of current biodiversity to enable the identification of priorities for conservation (Priego-Santander *et al.*, 2013). Conservation strategies require the quantification of biodiversity, although the time and cost limitations of biodiversity data collection make this a challenging task (Ewers *et al.*, 2005). Thus, the development of biodiversity indicators that reduce the effort of biodiversity estimation, therefore speeding up the decision-making process, has become a priority for conservation biologists (Rossi & van Halder, 2010; Laurila-Pant *et al.*, 2015).

There is a large body of literature in which different environmental variables such as, climate, land cover (Kivinen *et al.*, 2007; Mehr *et al.*, 2011), topography (Krömer *et al.*, 2013; Yu *et al.*, 2015), soil properties (Medinski *et al.*, 2010), human population density or habitat diversity (Moreno-Rueda & Pizarro, 2007) have been used to make spatial predictions of species richness. Currently, there is increasing agreement about the consideration of landscape as the most pertinent level for biodiversity management actions (Walz, 2011), since landscape-based evaluations provide a larger-scale perspective of ecological processes than traditional site-based ones (Pino *et al.*, 2000). The use of landscape metrics as a proxy of species richness has become a popular approach (Lindenmayer *et al.*, 2002; Rossi & van Halder, 2010), made easier by the continuous development of remote sensing techniques and Geographic Information Systems (GIS) (Wagner & Fortin, 1987). Amongst the large number of landscape metrics used as biodiversity surrogates, landscape heterogeneity is gaining valuable recognition within conservation strategies (Walz, 2011). It is generally accepted that landscape heterogeneity is positively related to ecological niche diversity (Katayama *et al.*, 2014). Furthermore, landscape heterogeneity plays an important role in population

dynamics, as it may control dispersal rates, movement patterns or foraging strategies (Johnson *et al.* 1992), which suggests some connection between landscape heterogeneity and species richness. Nevertheless, the estimation of biodiversity from landscape metrics is often affected by the methods employed to observe and analyse landscape patterns (Walz, 2011). Since landscape metrics, including landscape heterogeneity, describe geometric and spatial properties of landscape (Gimona *et al.*, 2009), the ecological response emerging from landscape analyses might be conditioned by the shape (i.e., delineated boundaries; Moser *et al.*, 2007; Cushman & Mc Garigal, 2008) or size (i.e., spatial scale) of the analytical unit used for landscape quantification (Plexida *et al.*, 2014; Ye *et al.*, 2015; Weibull *et al.*, 2000).

The landscape is a continuum, but for practical reasons it must be split into spatial analytical units providing a frame for landscape metrics quantification. This is often rather arbitrary (Verberk *et al.*, 2006; Walz, 2011). Difficulties arise as differently delineated spatial analytical units might provide different statistical relationships for the same ecological process, making the interpretation and applicability of landscape metrics estimations challenging (Saura & Martínez-Millán, 2001). Most studies addressing landscape heterogeneity as a surrogate of species richness (e.g. Atauri & de Lucio, 2001; Moreno-Rueda & Pizarro, 2007; Schindler *et al.*, 2013) are based on a systematic partition of the landscape using arbitrarily defined spatial analytical units, such as UTM grids or circular buffers. However, the use of spatial analytical units with eco-geographic meaning could also provide a useful approach when predicting biodiversity, as displayed by Priego-Santander *et al.* (2013). This study showed the potential of landscape heterogeneity as a predictor of plant richness on the basis of land units defined from geomorphology, geology, relief, climate, soil and land cover features. Watersheds are increasingly being used in environmental modelling and management, as they represent integrated socio-ecological (Mayer *et al.*, 2014), geomorphological (Montgomery *et al.*, 1995) and multifunctional units (Karadağ, 2013) with potential application for analyses at multiple scales (Tinker *et al.*, 1998). For example, watersheds have been considered as operational spatial units to assess the relationship between soil erosion and landscape change (Li & Zhou,

2015), to identify and manage natural resources (Baloch & Tanik, 2008) and to analyse land cover change (Mendoza *et al.*, 2011; Álvarez-Martínez *et al.*, 2014). However, the application of eco-geographical units, including watersheds, as spatial analytical units in biodiversity modelling is under-evaluated. There is a clear need to explore the role of eco-geographical spatial analytical unit approaches, as an alternative to traditional arbitrary ones, in biodiversity studies.

Similarly, the influence of the size of the spatial analytical unit on the detection of relationships between landscape heterogeneity and species richness has been highlighted in different studies (e.g. Tews *et al.*, 2004; Morelli *et al.*, 2013; Schindler *et al.*, 2013). Relationships emerging from the use of a particular spatial analytical-unit size are not necessarily consistent across different sizes. This is a consequence of the operational scale at which organisms interact with their environment (Tews *et al.*, 2004). Taxa with a higher mobility and a strong demand for space are expected to be more influenced by larger landscape surface areas than smaller or sedentary species (Suárez-Seoane & Baudry, 2002; Schindler *et al.*, 2013). Thus, multiscale analyses are required to detect the scale at which the ecological phenomena show their biological signal (Lechner *et al.*, 2012).

In comparison with other systems, the higher environmental variability found in mountains provides a large diversity of habitats, and therefore landscape heterogeneity (Jobbágy *et al.*, 1996), which allows for higher species richness (Dufour *et al.*, 2006). In fact, mountains have been largely recognized as important sources of biodiversity worldwide (La Sorte & Jetz, 2010). Meanwhile, they are highly prone to biodiversity loss, due to their susceptibility to human and natural disturbances (Martinelli *et al.*, 2007). Therefore, the need to explore potential biodiversity predictors, such as landscape heterogeneity, becomes particularly relevant in mountain systems.

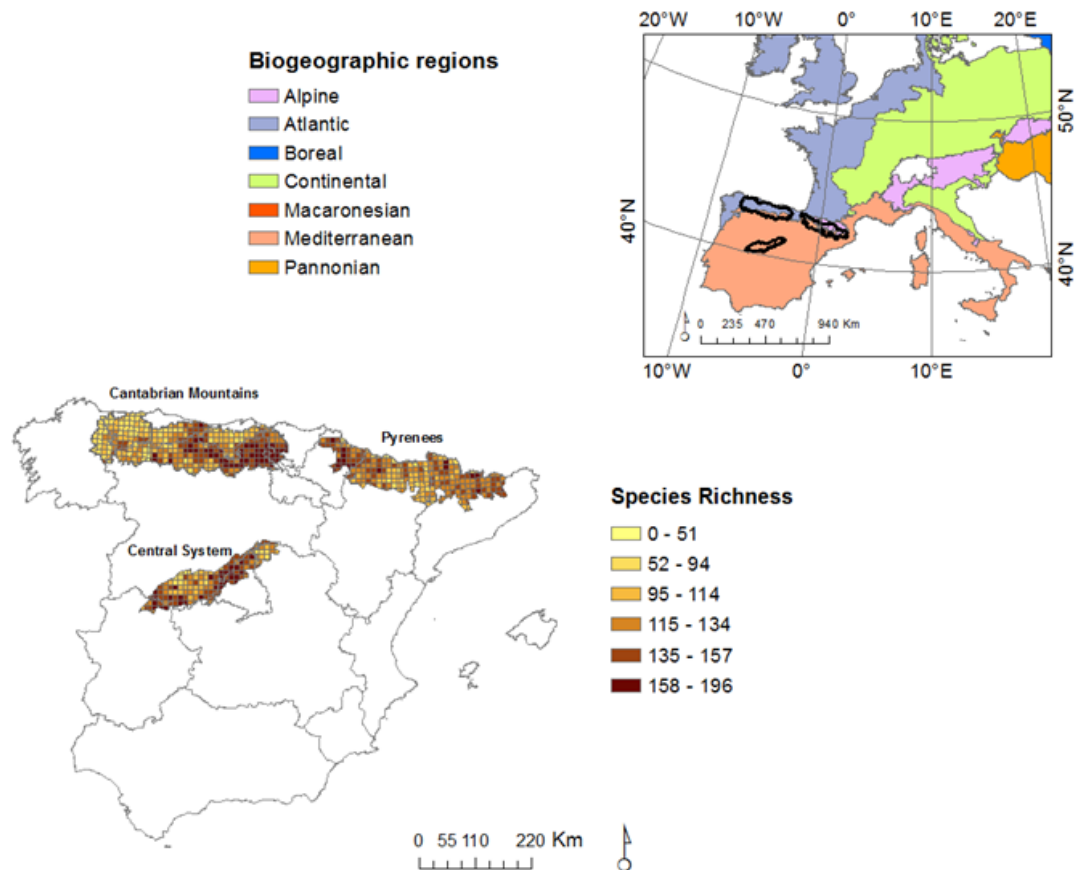
The main goal of this study was to evaluate the potential of the landscape heterogeneity as an indicator of species richness, assessing the effect of different methodological choices on the detection of significant ecological relationships. Specifically, we assessed the impact of using analytical units of different shape and size, i.e. following an eco-geographic (watersheds) versus an arbitrary (square

windows of different size) spatial analytical approach, to quantify species richness and landscape heterogeneity. As a study case, we evaluated the effect of the different choices on the relationship between landscape heterogeneity and species richness of vertebrates (total and per taxonomic group) in three mountain systems with different biogeographical influences in Spain.

## **2. Material and methods**

### **2.1. Study area**

The study area includes three mountain ranges located across Spain (Figure 2.1): the Cantabrian Mountains (CM), the Central System (CS) and the Spanish Pyrenees (SP). CM represent the transition between Atlantic and Mediterranean regions, CS is a typical example of the Mediterranean area and SP are located at the transition between the Mediterranean, Atlantic and Alpine regions (Rivas-Martínez *et al.*, 1987). All of them present a great diversity of climatic conditions. Annual rainfall ranges from 700 to 2400 mm in CM, 500 to 1500 mm in CS and 600 to 1400 mm in SP. Mean annual temperature ranges from -2.5 to 22.5 °C in all cases. These mountain systems are of particular interest as they are partially or totally included in the Mediterranean Basin, often considered as a biodiversity hotspot (Myers *et al.* 2000; Maiorano *et al.*, 2013), and they have a wide variety of ecosystems, habitats and endemic species. In particular, CM and SP represent the southern limit of a wide range of species of Euro-Siberian origin and the northernmost distribution of species of Iberian and Ibero-African origin (Martínez-Rica & Recoder, 1990; Morán-Ordóñez, 2012), while CS has been recognized as a migratory route and speciation centre (López-Sáez *et al.*, 2014).



**Figure 2.1.** Study area: The Cantabrian Mountains, the Central System and the Spanish Pyrenees. Information on biogeographic regions was obtained from the Spanish Ministry of Agriculture, Food and Environment (<http://www.magrama.gob.es/>). Additionally, total species richness in the three mountain systems. Information on species richness was obtained from the official database of vertebrates of Spain (Ministry of Agriculture, Food and Environment 2012; [www.magrama.gob.es](http://www.magrama.gob.es)).

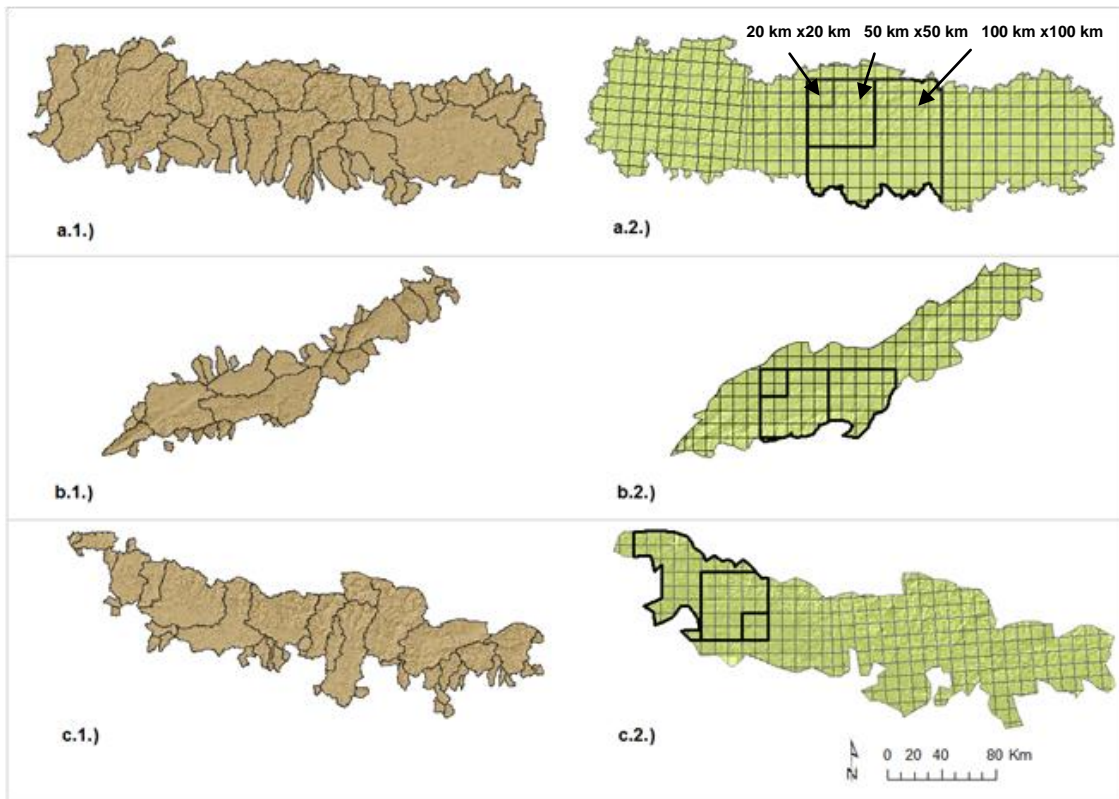
In CM, where altitude ranges from sea level up to 2650 m.a.s.l., dominant land covers are crop fields in lowlands and natural formations, such as heathlands, shrublands and deciduous forests (dominated by *Fagus sylvatica*, *Betula pubescens*, *Quercus petraea* and *Q. robur*, on northern slopes or by *Q. pyrenaica* and *Q. rotundifolia*, on southern slopes), in mid-highlands (Morán-Ordóñez *et al.*, 2011). Natural grasslands mainly cover areas at the highest altitudes. In CS, altitude ranges from 280 to 2592 m.a.s.l. The landscape is dominated by forests of *Q. pyrenaica*, *Q. ilex subsp. rotundifolia* and *Q. suber* (especially in the western sector) and *Pinus sylvestris* and *P. nigra* eastwards (López-Sáez *et al.*, 2014). Shrublands

and heathlands of *Cytisus oromediterraneus*, *Echinopartum ibericum*, *E. barnadesii* or *Erica australis* constitute the main features of the landscape above 1600 m.a.s.l. (Rivas-Martínez *et al.*, 1987), while grasslands dominate in the areas at the highest altitudes (López-Sáez *et al.*, 2014). In SP, the altitude ranges from 100 to 3404 m.a.s.l. The landscape mosaic is mainly dominated by natural formations such as *Quercus pubescens* and *Q. ilex* and *Pinus sylvestris* and *Fagus sylvatica* forests covering, respectively, sunny and shaded slopes, while *P. uncinata* forests appear above 1800 m.a.s.l. (Lasanta-Martínez *et al.*, 2005; Roura-Pascual *et al.*, 2005), along with scrublands and natural grasslands. Crop fields can be found in valley bottoms.

## **2.2. Spatial analytical unit approach**

To assess the influence of the spatial analytical unit chosen to evaluate the relationship between landscape heterogeneity and species richness, we considered two different approaches that consisted of splitting the study area according to either geographic-ecological or arbitrary criteria (Figure 2.2). The first approach (the “eco-geographic approach”) involved the delineation of a set of watersheds that were derived from a Digital Elevation Model (DEM) at 25 m resolution ([www.ign.es](http://www.ign.es)) using ArcGIS 10.2 (Esri, 2014), for each mountain system. Only watersheds of the highest order (i.e., fourth order) were considered, since those of lower order were smaller than the 10 km x 10 km UTM square (the basic resolution of the analyses, constrained by species data availability). Watersheds covering only one 10 km x 10 km UTM square were also excluded from the analyses since they did not allow for landscape heterogeneity quantification. As a result, we selected 76 watersheds for further analyses (39 in CM, 13 in SC and 24 in SP); mean area size  $582 \pm 652$  km<sup>2</sup> (range 102.33-4227.79 km<sup>2</sup>).





**Figure 2.2.** Analytical units: watersheds on the left (a.1 to c.1) vs. square windows of different size (20 km x 20 km, 50 km x 50 km and 100 km x 100 km) on the right (a.2 to c.2) in the three mountain systems studied: a) the Cantabrian Mountains; b) the Central System; c) the Spanish Pyrenees

The second spatial analytical unit approach (the “arbitrary approach”) involved the definition of square windows of different size (20 km x 20 km, 50 km x 50 km, 100 km x 100 km), which were obtained by successive aggregation of the original UTM grid system of 10 km x 10 km. The different sizes made it possible to assess the role of scale on the performance of spatial analytical units. The 20 km x 20 km and 50 km x 50 km window sizes were chosen as proximal sizes to the mean  $\pm$  SD watershed area. Furthermore, conservation planning in Spain is often conducted at a regional or sub-regional scale, thus we selected the 100 km x 100 km window size as a proximal size to a sub-regional spatial scale. The need of adapting square windows to the biogeographic limits of the mountain systems implied that coverage was not complete for some windows located across the borders of the study area. Incomplete windows are usually excluded from the analyses (Li *et al.*,

2017) in order to avoid potential bias on species richness and landscape heterogeneity. However, aiming to include as much as possible of the area of the mountain systems, we only excluded from further analyses windows with a coverage lower than 75% (at 20 km x 20 km and 50 km x 50 km window size) and 45% (at 100 km x 100km window size). This resulted in 154 windows of 20 km x 20 km (75 in CM, 28 in SC and 51 in SP), 20 of 50 km x 50 km (10 in CM, 4 in SC and 6 in SP) and 12 of 100 km x 100 km (5 in CM, 3 in SC and 4 in SP).

### **2.3. Vertebrate species data**

Distribution of terrestrial vertebrate species was obtained from the official database of vertebrates of Spain (Ministry of Agriculture, Food and Environment 2012; [www.magrama.gob.es](http://www.magrama.gob.es)), which combines field records gathered by volunteers with information from published sources. The data consist of species presence and absence locations for the period 1980-2007, collected on the basis of direct observations and indirect methods (pellets, tracks, bed sites) and assembled in a regular UTM grid system of 10 km x 10 km size (Pleguezuelos *et al.*, 2002; Martí & del Moral, 2003; Palomo *et al.*, 2007).

The value for species richness was calculated for each 10 km x 10 km UTM square as: (i) “total richness” or total number of species; and (ii) “taxonomic richness” or the number of species per taxonomic group (mammals, breeding birds, reptiles and amphibians; see Figure 2.1 and Annex II, Table S2.1). Only squares with at least 75% coverage of their area included within the limits of each mountain system were considered for analyses, resulting in a set of 624 squares. Based on these squares, total and species richness per taxonomic group were also computed for both watersheds and square windows of different size, by aggregating the original information from the 10 km x 10 km UTM grid system. The 10 km x 10 km squares intersecting boundaries between watersheds were fully considered as part of the watershed for which the intersection covered more than 50% of the square.

## **2.4. Estimators of landscape heterogeneity**

Landscape heterogeneity was calculated on the basis of a landscape classification elaborated by integrating variables accounting for topography, urban influence and land cover. Land cover was obtained from the categorical map CORINE Land Cover 2006 (derived from LANDSAT at 30m; <http://land.copernicus.eu/pan-european/corine-land-cover>), which had previously been converted into independent continuous variables by calculating the proportion covered by each class at each pixel. Topographic variables consisted of elevation, solar radiation and slope. They were derived from a Digital Elevation Models (DEM) (25 m spatial resolution), obtained from the Spanish Geographic Institute ([www.ign.es](http://www.ign.es)) and resampled at the resolution of the land cover variables (i.e. 30 m) by applying the nearest neighbor method. Urban influence was measured as the Euclidean distance from each 30 m pixel to the nearest settlement, using input data downloaded from the Spanish Geographic Institute site ([www.ign.es](http://www.ign.es)) at 1:25000 and 1:200000 spatial resolution. Landscape classification consisted of running a Principal Component Analysis (PCA) over the pool of variables, followed by a cluster analyses (unsupervised classification); this aggregated pixels into coherent classes. The number of classes was defined aiming to represent at best the ecological framework of the study area, according to our expert knowledge. To do this, classes resulting from the classification process were characterized by using thematic information related to topography, urban influence and land cover and when necessary, they were combined or reclassified. The classification process led to 11 landscape classes in the CM, 13 in the CS and 8 in the SP (Annex II, Figure S2.1 and Table S2.2). The overall accuracy of classifications and user's and producer's accuracy per class were evaluated through confusion error matrixes (Congalton, 2001), by using thematic information related to topography, urban influence, land cover and ortho-photographs (years 2006 to 2009, scale 1:5000 to 1:10000). Overall accuracy was 88% for the CM and the SP and 84% for the CS (Annex II, Table S2.3). See García-Llamas *et al.* (2016) for more technical details on the landscape classification method.

Landscape heterogeneity was estimated as beta diversity ( $H'_\beta$ ; Eq. 1) for each spatial analytical unit (watershed or regular window) using an additive model based on the comparison of both alpha and gamma diversity (Lande, 1996; Tárrega *et al.*, 1997; Jost, 2006, 2007).

$$H'_\beta = H'_\gamma - \frac{\sum_{i=1}^N H'_{\alpha_i}}{N} \quad (\text{Eq. 1})$$

where  $H'_\gamma$  is the gamma diversity (i.e., the diversity of landscape classes at each spatial analytical unit) and  $H'_{\alpha_i}$  is the alpha diversity (i.e., the diversity of landscape classes at each 10 km x10 km UTM squares within each spatial analytical unit). Both  $H'_\gamma$  and  $H'_{\alpha_i}$  were calculated using the Shannon diversity index (Shannon, 1948) (Eq. 2),

$$H' = - \sum_{i=1}^R p_i \ln p_i \quad (\text{Eq. 2})$$

where  $p_i$  is the proportion of each landscape class within the spatial analytical unit or the 10x10 km UTM square, respectively.

All analyses were done in ArcGIS 10.2 (Esri, 2014) and by using the extension Patch Analyst (Rempel *et al.*, 2012).

## 2.5. *Statistical analyses*

To analyse the relationship between landscape heterogeneity and richness (total and species richness per taxonomic group) of terrestrial vertebrates, separate linear models were fitted for each of the considered spatial analytical unit approaches (eco-geographic approach vs. arbitrary approach). In the particular case of mammals and amphibians, richness data were transformed for normality by using the log (x) function.

Species richness was considered in the models as the dependent variable and landscape heterogeneity ( $H'_\beta$ ) as the predictor. For the arbitrary approach, in order to avoid potential biased due to the incomplete coverage of some windows across borders of mountain systems, we included the logarithm of the area of the square window (i.e. proportion of the square window included within the study

area) as an additional predictor in models. For the eco-geographical approach, we included the logarithm of the watershed area as an additional predictor of landscape heterogeneity in order to partial-out the confounding effect of the different areas of individual watersheds (which is expected to affect both species richness and landscape heterogeneity *per se*). To control for intrinsic differences in species richness between the three study areas, "mountain system" was also included in both approaches as a predictor (Gelman & Hill, 2006; Seoane, 2014). In all cases, we checked model residuals to assess the appropriateness of the model and confirmed the absence of spatial autocorrelation by computing correlograms. Data analyses were carried out with the *R* 3.1.2 statistical programme (R Development Core Team 2014) using the 'lm' function (R Development Core Team 2014). Correlograms were computed with the 'correlog' function in the 'ncf' *R* package (Bjornstad, 2013).

In addition, the relative effect of the explanatory variables in each model was also assessed by commonality analysis (Legendre & Legendre, 2012; Ray-Mukherjee *et al.*, 2014). This method, based on the normal  $R^2$  of partial and complete regression models, apportions the variation of the response (species richness) in several fractions: the pure effect of the singular predictors, the shared effect of each pair, triplet or any subset of predictors and the shared effect of the total set of predictors. For this, we used the 'commonality coefficients' function in the *R* package 'Yhat' (Nimon & Oswald, 2013).

### 3. Results

Landscape heterogeneity exerted a positive effect on species richness in all the fitted models. The magnitude and significance of its effects, however, varied according to the spatial analytical unit approach and the taxonomic group (Table 2.1 and 2.2; Annex II, Tables S2.4-S2.5). For the case of the eco-geographic approach, models accounted for more than 53% of the variance of species richness (Table 2.1). Landscape heterogeneity was a significant predictor of species richness in all cases, except in mammals. It explained between 28% (mammals) and 50% (all taxa together) of the variance of species richness, although between 24% and 40% of this variation was shared with the logarithm of watershed area

(Figure 2.3). Indeed, the logarithm of watershed area had a significant effect on species richness in all taxa considered, explaining between 37% (reptiles) and 55% (total richness) of the variance of species richness. The mountain system had a significant effect in all cases, except for both amphibians and for total species richness (Table 2.1). It explained between 3% (total richness) and 14% (reptiles) of the total variance (Figure 2.3).

**Table 2.1.** Table of Anova including: the explained sum of squares (*Sum. Sq.*), *F* value, significance (*Sig.*) and normal coefficients of determination (*R*<sup>2</sup>) of regression linear models achieved when working with watersheds as spatial analytical units and landscape heterogeneity.

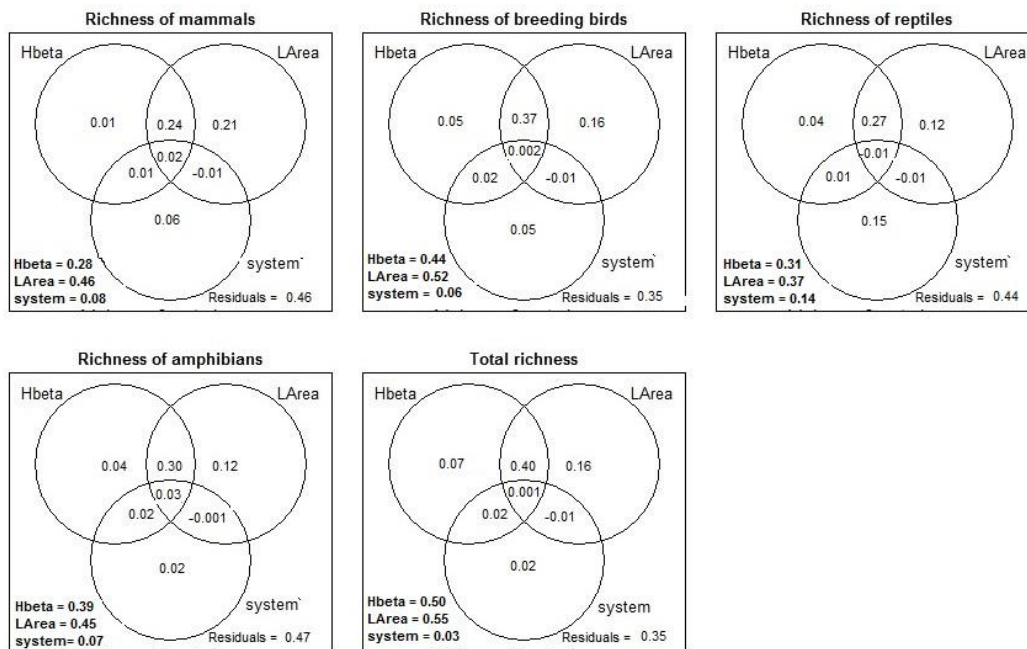
	Sum Sq	F value	Sig.	R <sup>2</sup>
<i>Mammal richness</i>				0.54
H <sub>β</sub>	0.09	0.86	n.s.	
log(A)	3.54	32.13	***	
Mountain system	0.95	4.29	*	
<i>Breeding bird richness</i>				0.65
H <sub>β</sub>	1555.90	9.53	**	
log(A)	5167.20	31.64	***	
Mountain system	1782.90	5.46	**	
<i>Reptile richness</i>				0.56
H <sub>β</sub>	92.12	5.90	*	
log(A)	301.07	19.28	***	
Mountain system	366.81	11.75	***	
<i>Amphibian richness</i>				0.53
H <sub>β</sub>	33.83	6.55	*	
log(A)	96.45	18.68	***	
Mountain system	14.77	1.43	n.s.	
<i>Total richness</i>				0.65
H <sub>β</sub>	7214.00	12.76	***	
log(A)	17726.00	31.35	***	
Mountain system	1694.00	1.50	n.s.	

H<sub>β</sub> landscape heterogeneity; log(A) logarithm of watershed area; \*\*\*significance at level <0.001;

\*\*significance at level 0.01; \*significance at level 0.05; n.s. no significance.

The performance of the arbitrary approach was poorer than the eco-geographical one, with a clear influence of windows size on the significance of relationships. Models accounted for more than 24% of the variance of species richness at 20 km x 20 km, more than 46% at 50 km x 50 km and more than 71% at 100 km x 100 km window size. Significant relationships between landscape heterogeneity and

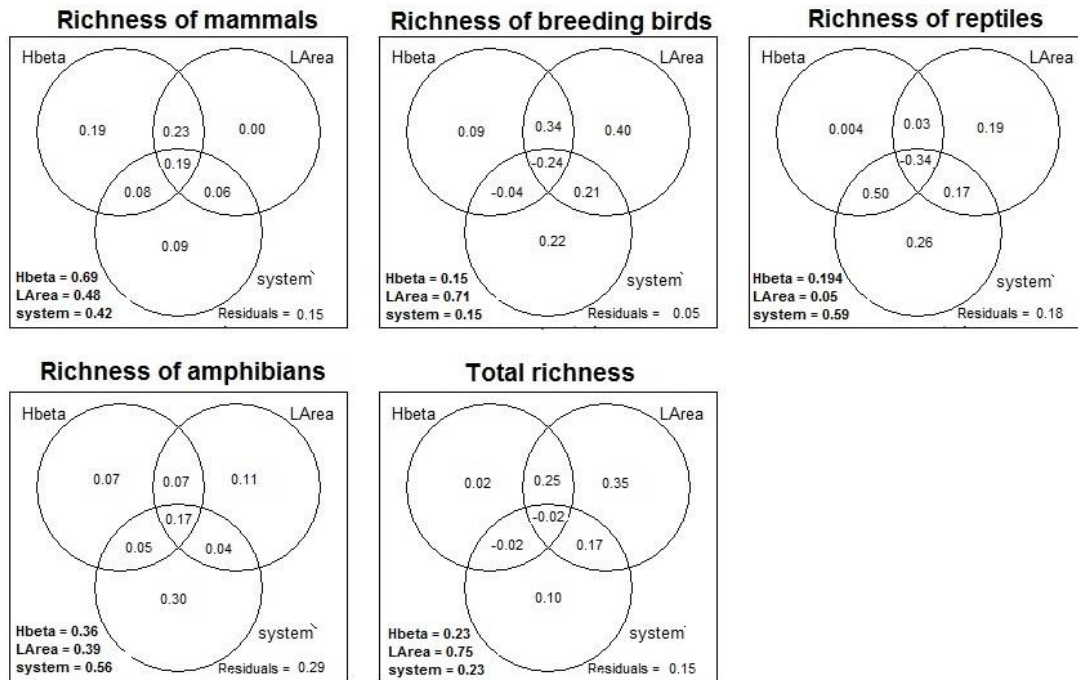
species richness were only found for mammals and breeding birds at the largest window size (100 km x 100 km) (Table 2.2). The percentage of total variation explained by the landscape heterogeneity was between 69% (mammals) and 15% (breeding birds), although between the 42% and the 10% of this variance was shared with the logarithm of the area of the square window, and between the 27% and -28% with the mountain system (Figure 2.4). The significance of the effect and predictive power of landscape heterogeneity decreased for all taxa for the smallest windows sizes (i.e. 50 km x 50 km and 20 km x20 km) (Table 2.2; Annex II, Table S2.5 and Figure S2.2).



**Figure 2.3.** Variance partitioning of species richness in watersheds explained by the pure and combined effect of landscape heterogeneity (Hbeta), logarithm of watershed area (Larea) and mountain system (system). Total variance (pure and combined effect) explained by predictors is in bold. For example, for richness of mammals total variance of Hbeta = 0.01 (pure effect) + (0.24+0.02+0.01; shared effect) = 0.28. Negative effects arise from the presence of suppression among predictors due to correlation among variables (Ray-Mukherjee *et al.*, 2014).

Further, we found an influence of the mountain system and the logarithm of the area of the square windows, depending on the window size and taxonomic group. Mountain system and area had a significant effect on total richness and richness of

all taxonomic groups, at 20 km x 20 km window size, these variables mainly explaining total variance of models.



**Figure 2.4.** Variance partitioning of species richness explained by pure and combined effects of landscape heterogeneity (Hbeta), logarithm of window area (Larea) and mountain system (system) for windows of 100 km x 100 km (or less if they intersected the limits of the study area). Total variance (pure and combined effect) explained by predictors is in bold. For example, for richness of mammals total variance of Hbeta = 0.19 (pure effect) + (0.23+0.19+0.08; combined effect) = 0.69. Negative effects arise from the presence of suppression among predictors due to correlation among variables (Ray-Mukherjee *et al*, 2014).

At 50 km x 50 km size only the mountain system significantly influenced results, this accounting for most of the species richness total variance (Table 2.2; Annex II, Table S2.5 and Figure S2.2). At 100 km x 100 km the mountain system and the logarithm of the area influenced significantly to breeding birds, reptiles and total species richness (only the area in this case). The mountain system accounted for between 15% (breeding birds) and 59% (reptiles) and the area between 5% (reptiles) and 75% (total richness) of the total variance of models (Table 2.2; Figures 2.4 and Annex II, Table S2.5).



## 4. Discussion

Landscape heterogeneity has been largely recognized as a cost-effective instrument to predict biodiversity (Ewers *et al.*, 2005), especially in large areas. However, as we demonstrated in this study, the predictive power of this indicator depends on the spatial analytical unit approach. Thus, the selection of an appropriated analytical framework for assessing landscape heterogeneity-species richness relationships requires careful consideration in view of a practical implementation. In this sense, our study advocates the need to incorporate eco-geographically relevant spatial analytical units, based on linkages between physical and biological resources and processes (Montgomery *et al.*, 1995), rather than arbitrarily delineated ones (typical of traditional approaches) within the framework of biodiversity studies.

The eco-geographic spatial analytical unit approach, based on the use of watersheds, enabled the detection of significant relationships between landscape heterogeneity and species richness for almost all taxonomic groups. Generally, species richness depends on the presence of 'keystone structures' (i.e., distinct spatial landscape structures providing resources, shelter or goods crucial for species; Tews *et al.*, 2004), which are the result of the interaction between biotic and abiotic features (e.g. climate, soil type, watering, human perturbations; Blasi *et al.*, 2008) and influence the use of territory by animals (Mazía *et al.*, 2006). In this context, watersheds may better reflect these keystone structures than arbitrary spatial analytical units, as they represent areas where climate, hydrology, geomorphology and land use history interact in predictable and repetitive ways, determining the composition and structure of landscapes and their biotic communities (Karadağ, 2013). In fact, for example, watershed characteristics have been employed to effectively predict the existence of protected habitats (Baattrup-Pedersen *et al.*, 2012).

**Table 2.2.** Table of Anova including: explained sum of squares (*Sum. Sq.*), *F* value, significance (*Sig.*) and normal coefficients of determination ( $R^2$ ) of linear models based on square windows of different sizes (20 km x 20 km, 50 km x 50 km and 100 km x 100 km).

	20 km x 20 km				50 km x 50 km				100 km x 100 km			
	Sum Sq	F value	Sig.	R <sup>2</sup>	Sum Sq	F value	Sig.	R <sup>2</sup>	Sum Sq	F value	Sig.	R <sup>2</sup>
<i>Mammal richness</i>				0.24				0.46				0.83
H <sub>β</sub>	0.16	1.54	n.s.		0.004	0.53	n.s.		0.02	7.38	*	
log(A)	2.08	20.18	***		0.001	0.21	n.s.		0.00	0.001	n.s.	
Mountain system	2.17	10.53	***		0.05	2.72	n.s.		0.01	1.86	n.s.	
<i>Breeding bird richness</i>				0.35				0.47				0.95
H <sub>β</sub>	98.50	0.47	n.s.		40.49	0.76	n.s.		163.01	11.14	*	
log(A)	11924.9	56.55	***		142.63	2.68	n.s.		754.46	51.59	***	
Mountain system	3291.1	7.80	***		325.67	3.05	n.s.		410.50	14.04	**	
<i>Reptile richness</i>				0.35				0.85				0.82
H <sub>β</sub>	52.77	3.36	n.s.		0.37	0.14	n.s.		0.35	0.16	n.s.	
log(A)	234.07	14.92	***		2.09	0.76	n.s.		16.63	7.40	*	
Mountain system	922.96	2941	***		221.53	40.44	***		22.78	5.07	*	
<i>Amphibian richness</i>				0.27				0.64				0.71
H <sub>β</sub>	24.83	3.36	n.s.		15.55	4.42	n.s.		2.79	1.70	n.s.	
log(A)	107.20	7.24	**		4.72	1.98	n.s.		0.45	0.27	n.s.	
Mountain system	139.34	18.83	***		29.21	6.12	*		11.86	3.61	n.s.	
<i>Total richness</i>				0.38				0.60				0.85
H <sub>β</sub>	1675.00	2.96	n.s.		190.22	1.99	n.s.		115.82	0.91	n.s.	0
log(A)	37761.00	66.83	***		157.27	1.65	n.s.		2156.07	16.85	**	
Mountain system	5970.00	5.28	**		902.48	4.73	*		584.81	2.28	n.s.	

H<sub>β</sub> landscape heterogeneity; \*\*\*significance at level <0.001; \*\*significance at level 0.01; \*significance at level 0.05; n.s. no significance

Although watersheds might offer a good sampling scheme to analyze the relationships between landscape heterogeneity and species richness, we found the predictive capacity of the landscape heterogeneity to be mainly associated with the watershed area. Two of the major mechanisms of increased species richness are the increase in area (spatial analytical unit size) and variety of habitat types (here expressed as landscape heterogeneity) (Kohn & Walsh, 1994). Both mechanisms are mutually complementary, thus one can act as a surrogate of the effect of the other, making it difficult to discern their direct effect on species richness patterns (Triantis *et al.*, 2003). Consequently, although both area and landscape heterogeneity partially contributed to explaining species richness separately, their large combined effect on species richness means that these two variables should be considered in conjunction (Kallimanis *et al.*, 2008) when working with eco-geographic spatial analytical units, in conservation planning.

Despite being widely accepted in landscape analysis (e.g. Nogués-Bravo & Martínez-Rica, 2004; Flick *et al.*, 2012), the arbitrary spatial analytical unit approach, based on the use of square windows, revealed some limitations with regards to modelling landscape heterogeneity-species richness relationships. Only two taxonomic groups (i.e. mammals and breeding birds) showed significant effects of landscape heterogeneity. Further, the size of the spatial analytical unit also largely influenced the predictive capacity of landscape heterogeneity, as demonstrated in other studies (Morelli *et al.*, 2013, Schindler *et al.*, 2013; Chambers *et al.*, 2016). In our particular case we only found significant relationships between landscape heterogeneity and species richness at 100 km x 100 km window size. Such an outcome might be related to the fact that species attributes (e.g. mobility or dispersal capacity) widely rule the effect of landscape heterogeneity (Barbaro & Van Halder, 2009; Perović *et al.*, 2015) and the spatial scale (i.e. size of the spatial analytical unit) at which this effect emerges (Miguet *et al.*, 2016). Consequently, it would be expected that the spatial scale at which landscape heterogeneity exerts its effect would be larger for taxa with greater mobility or space demand, (e.g. mammals or birds) than for less mobile ones (e.g. reptiles or amphibians), because they interact with the landscape over a larger spatial extent (Schindler *et al.*, 2013; Miguet *et al.*, 2016). As a result, the lack of explanation of mammal richness within watersheds might suggest that the

watersheds in this study are not large enough to efficiently capture the effect of landscape heterogeneity over species richness of this taxon. These results emphasise the need to consider the spatial scale appropriate for both the subject of study and the ecological question posed (Wu, 2004), i.e., it might be associated with the scale at which organisms perceive the landscape.

The arbitrariness of the spatial analytical unit influences both the size and the shape of the selected spatial analytical units. Any change in these settings will provide a different description of the area of analysis, which is linked to the modifiable areal unit problem (MAUP); and which might affect results of statistical models (Dungan *et al.*, 2002; Dark & Bram, 2007; Nouri *et al.*, 2017). We tried to minimize the usual bias associated to the scale problem of the MAUP (inflated correlation at higher levels of aggregation; Wong, 2009), by estimating both the response (species richness) and the explanatory variables (landscape heterogeneity) as cumulative figures obtained from the 10 x 10 km raw data, rather than as averages or any other measure of central tendency of smaller units. However, contrarily to our results with watershed units, for arbitrary windows with a size close to the mean  $\pm$  SD watershed area (i.e., 20 km x 20 km and 50 km x 50 km window), no significant effects of landscape heterogeneity on vertebrate species richness were detected. This inconsistency when changing boundary delineation of spatial analytical units could be a result of the different description of the region leading to different analytical results, which is related to the zoning problem of the MAUP (Jelinski & Wu, 1996). Further, when boundaries of spatial analytical units are arbitrarily set, they could not reflect the spatial structure of the environmental and the biological components of the landscape (Wagner & Fortin, 2005). Thus, arbitrary boundaries may mask relationships between landscape heterogeneity and species richness. As an example, amphibians are usually favored by landscape heterogeneity, as they use a complex landscape matrix of terrestrial and aquatic habitats during different stages of their life cycles (Mawangi, 2010). Further, different species of amphibians could require different aquatic environments, from the headwater to the lower reaches. However, arbitrary spatial analytical units might not necessarily encompass both terrestrial and aquatic habitat patches, or all aquatic environments. Consequently, watershed might be a proper landscape approach to include amphibians breeding, foraging

and overwintering habitat patches (Maxell, 2009). In the case of reptiles, some studies (e.g., Shipam *et al.*, 2004) have highlighted the importance of preserving watershed-level heterogeneous landscape conditions for preserving their diversity. In fact, the physiography of watersheds (i.e. slope, elevation or naturally-occurring aquatic habitats) determines the diversity of canopy covers and aquatic habitats that ultimately influence variation of humidity and soil mixture, on which reptiles are highly dependent (Shipam *et al.*, 2004). Therefore, analyzing watersheds, rather than arbitrary spatial analytical units, might give ground for better understanding landscape heterogeneity-reptile richness relationship.

Results on the performance of eco-geographical and arbitrary spatial analytical unit approaches have important implications from a practical perspective. Developing an eco-geographical approach based on watersheds is not a new approximation in analysis and conservation management. For example, the unit plan used by the U.S. Forest service until mid-1970s was based on watersheds delineation (Montgomery *et al.*, 1995). Also in the mid-nineties, ecosystem management based on watershed analysis was implemented in the Pacific Northwest federal lands and, on a volunteer basis, on forested watersheds in Washington (WFPB 1992, 1993). In the case of Spain, conservation management is generally addressed independently by different regional autonomous administrations (Morillo & Gómez-Campo, 2000), except for some protected areas (i.e. national parks covering different regions) for which collaborative networks do exist. Consequently, management actions have usually been carried out according to varying arbitrary management units at regional or sub-regional scale, such as administrative boundaries. As our results show, the performance of arbitrary units could not be considered satisfactory. Even for the larger unit size considered (100 km x 100 km window), richness for some taxa (and total richness also) appeared unrelated to landscape heterogeneity so, at least with the sizes considered in our study, the arbitrary approach could not be considered an appropriate approximation to a sub-regional scale of management on the ground. On the contrary, our results showed that watersheds, i.e., eco-geographical rather than regular windows, or political or administrative boundaries, might provide a more rational basis for the management of biodiversity, based on potential indicators such as the landscape heterogeneity. Thereby, this study revealed the major

importance of adopting a trans-bordering and inter-regional management framework that advocates for a continuous and integrated engagement of all entities involved in decision-making.

Notwithstanding the important role of landscape heterogeneity as an indicator of species richness, caution is urged as high landscape heterogeneity might lead to fragmentation and, may thus have negative effects on biodiversity (Duflot *et al.*, 2014). Further, it should be note that the detected relationships between landscape heterogeneity and species richness depend on the landscape metrics used for analyses (Cale & Hobbs, 1994). Although there is no consensus regarding the most appropriate and informative index for landscape heterogeneity, the Shannon diversity index has been successfully used in several studies (e.g. Pino *et al.*, 2000; Oindo *et al.*, 2003; Priego-Santander *et al.*, 2013; Lee & Martin, 2017), along with other metrics such as the patch richness, Simpson's diversity index or Simpson's evenness (Schindler *et al.*, 2013). We are unaware of the use of a beta-diversity metric in landscape analyses, although our study results suggest its use in further studies. We claim, for the convenience of using a landscape classification adapted to the study site (i.e. the mountain system), thus allowing the ecological meaning and reliability of landscape classification to be increased and therefore, the reliability of landscape indices (Shao & Wu, 2008). Additionally, the influence of landscape heterogeneity on species richness may depend not only on the spatial analytical unit approach or the used landscape metrics, but also on the study site considered (Amano *et al.*, 2008; Oliver *et al.*, 2010).

## 5. Conclusions

Our study has shown how landscape heterogeneity, measured by a beta-diversity metric, could predict terrestrial vertebrate richness in mountain systems, although conditioned by the spatial analytical unit approach used for evaluation. This study indicates the high potential of eco-geographical spatial analytical unit approaches, based on watersheds, in biodiversity studies. The arbitrary spatial analytical units approach reflects how limiting it could be to apply spatial analytical units unrelated to the phenomena under study. In connection with this, we corroborate the effect of the size of arbitrary spatial analytical units on

predictive power of landscape heterogeneity, which is generally better at larger sizes. These findings have important practical implications as they underline the need to consider landscape heterogeneity in biodiversity conservation strategies. Furthermore, this study offers a valuable cost-effective framework for environmental management and spatial modeling, with potential to be adapted for national and global applications. Simultaneously, it makes visible important methodological issues that may affect biodiversity estimations and that should be considered in decision-making.

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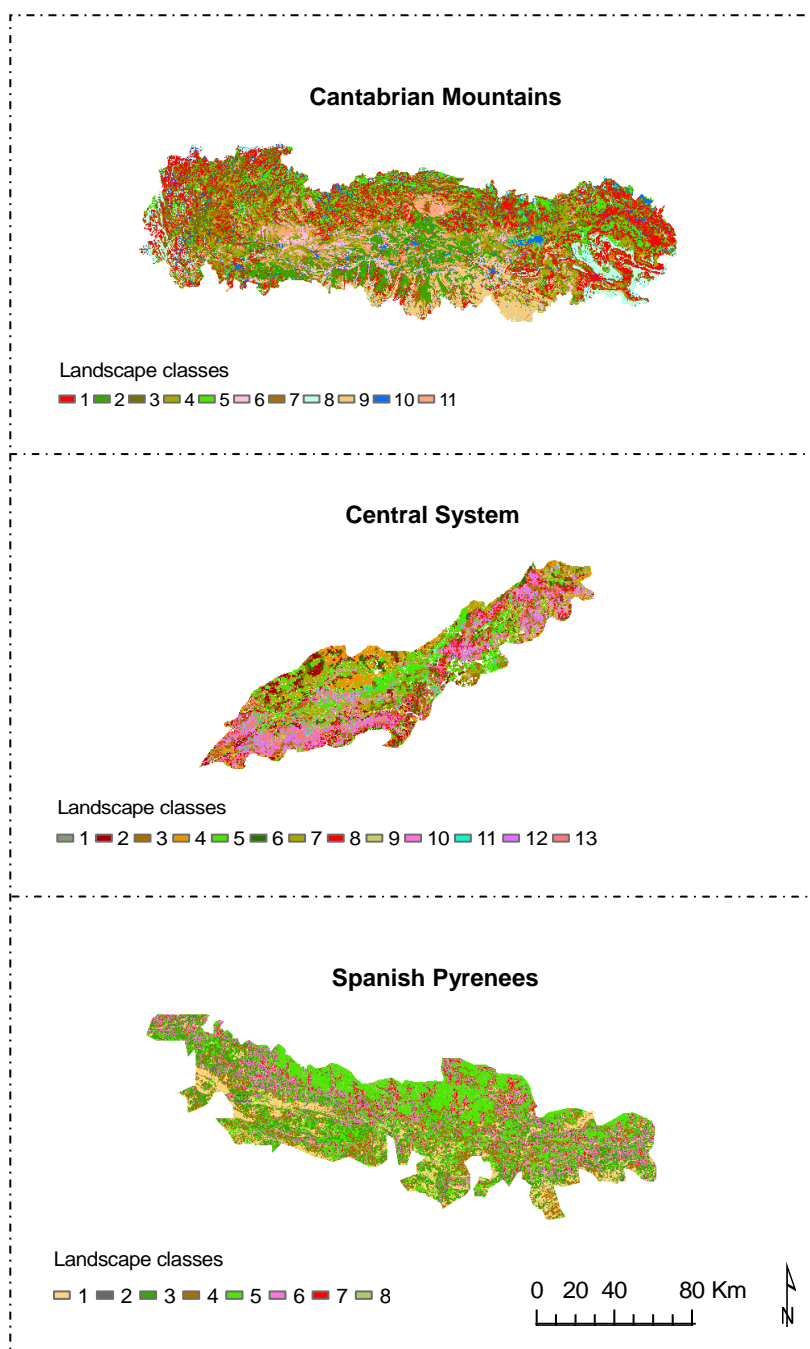
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## ANNEX II

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**Table S2.1.** Values of species richness: total and taxonomic (mammals, breeding birds, reptiles and amphibians) richness for each mountain system (Cantabrian Mountains, Central System and the Spanish Pyrenees).

	Cantabrian Mountains	Central System	Spanish Pyrenees
Mammals	88	85	64
Breeding birds	198	188	166
Reptiles	29	30	20
Amphibians	19	17	15
<b>Total species</b>	<b>334</b>	<b>320</b>	<b>265</b>



**Figure S2.1.** Landscape classifications based on CORINE, topography and urban influence variables for a.1) the Cantabrian Mountains; b.1) the Central System; c.1) the Spanish Pyrenees.



**Table S2.2.** Description of landscape classes obtained from a set of variables accounting for topography, urban influence and land cover (CORINE).

Class	Description
Cantabrian Mountains	
1	Forests covering coastal and middle-mountain areas at an average altitude of $688.16 \pm 299.69$ m.a.s.l. in areas with moderate to steep slope (mean value $20.73^\circ \pm 10.72^\circ$ ) and at mid-distance to settlements (mean value $3.65 \pm 4.05$ km)
2	Forests covering central mountains and piedmont areas at an average altitude of $1267.14 \pm 240.47$ m.a.s.l. with moderate slope (mean value $17.56 \pm 9.77^\circ$ ), those being at mid-distance to settlements (mean distance $2.67 \pm 2.48$ km)
3	Transitional to woodlands with low urban influence (mean distance to settlements $5.24 \pm 4.92$ km), covering mainly Atlantic and Sub-Atlantic mountains located at low altitudes (mean value $624 \pm 213.42$ m.a.s.l.), with moderate to steep slope (mean value $24.08^\circ \pm 9.86^\circ$ )
4	Transitional woodlands from central and southern areas of the Cantabrian Mountains, with relatively low urban influence (mean distance to settlements $3.9 \pm 4.11$ km), those being located at an average altitude of $1207.40 \pm 290.56$ m.a.s.l., in areas with moderate slope (mean value $18.05^\circ \pm 10.30^\circ$ )
5	Pastures from mid-low Atlantic mountains and coastal areas (mean altitude $520.22 \pm 263.10$ m.a.s.l.), with moderate slope (mean value $15.87^\circ \pm 9.68^\circ$ ) and at mid-distance to settlements (mean value $3.66 \pm 4.69$ km)
6	Pastures covering bottom valleys and hillsides of the central Cantabrian Mountains, lying at an average altitude of $1216.65 \pm 290.14$ m.a.s.l., in areas with moderate slope (mean value $16.22^\circ \pm 10.51^\circ$ ) at mid-distance to settlements (average distance $2.8 \pm 3.54$ km)
7	Shrub-herbaceous associations lying at an average altitude of $816.66 \pm 378.43$ m.a.s.l., in hillsides with moderate slope (mean value $19.27^\circ \pm 10.88^\circ$ ) and at mid-distance to settlements (mean distance $3.63 \pm 3.83$ km)
8	Croplands from depressions and coastal plains (average slope $8.84^\circ \pm 8.18^\circ$ ) lying at the lowest altitudes (mean value $605.05 \pm 241.81$ m.a.s.l.) and those being close to settlements (mean distance $1.64 \pm 1.80$ km)
9	Croplands (non-irrigated arable lands) from paramos and countrysides (mean slope $5.70^\circ \pm 5.79^\circ$ ) lying at an average altitude of $977.27 \pm 99.30$ m.a.s.l. and those being the closest class to settlements (mean distance $1.26 \pm 0.99$ km)
10	Water surfaces and artificial surfaces lying at an average altitude of $654.15 \pm 393.13$ m.a.s.l., in areas with moderate slope (mean slope $14.58^\circ \pm 11.05^\circ$ ) and at mid-distance to settlements (mean value $2.56 \pm 3.54$ km)
11	Rocks and areas with little or no vegetation covering the highest altitudinal ranges (mean value $1352.71 \pm 485.47$ m.a.s.l.), in areas with steep slope (mean value $25.94^\circ \pm 12.54^\circ$ ), those being far from settlements (mean distance $4 \pm 3.58$ km)

**Table S2.2. (Cont.)**

Central System	
1	Forests covering lowlands and valley bottoms (mean slope $5.28^\circ \pm 2.47^\circ$ ), at an average altitude of $1131.37 \pm 253.73$ m.a.s.l. and at mid-distance to settlements (mean value $2.63 \pm 1.38$ km)
2	Forests lying at an average altitude of $1226.79 \pm 305.41$ m.a.s.l. on hillsides with moderate slope (mean value $13.32^\circ \pm 3^\circ$ ) and at mid-distance to settlements (mean value $28.55 \pm 15.36$ km)
3	Forests lying at an average altitude of $1223.95 \pm 336.03$ m.a.s.l., on hillsides with moderate to steep slope (mean value $22.60^\circ \pm 6.25^\circ$ ) and at a mid-distance to settlements (mean value $28.62 \pm 15.68$ km)
4	Transitional to woodlands covering lowlands (mean altitude $1252.28 \pm 275.44$ m.a.s.l.) and areas with slight slope (mean value $5.31^\circ \pm 2.37^\circ$ ), those being at mid-distance to settlements (mean value $2.50 \pm 14.51$ km)
5	Transitional to woodlands covering middle-hillsides (mean altitude $1352.24 \pm 332.77$ m.a.s.l.) with moderate slope (mean value $12.80^\circ \pm 2.79^\circ$ ), those being at mid-distance to settlements (mean value $2.86 \pm 1.66$ km)
6	Transitional to woodlands covering the highest altitudes (mean value $1436.55 \pm 339.83$ m.a.s.l.) with moderate to steep slope (mean value $24.69^\circ \pm 6.04^\circ$ ), those being at mid-distance to settlements (mean value $3.55 \pm 1.84$ km)
7	Pastures covering valley bottoms (mean altitude $1181.78 \pm 246.51$ m.a.s.l.) and hillsides with slight slope (mean value $5.16^\circ \pm 3.22^\circ$ ) and at mid-distance to settlements (mean value $2.29 \pm 1.70$ km)
8	Pastures covering middle mountain areas (mean value $1348.88 \pm 314.95$ m.a.s.l.) with moderate slope (mean value $14.62^\circ \pm 3.25^\circ$ ) and at mid-distance to settlement (mean value $2.60 \pm 1.72$ km)
9	Shrub-herbaceous associations located at low altitudinal ranges (mean value $1177.51 \pm 301.89$ m.a.s.l.), on hillsides with moderate slope (mean value $13.17^\circ \pm 8.63^\circ$ ) and at mid-distance to settlements (mean value $2.75 \pm 1.64$ km)
10	Croplands (herbaceous) covering valley bottoms and plains (mean slope $5.01^\circ \pm 4.70^\circ$ ) at an average altitude of $1028.33 \pm 201.01$ m.a.s.l., those being close to settlements (mean value $1.46 \pm 0.9$ km)
11	Woody croplands covering valley bottoms and plains (mean slope $6.75^\circ \pm 5.40^\circ$ ) at an average altitudinal range of $962.96 \pm 233.65$ m.a.s.l., those being close to settlements (mean value $2.06 \pm 1.34$ km)
12	Water surfaces and artificial surfaces located at an average altitude of $1002.28 \pm 229.45$ m.a.s.l., in areas of slight slope (mean value $4.87^\circ \pm 4.22^\circ$ ), those being close to settlements (mean value $1.31 \pm 1.25$ km)
13	Rocks and areas with little or no vegetation covering the highest altitudes (mean value $1481.65 \pm 371.04$ m.a.s.l.), in areas with moderate to steep slope ( $20.08^\circ \pm 10.21^\circ$ ) at mid-distance to settlements (mean distance $3.54 \pm 2.17$ km)
Spanish Pyrenees	
1	Forests lying at an average altitude of $1000.49 \pm 323.21$ m.a.s.l., covering hillsides with moderate slope (mean value $14.28^\circ \pm 5.29^\circ$ ) at mid-distance to settlements (mean distance $2.95 \pm 1.74$ km)
2	Forests lying at an average altitude of $1163.56 \pm 368.78$ m.a.s.l., covering hillsides with steep slope (mean value $27.97^\circ \pm 3.57^\circ$ ), those being at mid-distance to settlements (mean value $2.97 \pm 1.77$ km)
3	Forests lying at an average altitude of $1313.67 \pm 397.56$ m.a.s.l., in areas with very steep slope (mean value $39.39^\circ \pm 4.23^\circ$ ), those being at mid-distance to settlements (mean value $2.98 \pm 1.83$ km)
4	Mosaic of grasslands, rocks and areas with little or no vegetation and transitional to woodlands, covering the highest altitudinal ranges (mean value $1547.19 \pm 623.41$ m.a.s.l.), in areas with moderate slopes (mean value $20.09^\circ \pm 9.55^\circ$ ) and at mid-distance to settlements (mean value $3.69 \pm 2.61$ km)
5	Mosaic of grasslands, rocks and areas with little or no vegetation, covering the highest altitudinal ranges (mean value $1588.50 \pm 653.16$ m.a.s.l.), in areas with very steep slopes (mean value $44.02^\circ \pm 9.07^\circ$ ) and relatively far from settlements (mean value $3.83 \pm 2.64$ km)
6	Shrub-herbaceous associations laying at an average altitude of $1080.83 \pm 414.27$ m.a.s.l., covering hillsides with moderate slope (mean value $19.17^\circ \pm 9.36^\circ$ ) and at mid-distance to settlements (mean value $2.53 \pm 1.58$ km)
7	Croplands covering bottom valleys lying at the lowest altitudinal ranges (mean value $775.08 \pm 219.38$ m.a.s.l.) in areas with slight slope (mean value $10.56^\circ \pm 8.04^\circ$ ), those being close to settlements (mean value $1.89 \pm 1.51$ km)
8	Water surfaces and artificial surfaces lying at an average altitude of $803.85 \pm 395.78$ m.a.s.l., in areas with moderate slope (mean value $14.21^\circ \pm 10.07^\circ$ ), those being close to settlements (mean distance $2.05 \pm 1.91$ km)

**Table S2.3.** Overall accuracy of landscape classifications and user's and producer's accuracy per class, obtained from topography, urban influence and CORINE (as a proxy of land cover) data.

	Class	User's accuracy (%)	Producer's accuracy (%)	Overall accuracy (%)
Cantabrian Mountains	1	93.33	88.89	
	2	85.29	78.38	
	3	83.33	68.97	
	4	86.49	96.97	
	5	100.00	91.18	88.33
	6	94.12	94.12	
	7	96.15	100.00	
	8	89.47	85.00	
	9	85.00	89.47	
	10	50.00	100.00	
	11	93.33	100.00	
Central System	1	50.00	100.00	
	2	90.00	81.81	
	3	100.00	84.62	
	4	92.30	80.00	
	5	69.23	75.00	
	6	77.78	80.00	
	7	88.00	91.66	84.39
	8	100.00	37.05	
	9	92.30	100.00	
	10	100.00	84.62	
	11	100.00	100.00	
	12	100.00	100.00	
	13	88.00	91.67	
Spanish Pyrenees	1	85.29	87.87	
	2	95.23	66.67	
	3	85.00	71.51	
	4	80.49	97.05	88.00
	5	100.00	66.67	
	6	100.00	100.00	
	7	89.47	100.00	
	8	50.00	100.00	

**Table S2.4.** Estimate, standard error (*Std. error*) and significance (*Sig.*) of regression lineal models, achieved when working with watersheds as spatial analytical units and landscape heterogeneity calculated from landscape classifications. The intercept represents the Cantabrian Mountains.

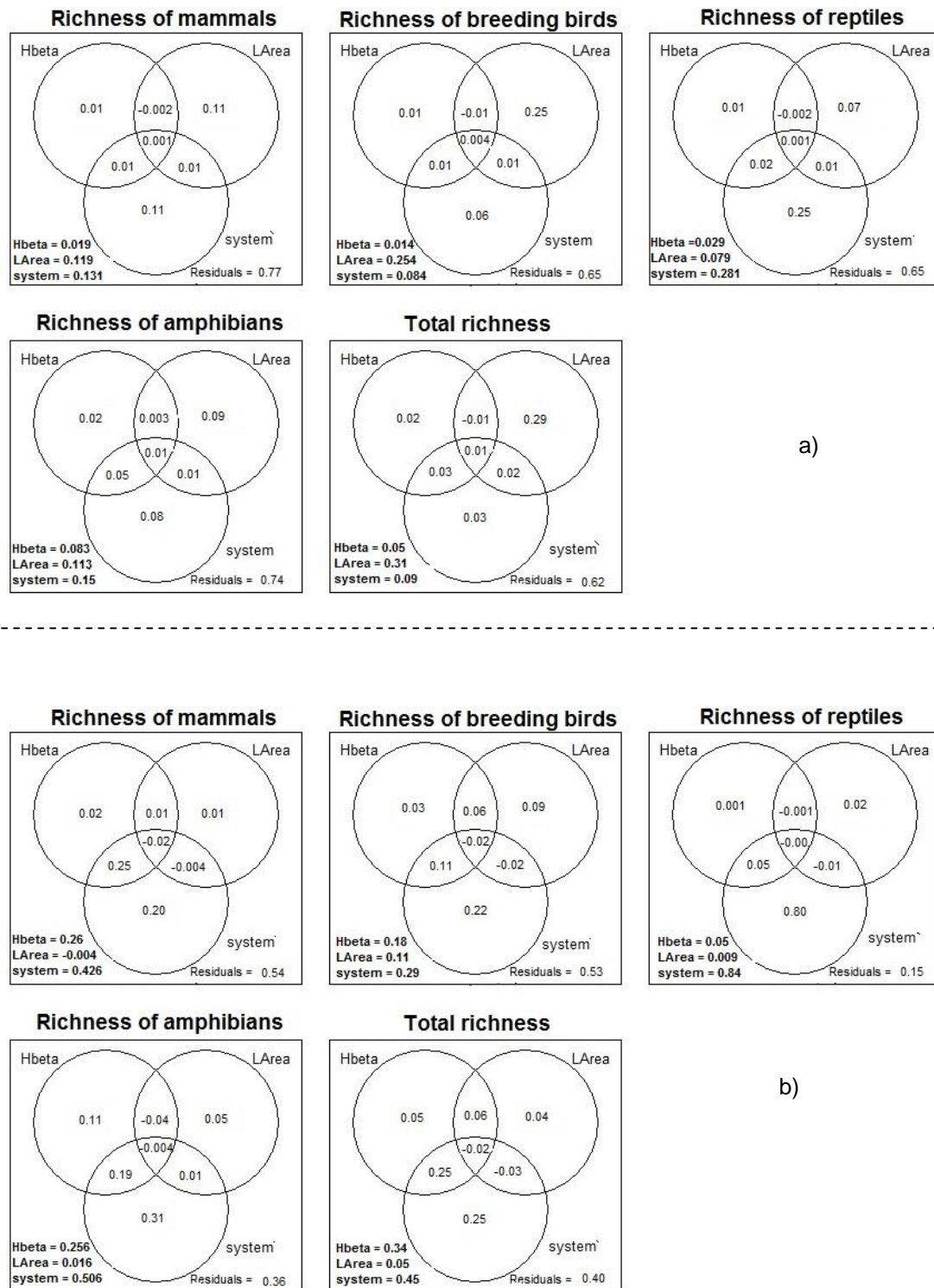
	Estimate	Std. Error	Sig.
<i>Mammal richness</i>			
Intercept	2.03	0.26	***
H <sub>β</sub>	0.43	0.47	n.s.
log(A)	0.23	0.05	***
Central System	-0.08	0.11	n.s.
Spanish Pyrenees	-0.26	0.09	**
<i>Breeding birds richness</i>			
Intercept	37.18	9.93	***
H <sub>β</sub>	56.66	18.36	**
log(A)	11.18	1.99	***
Central System	12.74	4.23	*
Spanish Pyrenees	7.20	3.47	**
<i>Reptiles richness</i>			
Intercept	-6.73	2.93	*
H <sub>β</sub>	13.49	5.55	*
log(A)	2.56	0.58	***
Central System	4.64	1.30	***
Spanish Pyrenees	4.31	1.05	***
<i>Amphibian richness</i>			
Intercept	-0.22	1.69	n.s.
H <sub>β</sub>	8.21	3.21	*
log(A)	1.45	0.34	***
Central System	-0.27	0.61	n.s.
Spanish Pyrenees	-1.04	0.75	n.s.
<i>Total richness</i>			
Intercept	34.41	19.06	n.s.
H <sub>β</sub>	120.18	33.65	***
log(A)	20.89	3.73	***
Central System	13.09	5.98	n.s.
Spanish Pyrenees	5.98	13.09	n.s.

H<sub>β</sub> landscape heterogeneity; log(A) logarithm of watershed area; \*\*\*significance at level <0.001; \*\*significance at level 0.01; \*significance at level 0.05; n.s. no significance

**Table S2.5.** Estimate, standard error (*Std. error*) and significance (*Sig.*) of regression lineal models, achieved when working with regular squared windows as spatial analytical units and landscape heterogeneity calculated from landscape classifications. The intercept represents the Cantabrian Mountains.

	20 km x20 km			50 km x50 km			100 km x100km		
	Estimate	Std. Error	Sig.	Estimate	Std. Error	Sig.	Estimate	Std. Error	Sig.
<i>Mammal richness</i>									
Intercept	1.98	0.40	***	3.71	0.88	***	3.52	0.31	***
H <sub>β</sub>	0.22	0.17	n.s.	0.23	0.32	n.s.	1.50	0.55	*
log(A)	0.31	0.07	***	0.06	0.12	n.s.	0.001	0.05	n.s.
Central System	-0.14	0.07	n.s.	-0.08	0.06	n.s.	0.16	0.1	n.s.
Spanish Pyrenees	-0.26	0.06	***	-0.14	0.07	*	0.21	0.10	n.s.
<i>Breeding birds richness</i>									
Intercept	-31.34	18.11	n.s.	20.76	68.22	n.s.	-81.54	23.43	*
H <sub>β</sub>	5.40	7.90	n.s.	21.58	24.77	n.s.	114.42	34.47	*
log(A)	23.16	3.08	***	15.28	9.34	n.s.	20.90	2.91	***
Central System	5.42	2.64	*	9.84	4.32	*	36.14	7.05	**
Spanish Pyrenees	12.57	3.26	***	-1.54	5.10	n.s.	29.14	7.07	**
<i>Reptiles richness</i>									
Intercept	-9.99	4.94	*	28.08	15.46	n.s.	-4.32	8.39	*
H <sub>β</sub>	3.95	2.15	n.s.	2.07	5.61	n.s.	-5.22	13.18	n.s.
log(A)	3.24	0.84	***	-1.85	2.11	n.s.	3.04	1.12	
Central System	6.27	0.89	***	8.49	0.98	***	5.32	2.59	n.s.
Spanish Pyrenees	3.69	0.72	***	5.44	1.16	***	2.03	2.58	*
<i>Amphibian richness</i>									
Intercept	-7.97	3.59	*	29.11	14.57	n.s.	3.22	7.16	n.s.
H <sub>β</sub>	5.96	3.25	n.s.	11.10	5.28	n.s.	14.70	11.26	n.s.
log(A)	2.65	0.61	***	-2.79	1.99	n.s.	0.50	0.95	n.s.
Central System	2.04	0.63	**	0.05	0.91	**	2.82	2.21	n.s.
Spanish Pyrenees	-0.63	0.51	n.s.	3.10	1.13	n.s.	0.25	2.20	n.s.
<i>Total richness</i>									
Intercept	-75.40	29.65	*	100.99	91.30	n.s.	-75.24	63.26	n.s.
H <sub>β</sub>	22.26	12.93	n.s.	46.79	33.15	n.s.	94.61	99.46	n.s.
log(A)	41.21	5.04	***	16.05	12.51	n.s.	34.56	8.42	**
Central System	14.61	5.34	**	14.71	5.79	*	29.82	0.72	n.s.
Spanish Pyrenees	-3.40	4.32	n.s.	-6.62	6.83	n.s.	13.98	1.52	n.s.

H<sub>β</sub> landscape heterogeneity; log(A) logarithm of square window area \*\*\*significance at level <0.001; \*\*significance at level 0.01; \*significance at level 0.05; n.s. no significance.



**Figure S2.2.** Variance partitioning among pure and combined effects of landscape heterogeneity (Hbeta), logarithm of watershed area (LArea) and mountain system (system), as explanatory variables explaining species richness of mammals, breeding birds, reptiles and amphibians and total species richness, based on squared windows of: a) 20 km x 20 km and b) 50 km x 50 km as units of analysis. Total effect of predictors (share and pure) are in bold.



*Picture's author: Pablo Rodríguez*

## **Chapter 3**

# **Linking species functional traits of terrestrial vertebrates and environmental filters: a case study in temperate mountain systems<sup>3</sup>**

<sup>3</sup> The content of this chapter has been submitted for publication consideration to *Landscape Ecology*.

García-Llamas, P., Rangel, T.F., Calvo, L., & Suárez-Seoane, S. (2017) Linking species functional traits of terrestrial vertebrates and environmental filters: a case study in temperate mountain systems.

## Abstract

Knowledge on the relationship between species functional traits and environmental filters is relevant to understand the drivers of biodiversity loss from a multi-taxa perspective. The aim of this study is to analyze the species functional trait-environment relationships across terrestrial vertebrate species (mammals, breeding birds, reptiles and amphibians), identifying common response patterns of functional groups to environmental filtering. Using the Cantabrian Mountains (NW of Spain) as a case study, we selected three species functional traits, including feeding guild, habitat use type and daily activity. For each trait, we described a set of functional groups considering common functional characteristics among vertebrate species. The richness of each functional group was calculated in a 10 km x 10 km UTM grid system, on the basis of the Spanish Inventory of Terrestrial Vertebrates Species. The relationship between the richness of each functional group and the environmental filters (climate, topography, land cover, physiological state of vegetation, landscape heterogeneity and human influence) was determined by fitting ordinary least squares regression models and simultaneous and conditional autoregressive models. The results showed that the response of functional groups to environmental filters was not random. Climate, topography and human influence systematically contributed to explaining the richness of each functional group in mountain systems. Nevertheless, land cover, physiological state of vegetation and landscape heterogeneity did not show a clear predictive pattern and their effect was dependent on the functional group. Overall, this study might help to identify general rules of species functional trait assemblage and illustrate the importance of environmental filters in community assembly in mountain systems.

**Keywords:** Assembly, functional group, landscape heterogeneity.



## 1. Introduction

The rapid decrease in biodiversity as a consequence of land use and climate change, jointly with other factors, such as species introduction or nitrogen deposition, is a major key environmental problem impacting biological systems worldwide (Chapin *et al.*, 2000; Sala *et al.*, 2000), and in particular mountain systems (El-Keblawy, 2014). Mountains have been considered as highly fragile systems, especially susceptible to biodiversity loss, due to their vulnerability to human and natural disturbances (Martinelli, 2007). However, at the same time, they harbor a great proportion of the world's biodiversity (La Sorte & Jetz, 2010). Mountains constitute centers of endemisms and endangered species and ecosystems, with influence in the surrounding lowlands (Nogués-Bravo *et al.*, 2007), mainly as a result of biotic evolutive response to climatic and geological history and the effect of topo-climatic gradients (Sarmiento, 2002; González-Prieto *et al.*, 2016). Therefore, studies involving mountain systems are key to understanding biodiversity loss worldwide.

Biodiversity decline might affect ecosystem processes and functioning (Duffy, 2003) and, ultimately, compromise the capacity of ecological systems to provide ecosystem goods and services that support human well-being (Flynn *et al.*, 2009). Accordingly, the quantification of biodiversity loss seems to be of utmost importance within the framework of conservation strategies (Turner *et al.*, 2003). Biodiversity estimation has usually been focused on taxonomic species richness, but other biodiversity components (i.e., composition of genotype, species functional types and landscape units) have been underestimated (Díaz & Cabido, 2001). Nevertheless, ecological processes are mainly ruled by functional attributes of organisms rather than by their taxonomic status, as very different species may be functionally similar (Hooper *et al.*, 2002). Therefore, the specific evaluation of species functional traits -henceforth SFT- (i.e. any morphological, biochemical, physiological, structural, phenological or behavioural characteristic of an organism, that potentially influences its fitness, response to the environment and/or its effect on ecosystem properties; Cadotte *et al.*, 2011; Díaz *et al.*, 2013) not only contribute to better explaining ecological functioning and processes, but also to achieve ecological stability against environmental changes (Chapin *et al.*,

2000). Consequently, the identification of functional groups and the measurement of functional diversity, as a key aspect in approaches determining ecological processes, is attracting growing interest among the scientific community (Ernst *et al.*, 2006).

The role of biodiversity in ecological processes and functioning is, however, conditioned by ecological differences among the species in the community (Schmid *et al.*, 2003). The assembly of SFT at any particular site results from the response of the regional species pool against environmental filters (Cornwell *et al.*, 2006), which is determined by the ecological requirements of organisms (Araújo *et al.*, 2005). Environmental filters are non-random ecological factors that may restrict or exclude some types of species from coexisting or entering a community, according to unfeasible physiological limits (Poff, 1997; Mayfield *et al.*, 2010). SFT are not filtered independently from each other, but tend to be associated in patterns that enable the multiple pool of species in the community to be classified in fewer functional types, showing a similar response to environmental conditions and having a similar influence on the prevailing ecosystem process (Diaz *et al.*, 1998). Climate variables, disturbance regimes or landscape heterogeneity are generally some of the major filters strongly determining SFT at any specific site (Díaz *et al.*, 2007). For example, variations in temperature and summer drought along altitudinal gradients have been demonstrated to affect the SFT of plants in Mediterranean mountain systems (Pescador *et al.*, 2015). Similarly, temperature gradients might constrain the functional response of species, in relation to attack and maximal intake rate, according to their thermal optimum (Englund *et al.*, 2011). Landscape heterogeneity may condition the range of SFT present in a bird community according to the species habitat requirements (Devictor *et al.*, 2010). However, global change might modify these environmental filters, leading to a non-random biodiversity loss (Lehikoinen *et al.*, 2016) and functional shifting (Diaz *et al.*, 1998, 2007; Suding *et al.*, 2008). Thus, understanding the SFT-environment relationship is of great importance in determining the spatial distribution of SFT, which helps to comprehend biodiversity loss under different scenarios of global change (Scherer *et al.*, 2015). In this context, steep environmental gradients in mountains (i.e. temperature, humidity, precipitation or solar radiation among others), associated to altitudinal gradient, influence the distribution of plants and

animals, hence providing an interesting context to assess how environmental filters act on SFT (Nunes *et al.*, 2016).

Several authors have highlighted the need of multi-taxa approaches (Barbaro & van Halder, 2009; Dufлот *et al.*, 2014) to assess the responses of SFT against environmental filtering. Nevertheless, most recent literature has been restricted to specific taxonomic groups, mainly plants, invertebrates and birds (Maire *et al.*, 2012; Aiello-Lammens *et al.*, 2016; Concepción *et al.*, 2016; Ding *et al.*, 2017), probably due to the availability of free accessible traits databases for these groups (Mbaka *et al.*, 2015) and working with other groups of vertebrates is challenging because of high variability in animal behavior, morphology and foraging strategies (Blaum *et al.*, 2011). Multi-taxa approaches are, however, based on grouping similar functional responses across taxa, which matches the ecological concept of functional convergence and this implies a similar adaptive response to environmental factors (Grime, 2006). These approaches allow for the generalization of results, determining general patterns in species responses, which can be a helpful tool for conservation management (Aubin *et al.*, 2013).

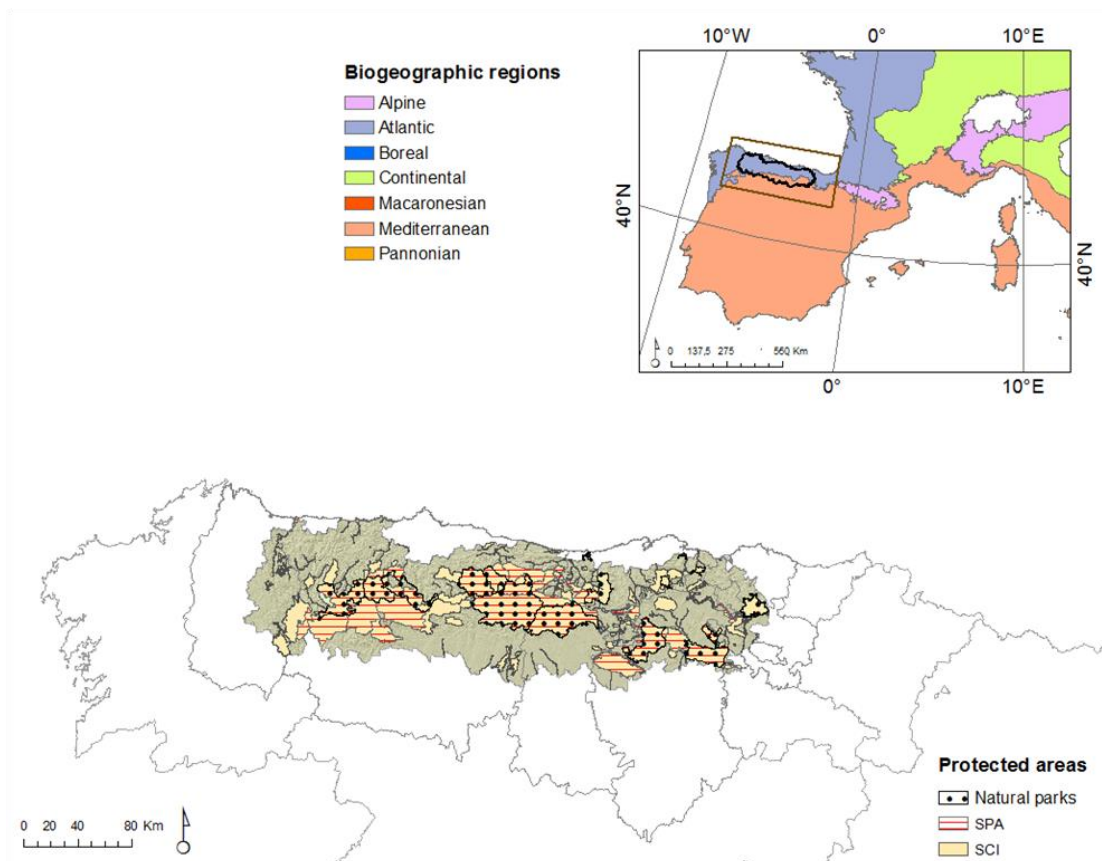
In this study we developed a multi-taxa approach analyzing SFT-environment relationships across terrestrial vertebrates (mammals, breeding birds, reptiles and amphibians) with the aim of assessing the role of environmental filters in structuring the SFT assembly and using a temperate mountain system (the Cantabrian Mountains, NW Spain) as a case study. In particular, our goals were to identify: (i) common patterns of response of functional groups to environmental filters; (ii) major groups of environmental variables that govern the spatial distribution of functional groups.

## **2. Material and Methods**

### **2.1. Study area**

The Cantabrian Mountains (NW of Spain) cover approximately 31494 km<sup>2</sup>, with altitude ranging from sea level to 2631 m.a.s.l. (Fig. 3.1). They lie at the limit between the Eurosiberian (northern slope) and Mediterranean (southern slope) biogeographic regions (Rivas-Martínez *et al.*, 1987). Climate varies between both slopes, from

Temperate-Oceanic to Mediterranean (Rivas-Martínez *et al.*, 2004), which is expected to define significant variations in species distribution (Araújo *et al.*, 2005). Average annual precipitation varies from 700 to 2400 mm and mean annual temperature from 4°C to 22°C. These particular climatic characteristics, jointly with the uneven topography and land management in the area during centuries (burning, cutting and grazing), have given rise to a very heterogeneous landscape mosaic of special relevance from a conservation perspective (Morán-Ordóñez, 2012).



**Figure 3.1.** Study area: The Cantabrian Mountains located in NW Spain. Information on biogeographic regions was obtained from the Spanish Ministry of Agriculture Food and Environment (<http://www.magrama.gob.es/>). Information on protected areas was obtained from the BCN200 database of the Spanish Geographic Institute ([www.ign.es](http://www.ign.es)); SPC Special Protection Areas, SCI Sites of Community Importance.

This area hosts a wide variety of ecosystems, habitats and endemic species, making it a recognized biodiversity hotspot (Worboys *et al.*, 2010), with around 40% of the surface being protected under different figures since 1918. The landscape is dominated by pastures and croplands in valley bottoms and lowlands, being substituted in mid-high

slopes by heathlands, shrublands and deciduous forests dominated by *Fagus sylvatica*, *Betula pubescens*, *Quercus petraea* and *Q. robur*, on northern slopes, and *Q. pyrenaica* and *Q. rotundifolia* on southern slopes. Plantations of *Pinus pinaster*, *P. radiata* and *Eucalyptus globulus* also cover middle slopes replacing scrubs and heathers. The top of the mountains is covered by natural grasslands and rock formations.

## 2.2. Functional traits of vertebrate species

SFT were selected according to the criteria of Chillo & Ojeda (2012) and Gravel *et al.* (2016). The target traits were related to resource capture (feeding guild) and behavior (habitat use type and daily activity). These traits can be considered as drivers of biodiversity-ecosystem function relationships (Flynn *et al.*, 2009). Feeding guild is related to the resource requirements of species in the community (Belmaker *et al.*, 2012), while habitat use type and activity are associated to the spatial distribution and temporal use of resources (Petchey *et al.*, 2007; Barbaro & van Halder, 2009). For each trait, a range of functional groups was identified considering common functional characteristics among groups of terrestrial vertebrate species (mammals, breeding birds, reptiles and amphibians). This implies a similar functional adaptive response to environmental factors across taxa which allows comparability. As a result, three traits and 17 functional groups were identified (Table 3.1).

**Table 3.1.** Classification of species' functional traits and functional groups considered in this study

Trait	Range of functional groups
Feeding guild	Carnivore, granivore, herbivore, omnivore, insectivore
Habitat use type	Tree-dwelling, terrestrial, ground-dwelling, cave-dwelling, rock-dwelling, semi-aquatic, shrub-dwelling, anthropogenic environments, generalist
Daily activity	Nocturnal, diurnal, multiphasic

Functional groups were identified based on experts' knowledge, using the species list included in the official database of vertebrates of Spain (Ministry of Agriculture, Food and Environment 2012; [www.magrama.gob.es](http://www.magrama.gob.es); see Annex III, Table S3.1). This database contains information on species occurrence

(presence/absence) in a 10 km x 10 km UTM grid system for the period 1980-2007. Occurrence data derive from published sources and field surveys carried out by volunteers on the basis of direct and indirect observations (pellets, tracks, bed sites; Pleguezuelos *et al.*, 2002; Martí & del Moral, 2003; Palomo *et al.*, 2007). Using this database, we estimated the richness (total number of species) of each functional group in each UTM 10x10 km square, requiring 388 squares to completely cover the study area.

### **2.3. Environmental filters**

A set of 43 environmental variables accounting for climate, topography, land cover, physiological state of vegetation, landscape heterogeneity, human influence and accessibility were chosen as environmental filters determining the spatial distribution of functional groups (Annex III, Table S3.2; Hawkins & Porter, 2003a; Ortiz-Yusty *et al.*, 2013; Suárez-Seoane *et al.*, 2014).

Climatic variables are expected to define significant variations in species distribution both at regional and continental scale (Araújo & Luoto, 2007). The maximum and minimum temperature and the mean precipitation were obtained on a monthly basis (period 1951-1999) from the Climatic Atlas of Ninyerola *et al.* (2005) at 200 m of spatial resolution. These values were averaged (i.e. mean value) for summer (July, August, September) and winter (December, January and February) because they are the most limiting seasons for temperate and Mediterranean species (Virgós & Tellería, 1998; Acevedo *et al.*, 2005; Ferretti *et al.*, 2011; Álvarez-Martínez *et al.*, 2015). We calculated the mean and the standard deviation of the seasonal climate variables (as an expression of the general climate pattern and climate variability, respectively) for each 10 km x 10 km UTM square, in correspondence with the grid reference system of the vertebrate species inventory.

Topography influences land cover characteristics, as well as microclimatic conditions, and species movement, iterations or species visual communication (Coughenour, 2006; Alonso *et al.*, 2012). Topographic variables (altitude, slope and solar radiation) were derived from a Digital Elevation Models (DEM) at 90 m resolution obtained from the Spanish Geographic Institute ([www.ign.es](http://www.ign.es)). The mean

and the standard deviation of each topographic variable were calculated for each 10 km x 10 km UTM square.

Land cover is known to influence species habitat selection as it mainly reflects resource quality and availability (Borkowski, 2004; Alves *et al.*, 2014). Land cover information was obtained from the CORINE Land Cover database for the year 2006 at 30 m resolution. (<http://www.eea.europa.eu/publications/COR0-landcover>). A reclassification of the original CORINE dataset (44 classes) was carried out, with the purpose of simplifying the original dataset, considering the vertical structure of vegetation. This resulted in 12 land cover classes (see more details in Table S3.3 and García-Llamas *et al.*, 2016). The relative frequency of each land cover class was subsequently calculated in each 10 km x 10 km UTM square.

The normalized difference vegetation index (NDVI) was used as an indicator of the physiological state of vegetation. It varies from -1 (in non-vegetated areas) to +1 (indicating increasing green vegetation) (Tognelli & Kelt, 2004). This index has been broadly recognized as a driver of species distribution and resource availability relationships (Suárez-Seoane *et al.*, 2014). The mean value of annual NDVI was derived from a temporal monthly series of NDVI for years 1983, 1985, 1990, 1993, 1996 and 1999, obtained from NOAA-AVHRR at 1km resolution (see Osborne *et al.*, 2007 for technical details).

This NDVI database was also used to calculate landscape heterogeneity (see Seto *et al.*, 2004 for similar approaches) as an indicator of habitat heterogeneity, since landscape heterogeneity can give rise to large spatial variations of reflectance and consequently, of NDVI spatial patterns (Tchuenté *et al.*, 2011). NDVI values were divided in 20 classes according to data distribution in a frequency histogram. Landscape heterogeneity was estimated as the number of NDVI classes in each 10 km x 10 km UTM square, considering the total of pixels per class in each 10 km x 10 km UTM square.

Human influence variables reflect the degree of anthropogenic disturbances (Alonso *et al.*, 2012). We used the minimum Euclidean distance to urban settlements (mean and standard deviation values at each 10 km x 10 km UTM square), the surface of protected areas (in km<sup>2</sup>) and the status of conservation at each pixel (i.e. presence/absence of protected areas) as indicators of human influence.

A major concern of direct observation methods in species surveys is related to differences in detectability between the habitats or species (Alves *et al.*, 2014). Therefore, although not considered as an environmental filter, accessibility was also included in models trying to account for the potential sampling bias in species surveys. We mapped the mean cost of accessibility for each 10 km x 10 km UTM square at 90 m of spatial resolution by integrating data on slope, distance to paths and roads and distance to settlements. Total length of paths and roads in each 10 km x 10 km UTM square was also used as an indicator of accessibility. Information on settlements, roads, paths and protected areas was obtained at 1:200000 spatial resolution from the BCN200 database of the Spanish Geographic Institute ([www.ign.es](http://www.ign.es)). Slope was derived from a DEMs at 90 m resolution ([www.ign.es](http://www.ign.es)).

## **2.4. Data analysis**

In order to explore the relationship between the response variable (species richness of each functional group) and the predictors (environmental filters), separated multi regression linear models (ordinary least squares; OLS) were fitted for each of the 17 considered functional groups (Table 3.1).

To avoid multicollinearity problems, we previously evaluated Spearman's bivariate correlations among all predictors. When pairs of variables were highly correlated ( $r^2 > 0.7$ ), we excluded the one with the least biological meaning (Alonso *et al.*, 2012). Thus the original pool of variables was simplified to 28 variables, which were further entered as predictors in OLS models (Table 3.2). We also calculated variance inflation factors (VIF). In our models VIF was lower than 5 (Zuur *et al.*, 2010).

A stepwise procedure (backward and forward variable selection) according to Akaike's information criterion (AIC) was used to test the effect of all predictors considered in OLS models on species richness in functional groups and selected the best-fit model (Venables & Ripley, 2002; Concepción *et al.*, 2016). Residuals of OLS models were graphically checked to ensure the appropriateness of models (i.e. residuals' distribution, independence and homoscedasticity). Spatial autocorrelation in the residuals, which violates the assumption of independence in their distribution, was further evaluated by using Moran's index (Moran, 1950). When evidence of spatial autocorrelation was detected (Moran's index  $> 0.1$ ), we applied simultaneous or



conditional autoregressive (SAR and CAR, respectively) models to remove the spatial autocorrelation in the residuals (Wall, 2004; Stefanescu *et al.*, 2011).

All statistical analyses were performed using SAM v4.0 statistical software (Rangel *et al.*, 2010). Environmental variables were processed using ArcGIS 10.2 (Esri, 2014).

### 3. Results

Considering the performance of models for the three SFT, feeding guild SFT achieved values of  $R^2$  between 0.25 (for granivores) and 0.44 (for omnivores). For habitat use SFT, models accounted for 18% to 59% of the variance of species richness of functional groups, with the lowest value of  $R^2$  being recorded by cave-dwelling groups, and the highest value by ground-dwelling ones. Finally, in the case of daily activity SFT, the multiphasic functional group obtained an  $R^2$  of 0.21, while the highest value was obtained by the diurnal functional group ( $R^2=0.52$ ) (Table 3.3).

As a general trend, species richness in functional groups was mainly explained by climate, topography, human influence and accessibility (Table 3.3 and 3.4). Particularly, maximum summer temperature, standard deviation of slope and surface of protected areas were systematically ranked as the top variables filtering species richness for the target functional groups. No clear trends were detected for land cover, physiological state of vegetation or landscape heterogeneity, their effect being dependent on the functional group (Table 3.3 and 3.4).

In detail, the maximum summer temperature had a positive significant effect on species richness in most functional groups, for the three SFT traits. The influence of topographic descriptors varied however among functional groups. The standard deviation of slope was the most relevant filter explaining richness for the three SFT. Similarly, solar radiation also greatly affected functional groups, specifically those of feeding guild STF (i.e. insectivores, carnivores and omnivores), but also tree-dwelling, ground-dwelling, shrub-dwelling (i.e. habitat use STF) and diurnal groups (i.e. activity STF). Only cave-dwelling, terrestrial and multiphasic groups were not associated with topography. In contrast, there was not a clear trend in response against land cover, this response being closely dependent on the particular functional group. Generalist, terrestrial, multiphasic and nocturnal

groups were not significantly related to any land cover class. Insectivores, herbivores, carnivores, tree-dwellers, cave-dwellers, ground-dwellers, shrub-dwellers and diurnals increased with the presence of woody land cover, while anthropogenic and semi-aquatic groups decreased. Herbivores, cave-dwellers, ground-dwellers and shrub-dwellers were also favored by the existence of open areas, such as herbaceous croplands and pasturelands. However, the presence of agricultural areas negatively affected omnivorous, tree-dwelling and diurnal richness. Likewise, richness of omnivores, ground-dwellers, rock-dwellers, semi-aquatics and diurnals showed a significant negative response to human infrastructures, with an additional negative effect of bare areas on ground-dwellers. On the other hand, richness of semi-aquatic group was positively influenced by water. Richness of granivores, omnivores, shrub-dwellers, nocturnals and diurnals was disfavored by scrub and sclerophyllous-herbaceous vegetation. Further, physiological state of vegetation, measured as NDVI was the variable that least contributed, only explaining richness of anthropogenics and ground-dwellers (negatively) and terrestrials (positively). Similarly, the predictive power of landscape heterogeneity did not show a clear pattern. The presence of heterogeneous landscapes particularly favored the richness of insectivores, granivores, omnivores, tree-dwellers, cave-dwellers, rock-dwellers, shrub-dwellers and diurnals. The filtering effect of protected areas was high, as the richness of nearly all functional groups, for the three SFT, increased in these areas (Table 3.3 and 3.4).

In addition, the results of models showed some degree of sampling bias in the vertebrate species survey. The cost of accessibility showed negative significant relationships with the richness of the three SFT. We must point out the effect on insectivorous, carnivorous, omnivorous, tree-dwelling, anthropogenic, generalist, rock-dwelling, shrub-dwelling, diurnal and multiphasic groups. Further, road length also showed statistically significant relationships with herbivorous, omnivorous and rock-dwelling groups (Table 3.3 and 3.4).

**Table 3.2.** Environmental variables entered as predictors in ordinary least squares regression models after excluding correlated variables. The mean and/or the standard deviation value of the environmental variables were extracted for each 10 km x 10 km UTM sampling unit (See Annex III, Table S3.2 for more details).

Family	Code	Description of the variable	Source
Climate	PRECWIN	Mean precipitation (mm) in winter	Ninyerola's Climatic Atlas (Ninyerola <i>et al.</i> , 2005) at 200m spatial resolution
	TMAXWIN	Maximum temperature (°C) in winter	
	TMAXSUM	Maximum temperature (°C) in summer	
	stdPRECWIN	Standard deviation of mean precipitation (mm) in winter	
	stdTMAXSUM	Standard deviation of maximum temperature (°C) in summer	
Topography	SOLR	Solar radiation (*10 <sup>6</sup> W/h)	Digital Elevation Model at 90 m spatial resolution ( <a href="http://www.ign.es">http://www.ign.es</a> )
	stdDEM	Standard deviation of elevation (m)	
	stdSLO	Standard deviation of slope (%)	
Land cover	INFRA	Frequency of class human infrastructures	CORINE Land Cover 2006 at 30 m spatial resolution
	MIN	Frequency of class mineral extraction sites	
	HERC	Frequency of class herbaceous croplands	
	WOOC	Frequency of class woody cropland	
	PAS	Frequency of class pasturelands	
	FOR	Frequency of class forest	
	TWOOD	Frequency of class transitional woodland-shrublands	
	SCRUB	Frequency of scrub and sclerophyllous-hebaceous formations	
	SPAR	Frequency of class sparsely vegetated areas	
	BARE	Frequency of class bare areas	
WET	Frequency of class wetlands		
WAT	Frequency of class water		
Physiological state of vegetation	NDVI	Annual average NDVI index	NDVI from NOAA-AVHRR at 1 km of spatial resolution
Landscape heterogeneity	LANDHET	Landscape heterogeneity considering the total number of pixels in each sampling unit	NDVI from NOAA-AVHRR at 1 km of spatial resolution
Human influence	UD	Euclidean distance to the nearest settlement (m)	Vector layers at 1:200000 spatial resolution ( <a href="http://www.ign.es">http://www.ign.es</a> )
	stdUD	Standard deviation of Euclidean distance to the nearest settlement (m)	
	SURFPA	Surface covered by protected areas in each sampling unit (km <sup>2</sup> )	
	PREPA	Presence/absence of protected areas	
Accessibility	LROAD	Total length of roads and paths (km)	Vector layers of roads at 1:200000 spatial resolution
	ACOST	Accessibility cost at 90m and 180m spatial resolution	Digital Elevation Models at 90 m spatial resolution and vector layers of roads and settlements at 1:200000 spatial resolution ( <a href="http://www.ign.es">http://www.ign.es</a> )

**Table 3.3.** Results of the most parsimonious models (ordinary least squares regression and autoregressive models SAR or CAR) testing the effect of environmental predictors on the richness of each functional group. Significance levels, sign of the effect and variance explained by models are indicated. See Table 3.2 for codes of environmental variables. Only variables included as predictors in some of the most parsimonious models are shown (wholes).

Environmental variables		Feeding guild				Habitat use type						Activity						
		Insec.	Gran.	Herb.	Carn.	Omn.	Arb.	Anthr.	*CD.	Gen.	*GD	RD	*SA	*Shru.	Terr.	*Di.	Noc.	Mu.
Climate	PRECWIN	▽									▽	▽				△		
	TMAXSUM	▲	▲	△	▲	▲	▲	▲	▲	▲	▲	▲	▲	▲	△	▲	▲	△
Topography	SOLR	▲		△	▲	▲	▲				▲	△		▲	▲			
	stdDEM			△			▲											
	stdSLO	▲			▲	▲		▲	▲	▲	▲	▲	▲	▲		▲	▲	△
Land cover	INFRA					▽					▽	▽	△			▽		
	MIN	▽			▽						▽	▽				▽	▽	▽
	HERC			▲							▲			▲		▽		▽
	WOOC	▽						▽		▽						▽	▽	▽
	PAS			△		▽			▲		▽	▽						▽
	FOR	▲	△	▲	▲		▲		▲			△		▲		▲	△	△
	TWOOD	△			▲		▲	▽			▲	△	▽	▲		▲	△	△
	SCRUB	▽	▽			▽						▽	▽	▲	▽	▽	▽	▽
	SPAR					▲			▲			△				▲		△
	BARE										▽	△						
	WET								▽		▽				▽			
	WAT												▲					
	Physiological state of vegetation	NDVI							▽			▽			▲		△	
	Landscape heterogeneity	LANDHET	▲	▲	△	△	▲	▲		▲		▲	△	▲	△	▲	△	△
stdUD					△				▲									
Human influence	SURFPA	▲	▲	▲	▲	▲	▲	▲		▲	▲	▲		▲	▲	▲	▲	▲
	PREPA			△						△		△	▲		△	▲	△	△
Accessibility	LROAD			△		▲						▲	▲					
	ACOST	▽		▽	▽	▽	▽	▽		▽	▽	▽		▽	▽	▽	▽	▽
Model fit	R-square	0.43	0.25	0.30	0.43	0.44	0.46	0.33	0.18	0.21	0.59	0.42	0.33	0.30	0.28	0.52	0.27	0.21

Insec. (Insectivore); Gran. (Granivore); Herb. (Herbivore); Carn. (Carnivore); Omn. (Omnivore); Arb. (Tree-dwelling); Anthr. (Anthropogenic); CD (Cave-dwelling); Gen (Generalist); GD (Ground-dwelling); RD (Rock-dwelling); SA (Semi-aquatic); Shru. (Shrub-dwelling); Terr. (Terrestrial); Di (Diurnal); Noc. (Nocturnal); Mu. (Multiphasic). \* Correspond to models not affected by spatial autocorrelation and thus, not corrected by autoregressive models (SAR and CAR). ▲ Significance at level <0.001; ▲ significance at level 0.01 ▲ significance at level 0.05 △ no significance. Direction of arrows indicates the sign of the effect (positive or negative).

**Table 4.3.** Results of the most parsimonious models (ordinary least squares regression and autoregressive models SAR or CAR) testing the effect of environmental predictors on the richness of each functional group, including the sign of the effect and standardized coefficient estimates of distinct predictors. Significant predictors are in bold. See Table 3.2 for codes of environmental variables. Only variables included as predictors in some of the most parsimonious models are shown (wholes).

Environmental variables	Feeding guild							Habitat use type							Activity			
	Insec.	Gran.	Herb.	Carn.	Omn.	Arb.	Anthr.	*CD.	Gen.	*GD	RD	*SA	*Shru.	Terr.	*Di.	Noc.	Mu.	
Climate	PRECWIN	-0.18		+0.01							-0.10	<b>-0.16</b>				<b>-0.14</b>		
	TMAXSUM	<b>+0.38</b>	<b>+0.47</b>		<b>+0.39</b>	<b>+0.33</b>	<b>+0.56</b>	<b>+0.34</b>	<b>+0.26</b>	<b>+0.25</b>	<b>+0.38</b>	<b>+0.18</b>	<b>+0.44</b>	<b>+0.35</b>	+0.08	<b>+0.01</b>	<b>+0.26</b>	+0.12
Topography	SOLR	<b>+0.30</b>			<b>+0.29</b>	<b>+0.28</b>	<b>+0.32</b>			<b>+0.54</b>	+0.08		<b>+0.30</b>	+0.04	<b>+0.01</b>			
	stdDEM			+0.13			<b>+0.37</b>											
	stdSLO	<b>+0.42</b>			<b>+0.47</b>	<b>+0.28</b>		<b>+0.30</b>	<b>+0.23</b>	<b>+0.029</b>	<b>+0.29</b>	<b>+0.43</b>	<b>+0.13</b>	<b>+0.43</b>		<b>+0.004</b>	<b>+0.21</b>	+0.10
Land cover	INFRA						<b>-0.12</b>			<b>-0.09</b>	<b>-0.10</b>	+0.08			-0.001			
	MIN	-0.05			-0.05						-0.02	<b>-0.10</b>				-0.02	-0.06	
	HERC			<b>+0.20</b>									<b>+0.27</b>					
	WOOC	-0.06						<b>-0.08</b>	-0.07		-0.03					-0.04	-0.07	
	PAS			+0.08		<b>-0.11</b>			<b>+0.14</b>		-0.06				<b>-0.001</b>			
	FOR	<b>+0.15</b>	+0.05	<b>+0.11</b>	<b>+0.12</b>		<b>+0.32</b>	<b>-0.15</b>	<b>+0.12</b>			+0.07		<b>+0.32</b>		<b>+0.001</b>	0.08	+0.03
	TWOOD	+0.07			<b>+0.16</b>		<b>+0.14</b>				<b>+0.14</b>	+0.06	<b>-0.12</b>	<b>+0.24</b>		<b>+0.001</b>		
	SCRUB	-0.03	<b>-0.09</b>			<b>-0.11</b>						-0.03	-0.08	<b>+0.11</b>	-0.05	<b>-0.001</b>	-0.06	-0.05
	SPAR					<b>0.08</b>			<b>+0.05</b>			+0.05				<b>-0.001</b>		+0.03
	BARE										<b>-0.09</b>	+0.04						
	WET								-0.07		+0.06							
WAT												<b>+0.10</b>		-0.02				
Physiological state of vegetation	NDVI						<b>-0.11</b>			<b>-0.16</b>				<b>+0.21</b>		+0.07		
Landscape heterogeneity	LANDHET	<b>+0.09</b>	<b>+0.12</b>	+0.09	+0.06		<b>+0.11</b>	<b>+0.07</b>			<b>+0.11</b>	+0.08	<b>+0.11</b>	+0.02		+0.02	+0.01	
Human influence	stdUD				+0.07		<b>+0.13</b>											
	SURFPA	<b>+0.31</b>	<b>+0.21</b>	<b>+0.43</b>	<b>+0.37</b>	<b>+0.28</b>	<b>+0.37</b>	<b>+0.17</b>		<b>+0.16</b>	<b>+0.21</b>	<b>+0.034</b>	<b>+0.21</b>		<b>+0.35</b>	<b>+0.004</b>	<b>+0.33</b>	<b>+0.29</b>
	PREPA			+0.07						+0.06		+0.03	<b>+0.13</b>	+0.05		+0.06	+0.09	
Accessibility	LROAD			+0.08		<b>+0.10</b>					<b>+0.09</b>							
	ACOST	<b>-0.20</b>		<b>-0.29</b>	<b>-0.40</b>	<b>-0.24</b>	<b>-0.32</b>	<b>-0.42</b>		<b>-0.43</b>		<b>-0.37</b>		<b>-0.32</b>		<b>-0.002</b>		<b>-0.27</b>

Insect. (Insectivore); Gran. (Granivore); Herb. (Herbivore); Carn. (Carnivore); Omn. (Omnivore); Arb. (Tree-dwelling); Anthr. (Anthropogenic); CD (Cave-dwelling); Gen (Generalist); GD (Ground-dwelling); RD (Rock-dwelling); SA (Semi-aquatic); Shru. (Shrub-dwelling); Terr. (Terrestrial); Di (Diurnal); Noc. (Nocturnal); Mu. (Multiphasic). \* Correspond to models not affected by spatial autocorrelation and thus, not corrected by autoregressive models (SAR and CAR).

## 4. Discussion

Our study showed that the richness of functional groups was non-randomly distributed and highlighted how environmental filtering is structuring species functional traits assemblage in our study area, as has been observed in other studies carried out in coastal landscapes and semi-arid African savannas (Cornwell & Ackerly, 2009; Scherer *et al.*, 2015). We stressed the importance of climatic variables (in particular the maximum summer temperature) as filters of richness for the target functional groups, which might be related to the strategic geographic position of the Cantabrian Mountains, which are under the influence of both Mediterranean and Temperate-Oceanic climates (Rivas-Martínez *et al.*, 2004). In areas of Mediterranean influence, summer temperature is highly correlated with biodiversity, as it constitutes a seasonal limiting factor for species due to its restrictive effect on food and water flows (Virgós & Tellería, 1998; Rueda *et al.*, 2008). Meanwhile, in temperate areas, cool temperatures might be limiting for species, generally increasing richness in warmer areas (Hawkins *et al.*, 2003b; Menéndez *et al.*, 2006), as in our particular case. Therefore, transitional climatic conditions in our study area, with hot summers and a dry summer period of less than two months (Rivas-Martínez & Rivas-Sáenz, 2015; Calvo-Fernández *et al.*, 2017), allowed the coexistence of species with both Mediterranean and temperate requirements, which likely explained the co-occurrence of functional groups. Further according to the energy hypothesis, the energy available to the system is somehow a limiting factor of biodiversity (Wright, 1983; Kerr & Packer, 1997), so that more species tend to coexist in areas of high energy availability (Tognelli & Kelt, 2004). Temperature and solar radiation, are variables highly correlated with the energy supply in the environment (Rohde, 1992; Tognelli & Kelt, 2004) contributing therefore, to explaining the filtering effect of these variables (Meynard *et al.*, 2011).

The importance of topography in the assembly of functional groups in mountain areas, a common pattern in other areas such as tropical forests covered by ridges and canyons (Menger *et al.*, 2017), was also evidenced by the role of the standard deviation of the slope as a driver of the richness of the target functional groups. Slope is related to the roughness of terrain, which can affect the energetic and

timely cost of individual movements and, hence, the use of resources and habitat by species (Coughenour, 2006). Slope variability, which was expressed as standard deviation, may therefore favor the presence of different functional groups through complementarity of resources used by different species (Díaz *et al.*, 2007), since they could exploit different parts of the mountain according to their dispersal and movement abilities. Furthermore, the increase in richness of the target functional groups with slope variability might contribute to maintaining properties of ecosystems, since the greater number of functional similar species (i.e. functional redundancy), the greater probability that at least some species will overcome perturbations or changes in the system (Laliberté *et al.*, 2010).

The role of land cover did not show a clear pattern of response, as the relationship between land cover and richness of functional groups were strongly affected by their ecological requirements. For example, functional groups with generalist behaviour and wide requirements of land cover (i.e. generalist, terrestrial or multiphasic categories) did not show, in general, any particular significant response to land cover classes. This might explain the poor performance of models for these groups, as also stated in other studies (Grenouillet *et al.*, 2011). Similarly, the weak association of granivores to land cover types could be linked to their foraging strategy (Pyke, 1984), which might involve different habitat requirements according to different seed preferences, distribution or detectability of seeds, toxic minimization, predation risk, competitors (Hulmen & Benkman, 2002) or food seasonal availability (Díaz & Diaz, 1992; Marone *et al.*, 1997; Šálek *et al.*, 2015). Carnivores, in turn, were common in landscapes dominated by forest formations with open patches, which provide a favourable combination of refuge and foraging supply, which is consistent with other studies such as Pita *et al.* (2009) or Scherer *et al.* (2015). Likewise, herbivores benefited from the combination of woody cover and open grazing areas that embody shelter and foraging provision. Furthermore, tree-dwelling species were favored by tree canopy, while the negative effect of woody land cover on species richness from anthropogenic environments may be related to the structural simplification of vegetation (McKinney, 2008). Further examples could be found in the positive contribution of water surfaces to explaining the functional richness of the semi-aquatic group.

The filtering effect of landscape heterogeneity has been widely reported by several authors from a functional perspective (Flynn *et al.*, 2009; Devictor *et al.*, 2010). Indeed, Lee & Martin (2017) stated that functional diversity is limited by the accessibility of ecological niches and, in turn, heterogeneous landscapes offer more niches and complementary resources (Tews *et al.*, 2004) for shelter, predation refuge or feeding (Coughenour, 2006). Thus, the more heterogeneous an area, the more functional groups could be expected to coexist. Because of topographic and climatic complexity and historic human intervention, mountains are usually characterized by heterogeneous landscapes (Morán-Ordóñez, 2012). Nevertheless, the response of functional groups to landscape heterogeneity in our study did not show any clear trend. Significant relationships were only found with functional richness of some groups. Explanations may be related to the fact that not all SFT and functional groups respond equally to landscape heterogeneity (Barbaro & van Halder, 2009). Indeed, we selected traits based on resource capture and behavioral traits, but traits not considered here, such as those related to dispersal capacity, body size or colonization could be more related to landscape heterogeneity (Duflot *et al.*, 2014; Perović *et al.*, 2015; Scherer *et al.*, 2015). Consequently, we suggest future research including these traits for an enhanced understanding of the role played by landscape heterogeneity as a limiting factor for the functional response of species.

Anthropogenic disturbances usually act as a filter with negative functional consequences (Chillo & Ojeda, 2012; Concepción *et al.*, 2016), since they may exclude species with more stable habitat requirements or when exceeding species' physiological tolerance range, while possibly favoring the entry of new species according to their functional attributes (Chapin *et al.*, 2000; e.g. generalist species). This might result in an increasing vulnerability of particular functional groups and, therefore, in strong alterations of ecosystem processes (Elmqvist *et al.*, 2003). In this respect, protected areas are subject to regulation of uses and human activities, generally supporting high quality habitats and reducing threats (e.g. chemical inputs, persecutions or disturbances) compared to the habitats outside protected areas (Thomas *et al.*, 2012), that may benefit the presence of a wider range of functional groups and richness. For example, the presence of carnivores usually comes into conflict with human interests, such as competition for resources or



livestock predation. Low human pressure over protected areas may benefit carnivores in terms of conservation, habitat quality and human conflict limitation (Pia *et al.*, 2013). Coughenour (2006) or Marchand *et al.* (2014) also pointed out the positive contribution of protected areas on herbivore populations due to lower hunting pressure. In our particular case, protected areas provided a high representation of functional groups, in contrast to other studies in France (Devictor *et al.*, 2010) and in the Iberian Peninsula, regarding other taxa such as macroinvertebrates (Guareschi *et al.*, 2015). As these studies state, differences with our results may occur because in protected areas the focus has traditionally been on taxonomic diversity. Besides, these areas are located around particular systems, such as mountains because they usually contain relatively unimpacted areas, whereas low lands are underestimated.

Although not considered as an environmental filter, significant association of richness of most functional groups with accessibility might suggest some degree of bias in species survey, which was a main difficulty in our study. However, in spite of this potential bias, it was possible to extract relevant ecological information related to the response of species richness of functional groups to environmental filters. Unfortunately, as also reported in other studies (Lobo *et al.*, 2007; Hortal *et al.*, 2008; Pardo *et al.*, 2016), most of the species databases currently available present important sampling bias and gaps (Hortal *et al.*, 2007). Differences in detectability of animals or signs, but also observers' behavior are main constraints in direct presence/absence observation methods (Alves *et al.*, 2014). Nevertheless, direct observation methods can avoid uncertainties related to predictive models, such as problems of independence among samples or arbitrariness in the selection of the study areas (McDonald *et al.*, 2005). As a consequence, despite limitations, they have been widely used in biodiversity studies (Lorenzo, 2012).

## 5. Conclusions

This study highlights the role played by climate, topography and human influence as main environmental filters determining the richness of functional groups in mountain systems. The filtering effect of land cover depended on the particular ecology of each functional group, although the richness of functional groups was generally favored by

the presence of heterogeneous landscapes. Overall, this study might help to identify general rules involved in the assemblage of species functional traits and illustrates the importance of environmental filters on community assembly in mountain systems. This study stresses the need to focus on the functional ecology of species, from a multi-taxa perspective in environmental management and conservation studies. Further, it might offer a valuable framework to better understand mechanisms of biodiversity loss within the context of environmental change.

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## ANNEX III

**Table S3.1.** List of species of mammals, breeding birds, reptiles and amphibians included in the official database of vertebrates of Spain (Ministry of Agriculture, Food and Environment 2012; [www.magrama.gob.es](http://www.magrama.gob.es)), from which we derived species functional groups

Species of mammals			
<i>Apodemus flavicollis</i>	<i>Hypsugo savii</i>	<i>Myocastor coipus</i>	<i>Pipistrellus pygmaeus</i>
<i>Apodemus sylvaticus</i>	<i>Lepus castroviejoii</i>	<i>Myodes glareolus</i>	<i>Plecotus auritus</i>
<i>Arvicola sapidus</i>	<i>Lepus europaeus</i>	<i>Myotis becnsteinii</i>	<i>Plecotus austriacus</i>
<i>Arvicola terrestris</i>	<i>Lepus granatensis</i>	<i>Myotis blythii</i>	<i>Rattus norvegicus</i>
<i>Barbastella barbastellus</i>	<i>Lutra lutra</i>	<i>Myotis daubentonii</i>	<i>Rattus rattus</i>
<i>Canis lupus</i>	<i>Martes foina</i>	<i>Myotis emarginatus</i>	<i>Rhinolophus euryale</i>
<i>Capra pyrenaica</i>	<i>Martes martes</i>	<i>Myotis myotis</i>	<i>Rhinolophus ferrumequinu</i>
<i>Capreolus capreolus</i>	<i>Meles meles</i>	<i>Myotis mystacinus</i>	<i>Rhinolophus hipposideros</i>
<i>Cervus elaphus</i>	<i>Micromys minutus</i>	<i>Myotis nattereri</i>	<i>Rhinolophus mehelyi</i>
<i>Chionomys nivalis</i>	<i>Microtus agrestis</i>	<i>Neomys anomalus</i>	<i>Rupicapra pyrenaica</i>
<i>Crocidura russula</i>	<i>Microtus arvalis</i>	<i>Neomys fodiens</i>	<i>Sciurus vulgaris</i>
<i>Crocidura suaveolens</i>	<i>Microtus duodecimcostatus</i>	<i>Neovison vison</i>	<i>Sorex coronatus</i>
<i>Dama dama</i>	<i>Microtus gerbei</i>	<i>Nyctalus lasiopterus</i>	<i>Sorex granarius</i>
<i>Eliomys quercinus</i>	<i>Microtus lusitanicus</i>	<i>Nyctalus leisleri</i>	<i>Sorex minutus</i>
<i>Eptesicus serotinus</i>	<i>Mus musculus</i>	<i>Nyctalus noctula</i>	<i>Suncus etruscus</i>
<i>Felis silvestris</i>	<i>Mus spretus</i>	<i>Oryctolagus cuniculus</i>	<i>Tadarida teniotis</i>
<i>Galemys pyrenaicus</i>	<i>Mustela erminea</i>	<i>Ovies aries</i>	<i>Talpa europaea</i>
<i>Genetta genetta</i>	<i>Mustela lutreola</i>	<i>Pipistrellus kuhlii</i>	<i>Talpa occidentalis</i>
<i>Glis glis</i>	<i>Mustela nivalis</i>	<i>Pipistrellus nathusii</i>	<i>Ursus arctos</i>
<i>Herpestes ichneumon</i>	<i>Mustela putorius</i>	<i>Pipistrellus pipistrellu</i>	<i>Vulpes vulpes</i>

**Table S3.1. (cont.).**

Species of breeding birds			
<i>Accipiter gentilis</i>	<i>Aythya ferina</i>	<i>Cisticola juncidis</i>	<i>Emberiza hortulana</i>
<i>Accipiter nisus</i>	<i>Aythya fuligula</i>	<i>Clamator glandarius</i>	<i>Emberiza schoeniclus</i>
<i>Acrocephalus arundinaceus</i>	<i>Bubo bubo</i>	<i>Coccothraustes coccothraustes</i>	<i>Erithacus rubecula</i>
<i>Acrocephalus scirpaceus</i>	<i>Bubulcus ibis</i>	<i>Columba domestica</i>	<i>Falco naumanni</i>
<i>Actitis hypoleucos</i>	<i>Burhinus oediconemus</i>	<i>Columba livia/domestica</i>	<i>Falco peregrinus</i>
<i>Aegithalos caudatus</i>	<i>Buteo buteo</i>	<i>Columba oenas</i>	<i>Falco subbuteo</i>
<i>Alauda arvensis</i>	<i>Calandrella brachydactyla</i>	<i>Columba palumbus</i>	<i>Falco tinnunculus</i>
<i>Alcedo atthis</i>	<i>Caprimulgus europaeus</i>	<i>Coracias garrulus</i>	<i>Ficedula hypoleuca</i>
<i>Alectoris rufa</i>	<i>Carduelis cannabina</i>	<i>Corvus corax</i>	<i>Fringilla coelebs</i>
<i>Anas acuta</i>	<i>Carduelis carduelis</i>	<i>Corvus corone</i>	<i>Fulica atra</i>
<i>Anas clypeata</i>	<i>Carduelis chloris</i>	<i>Corvus frugilegus</i>	<i>Galerida cristata</i>
<i>Anas crecca</i>	<i>Carduelis spinus</i>	<i>Corvus monedula</i>	<i>Galerida theklae</i>
<i>Anas platyrhynchos</i>	<i>Cecropis daurica</i>	<i>Coturnix coturnix</i>	<i>Gallinula chloropus</i>
<i>Anas strepera</i>	<i>Certhia brachydactyla</i>	<i>Cuculus canorus</i>	<i>Garrulus glandarius</i>
<i>Anthus campestris</i>	<i>Certhia familiaris</i>	<i>Delichon urbicum</i>	<i>Gyps fulvus</i>
<i>Anthus pratensis</i>	<i>Cettia cetti</i>	<i>Dendrocopos major</i>	<i>Haematopus ostralegus</i>
<i>Anthus spinoletta</i>	<i>Charadrius alexandrinus</i>	<i>Dendrocopos medius</i>	<i>Hieraaetus fasciatus</i>
<i>Anthus trivialis</i>	<i>Charadrius dubius</i>	<i>Dendrocopos minor</i>	<i>Hieraaetus pennatus</i>
<i>Apus apus</i>	<i>Chersophilus duponti</i>	<i>Dryocopus martius</i>	<i>Hippolais polyglotta</i>
<i>Apus melba</i>	<i>Ciconia ciconia</i>	<i>Egretta garzetta</i>	<i>Hirundo rustica</i>
<i>Aquila chrysaetos</i>	<i>Cinclus cinclus</i>	<i>Elanus caeruleus</i>	<i>Hydrobates pelagicus</i>
<i>Ardea cinerea</i>	<i>Circaetus gallicus</i>	<i>Emberiza calandra</i>	<i>Ixobrychus minutus</i>
<i>Asio flammeus</i>	<i>Circus aeruginosus</i>	<i>Emberiza cia</i>	<i>Jynx torquilla</i>
<i>Asio otus</i>	<i>Circus cyaneus</i>	<i>Emberiza cirius</i>	<i>Lanius collurio</i>
<i>Athene noctua</i>	<i>Circus pygargus</i>	<i>Emberiza citrinella</i>	<i>Lanius excubitor</i>
<i>Accipiter gentilis</i>	<i>Aythya ferina</i>	<i>Cisticola juncidis</i>	<i>Emberiza hortulana</i>
<i>Accipiter nisus</i>	<i>Aythya fuligula</i>	<i>Clamator glandarius</i>	<i>Emberiza schoeniclus</i>

**Table S3.1. (cont.).**

Species of breeding birds			
<i>Lanius senator</i>	<i>Larus fuscus</i>	<i>Otis tarda</i>	<i>Podiceps cristatus</i>
<i>Larus fuscus</i>	<i>Otis tarda</i>	<i>Otus scops</i>	<i>Podiceps nigricollis</i>
<i>Larus michahellis</i>	<i>Otus scops</i>	<i>Podiceps cristatus</i>	<i>Strix aluco</i>
<i>Locustella naevia</i>	<i>Parus ater</i>	<i>Podiceps nigricollis</i>	<i>Sturnus unicolor</i>
<i>Loxia curvirostra</i>	<i>Parus caeruleus</i>	<i>Porzana porzana</i>	<i>Sturnus vulgaris</i>
<i>Lullula arborea</i>	<i>Parus cristatus</i>	<i>Porzana pusilla</i>	<i>Sylvia atricapilla</i>
<i>Luscinia megarhynchos</i>	<i>Parus major</i>	<i>Prunella collaris</i>	<i>Sylvia borin</i>
<i>Luscinia svecica</i>	<i>Parus palustris</i>	<i>Prunella modularis</i>	<i>Sylvia cantillans</i>
<i>Melanocorypha calandra</i>	<i>Passer domesticus</i>	<i>Pterocles orientalis</i>	<i>Sylvia communis</i>
<i>Merops apiaster</i>	<i>Passer hispaniolensis</i>	<i>Ptyonoprogne rupestris</i>	<i>Sylvia conspicillata</i>
<i>Milvus migrans</i>	<i>Passer montanus</i>	<i>Pyrrhocorax graculus</i>	<i>Sylvia hortensis</i>
<i>Milvus milvus</i>	<i>Perdix perdix</i>	<i>Pyrrhocorax pyrrhocorax</i>	<i>Sylvia melanocephala</i>
<i>Monticola saxatilis</i>	<i>Pernis apivorus</i>	<i>Pyrrhula pyrrhula</i>	<i>Sylvia undata</i>
<i>Monticola solitarius</i>	<i>Petronia petronia</i>	<i>Rallus aquaticus</i>	<i>Tachybaptus ruficollis</i>
<i>Montifringilla nivalis</i>	<i>Phalacrocorax aristotelis</i>	<i>Regulus ignicapilla</i>	<i>Tetrao urogallus</i>
<i>Motacilla alba</i>	<i>Phalacrocorax carbo</i>	<i>Regulus regulus</i>	<i>Tetrax tetrax</i>
<i>Motacilla cinerea</i>	<i>Phasianus colchicus</i>	<i>Remiz pendulinus</i>	<i>Tichodroma muraria</i>
<i>Motacilla flava</i>	<i>Phoenicurus ochruros</i>	<i>Riparia riparia</i>	<i>Tringa totanus</i>
			<i>Troglodytes</i>
<i>Muscicapa striata</i>	<i>Phoenicurus phoenicurus</i>	<i>Saxicola rubetra</i>	<i>troglodytes</i>
<i>Neophron percnopterus</i>	<i>Phylloscopus bonelli</i>	<i>Saxicola torquatus</i>	<i>Turdus merula</i>
<i>Numenius arquata</i>	<i>Phylloscopus collybita/ibericus</i>	<i>Scolopax rusticola</i>	<i>Turdus philomelos</i>
<i>Nycticorax nycticorax</i>	<i>Phylloscopus ibericus</i>	<i>Serinus citrinella</i>	<i>Turdus torquatus</i>
<i>Oenanthe hispanica</i>	<i>Phylloscopus sibilatrix</i>	<i>Serinus serinus</i>	<i>Turdus viscivorus</i>
<i>Oenanthe oenanthe</i>	<i>Phylloscopus trochilus</i>	<i>Sitta europaea</i>	<i>Tyto alba</i>
<i>Oriolus oriolus</i>	<i>Pica pica</i>	<i>Streptopelia decaocto</i>	<i>Upupa epops</i>
<i>Lanius senator</i>	<i>Picus viridis</i>	<i>Streptopelia turtur</i>	<i>Vanellus vanellus</i>

**Table S3.1. (cont.).**

Species of reptiles			
<i>Anguis fragilis</i>	<i>Eretmochelys imbricata</i>	<i>Mauremys leprosa</i>	<i>Psammodromus hispanicus</i>
<i>Chalcides bedriagai</i>	<i>Iberolacerta monticola</i>	<i>Natrix maura</i>	<i>Rhinechis scalaris</i>
<i>Chalcides striatus</i>	<i>Lacerta bilineata</i>	<i>Natrix natrix</i>	<i>Tarentola mauritanica</i>
<i>Coronella austriaca</i>	<i>Lacerta lepida</i>	<i>Podarcis bocagei</i>	<i>Trachemys scripta</i>
<i>Coronella girondica</i>	<i>Lacerta schreiberi</i>	<i>Podarcis hispanica</i>	<i>Vipera aspis</i>
<i>Dermochelys coriacea</i>	<i>Lacerta vivipara</i>	<i>Podarcis muralis</i>	<i>Vipera latasti</i>
<i>Emys orbicularis</i>	<i>Malpolon monspessulanus</i>	<i>Psammodromus algirus</i>	<i>Vipera seoanei</i>
Species of amphibians			
<i>Alytes obstetricans</i>	<i>Discoglossus jeanneae</i>	<i>Pelobates cultripes</i>	<i>Rana perezi</i>
<i>Bufo bufo</i>	<i>Hyla arborea</i>	<i>Pelodytes punctatus</i>	<i>Rana temporaria</i>
<i>Bufo calamita</i>	<i>Lissotriton boscai</i>	<i>Pleurodeles waltl</i>	<i>Salamandra salamandra</i>
<i>Chioglossa lusitanica</i>	<i>Lissotriton helveticus</i>	<i>Rana dalmatina</i>	<i>Triturus marmoratus</i>
<i>Discoglossus galganoi</i>	<i>Mesotriton alpestris</i>	<i>Rana iberica</i>	

**Table S3.2.** Environmental variables used as predictors. The average value and/or the standard deviation value (*std*) of the environmental variables was extracted at each UTM 10 km x 10 km sampling unit.

Family	Code	Variables description	Source
	PRECSUM	Mean precipitation in summer (mm)	Ninyerola's Climatic Atlas (Ninyerola <i>et al.</i> , 2005) at 200 m spatial resolution
	PRECWIN	Mean precipitation in winter (mm)	
	TMWIN	Mean temperature in winter (°C)	
	TMSUM	Mean temperature in summer (°C)	
	TMAXWIN	Maximum temperature in winter (°C)	
	TMAXSUM	Maximum temperature in summer (°C)	
	TMINWIN	Minimum temperature in winter (°C)	
	TMINSUM	Minimum temperature in summer (°C)	
	stdPRECSUM	Standard deviation of mean precipitation in summer (mm)	
	stdPRECWIN	Standard deviation of mean precipitation in winter (mm)	
	stdTMWIN	Standard deviation of mean temperature in winter (°C)	
	stdTMSUM	Standard deviation of mean temperature in summer (°C)	
	stdTMAXWIN	Standard deviation of maximum temperature in winter (°C)	
	stdTMAXSUM	Standard deviation of maximum temperature in summer (°C)	
	stdTMINWIN	Standard deviation of minimum temperature in winter (°C)	
	stdTMINSUM	Standard deviation of minimum temperature in summer (°C)	
Topography	DEM	Elevation (m)	
	SLO	Slope (%)	
	SOLR	Solar radiation (*10 <sup>6</sup> W/h)	
	stdDEM	Standard deviation of elevation (m)	
	stdSLO	Standard deviation of slope (%)	
	stdSOLR	Standard deviation of solar radiation (*10 <sup>6</sup> W/h)	

**Table S3.2. (cont.).**

Family	Code	Description of the variable	Source
Land cover	INFRA	Frequency of class human infrastructures	CORINE Land Cover 2006 at 30 m spatial resolution ( <a href="http://www.eea.europa.eu/publications/COR0-landcover">http://www.eea.europa.eu/publications/COR0-landcover</a> )
	MIN	Frequency of class mineral extraction sites	
	HERC	Frequency of class herbaceous croplands	
	WOOC	Frequency of class woody croplands	
	PAS	Frequency of class pasturelands	
	FOR	Frequency of class forest	
	TWOOD	Frequency of class transitional woodland-shrublands	
	SCRUB	Frequency of class scrub and sclerophyllous-herbaceous formations	
	SPAR	Frequency of class sparsely vegetated areas	
	BARE	Frequency of class bare areas	
	WET	Frequency of class wetlands	
WAT	Frequency of class water		
Physiological state of vegetation	NDVI	Annual mean NDVI index (no units, ranging from -1 to +1)	NDVI from NOAA-AVHRR at 1km of spatial resolution
Landscape heterogeneity	LANDHET	Landscape heterogeneity measured as the number of landscape classes (considering the total number of pixels in each sampling unit)	NDVI from NOAA-AVHRR at 1km of spatial resolution
Human influence	UD	Distance to the nearest settlement measured as Euclidian distance (m)	Vector layers at 1:200000 spatial resolution ( <a href="http://www.ign.es">www.ign.es</a> )
	stdUD	Standard deviation of the distance to the nearest settlement (m)	
	SURFPA	Surface of sampling unit covered by protected areas (km <sup>2</sup> )	
	PREPA	Presence/absence of pixels owing to protected areas	
Accessibility	LROAD	Total length of roads and paths (km)	Vector layers of roads at 1:200000 spatial resolution
	ACOST	Accessibility cost at 90 m spatial resolution elaborated by integrating data of slope, distance to settlements and distance to roads and paths.	Digital Elevation Models (DEM) at 90m spatial resolution and vector layers of roads and settlements at 1:200000 spatial resolution ( <a href="http://www.ign.es">www.ign.es</a> )





*Picture's author: Pablo Rodríguez*

## **Chapter 4**

# **Impact of land cover change on ecosystem service supply in mountain systems<sup>4</sup>**

<sup>4</sup> The content of this chapter has been submitted for publication consideration to *Ecosystem Services*.

García-Llamas, P., Geijzendorffer, I.R., García-Nieto, A.P., Calvo, L., Suárez-Seoane, S., & Cramer, W. (2017) Impact of land cover change on ecosystem service supply in mountain systems.

## Abstract

Land abandonment and the subsequent loss of traditional farming practices are thought to control land cover dynamics at different scales and, hence, ecosystem services' supply in traditionally managed mountain landscapes. We aim to evaluate the impact of the land cover changes occurred in the Cantabrian Mountains (NW Spain) during the last two decades (period 1990-2012) on the potential supply capacity of ecosystem services (regulating, provisioning and cultural), at both regional and local scale. We also target to compare trends in the use of ecosystem services with estimates of their potential supply at local scale. Net overall land cover changes for the whole study period, as well as short-time fluctuations (1990-2000, 2000-2006, 2006-2012), were estimated by using CORINE Land Cover database. Patterns of ecosystem service potential supply were assessed by applying an ecosystem service supply capacity matrix and trends in their actual use were analyzed using records provided by the regional administration. At both scales, the most prevalent changes in land cover and ecosystem service supply were detected over 1990-2000. Main trajectories of land cover change encompassed woody vegetation spread in semi-natural open systems due to land abandonment in marginal zones and agricultural expansion in the most suitable areas. The capacity of landscape to provide ecosystem services improved over the whole period at both scales. Woody vegetation expansion mainly benefited the potential supply of regulating and provisioning services. Conversely, it negatively affected the potential supply of livestock and cultural services associated to traditionally managed landscapes. Changes in the potential supply of ecosystems services matched trends in ecosystem service use, thus suggesting enhancement of particular uses associated to changes in land cover. The results of this study could help to develop future scenarios to tackle upcoming challenges in ecosystem service supply.

**Key words:** CORINE land cover, provision services, capacity matrix, transhumance, cultural services, regulation services, semi-natural landscapes.

## 1. Introduction

Mountains systems are key centers of ecological and cultural diversity. They cover 24% of the Earth's land surface and hold 12% of the world's population, providing half of humanity with vital goods and services. They also support 25% of terrestrial biodiversity, with almost half of the world's biodiversity hot spots (Körner *et al.*, 2005). However, mountains are highly vulnerable to socio-economic and environmental changes (Balthazar *et al.*, 2015). In European mountains, the landscape has been shaped since historical times through human interventions associated with low intensive agro-silvopastoral activities (Lasanta *et al.*, 2006; Daugstad *et al.*, 2014). Thereby, the combination of traditional farming practices, livestock grazing and forest management has resulted in highly heterogeneous and spatially structured cultural landscape mosaics (Farina, 2000). During the 20th century, the mountains of southern Europe have experienced a progressive socio-economic marginalization process associated to rural depopulation, land abandonment and a decrease in extensive livestock rearing (Conti & Fagarazzi, 2005; Gracia *et al.*, 2011). A particularly relevant change has been the decrease of the transhumance practices, associated to seasonal movements of sheep flocks to exploit the natural vegetation growth in summer mountain pastures (Vicente-Serrano *et al.*, 2004; Morán-Ordóñez, 2012). As a consequence of these factors, the landscape has suffered major transformations driving to the expansion of forests and shrublands, in the most marginal areas, and the intensification of agricultural practices, in the most fertile and accessible lands (Sidiropoulou *et al.*, 2015; Álvarez-Martínez *et al.*, 2016).

Managed mountainous landscapes have traditionally been an important source of ecosystem services (Zoderer *et al.*, 2016). In fact, they provide many ecological, socio-cultural and economic benefits for society that include: regulating services, such as water cycling regulation or control and mitigation of extreme climatic events; provisioning services, such as grazing, wood-fuel or medicinal plants; and cultural services, such as traditional knowledge or cultural identity (Körner *et al.*, 2005; Foggin, 2016). Over time, ecosystem processes that support ecosystem services may be affected by land use changes and the associated land cover changes (Reyers *et al.*, 2009; Dick *et al.*, 2016), ultimately impacting on benefits for

society and human well-being (Rescia *et al.*, 2008; Sonter *et al.*, 2017). Each particular land cover change might drive to a variation in the potential supply (i.e. the hypothetical maximum yield of a service that can be provided by natural components of the ecosystem without stakeholders interventions; Geijzenborffer *et al.*, 2015) of multiple ecosystem services (Vallet *et al.*, 2016). However, it is important to consider that not only the supply of ecosystem services changes over time, but also their value and use (i.e. the quantity and type of an ecosystem service which is consumed or utilized by stakeholders; Geijzenborffer *et al.*, 2015) for society. For instance, ecosystem services of high relevance for past traditional lifestyle, as provisioning services like wool or fuels, have become marginal nowadays; while others less appreciated in the past, such as cultural services like aesthetic value or recreation, are in increasing value for current society (Morán-Ordóñez *et al.*, 2013a; de Lima *et al.*, 2016).

The implications of land cover change for the capacity of mountain systems to provide ecosystem services remains, however, a controversial issue due to the spatio-temporal variability of its impact on ecosystem services (de Lima *et al.*, 2016; Locatelli *et al.*, 2017) and to the existence of trade-offs among ecosystems services (Pereira *et al.*, 2005). Thereby, enhanced knowledge of spatial and temporal patterns of land cover change is required to assess mountain landscape dynamics in relation to multiple ecosystem services (regulation, provisioning, cultural) (Mottet *et al.*, 2006). Information on these temporal and spatial patterns can help land managers to develop strategies and policies to improve the inclusion of novel socio-ecological connections (MacDonald *et al.*, 2000) and ensure the future continuity of benefits to human well-being (Cabel & Oelofse, 2012; Dick *et al.*, 2016).

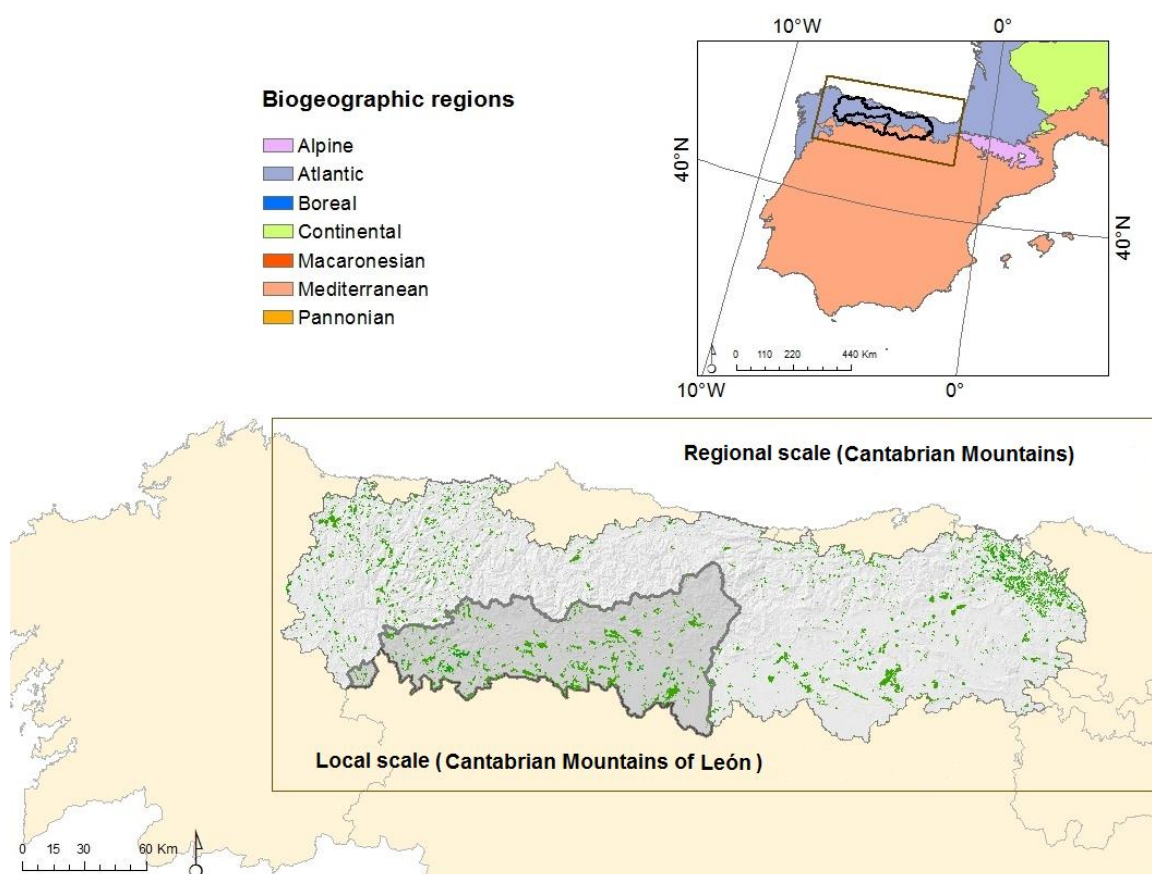
The objective of this paper was to analyze the impact of land cover changes on the potential supply and use of ecosystem services in mountain landscapes, using as case study the Cantabrian Mountains (NW of Spain). We specifically aimed to: (i) detect the main trajectories of land cover change occurred during the last two decades (period 1990-2012), considering short-time fluctuations (1990-2000, 2000-2006, 2006-2012), and estimate the potential impact on the supply of ecosystem services (regulating, provisioning and cultural services), at both

regional and local scale; (ii) analyze trends in the use of ecosystem services and compare them with potential supply estimates, at local scale. Finally, we provided recommendations for the long-term supply of ecosystem services in traditional managed mountain landscapes.

## 2. Study area: Definition of two scales of analysis

The study was conducted in the Cantabrian Mountains (Northwest of Spain) where two spatial scales of analysis were considered: (i) A regional scale, that includes the whole area of the Cantabrian Mountains, covering 31494 km<sup>2</sup> and (ii) a local scale, that includes the Cantabrian Mountains of the León province (one of the nine provinces that encompass this mountain system), covering 7151 km<sup>2</sup> (23% of the Cantabrian Mountains' surface) (Figure 4.1).

The Cantabrian Mountains are located at the transition between the Eurosiberian and Mediterranean biogeographic regions (Rivas-Martínez *et al.*, 1987). Annual rainfall varies from 700 to 2200 mm and mean annual temperature from -2.5 to 15 °C. Altitude ranges from the sea level up to 2650 m.a.s.l. In this mountain range, the main land covers are crop fields and grazed meadows at the valley bottoms, and heathlands, shrublands and deciduous forests, dominated by beech (*Fagus sylvatica*), birch (*Betula spp.*) and different oak species (*Quercus petraea* and *Q. robur* on northern slopes, *Q. pyrenaica* and *Q. ilex* subsp. *rotundifolia* on southern slopes), at the uplands (Morán-Ordóñez, 2012). These woody habitats can spatially intersperse with grazing systems (i.e. open semi-natural habitats mainly comprising pastures, grasslands or open scrublands with very few or no trees) at middle slope levels (Rescia *et al.*, 2008). The top of the mountains are dominated by rocky formations and natural grasslands. Furthermore, plantations of pines (*Pinus pinaster*, *P. radiata*) and eucalyptus (*Eucalyptus globulus*) cover medium-to-low slopes (García-Llamas *et al.*, 2016).



**Figure 4.1.** Location of the study area in NW Spain and analytical scales: Regional (Cantabrian Mountains) and local (Cantabrian Mountains of León). Information on biogeographic regions was obtained from the Spanish Ministry of Agriculture Food and Environment (<http://www.magrama.gob.es/>). Spots corresponding to land cover changes during period 1990-2012 are in green, and were obtained from the CORINE Land Cover change layers (<http://dataservice.eea.europa.eu>).

The Cantabrian Mountains of León are located on the southern slope of this mountain system. Annual rainfall ranges from 700 to 1800 mm and mean annual temperature are between -2.5 and 12.5 °C. The altitudinal gradient is 391-2650 m.a.s.l. Land cover pattern is similar to that described for the whole Cantabrian Mountains, with croplands and pasturelands at the valley bottoms and heathlands and shrublands of *Cytisus multiflorus*, *C. scoparius*, *Calluna vulgaris*, *Erica australis*, *Genista obtusiramea*, *G. florida* subsp. *polygaliphylla*, *G. hispanica* subsp. *occidentalis* and *Vaccinium myrtillus* at uplands. Forest formations vary with altitude and appearance. Beech forests dominate at low altitude in northern slopes,

with marked xericity and warm temperature, while they also cover southern humid slopes at higher altitudes. Forest dominated by Oak species (*Q. pyrenaica* and *Q. ilex* subsp. *rotundifolia*) are common in southern slopes at low altitudes, whereas the highest altitudes are covered by birch groves (*Betula celtiberica*). The top of the mountains are dominated by rocky formations and natural grasslands.

The main driving forces historically shaping the landscape across the Cantabrian Mountains have been extensive livestock (sheep, cattle and horses), uneven topography and diverse climatic conditions (Morán-Ordóñez, 2012). As a result of interactions among these factors, traditionally managed landscapes of high cultural value, consisting of a mosaic of open habitats, forests and shrubs, have been originated. Within the study area, transhumance sheep activity has played a major role as a driver of landscape change in León mountains (MAGRAMA, 2013), creating cultural landscapes consisting of an open heath-pasture mosaic predominantly associated to pastoral activity (Morán-Ordóñez *et al.*, 2013a). These particular cultural landscapes, associated to the transhumance activity, gave ground to selecting León province mountains as our local scale approximation. Nowadays, although livestock rearing (mainly cattle and horses) continues to represent an important economic resource, other activities, such as hunting (Morán-Ordóñez, 2012), forestry (Delgado-Viñas, 2015) or tourism (Álvarez & Pérez, 2016) have increased their importance. The loss of profitability and competitiveness of traditional agro-silvopastoral systems in the last decades, along with rural depopulation (overall rates of 16% and 66.69% between 1990 and 2012 in the whole Cantabrian Mountains and the Cantabrian Mountains of León province respectively; Annex IV, Table S4.1) have resulted in a loss of traditional management and a modification of landscape patterns and their related ecosystem services (Morán-Ordóñez *et al.*, 2013a).

### 3. Methods

#### 3.1 Temporal patterns of land cover change

We identified land cover changes that have occurred in the Cantabrian Mountains during 1990-2012, at both regional and local scale, on the basis of the change layers available in the CORINE land cover inventory (CLC) (<http://dataservice.eea.europa.eu>). This database provides a unique and consistent land cover dataset for Europe, comprising 44 land cover classes grouped in three hierarchical levels, of which 37 are present in our study area (Annex IV, Table S4.2) (Bossard *et al.*, 2000). This database was first available for 1990 and was subsequently updated in 2000, 2006 and 2012. CLC change data reveal changes in land cover with a minimum mapping unit of 5 ha (Nunes de Lima, 2005). Despite possible drawbacks to the CLC database, such as the existence of classification errors and uncertainties (García-Llamas *et al.*, 2016), its accessibility, pan-European comparability and availability at different time spans offer considerable advantages for studying land cover changes (Kroll *et al.*, 2012).

Land cover changes were reported as the net overall change for the whole study period (1990-2012) and also for the three sub-periods 1990-2000, 2000-2006 and 2006-2012 (corresponding with the availability of CLC data) to account for short-term temporal fluctuations. Land cover changes were estimated as the variation in the area ( $\Delta A$ ) occupied by each CLC class for a given time period (Eq. 1) and expressed in ‰ in relation to the study area.

$$\Delta A_i = \frac{A_{ij} - A_{i,j+1}}{SA} * 10000 \quad \text{Eq. 1}$$

Where  $A$  is the area in ha of each CLC class  $i$  and  $j$  are the periods of study and  $SA$  is the surface of the study area.

Additionally, we applied transition matrixes of change to identify the main land cover transitions during land cover changes.



### **3.2 Trends of change in the potential supply of ecosystem services**

The impact of land cover changes on ecosystem service supply was estimated independently at both regional and local scale through a semi-quantitative approach, namely the “ecosystem services capacity matrix method”. This method was originally developed by Burkhard *et al.* (2009) for a German region and further adapted by Stoll *et al.* (2015) for the whole of Europe. From here on, we will refer to this method as the “Stoll matrix”. This matrix provides estimates of the capacity of individual CLC classes to supply specific ecosystem services for the whole of Europe. The estimates in the matrix are based on averages of scores assigned by expert knowledge on a scale from “0” (no capacity to provide a particular ecosystem service) to “5” (very high capacity to provide a particular ecosystem service). Although the method has limitations, such as various degrees of generalization and poor capacity to capture spatial variability (Jacobs *et al.*, 2015), it constitutes a timely and cost-saving tool to evaluate the potential of ecosystems to supply services in changing environments (Balthazar *et al.*, 2015). We have estimated the potential supply capacity (PSC) of 31 ecosystem services (regulating, provisioning and cultural services) for the 37 CLC classes presented in the study area. PSC values were normalized between 0 and 1. Subsequently, the variation in the potential supply capacity ( $\Delta PSC$ ) for each ecosystem service, time period and analytical scale was computed as follows:

$$\Delta PSC_i = sPSC_{ij} * \Delta A_j \quad (\text{Eq.1})$$

where  $sPSC$  is the normalized potential supply capacity value and  $\Delta A$  represents the variation in the area occupied by each land cover at each time period.  $i$  corresponds to each ecosystem service and  $j$  to each CLC class.

### **3.3 Trends in the use of ecosystem services**

We compared temporal trends in the actual use of ecosystem services with trends in their potential supply at local scale, on the basis of visual analyses. The use of ecosystem services was estimated on the basis of field data provided by both the regional administration and Rodríguez (2004) for 1990, 2000, 2006 and 2012

(or nearest years) for a set of provisioning (timber, wild food and livestock) and cultural (recreation/tourism) services. This set includes services highly valued by traditional society, but also others of increasing value nowadays (Herruzo & Martinez-Jauregui, 2013; Morán-Ordóñez *et al.*, 2013a; Schulp *et al.*, 2014; Delgado-Viñas, 2015). Indicators of actual use of ecosystem services were selected on the basis of the available data (Table 4.1). For timber, we used information on wood harvested in public forests. The indicator of wild food was built from hunting data collected in game reserves. Additionally, we also included information on the actual potential supply of this service, which was derived from census of game species (*Capreolus capreolus*, *Cervus elaphus* and *Rupicapra rupicapra*). For livestock, we used information on the number of cows and transhumant sheep, which were transformed into livestock units (LU; 1 sheep = 1LU, 1 cow = 5LU; Olea & Mateo-Tomás, 2009). For recreation/tourism, we employed data on visitor flow to natural parks. We also included data on recreation/tourism actual supply (i.e. the current amount of an ecosystem service that is provided by the combination of the potential supply and the effect of operations by stakeholders in a particular area and within a given time period Geijzendorffer *et al.*, 2015) measured as the amount of available rural accommodation.

**Table 4.1.** Indicators of ecosystem service use, actual potential supply and actual supply at local scale for the Cantabrian Mountains of León.

Ecosystem service	Definition	Indicator	Data source and years	
Provisioning	Timber	Wood production	Use: Tonnes of wood/ha of public utility forests	Junta de Castilla y León; years from 1992 to 2012
	Wild food	Harvest of mushrooms, berries, animal hunting and fish catch	Use: number of hunted animals in game reserves/1000 ha Actual potential supply: density of hunting species in game reserves (number of animals/1000 ha)	Junta de Castilla y León; years 2000, 2006 and 2012
	Livestock	Production and utilization of domestic animals	Use: Number of livestock units per hectare of pastureland	Junta de Castilla y León and (Rodríguez, 2004); sheep: years 1990, 2003 and 2012, cows: years 1990 and 2012
Cultural	Recreation /tourism	Recreational activities including tourism associated with local environment or landscape	Use: Number of tourists visiting natural parks Actual supply: Amount of rural accommodation	Junta de Castilla y León; Amount of rural accommodation: from 2000 to 2012; number of tourists visiting national parks: from 1990 to 2009

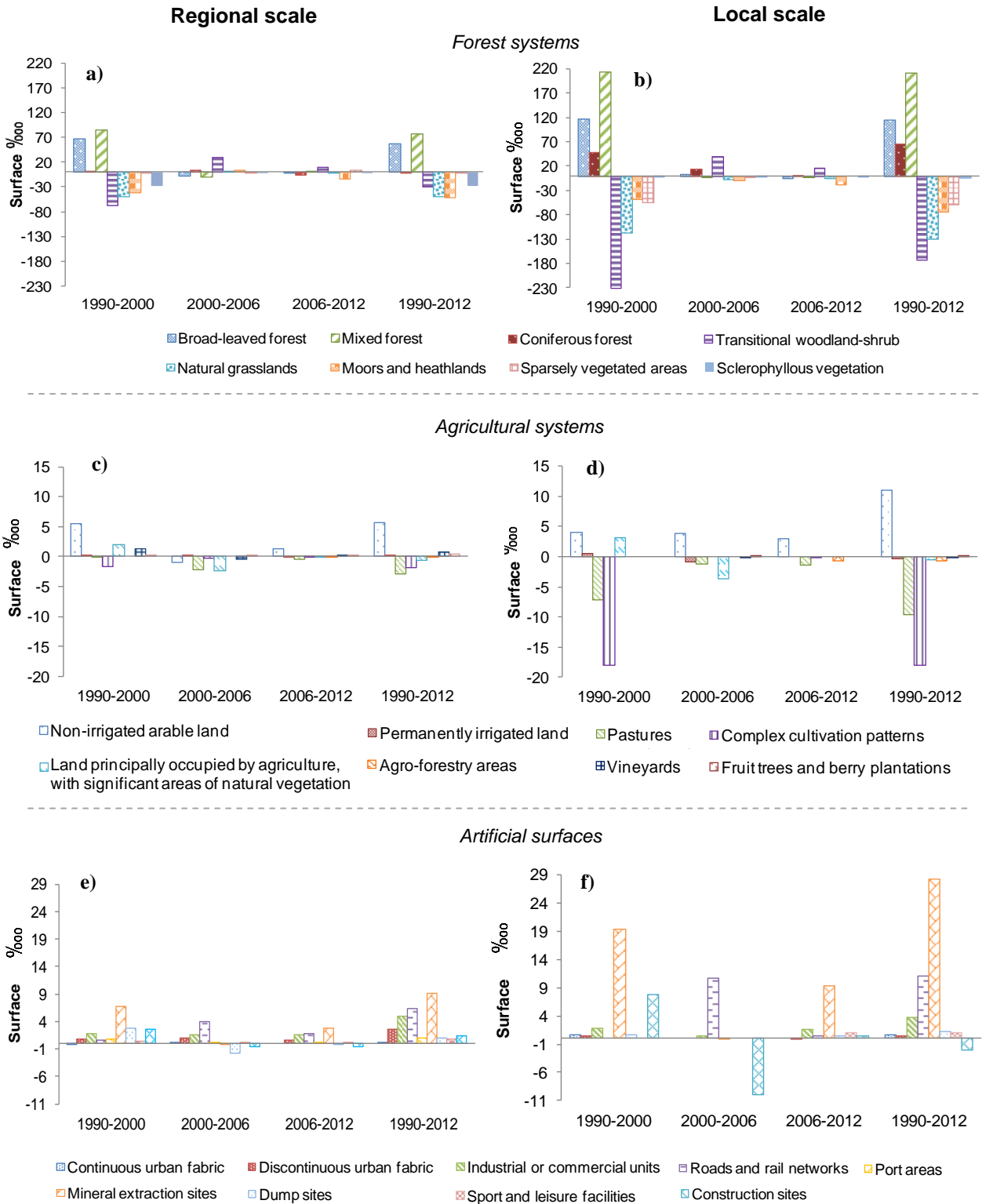
## 4. Results

### 4.1 Temporal patterns of land cover change

Land cover dynamics followed similar trends at both regional and local scale. However, changes were particularly pronounced at local scale (Figure 4.2). The most prevailing change was the expansion of woody vegetation, particularly during the sub-period 1990-2000 with few changes beyond 2000, which was mainly associated to a net increase in forests and a loss of open habitats (Figure 4.2 cases a, b). Patches of natural grasslands, moors-heathlands and sclerophyllous vegetation mostly turned into forests or transitional woodland-shrubs and those of transitional woodlands-shrubs into forests (Table 4.2; Annex IV, Table S4.3).

To a lesser extent, the study period 1990-2012 was also characterized by an expansion and geographic aggregation of agricultural lands in the most suitable areas. This change was linked to a noticeable increase in non-irrigated arable lands at the expense of small-holding agricultural lands, particularly in natural grasslands and areas of complex cultivation patterns. Additionally, during the sub-period 1990-2000, areas of complex cultivation patterns also turned into agricultural lands with natural vegetation. Small-holding agriculture also decreased due to its conversion (mainly of pasturelands) into forests, in marginal areas, and into artificial surfaces (Figure 4.2 cases c, d; Table 4.2 and Annex IV, Table S4.3). At regional scale, agricultural expansion and aggregation occurred particularly during 1990-2000 and, to a lesser extent, throughout 2006-2012. Conversely, agricultural decrease, due to land abandonment and urban expansion, mainly encompassed the period 2000-2006 (Figure 4.2, case c). At local scale, the increase in non-irrigated arable lands was constant over time, but agricultural land abandonment peaked between 1990 and 2000 (Figure 4.2 case d).

The expansion of artificial surfaces (i.e. discontinuous urban fabrics, industrial or commercial units, roads and rail networks, mineral extraction or construction sites) was a general trend in the whole area of the Cantabrian Mountains throughout all the reporting periods at both scales (Figure 4.2 cases e, f), mainly in forest areas and moors and heathlands (Table 4.2 and Annex IV, Table S4.3).



**Figure 4.2.** Land cover changes for the global period 1990-2012 and the sub-periods 1990-2000, 2000-2006 and 2006-2012 at both regional and local scale, representing: a), b) forest systems; c, d) agricultural systems; e, f) artificial surfaces. Source: CORINE Land Cover database.

**Table 4.2.** Transition matrix showing changes in land cover (in ‰) from 1990 (rows) to 2000 (columns) at regional scale (Cantabrian Mountains). The largest changes for each land cover type are in bold. Only 1990-2000 is shown as the most representative period.

		Land cover 2000																	
		ArtiS	NI	Pirriga	V	Fruit	Past	CCP	LPA	Forest	NG	Twood	Moor	SclV	SparV	Rock	Burnt	WatS	Total area
Land cover 1990	ArtiS						0.51	0.55		0.15	0.14	<b>1.63</b>	0.74	0.06				0.18	3.95
	NI	<b>0.79</b>		0.50			0.11	0.02		0.22		0.30		0.55					2.49
	Pirrigate	<b>0.12</b>								0.02			0.04			0.08			0.26
	Past	<b>2.33</b>						1.34	0.11	<b>2.04</b>		1.27					0.10	0.44	7.63
	CCP	1.80	<b>1.83</b>							<b>2.60</b>	0.61	0.17	0.02					1.71	8.11
	LPA	1.31	0.80	0.05	1.25		0.06	<b>1.89</b>		<b>1.89</b>	0.05	0.66	0.06	0.06			0.34		8.41
	Forest	3.71	0.33			0.07	0.98	0.99	1.22		0.47	<b>78.06</b>	1.25	0.23	0.03		2.43	0.64	90.40
	NG	2.53	<b>3.67</b>				0.35	1.44	2.61	<b>34.67</b>		<b>6.89</b>		0.36			1.42	1.39	55.43
	Moor	4.70					3.80		1.17	<b>10.70</b>	3.28	<b>15.44</b>			1.16		<b>11.40</b>	2.04	53.70
	SclV	0.18	0.63	0.10				0.05	1.33	<b>12.02</b>	0.11	<b>15.05</b>					1.39		30.88
	Twood	2.36	0.62				1.59	0.21	1.20	<b>181.84</b>	0.59		0.70	2.41			4.74		196.26
	Rock									0.03			0.09						0.13
	SparV	0.46										0.68	<b>2.74</b>				0.61	0.05	4.55
	Burnt							0.01	0.10	1.95		<b>7.32</b>	<b>6.69</b>		0.21				16.28
	WatS	0.67																	
	Total area	19.67	7.89	0.65	1.25	0.07	7.40	6.49	10.39	246.19	4.65	127.57	12.25	3.67	1.39	0.08	22.42		

ArtiS (continuous urban fabric, discontinuous urban fabric, industrial or commercial units, road and rail networks, port areas, mineral extraction sites, dump sites, construction sites, green urban areas, sport and leisure facilities); NI (non-irrigated arable land); Pirrigate (permanently irrigated lands); V (vineyards); Fruit (fruit trees); Past (pasturelands); CCP (complex cultivation patterns); LPA (land principally occupied by agriculture, with significant areas of natural vegetation); Forest (broad leaf forest, mixed forest and coniferous forest); NG (natural grasslands); Moor (moors and heathlands); SclV (sclerophyllous vegetation); Twood (transitional woodlands-shrub); Rock (bare rocks); SparV (sparsely vegetated areas); Burnt (burnt areas); WatS (water bodies, water courses, estuaries, sea

## ***4.2 Trends of change in the potential supply of ecosystem services***

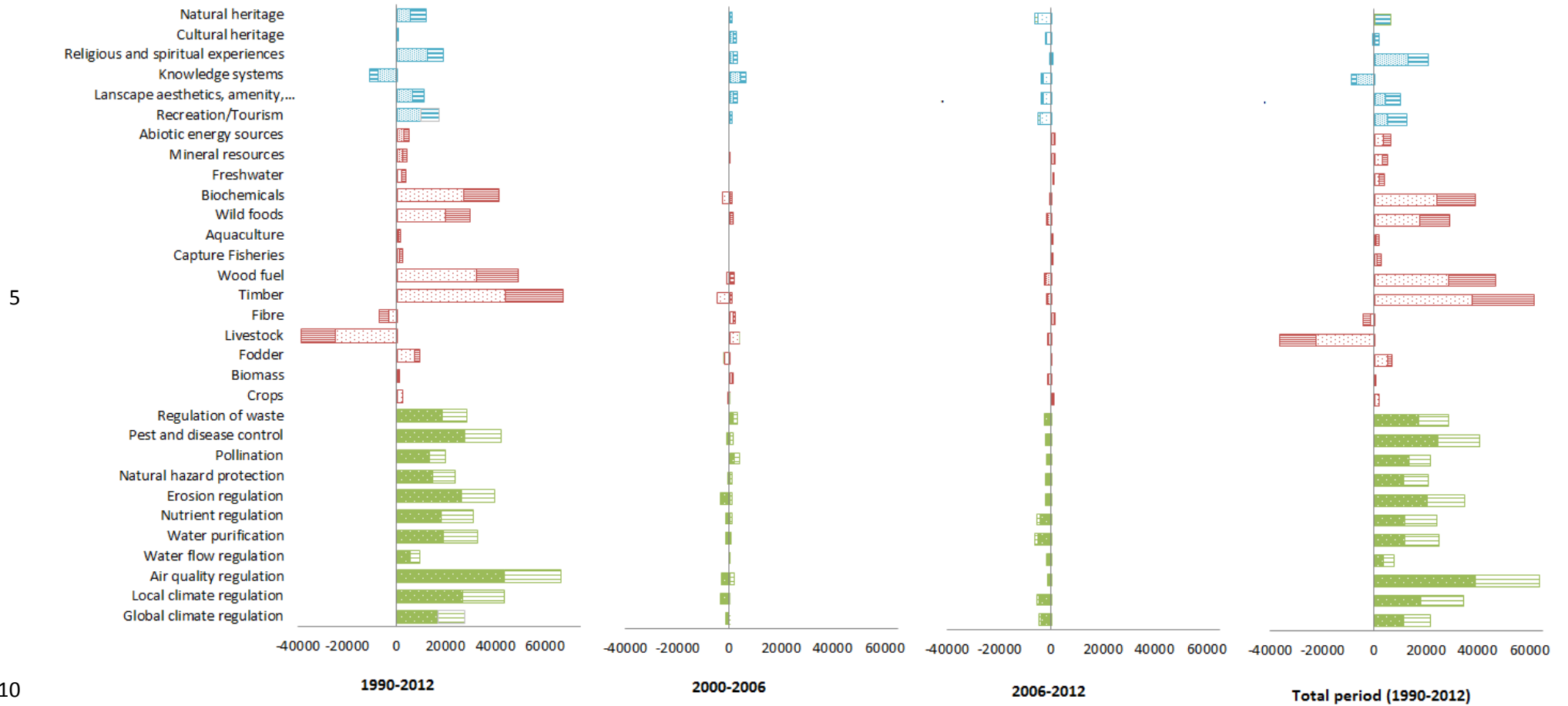
Trends of change in the potential supply of ecosystem service (see Figure 4.3) were similar at both scales, albeit changes were relatively larger at local scale and particularly remarkable for the sub-period 1990-2000. Beyond that moment, only slight changes were detected, which suggests stabilization. We found a net increase in the potential supply of all categories of ecosystem services (regulating, provisioning and cultural) during the whole study period (1990-2012), although some differences should be highlighted. The potential supply of regulating services strongly increased, especially air quality regulation, pest and disease control, erosion regulation and local climate regulation. Similarly, there was a substantial improvement in the potential supply of provisioning services related to the presence of trees or woodland, such as timber, wood fuel, biochemicals and wild food. However, there was a marked reduction in the potential supply of livestock. There were fewer changes in the potential supply of cultural services than for the case of regulating or provisioning ones. The greatest increase was estimated for recreation and tourism, landscape aesthetics and natural heritage, showing only a decrease in service knowledge systems.

## ***4.2 Trends in the use of ecosystem services***

Ecosystem service actual use at local scale showed similar temporal patterns to potential supply estimates (see Table 4.3 and Figure 4.3). We found an increasing trend in the tonnes of timber extracted from public forests from 1990 to 2012, which was analogous to trends in the potential supply of timber. The increasing density of game species in hunting reserves between 1990 and 2012 indicated an increase in the hunting actual potential supply, similar to the increasing trends of estimated wild food potential supply. Currently, the number of hunted animals (hunting use) declined from 2000 onwards. Similarly, the number of livestock units decreased over the whole study period, in line with estimates of livestock potential supply. However, analyzing independently the trends of change associated to different livestock species, we did not find a common pattern, as the number of sheep drastically decreased (70%; from 123380 to 37922 sheep), while

the number of beef cattle increased (65%; from 3569 to 9996 heads of cattle). Furthermore, the use/supply of recreation and tourism services showed an important increase. More than 300 new rural tourism establishments were created in twelve years, tripling from 2000, and the number of visitors to natural parks almost doubled in twenty years. These results were consistent with trends of estimations in tourism/recreation potential supply.





**Figure 4.3.** Changes in the ecosystem service potential supply capacity (cultural: blue, provisioning: pink and regulating cultural services: green) through sub-periods 1990-2000, 2000-2006 and 2006-2012 and all of 1990-2012. Spots refer to the regional scale and stripes to the local one.

**Table 4.3.** Changes in actual use of ecosystem services at local scale, including: timber, hunting, livestock, recreation/tourism, along with changes in potential supply estimates of these services, for the sub-periods 1990-2000, 2000-2006, 2006-2012 and for the whole study period 1990-2012. Information on the actual potential hunting supply and on the actual recreation/tourism supply are also shown. Negative values indicate a decrease.

Ecosystem service	1990-2000	2000-2006	2006-2012	<b>1990-2012</b>
Timber use (Tn/ha public forest)	458	16	-59	415
Potential timber supply	23452.07	817.26	-287.80	23981.53
Hunting use (No. of hunted animals/ 1000 ha)	-	-0.1	-1.27	-1.37
Potential wild food supply	10068.84	1339.66	-134.96	11270.15
Actual potential hunting supply (No. of hunted animals/ 1000 ha)	44.18	-18.98	10.66	35.86
Livestock use (livestock units/ha pastureland)	-	-	-	-1,85
Potential livestock supply	-	-	-	-14090.38
Tourism use (No. of tourists visiting natural parks)	1070000	250000	0	1070000
Potential tourism supply	7387.62	799.93	-287.79	23981.52
Actual recreation/tourism supply		103	93	196

## 5. Discussion

### 5.1 Temporal patterns of land cover change

The temporal analysis of the land cover changes that have occurred in the Cantabrian Mountains revealed landscape homogenization at both regional and local scale, which is consistent with the results of other studies carried out across other European mountains (Conti & Fagarazzi, 2005; Gracia *et al.*, 2011). We have found two main trends of change: (i) A woody vegetation (shrub and forest) expansion and a loss of opened habitats linked to extensification and land abandonment in marginal zones, (ii) to a lesser extent, an expansion and geographic aggregation of agricultural fields in the most suitable areas. These land cover changes have been particularly relevant during the sub-period 1990-2000, which might be attributable to the inclusion of Spain in the European Union

market in 1985 and the subsequent implementation of the Common Agricultural Policy (CAP), as identified in other studies (Martínez-Casasnovas *et al.*, 2010; Bernués *et al.*, 2011; Vidal-Legaz *et al.*, 2013). These policies prompted farming specialization and more productive and competitive agricultural systems, at the expense of small farming holdings and traditional practices (Donald *et al.*, 2002; Casas & Manzano, 2007). Transformations in farming and agricultural production drove to alterations in the equilibrium between low intensive agricultural lands, grazing and woody systems (Mottet *et al.*, 2006; Rescia *et al.*, 2008), typical of traditionally managed mountain landscapes, and favored secondary succession in different ranges, from grazing areas to transitional stands. Likewise, forest plantation subsidies within the CAP also favored the afforestation of abandoned lands (Rey-Benayas *et al.*, 2007), thus contributing to forest expansion. Notwithstanding, few changes in land cover from 2000 might indicate a new state of equilibrium in the landscape. This reduction in land cover change rates could represent a balance between current human and natural forces of change occurring in abandoned or less intensively-used land patches (Pelorosso *et al.*, 2011).

In addition to the aforementioned factors, the pronounced trends in land cover change at local scale may be partially related to a historical major role of transhumance in shaping landscape in this area, in comparison with other areas in the Cantabrian Mountains (MAGRAMA, 2013). The socio-economic crisis greatly affecting transhumance, during the 20<sup>th</sup> century, has caused an increase mainly in beef cattle, requiring less humane handling, at the expense of the traditionally migratory sheep flocks (Morán-Ordóñez *et al.*, 2013b). Cattle make a different use of grasslands, being less effective in controlling woody species than sheep (Calvo *et al.*, 2002). At the same time, the traditional transhumance model has been replaced in recent years by short movements from nearby lowlands where shepherds spend shorter and shorter periods of time in mountain areas (Olea & Mateo-Tomás, 2009). Further, they involve a lower number of animals, thus decreasing pressure over woody systems. Additionally, particular socio-economic factors occurring in the Cantabrian Mountains of León, such as the small size and isolation of villages, loss of facilities and lack of economic opportunities have encouraged depopulation.

This fact, along with population ageing, further explains the abandonment of small holding agriculture and traditional landscape management, inducing pronounced land cover trends at local scale (Morán-Ordóñez, 2012).

## ***5.2 Impact of land cover changes in ecosystem service supply and trends in ecosystem service use***

Land cover changes linked to socio-economic transformations and agricultural policies, mainly occurring during the sub-period 1990-2000, were identified as an important driver of ecosystem service change in traditionally managed landscapes in the Cantabrian Mountains. While the potential supply of ecosystem services associated to natural systems increased, that linked to traditional land uses was notably altered, at both regional and local scale, which is in line with other studies (Conti & Fagarazzi, 2005; Rey-Benayas *et al.*, 2007). The consideration of these trade-offs is key to understand the evolution of traditionally managed landscapes as suppliers of ecosystems services, thus allowing for sustainable policies to be desing. The expansion of woody vegetation positively influenced regulating services in the Cantabrian Mountains, in line with the findings of other studies, including the rise of air quality regulation (Chaparro & Terrasdas, 2009), reduction in erosion (García-Ruiz *et al.*, 2010; Anaya-Romero *et al.*, 2016), the improvement in water quality (Navas *et al.*, 2009) and the runoff regulation (Schulz *et al.*, 2010). Additionally, it also benefited the potential supply of timber, wood fuel, wild foods and biochemicals, enhancing the use of some services, such as timber (Maes *et al.*, 2015), a fact that we found at local scale. At the same time, the increasing density of game species at local scale evidenced how the expansion of woody vegetation, associated to a reduction of livestock pressure, is also likely to favor wildlife species, generally associated with forested areas (Nikolakaki, 2004; Conti & Fagarazzi, 2005). This fact contributes to natural heritage, which might also benefit tourism (Navarro & Pereira, 2012). This increase in density of game species was consistent with the increase in potential wild food supply with land cover changes, but it was not corroborated by the hunting use. However, the decline in the number of hunted animals (i.e. hunting use) might not be directly connected with land cover changes, but with other factors such as differences in the male-female

ratio, pests or weather events. Beyond this, hunting represents an ecosystem service of increasing use at national scale (Herruzo & Martínez-Jauregui, 2013), although it might be in conflict with biodiversity conservation (Morán-Ordóñez *et al.*, 2013a), generating opposed interests among stakeholders demanding different ecosystem services. Benefits from the expansion of woody vegetation have been identified as an opportunity for the regeneration of native ecosystems and present rewilding as a potential cost-saving alternative approach to conservation strategies (Regos *et al.*, 2016).

Notwithstanding, in the Cantabrian Mountains, the importance of preserving traditionally managed landscapes, related to acceptable levels of livestock production and traditional farming practices, as valuable sources of ecosystem services has been stated in previous studies (Rescia *et al.*, 2010; Morán-Ordóñez *et al.*, 2013b). However, the expansion of shrublands and forests into semi-natural grazing systems, mainly occurred over 1990-2000 at both local and regional scale, and the decrease in actual use drove a strong impact on the potential supply of livestock (Oteros-Rozas *et al.*, 2012), which might compromise these landscapes and their supplier character. The existence of opened habitats and pasture activities has been recognized as crucial in reducing the vulnerability of landscape against natural perturbations, like wildfires, being associated to a reduction in fuel accumulation and its continuity (Zumbrunnen *et al.*, 2012). At the same time, the conservation of high quality semi-natural grazing systems has benefits for the socio-economic welfare of mountain villages derived from the rental of mountain passes (Rodríguez, 2004). Further, despite the observed general increase the potential cultural service supply, mainly associated to woody vegetation expansion, traditionally managed landscapes are important cultural service suppliers. Beyond economic benefits, cultural heritage related to pastoralism culture and traditional landscape management is a valuable cultural service which may be endangered by the loss of traditional practices (Calvo-Iglesias *et al.*, 2009; Morán-Ordóñez *et al.*, 2013a). Similarly, the mosaic of semi-natural open habitats, forests and shrubs, jeopardized by the current landscape homogenization trend, is usually perceived as more aesthetically attractive (Schirpke *et al.*, 2016) than transitory degraded stages of forest (Pardini *et al.*, 2002). In parallel, traditionally

managed landscapes might also contribute to natural heritage. Many flora and fauna species of high conservation value (e.g. *Potentilla fruticosa* or *Luscinia svecica*) depend on these habitats and could thus being threatened by their detriment (MacDonald *et al.*, 2000; Sirami *et al.*, 2008).

Potential limitations of the Stoll matrix to depict local and regional peculiarities in different European regions (Burkhard *et al.*, 2009; Stoll *et al.*, 2015) might be associated with the increase in potential cultural service supply, despite the loss of cultural services linked to traditional managed landscapes in the Cantabrian Mountains. This may be explained by the challenge of generalizing cultural ecosystem services, whose value is highly site and context dependent (Locatelli *et al.*, 2017; Tolessa *et al.*, 2017). Further, it might highlight an overstatement of the relative role of forest to supply particular services by matrix methods (Maes *et al.*, 2015). Limitations of the Stoll matrix would suggest the advisability of using capacity matrixes adapted to different regional socio-ecological contexts in future studies. Safeguarding cultural values of traditional managed landscapes offers possibilities for the development of new services of increasing use in the Cantabrian Mountains, such as tourism (Rey-Benayas *et al.*, 2007). Further, the increasing use of tourism could potentially serve as an instrument to diversify economy and revitalize mountainous rural areas. Such a purpose would require greater engagement of rural society (Cánoves *et al.*, 2004) and a diversified concept of land use planning, which contributes to ecologically sustainably tourism (Höchtel *et al.*, 2005), while maintaining natural and cultural heritage, practices and landscapes.

In our study area, efforts towards the preservation of traditionally managed landscapes and their character as traditional and cultural ecosystem service suppliers have been put through management and policy actions (e.g. agro-environmental schemes of the CAP; Rescia *et al.*, 2008). In this context, the degree of restoration of lost ecosystem service values (livestock and cultural services) during 1990-2000 has been scarce, but results beyond 2000 in this study showed trends towards a relatively stable state. In this state, despite the existence of landscape homogenization, maintaining a certain degree of spatial heterogeneity of the landscape mosaic in mountain systems has been shown to be beneficial, as it

might enhance a more diversified bundle of ecosystem services provided by the different types of ecosystems. However, we must note that reported links between land cover and ecosystem service dynamics are temporal and spatial scale-dependent (Locatelli *et al.*, 2017). Therefore, even if we found similar trends in land cover and ecosystem services at local and regional scales, these trends might vary across other temporal and spatial scales. Besides, novel management and policy strategies, aiming at the preservation of traditional landscapes and their ecosystem services, would require adaptation in order to cover current socio-ecological needs. This can be achieved through the inclusion of socio-ecological connections and synergies among the primary, secondary and tertiary sectors (Lago & Sevilla, 2008), which enabled traditional ecosystem services to be maintained (e.g. livestock), complemented by current new sustainable ones (e.g. tourism).

## 5. Conclusions

Our analysis of land cover dynamics in the Cantabrian Mountains at both regional and local scale revealed a trend towards landscape homogenization and highlighted the importance of considering the temporal scale when analyzing land cover and ecosystem services dynamics. The spread of woodland systems increased the potential supply of regulating and provisioning services in the Cantabrian Mountains. At the same time, the decline in semi-natural opened landscapes negatively affected the supply of services linked to traditional uses, such as livestock. A poor depiction of the loss of cultural services associated to traditionally managed landscapes suggests the need to revise the Stoll matrix for its correct application in this type of systems. Changes in land cover produced an increase in the use of some ecosystem services that emphasized the need to integrate both the supply and the future use of all ecosystem services in management plans. The identification of trends in land cover change and ecosystem service supply and use reported in this study could help to develop future scenarios to tackle future challenges in ecosystem service supply.

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## ANNEX IV

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- 5 **Table S4.1.** Changes in human population in the provinces of the Cantabrian Mountains from 1991 to 2011 (number of inhabitants and percentage). Source: Spanish National Institute of Statistics.

Changes in population from 1991-2011	Álava	Asturias	Bizkaia	Burgos	Cantabria	León	Lugo	Palencia	Total C. Mountains
Nº inhabitants	-14128	-99784	-14316	-5195	+13544	-67759	-15013	-8907	-211558
%	-34,31	-25,86	-2,59	-14,17	+13,36	-66,69	-31,54	-23,93	-16,24

**Table S4.2.** CORINE Land Cover classes comprised in the Cantabrian Mountains.

Code	CORINE Land Cover classes
ArtiS	Continuous urban fabrics
	Discontinuous urban fabrics
	Industrial or commercial units
	Road and rail networks and associated land
	Port areas
	Airports
	Dump sites
	Construction sites
	Green urban areas
	Sport and leisure facilities
	Mineral extraction sites
NI	Non-irrigated arable lands
Pirriga	Permanently irrigated lands
V	Vineyards
Fruit	Fruit trees and berry plantations
Past	Pastures
AgroF	Agro-forestry areas
CCP	Complex cultivation patterns
LPA	Land principally occupied by agriculture, with significant areas of natural vegetation
Forest	Broad-leaved forests
	Mixed forests
	Coniferous forests
NG	Natural grasslands
Twood	Transitional woodland-shrub
Moor	Moors and heathlands
SclV	Sclerophyllous vegetation
Pbogs	Peat bogs
SparV	Sparsely vegetated areas
Beach	Beaches, dunes, sands
Rock	Bare rocks
Burnt	Burnt areas
WaterSurf	Inland marshes
	Salt marshes
	Water courses
	Water bodies
	Sea and ocean
	Estuaries



**Table S4.3.** Transition matrix showing changes in land cover (i‰) from 1990 (rows) to 2000 (columns) at local scale (Cantabrian Mountains of León). The largest changes for each land cover type are in bold. Only period 1990-2000 is shown, as the most representative period

		Land cover 2000															
		ArtiS	NI	Pirriga	Past	CCP	LPA	Forest	NG	Twood	Moor	ScIV	SparV	Rock	Burnt	WatS	Total area
Land cover 1990	ArtiS							0.54		<b>6.66</b>	1.83					0.69	9.73
	NI			0.91						0.53		<b>1.70</b>					3.14
	Pirriga						0.09				0.19		<b>0.30</b>				0.57
	Past					<b>3.48</b>		1.80							0.42	1.11	6.81
	CCP	2.32	<b>6.96</b>				<b>11.45</b>	0.31		0.27						0.72	22.02
	LPA	1.80		0.22		<b>4.15</b>		0.88	0.21	0.72		0.26			1.49		9.72
	Forest	8.01	0.17		0.09	0.37	0.28		1.24	<b>56.50</b>	0.12	1.03			4.98	2.63	75.42
	NG	10.22				2.26		<b>77.45</b>		<b>22.18</b>		1.23			3.78	6.10	126.34
	Moor	10.54			0.33		0.25	5.57	4.44	<b>12.27</b>					7.66	8.99	50.07
	ScIV	0.57					0.70	<b>28.06</b>	0.49	<b>30.21</b>					6.13		66.17
	Twood	4.48	0.10		0.69			<b>339.61</b>	1.36		0.16		7.14		9.36		363.22
	SparV	2.02														0.23	2.26
	Burnt							1.30							<b>3.64</b>		4.95
	Total area	39.99	7.23	1.13	0.43	10.96	12.77	455.93	7.76	132.35	2.30	4.22	7.15	0.30	37.46	20.49	

ArtiS (continuous urban fabric, discontinuous urban fabric, industrial or commercial units, road and rail networks, port areas, mineral extraction sites, dump sites, construction sites, green urban areas, sport and leisure facilities); NI (non-irrigated arable land); Pirriga (permanently irrigated lands); V (vineyards); Fruit (fruit trees); Past (pasturelands); CCP (complex cultivation patterns); LPA (land principally occupied by agriculture); Forest (broad leaf forest, mixed forest and coniferous forest); NG (natural grasslands); Moor (moors and heathlands); ScIV (sclerophyllous vegetation); Twood (transitional woodlands-shrub); Rock (bare rocks); SparV (sparsely vegetated areas); Burnt (burnt areas); WatS (water bodies, water courses, estuaries, sea and oceans).



## GENERAL DISCUSSION

Mountains are dynamic and heterogeneous socio-ecological systems where landscape heterogeneity has been identified as an important feature for explaining their relevant biodiversity, as well as their character as suppliers of a wide range of ecosystem services beneficial for society (Foggin, 2016). Such heterogeneity is mainly associated to topographic and climatic complexity (Korner *et al.*, 2005) and historic human intervention (Morán-Ordoñez *et al.*, 2011). Therefore, inclusion of landscape ecology and the assessment of landscape heterogeneity in mountain systems constitute a meaningful approach for exploring connections among ecological processes and their social dimension.

When addressing landscape studies, the importance of developing reliable classified landscape thematic maps is a core question, as they are usually the basis for landscape pattern analysis in such a way that, unreliable products might undermine inferences on relationships between patterns and processes (Shao & Wu, 2008). In this context, the combination of two of the most readily available remote sensing products informing on land cover, such as the CORINE Land Cover and the NDVI index derived from NOAA-AVHRR plus thematic data, were valuable tools for developing landscape classifications with a practical application. Indeed, landscape classifications developed in this Thesis were useful for evaluating relationships between landscape heterogeneity and richness of terrestrial vertebrate species. However, the representation of landscape patterns might be hampered by the spatial resolution of the input data (Lechner *et al.*, 2010). Our results demonstrated that the best landscape classification was never achieved at the original resolution of the land cover data, but at intermediate ones. Working with both low and high resolution input data might be challenging (Strahler *et al.*, 1986), thus increasing error and uncertainty. Such a difficulty at low resolution might arise from a distortion of information when representing objects or patterns occurring at a finer grain size (Foody, 2004); whereas at high resolution it would be related to high local spectral variability that might lead to intra-class variation and noise (Nagendra *et al.*, 2013; Rocchini *et al.*, 2013). Accordingly, selecting the appropriate spatial resolution acquires special relevance when addressing

landscape classification, in particular, and overall, when working with spatial information (Karl & Maurer, 2010).

The use of landscape metrics derived from categorical maps has become a common approach for biodiversity monitoring (Walz, 2011). Among them, the feasibility of landscape heterogeneity as a cost-effective surrogate of species diversity has been emphasized in previous studies, highlighting its influence on taxonomic (Atauri & de Lucio, 2001; Schindler *et al.*, 2013) and functional diversity (Perović *et al.*, 2015). This influence would be expected in relation to the habitat heterogeneity hypothesis (McArthur & Wilson, 1967) by which, an increase in the number of habitat types implies an increase in species diversity, through increasing niche availability and complementary resources (Cramer & Willig, 2005).

Notwithstanding, as follows from the results of this Thesis, the performance of landscape heterogeneity as a predictor of species diversity might be conditioned by the spatial analytical unit approach. Accordingly, the eco-geographical spatial analytical unit approach, based on watersheds, offered a rational framework for modelling terrestrial vertebrate species richness from landscape heterogeneity, with clear management application. This could be explained because this spatial analytical units allowed for a better representation of the keystone structure (Bohn & Kershner, 2002; Verhoeven *et al.*, 2008; Karadağ, 2013), which species depend on (Tews *et al.*, 2004), than traditionally used arbitrary spatial analytical approaches. Indeed, watersheds are not a novel approximation in analysis and conservation management studies (WFPB 1992, 1993; Montgomery *et al.*, 1995). Nevertheless, it must be taken into account that when working with this approach the shared effect of watershed area and the predictive power of landscape heterogeneity should not be neglected (Kallimanis *et al.*, 2008; Andrew *et al.*, 2011). At same time, possible limitations of arbitrary spatial analytical unit approaches, based on regular windows, were made evident with regards to modeling relationships between landscape heterogeneity and species richness. These limitations could arise from their inability to reflect the spatial structure of environmental and biological components of the landscape (Wagner & Fortin, 2005), while caution is also needed in relation to MAUP (Modifiable Areal Unit

Problem) issues (i.e. scale and zoning problems) (Dark & Bram, 2007; Nouri *et al.*, 2017).

Besides, the multi-scale arbitrary approach highlighted the influence of the spatial analytical unit size on the effect of landscape heterogeneity on species richness, and evidenced connections of this effect with species functional traits (Barbaro & van Halder, 2009; Perović *et al.*, 2015). Indeed, it is generally admitted that functional traits influence species response to landscape heterogeneity. Thus, landscape heterogeneity is recognized as an environmental filter that might influence community assembly via trait-based assembly (Concepción *et al.*, 2016). Nevertheless, after explicitly analyzing the effect of landscape heterogeneity on the richness of terrestrial vertebrate functional groups, we revealed a higher influence of other environmental filters such as climate (maximum summer temperature), topography (slope variability) and human influence (surface of protected areas). Such a filtering effect could be expected since climate and topography are known to constrain biota in mountain systems (Aiello-Lammens *et al.*, 2016; Zuloaga & Kerr, 2016). Further, anthropogenic disturbances usually act as a filter with negative functional consequences for organisms (Chillo & Ojeda, 2012). Therefore, the presence of protected areas, which are usually subject to regulation of human activities and uses, generally supporting higher quality habitats and reducing threats (Thomas *et al.*, 2012), might favor the presence of a higher number of functional groups. However, results on the effect of landscape heterogeneity on the richness of functional groups differed from the findings of other studies (Flynn *et al.*, 2009; Devictor *et al.*, 2010), which might be associated with the selected set of functional traits (Dufлот *et al.*, 2014; Perović *et al.*, 2015; Scherer *et al.*, 2015). These discrepancies did not allow the role of the landscape heterogeneity to be reliably determined as an environmental filter of functional traits of terrestrial vertebrates in mountain systems and further research would be advisable.

The relevance of preserving a heterogeneous landscape mosaic in mountain systems lies not just in its influence on biodiversity, but also on the benefits that this mosaic may provide for human well-being (Morán-Ordóñez *et al.*, 2013). In the Cantabrian Mountains, agricultural policies and socio-economic changes in recent decades have involved transformations in farming and agricultural production

(Donald *et al.*, 2002; Casas & Manzano, 2007), prompting land extensification and abandonment in marginal areas, while agricultural fields have been aggregated and increased in more suitable zones (Álvarez-Martínez, 2010). As a result, woody vegetation expansion into semi-natural open habitats (e.g. natural grasslands, pasturelands or moors and heathlands), mainly occurring during 1990-2000, has been identified as a main trend of land cover change, both at regional and local scale over the whole evaluated period 1900-2012. This land cover change has driven landscape homogenization and has put traditional managed landscapes at a risk of degradation, as identified in other European mountains (Conti & Fagarazzi, 2005; Gracia *et al.*, 2011).

In this context, land cover changes linked to shifts in relationships between humans and nature were found to be important drivers of change in the potential supply of ecosystem services provided by the Cantabrian Mountain landscapes, mainly during 1990-2000. They led to trade-offs between ecosystem services associated to natural systems, such as regulating and woodland provisioning services, and those associated to traditional land uses, such as livestock. However, despite the observed general increase in the potential supply of cultural service, limitations of the applied methodology (Stoll capacity matrix method; Burkhard *et al.*, 2009; Stoll *et al.*, 2015) did not allow for reliable determination of trends in these services. On the other hand, changes in land cover and ecosystem service dynamics across temporal scales showed trends towards a relatively stable state from 2000 onwards. In this state, despite landscape homogenization, preserving a certain degree of spatial landscape heterogeneity might enhance the supply of a more diverse bundle of ecosystem services. Currently, it has been evidenced that changes in the potential supply of ecosystems services are generally reflected in ecosystem service use, thus suggesting enhancement of particular uses associated to changes in land cover.

The temporal analyses of links between ecosystem services and land cover changes described in this Thesis will enhance knowledge of the dynamics of connected natural and human ecosystems. This could contribute to tackling future challenges in ecosystem service supply and use, by providing insight into the potential consequences of different human pressures.

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## GENERAL CONCLUSIONS

1. Remote sensing products associated with land cover, such as the CORINE Land Cover inventory or the spectral index NDVI, are suitable tools for developing meaningful landscape classifications with applicability in land management. Likewise, rescaling these products provides low levels of uncertainty and error in landscape classifications and the best classification results.

2. The use of CORINE Land Cover in landscape classifications is valuable for characterizing and interpreting landscape classes, as it reduces confusion in the classification process. Meanwhile, the use of the NDVI index increases the consistency of landscape classifications (typology and number of classes) across spatial resolutions.

3. Landscape heterogeneity is a suitable predictor of terrestrial vertebrates species richness in mountain systems, although the detection of its effect is determined by the spatial unit used for analyses.

4. The eco-geographical spatial unit approach, based on watersheds, provides a suitable analytical framework for modelling terrestrial vertebrates species richness using landscape heterogeneity. However, the arbitrary spatial analytical unit approach, based on square windows of different sizes, is not related to the phenomena under study; and, therefore, it is not appropriate for analyzing the landscape heterogeneity-species richness relationship.

5. Landscape heterogeneity is correlated with the terrestrial vertebrates richness of the following functional groups: insectivores, granivores and omnivores, tree-, cave-, rock- and shrub-dwellers, as well as diurnals. However, it cannot be considered as a major environmental filter of functional traits in mountain systems, since other predictors (climate, topography and human influence variables) are the main factors influencing the richness of these functional groups.

6. The main land cover changes in the Cantabrian Mountains during the last two decades are the expansion of the woody vegetation in semi-natural open habitats and the increase in agricultural fields in the most suitable areas. As a consequence of these land cover changes, the heterogeneity of the landscape mosaic decreases.

7. Land cover changes in the Cantabrian Mountains during the last two decades were a key factor driving the potential supply of ecosystem services. In particular, there was an increase in regulating and provisioning services associated to woody formations, and a decrease in services linked to traditional uses, such as livestock breeding.

8. The methodology applied for evaluating the potential supply of ecosystem services does not allow for properly evaluating trends in cultural services. It would be necessary to adapt this technique to the particular socio-ecological context of the mountain systems under evaluation.

9. Regardless of landscape homogenization in the Cantabrian Mountains during the last two decades, preserving a certain degree of spatial heterogeneity in the landscape mosaic is beneficial for diversifying the bundle of ecosystem services provided.

## CONCLUSIONES GENERALES

1. Los productos de teledetección relativos a los tipos de ocupación del suelo, como la clasificación CORINE Land Cover o el índice espectral NDVI, son herramientas adecuadas para desarrollar clasificaciones de paisaje con sentido ecológico y aplicabilidad en la gestión del territorio. Así mismo, el reescalado de estos productos de teledetección permite obtener bajos niveles de incertidumbre y error en las clasificaciones del paisaje y proporciona los mejores resultados de estas clasificaciones.

2. El uso del CORINE Land Cover en las clasificaciones de paisaje es ventajoso para la caracterización e interpretación de las clases de paisaje, disminuyendo la confusión en el proceso de clasificación. Mientras que el uso del índice NDVI da lugar a una mayor consistencia en la tipología y en el número de clases de paisaje en las distintas resoluciones espaciales.

3. La heterogeneidad del paisaje se considera como un predictor de la riqueza de especies de vertebrados terrestres en sistemas de montaña, aunque su efecto está condicionado por la unidad espacial de análisis utilizada.

4. El uso de la unidad espacial eco-geográfica, cuencas hidrográficas, proporciona un marco de análisis adecuado para modelar la riqueza de especies de vertebrados terrestres a partir de la heterogeneidad del paisaje. Sin embargo, las unidades espaciales de análisis arbitrarias, como las ventanas cuadrangulares de distinto tamaño, muestran muy baja relación con los procesos estudiados, por lo que se consideran menos apropiado para el análisis de la relación entre la heterogeneidad del paisaje y la riqueza de vertebrados terrestres.

5. La heterogeneidad del paisaje se correlaciona con la riqueza de vertebrados terrestres incluidos en los grupos funcionales de insectívoros, granívoros, omnívoros, especies arborícolas, cavernícolas, rupícolas, que viven en arbustos y diurnas. Sin embargo, esta característica no se puede considerar como un filtro ambiental clave de grupos funcionales en sistemas de montaña, ya que otros

predictores como el clima, la topografía y las variables de influencia humana presentan mayor contribución en la explicación de la riqueza de estos grupos funcionales.

6. Los principales cambios en los paisajes de montaña de la Cordillera Cantábrica, durante las últimas dos décadas, son la expansión de la vegetación leñosa en sistemas abiertos semi-naturales y el incremento de los cultivos agrícolas en las zonas más apropiadas para ello. Como consecuencia de estos cambios se reduce la heterogeneidad del mosaico de paisaje.

7. Los cambios en los tipos de ocupación del suelo ocurridos durante las dos últimas década en la Cordillera Cantábrica, fueron uno de los principales factores que modificaron la provisión potencial de servicios ecosistémicos. Se destaca un aumento en la provisión de los servicios de regulación y aprovisionamiento, ligados a sistemas forestales, y una disminución de los servicios relacionados con los usos tradicionales del territorio, como la ganadería.

8. La metodología aplicada para evaluar los cambios en la provisión potencial de servicios ecosistémicos no permite evaluar adecuadamente las tendencias de cambio de los servicios culturales. Por lo tanto, sería necesario desarrollar una adaptación de esta metodología al contexto socio-ecológico particular del sistema de montaña a estudiar.

9. A pesar de la tendencia hacia la homogenización del paisaje detectadas en el la Cordillera Cantábrica durante las dos últimas décadas, el mantenimiento de cierto grado de heterogeneidad espacial en el mosaico de paisaje es beneficiosa para la diversificación del conjunto de servicios ecosistémicos que proporciona.

