Incorporating the functional dimension of biodiversity through remote sensing into ecology and conservation

Incorporando la dimensión funcional de la biodiversidad a través de teledetección en ecología y conservación

Beatriz Pérez Cazorla
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CENTRO ANDALUZ PARA LA EVALUACIÓN
Y SEGUIMIENTO DEL CAMBIO GLOBAL

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Memoria presentada por Beatriz Pérez Cazorla para optar al Grado de Doctora en Ciencias Aplicadas y Medioambientales por la Universidad de Almería

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A las mujeres científicas

A Andrés

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SCIENTIFIC PUBLICATIONS THAT COMPOSES THE THESIS

The results section presented in this thesis consists of four chapters, three of them composed by articles listed below. Each article is referenced at the beginning of each chapter and included with the editing of the journal in the General appendix section.

1. **Cazorla, P.B.,** Cabello, J., Guirado, E., Reyes, A., Peñas, J., Pérez-Luque, A., Alcaraz-Segura D. (2020) A remote sensing-based dataset to characterize the ecosystem functioning and functional diversity of a Biosphere Reserve: Sierra Nevada (SE Spain). Earth System Science Data. Discuss., https://doi.org/10.5194/essd-2019-198, in review.

2. **Cazorla, P.B.,** Cabello, J., Peñas, J., Garcillán, P.P., Reyes, A., Alcaraz-Segura D. (2020). Incorporating ecosystem functional diversity into geographic conservation priorities using remotely-sensed Ecosystem Functional Types. Ecosystems, 1-17. https://doi.org/10.1007/s10021-020-00533-4

3. **Cazorla, P.B.,** Garcillán, P.P., Cabello, J., Alcaraz-Segura D., Reyes, A., Peñas, J. (2020). Patterns of ecosystem functioning as tool for biological regionalization: the case of the mediterranean-desert-tropical transition of Baja California. Mediterranean Botany. https://dx.doi.org/10.5209/mbot.68048. Accepted, in press.

ABSTRACT

Incorporating ecosystem functioning and functional diversity in ecology and nature conservation is key to promote sustainability and a safe operating space for humanity. Nowadays, numerous international agreements, such as the Convention on Biological Diversity (CBD), face the challenge of safeguarding the ecological processes and ecosystem functions that sustain the multiple facets of biodiversity and ecosystem services. Indeed, variables describing ecosystem functioning are widely demanded to define essential biodiversity variables, a framework to coordinate monitoring programmes worldwide. Ecosystem functioning is particularly relevant to track and forecast how environmental changes affect biodiversity and ecosystem services. To characterize ecosystem functioning, multiple remote sensing techniques can be used, such as the Ecosystem Functional Type (EFT) approach. EFTs can be defined as groups of ecosystems with similar dynamics of matter and energy exchanges between the biota and the physical environment. EFTs can be derived from biologically meaningful descriptors (named Ecosystem Functional Attributes -EFAs-) of the seasonal curves of spectral indices as surrogates of focal ecosystem functions, for instance, of primary production dynamics, one of the most essential and integrative indicators of ecosystem functioning.

The main objective of this thesis was to provide a remote-sensing based conceptual and methodological approach to incorporate the functional dimension of biodiversity at ecosystem level in ecology and conservation biology through the application of the Ecosystem Functional Type (EFT) concept. We achieved this goal in four steps: 1) First, we provide ground-based empirical evidence for the use of satellite-derived EFTs as descriptors of the regional heterogeneity in ecosystem functioning, i.e., satellite-derived EFTs as homogeneous patches of the land surface in terms of Net Ecosystem Exchange (NEE) dynamics measured on ground. 2) Second, we showed how EFTs can be used to describe the spatial heterogeneity and inter-annual variability of ecosystem functioning (i.e. EFAs and EFTs), ecosystem functional diversity (i.e. EFT richness and EFT rarity) and ecosystem

functional stability (interannual variability and dissimilarity) and released the associated dataset. 3) Third, we provide a proof of concept on how to use EFTs to incorporate ecosystem functional heterogeneity and singularity in setting geographic conservation priorities. 4) Finally, we also provide a proof of concept on how to use EFTs in biological regionalizations to complement the compositional and structural descriptions of biodiversity.

Theoretical and empirical models support the relationship between spectral indices derived from satellite images (e.g., Enhanced Vegetation Index -EVI-) and essential functional variables of ecosystems, such as primary production. In this thesis, we identified EFTs from three descriptors of the seasonal curves of MODIS/Terra EVI (MOD13Q1 product): annual mean (proxy of primary production), seasonal coefficient of variation or standard deviation (descriptors of seasonality), and date of maximum EVI (indicator of phenology).

Satellite-derived EFTs demonstrated to be an ecosystem functional classification that can inform on homogeneous patches on the land surface in terms of their NEE dynamics measured on ground. Given that NEE dynamics is related to primary production, a focal ecosystem function, EFTs can then be used (as essential variables) to describe, assess and monitor the regional heterogeneity of ecosystem functioning (Chapter I). EFTs also provide a straightforward approach to characterize the spatial diversity, i.e. EFT richness and EFT rarity, and functional stability, i.e. EFT interannual variability and dissimilarity, of ecosystem functioning to inform scientists and managers on ecosystem functional diversity patterns and trends (Chapter II). Furthermore, EFTs helped to both reinforce and complement traditional geographic conservation priorities based on biodiversity composition and structure by incorporating the heterogeneity and singularity of focal ecosystem functions (Chapter III). Finally, EFTs allowed us to understand the relationship between different dimensions of biodiversity in ecological regionalization exercises, i.e. based on biodiversity composition and structure (species distribution, endemisms, vegetation types) and on patterns of ecosystem functioning (Chapter IV).

Overall, the characterization of the spatial patterns and temporal variability of ecosystem functioning in terms of EFAs, EFTs, and EFT diversity metrics derived from satellite spectral indices related to a focal ecosystem function (e.g. Enhanced Vegetation Index, as a proxy for primary production), demonstrated to be a useful and innovative tool to incorporate ecosystem functioning at regional scale into ecology and conservation under the new conservation paradigm that considers ecological processes and ecosystem functions and services.

RESUMEN

La incorporación del funcionamiento de los ecosistemas y la diversidad funcional en la ecología y la conservación de la naturaleza es fundamental para promover la sostenibilidad y un espacio seguro para la humanidad. Hoy en día, numerosos acuerdos internacionales, como el Convenio sobre la Diversidad Biológica (CDB), se enfrentan al reto de salvaguardar los procesos ecológicos y las funciones de los ecosistemas que sustentan las múltiples facetas de la biodiversidad y los servicios ecosistémicos. De hecho, se demanda que variables que describen el funcionamiento de los ecosistemas definan las variables esenciales de la biodiversidad, un marco para coordinar los programas de vigilancia ambiental en todo el mundo. El funcionamiento de los ecosistemas es particularmente importante para el seguimiento y monitoreo de los cambios ambientales que afectan a la biodiversidad y los servicios de los ecosistemas. Para caracterizar el funcionamiento de los ecosistemas, pueden utilizarse múltiples técnicas basadas en teledetección, como la aproximación basada en tipos funcionales de ecosistemas (TFEs). Los TFEs pueden definirse como grupos de ecosistemas con una dinámica similar de intercambios de materia y energía entre la biota y el entorno físico. Los TFEs pueden derivarse de descriptores biológicamente significativos (denominados Atributos Funcionales del Ecosistema - AFE), obtenidos de las curvas estacionales de los índices espectrales, y utilizados como subrogados de las funciones focales del ecosistema, por ejemplo, de la dinámica de la producción primaria, uno de los indicadores más esenciales e integradores del funcionamiento del ecosistema.

El principal objetivo de esta tesis doctoral fue proporcionar un enfoque conceptual y metodológico basado en la teledetección para incorporar la dimensión funcional de la biodiversidad a nivel de ecosistema en la ecología y la biología de la conservación, mediante la aplicación del concepto de Tipo Funcional de Ecosistema (TFE). Logramos este objetivo en cuatro pasos: 1) En primer lugar, aportamos pruebas empíricas basadas en datos de campo para la utilización de los TFEs obtenidos mediante teledetección como descriptores de la heterogeneidad regional en el funcionamiento de los ecosistemas, es decir, determinamos

si los TFEs obtenidos mediante satélite son parches homogéneos de la superficie terrestre en términos de la dinámica de intercambio neto de ecosistemas (i.e. CO_2). 2) En segundo lugar, mostramos cómo pueden utilizarse los TFEs para describir la heterogeneidad espacial y la variabilidad interanual del funcionamiento de los ecosistemas (es decir, los AFE y los TFE), la diversidad funcional de los ecosistemas (es decir, la riqueza y la rareza de TFEs) y la estabilidad funcional de los ecosistemas (variabilidad y disimilitud interanuales), y ponemos a disposición de la comunidad científica el conjunto de datos correspondiente. 3) En tercer lugar, ofrecemos una prueba de concepto sobre cómo utilizar TFEs para incorporar la heterogeneidad y la singularidad funcional de los ecosistemas en el establecimiento de prioridades geográficas en conservación. 4) Por último, también proporcionamos una prueba de concepto sobre cómo utilizar TFEs en las regionalizaciones biológicas para complementar las descripciones composicionales y estructurales de la biodiversidad.

Los modelos teóricos y empíricos apoyan la relación entre los índices espectrales derivados de las imágenes satelitales (por ejemplo, el índice de vegetación mejorado -EVI-) y las variables esenciales del funcionamiento de los ecosistemas, como la producción primaria. En esta tesis, identificamos TFEs a partir de tres descriptores de las curvas estacionales del EVI de MODIS/Terra (producto MOD13Q1): media anual (proxy de la producción primaria), coeficiente de variación estacional o desviación estándar (descriptores de la estacionalidad) y fecha del EVI máximo (indicador de la fenología).

Los TFEs obtenidos mediante teledetección demostraron ser una clasificación funcional del ecosistema que puede informar sobre parches homogéneos en la superficie terrestre en términos de su dinámica de intercambio de CO_2 medida en tierra. Dado que esta dinámica está relacionada con la producción primaria, una función central del ecosistema, los TFEs pueden utilizarse (como variables esenciales) para describir, evaluar y vigilar la heterogeneidad regional del funcionamiento del ecosistema (Capítulo I). Los TFEs también proporcionan un enfoque directo para caracterizar la diversidad espacial, es decir, la riqueza y la rareza de TFEs, y la estabilidad funcional, es decir, la variabilidad y la disimilitud interanual de TFEs, del funcionamiento de los ecosistemas para informar a la comunidad científica y a la administración de los patrones y tendencias de la diversidad funcional de los ecosistemas (Capítulo II). Además, los TFEs contribuyeron a reforzar y complementar las prioridades tradicionales de conservación geográfica basadas en la composición y la estructura de la diversidad biológica al incorporar la heterogeneidad y la singularidad de las funciones focales de los ecosistemas (Capítulo III). Por último, los TFEs nos permitieron comprender la relación entre las diferentes dimensiones de la biodiversidad en los ejercicios de regionalización ecológica, es decir, basados en la composición y la estructura de la biodiversidad (distribución de las especies, endemismos, tipos de vegetación) y en los patrones de funcionamiento de los ecosistemas (Capítulo IV).

En general, la caracterización de los patrones espaciales y la variabilidad temporal del funcionamiento de los ecosistemas en términos de AFEs, TFEs y métricas de diversidad de TFEs derivadas de los índices espectrales satelitales relacionados con una función central del ecosistema (por ejemplo, el índice de vegetación mejorado, como sustituto de la producción primaria), demostró ser un instrumento útil e innovador para incorporar el funcionamiento de los ecosistemas a escala regional en la ecología y la conservación dentro del nuevo paradigma de conservación que considera los procesos ecológicos y las funciones y servicios de los ecosistemas.

1. INTRODUCTION

1. INTRODUCTION

1.1. The multidimensional nature of biodiversity and its importance for the integrity of ecosystems

Biodiversity is a central concept in ecology and conservation that can be understood as a measure of the total difference within a biological system (Lyashevska & Farnsworth, 2012). Since its proposal, the concept has received much attention due to its complex and hierarchical nature. In 1992, the United Nations Earth Summit in Rio de Janeiro defined biodiversity as "the variability among living organisms from all sources, including, terrestrial, marine, and other aquatic ecosystems, and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems" (Convention on Biological Diversity, 1992). From this declaration, several definitions have been proposed to provide a more comprehensive concept of biodiversity. While these definitions can vary enormously (Kaennel, 1998; Gastón and Spicer, 2013), a common feature among them is that biodiversity arises at multiple levels of biological organization (i.e. genetic, species, ecosystems and ecoregions) and it is inherently multidimensional (Noss, 1990; Lyashevska & Farnsworth, 2012; Naeem et al., 2016). Such complex nature implies the acknowledgement of biodiversity is organized in three main dimensions -composition, structure and function- (Noss, 1990; Walters and Scholes, 2017) (Figure 1.1). Composition deals with the identity and variety of entities in a collection (e.g., species lists and diversity indices); structure is the physical organization or pattern of a system (e.g., habitat complexity or physiognomy of vegetation); and function involves ecological processes (e.g., information, matter and energy exchanges). The acknowledgement of the importance of research on the development of new methodologies and analytic tools for measuring the natural variation of biodiversity embracing all its dimensions is currently one of the mainstays of biological sciences.

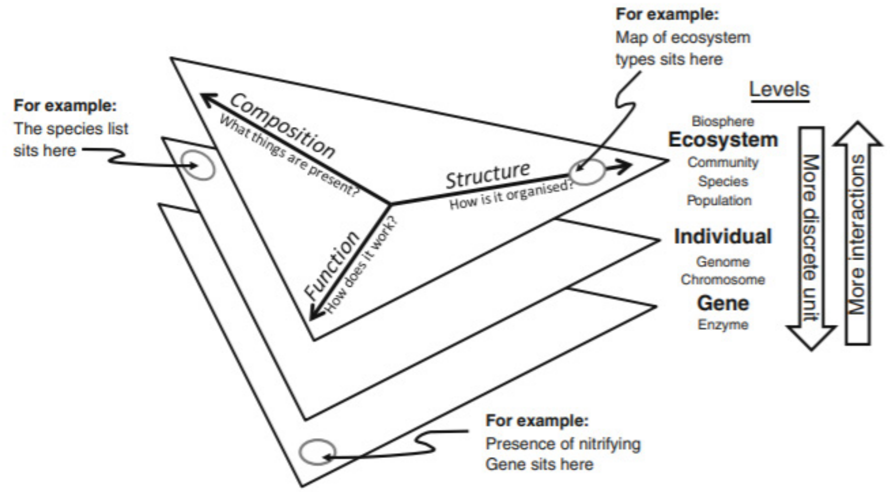

Figure 1.1. Biodiversity dimensions from Scholes et al., (2017) based on Noss, (1990).

The growing awareness that biodiversity is a precious global asset to human well-being and that the integrity of habitats and ecosystems are at serious risk, has increased the importance of biodiversity-related research. Such an investigation has shown that the characterization and monitoring of all dimensions of biodiversity is key to maintaining ecosystems healthy and resilient to global change (Walters and Scholes, 2017). First, nowadays it is widely recognized that healthy ecosystems are the basis of human well-being since they provide the multiple benefits that we need to have an good life (MEA, 2005). Such benefits, the so-called ecosystem services, are obtained only if ecosystems hold adequate biodiversity composition and structure that guarantees the functional processes necessary to deliver them (Cardinale et al., 2012). Second, ecosystems have been resilient enough to gradually adapt to environmental changes. However, the demographic growth of the human population and the exploitation of natural resources have dramatically reduced biological diversity (Bongaarts, 2019) undermining ecosystems' abilities to function efficiently and thereby diminishing their ability to respond to environmental changes (Oliver et al., 2015).

1.2. Compositionalism vs functionalism

Even though traditionally compositional and structural biodiversity has been more important in ecology and conservation than functional biodiversity (Calicott 1999; Lovett et al., 2005), in recent decades the role of ecosystem functions in biodiversity studies has significantly increased (Oliver et al., 2015; Navarro et al., 2017; Pettorelli et al., 2018). Indeed, biodiversity research has moved from a compositional approach oriented towards the biological hierarchy of organisms and populations of species that interact in biotic communities, to a functional approach that aims to know the ecological processes that sustain biodiversity (Jax, 2010). Both approaches have a different conceptual basis, since while compositionalism is based on evolutionary ecology, functionalism adopts the principles of thermodynamic ecology (Callicott et al., 1999, Rodríguez, 2016) (Figure 1.2). According to Cabello et al., (2012), the higher tangibility of the discrete entities that study evolutionary ecology (such as species) has made it possible to make more and earlier progress in the use of biodiversity composition and structure in ecology and conservation. In contrast, the fact that thermodynamic ecology (e.g. functions) is based on continuous and intangible units using aggregation criteria such as biomass or matter and energy flows has delayed and limited its use. Despite their methodological and theoretical differences, in practice, both approaches are complementary, since they offer the opportunity to address the current biodiversity crisis from a wide variety of arguments that as a whole deal to the intrinsic, instrumental and relational values of biodiversity (Tallis and Lubchenco, 2014).

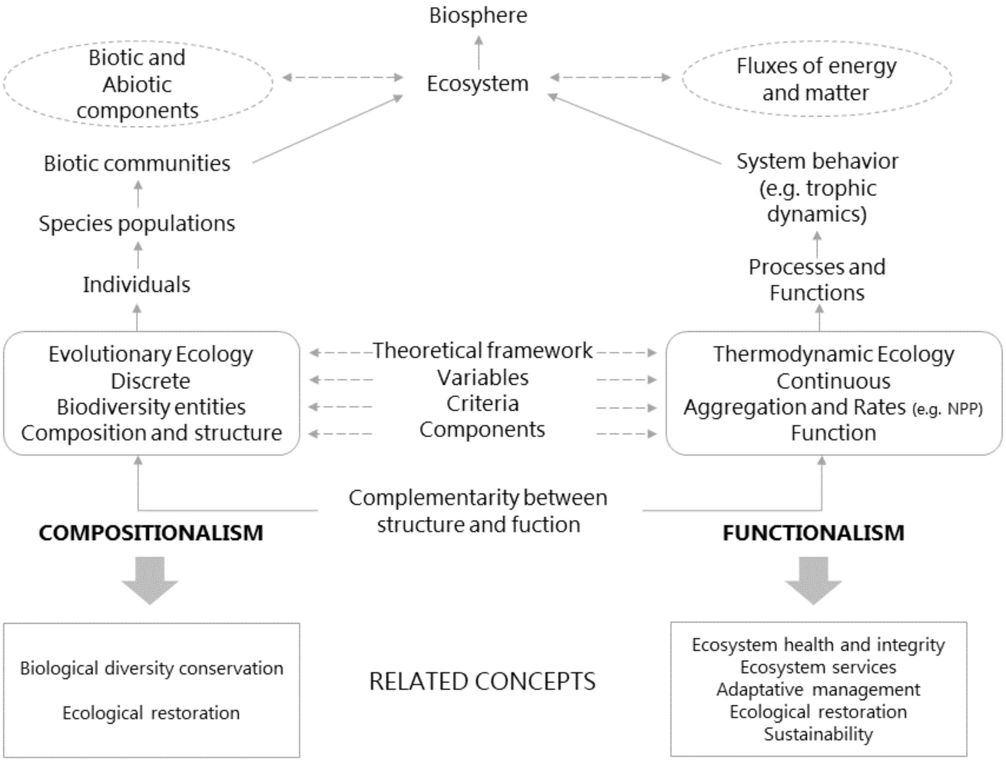

Figure 1.2. Compositionalism vs functionalism. Based on Callicott, (1999) and Rodriguez, (2016).

1.3. Ecosystem functioning as a focus in the study of the functional dimension of biodiversity

The incorporation of ecosystem functioning in ecological research offers a better understanding of spatial and temporal patterns of biodiversity (Garnier et al., 2016). Research on the functional aspects of biodiversity has primarily focused on reflecting the variability of ecological attributes among species that provides a mechanistic link to ecosystem resistance, resilience and functioning (Petchey & Gaston, 2006; Lavorel et al., 2007). However, because the final goal of the functional biodiversity dimension research is to focus on processes that arise as an integral response at the ecosystem level, in practice, it has been expanded to deal with the characterization of ecosystem functioning (e.g., Cabello et al., 2012). Nowadays, the ecosystem functioning has an essential role in biodiversity research, since through it, we can address how systems perform, and provide the links between biological diversity (Díaz et al., 2007; Chapin et al., 2010; Cadotte et al., 2011; Asner et al., 2017), ecosystem services (Balvanera et al., 2006; Duncan et al., 2015), and ecological resilience (Petchey and Gaston, 2006). In this sense, variables describing ecosystem functioning are widely demanded to define essential biodiversity variables, a framework to coordinate monitoring programmes worldwide (Pereira et al., 2013). Functional variables have also been claimed to predict, for example, how communities and ecosystems respond to environmental change (Bengtsson, 1998) and on understanding how declining diversity influences ecosystem services on which humans depend (Costanza et al., 1997; Pettorelli et al., 2018). Furthermore, variables capable of describing ecosystem functioning at regional to global scales are needed to advance in the definition of one of the nine critical, but still unassessed planetary boundaries, i.e. functional diversity (Steffen et al., 2015).

Multiple definitions of ecosystem functioning and related terms of its semantic field (i.e. ecological processes, ecosystem functions) can be found in the literature (Jax 2010; Pettorelli et al., 2018). All of them try to reflect the collective life activities of plants, animals, and microbes and the effects that these activities (e.g., feeding, growing, moving, excreting waste) have on the physical and chemical conditions of their environment. In this thesis, we considered the following definitions: 1) Ecological processes as “the resulting activities from interactions among organisms and with their environment” (Martinez, 1996); 2) Ecosystem processes as “the transfer of energy, material, or organisms among pools in an ecosystem” (Lovett et al., 2006); 3) Ecosystem functions as “attributes related to the performance of an ecosystem that is the consequence of one or of multiple ecosystem processes” (Lovett et al., 2006); and 4) Ecosystem functioning as the sum of all ecosystem functions, in particular, we will refer to the ecosystem functioning as the information contained in magnitudes of stocks and rates of processes involving exchanges of energy and matter between the biota and the environment (Paruelo et al., 2001).

1.4. Ecosystem functioning research in conservation

A better understanding of ecosystem functioning and functional diversity is key to biodiversity conservation and its services. The emergence of the biodiversity-ecosystem functioning paradigm has recognized the bidirectional relationship between the conservation status of biodiversity and of ecosystem processes (Naeem, 2002; Hooper et al., 2005). Accompanied by the challenge of safeguarding the ecological processes necessary for the persistence of biodiversity over time (CBD, 2010; GBO4, 2014; Mace, 2014) appeared a general concern for maintaining the capacity of ecosystems to sustain and regulate their functions (Chapin et al., 2010; Prober et al., 2019) and services (Naidoo et al., 2008; Costanza et al., 2014; Doak et al., 2015). Indeed, a growing number of international commitments, such as the Convention on Biological Diversity or the Aichi Targets, require specific management plans that specifically address ecosystem functioning (CBD, 2011; Visconti et al., 2019).

From the planning and management perspective, the importance of incorporating ecosystem processes and functions into systematic conservation planning, ecosystem management and adaptive management is also noted (Margules and Pressey, 2000; Possingham et al., 2005; Klein et al., 2009; Jax, 2010). Systematic approaches to conservation planning have been developed over the last two decades to guide the allocation of the scarce resources available for protecting biodiversity (Carwardine et al., 2007). These approaches should be supported by the identification of explicit targets for biodiversity features to guide decisions for setting conservation priorities (Possingham et al., 2000). The identification of conservation priorities areas is usually based on the important metrics in ecology and conservation, such as richness or rarity (Ceballos and Brown, 1995). Nowadays, the need for a larger and more representative and comprehensive global protected area network (Aichi target 11, CBD 2011) that accounts for all dimensions of biodiversity could greatly benefit from the explicit inclusion of the ecosystem functions and processes that support biodiversity and ecosystem services (Naidoo et al., 2008).

Ecosystem functioning provides several advantages in conservation schemes over compositional and structural dimensions. Ecosystem functioning offers a more rapid response to environmental changes, allowing adaptive management and early detection of impacts (Milchunas and Lauenroth, 1995). Besides, the large-scale changes in ecosystem functioning across Earth has important consequences for biodiversity and resources availability to support biological conservation and human well-being (Olson et al., 2001). In consequence, a growing number of authors have identified the need to integrate new concepts and methodologies to connect classical ecology and contemporary conservation with ecosystem functioning (Violle et al., 2014). Thus, new approaches aimed at characterizing biodiversity based on ecosystem functioning could help to address such conceptual and operational challenges.

1.5. Remote sensing of ecosystem functioning

Ecosystem functioning can be systematically and easily monitored through satellite images over large areas, providing us a dynamic characterization of ecosystems (Paruelo et al., 2001). Consequently, remote sensing appears as a tool that allows us to incorporate ecosystem functioning indicators to biodiversity conservation (Duro et al., 2007; Cabello et al., 2012; O'Connor et al., 2015; Skidmore et al., 2015; Pettorelli et al., 2019).

Remote sensing has been around as a tool for nature science development for several decades, improving the knowledge on ecology and conservation. Over the last decades, technological advancements in sensors (e.g. increasing spatial, temporal and spectral resolution), computer processing capacity of large-datasets and associated development of analytic tools have opened new opportunities to biodiversity research (Pettorelli et al., 2018). Remote sensing offers the opportunity to understand the spatial and temporal patterns of the ecological processes that operate over large scales to support biodiversity and ecosystem services (Pettorelli et al., 2016). In fact, remote sensing has repeatedly been identified as a promising and powerful tool to aid biodiversity mapping and monitoring (e.g., Stoms and Estes 1993; Turner et al., 2003; Nagendra et al., 2013; Corbane et al., 2015;

Pettorelli et al., 2016, 2018). Through remote sensing techniques, ecologists have more integrative functional measures of the whole ecosystem performance that complement our traditional view of ecosystems (Butchart et al., 2010; Asner et al., 2017).

Currently, the use of satellite images provides suitable methods to produce a spatially continuous characterization of ecosystem (Xiao and Moody, 2004; Alcaraz-Segura et al., 2006). The spectral response of the vegetation changes according to physical parameters (i.e. in wavelengths in the red, infrared and thermal range) allowing us to obtain continuous information of these parameters and to study different functional attributes over large extensions of territory (Box et al., 1989; Running et al., 2000; Peñuelas et al., 2004). In particular, both theoretical and empirical models support the relationship between spectral indices derived from satellite images and functional attributes of ecosystems such as evapotranspiration, surface temperature, albedo or net primary production (Running et al., 2000; Pettorelli et al., 2005, 2018). For us, the variable of interest is primary productivity for the reasons which we will explain below. Among the most important and used spectral indices related with primary productivity and derived from satellite images are the vegetation indices (VI), we found the NDVI (Normalized Difference Vegetation Index) and the EVI (Enhanced Vegetation Index). Both spectral indices (i.e. NDVI and EVI) are linear estimators of the fraction of Photosynthetically Active Radiation (fPAR) intercepted by vegetation, which is the main control of carbon gains (Monteith, 1972) (see section 3. General methodology).

Among the functional variables, primary productivity appears as the most integrative descriptor of ecosystem functioning (Virginia and Wall, 2001), since primary productivity represents the energy that enters into the life cycle, and it is linked to multiple ecosystem processes and services (Paruelo et al., 2016). In essence, primary productivity shows a comprehensive response to environmental changes, being a synthetic indicator of ecosystem health (Costanza et al., 1992; Skidmore et al., 2015).

Ecological research based on spectral vegetation indices has great value in conservation biology (Cabello et al., 2012; Pettorelli 2016, 2018), as a support to management (Pelkey et al., 2003; Cabello et al., 2016) and in the study of biodiversity responses to environmental changes (Alcaraz-Segura et al., 2017). Among the many advantages of using these indices to study the spatial and temporal variability of vegetation dynamics are the use of common protocols across the Earth (Pettorelli et al., 2018), their high sensitivity and rapid response to environmental changes (Milchunas and Lauenroth, 1995), their clear biological significance (Pettorelli et al., 2005), and their connection to the assessment of ecosystem functions and services (Volante et al., 2012; Paruelo et al., 2016).

1.6. Ecosystem Functional Types: a concept to incorporate the spatial heterogeneity of ecosystem functioning into conservation practice and landscape ecology

Ecosystem functioning has been characterized from spectral vegetation indices, in particular from Ecosystem Functional Attributes (EFAs). Recently, the use of Ecosystems Functional Attributes derived from spectral vegetation indices in species distribution models is allowing the assessment of habitat suitability for plant (Arenas-Castro et al., 2018) and animal species (Requena-Mullor et al., 2017, Regos et al., 2019) with great spatial and temporal precision, and can even anticipate expected changes in the distribution of threatened plant species as a result of climate change (Alcaraz-Segura et al., 2017). In addition, based on the Ecosystems Functional Attributes, have been possible to evaluate the functional changes in ecosystems at regional scale and at the protected area level (Alcaraz-Segura et al., 2009; Lourenço et al., 2018). In fact, a monitoring program has been designed for the Spanish National Park Network, which allows changes and anomalies in functioning to be identified, informing managers of the health and state of conservation of the ecosystems (Cabello et al., 2016).

Satellite-derived Ecosystem Functional Attributes can be grouped together (i.e. getting a functional classification), providing a useful framework to understand these large-scale ecological changes in relation to ecosystem function and processes, and allowing the identification of homogeneous categorical groups that showed a similar and coordinated response to environmental factors (Díaz et al., 2013). Functional classifications have been widely used to simplify a number of categories for regional-to-global synthesis and modeling studies (Wullschleger et al., 2014). The understanding changes in ecosystem functioning across large-scales can benefit from a greater ability to represent and define biotic communities (Reichstein et al., 2014). This leads the functional classifications to have been widely used for ecologists historically.

In 1992, Soriano and Paruelo proposed the concept of Biozones referred to vegetation units that share ecosystem functional characteristics, identified using time-series of satellite images of spectral vegetation índices. Biozones were later renamed to Ecosystem Functional Types (EFTs) by Paruelo et al., (2001), using an equivalent definition and methodology. Shugart (1997) used for the first time the term EFT as "aggregated components of ecosystems whose interactions with one another and with the environment produce differences in patterns of ecosystem structure and dynamics". Walker (1997) proposed the use of a similar term, vegetation functional types, for "groups of PFTs in sets that constitute the different states of vegetation succession in non-equilibrium ecosystems". Scholes et al., (1997) also applied the term, in a wider sense for those areas having similar ecological attributes, such as PFTs composition, structure, phenology, biomass or productivity. Since then, several studies have applied hierarchy and patch dynamic theories (Reynolds and Wu, 1999; Wu et al., 2003) for the definition of ecosystem and landscape functional types at different spatial scales. Valentini et al., (1999) defined land functional units by focusing on "patches of the land surface that are able to exchange mass and energy with the atmosphere and show a coordinated and specific response to environmental factors". Paruelo et al., (2001) and Alcaraz-Segura et al., (2006, 2013) refined the EFT concept and proposed a remote-sensing based methodology to derive them from VI. Both defined EFTs as "patches of the land surface that share similar dynamics of matter and energy exchanges between the biota and the physical environment" (Paruelo et al., 2001; Alcaraz-Segura et al., 2006, 2013). In practice, EFTs group ecosystems (at large scales) on the basis of shared ecosystem functioning without prior knowledge of vegetation type or canopy architecture (Fernández et al., 2010; Pérez-Hoyos et al., 2014; Villarreal et al., 2018). In other words, EFTs capture dynamics of ecosystem functioning, a different dimension to the structural vegetation types

(Noss, 1990). As species can be grouped into plant functional types (PFTs) based on common species traits, ecosystems can be grouped into ecosystem functional types (EFTs) based on their similar ecosystem functioning (Noble and Gitay 1996). In this sense, we follow the holistic approach by Naeem (1998, 2002), Hooper et al., (2005), and Loreau (2008), focusing on the overall operation or performance of the ecosystem as a whole (see review in Jax, 2010). EFTs adopt a top-down approach to understand and map functional aspects of ecosystem heterogeneity and diversity at the regional scale, while PFTs follow a bottom-up approach to derive ecological properties at the regional scale by aggregation of species functional traits used in their classification.

Regardless of the definition or methodology, since the concept of EFT appeared in 2001 (Paruelo et al., 2001), its implementation or that of similar methodologies has not stopped growing to characterize functional heterogeneity at a regional scale (Alcaraz-Segura et al., 2006; Duro et al., 2007; Fernández et al., 2010; Geerken, 2009; Alcaraz-Segura et al., 2013; Ivits et al., 2013; Pérez-Hoyos et al., 2014; Müller et al., 2014; Wang and Huang, 2015; Villarreal et al., 2018; Coops et al., 2018; Mucina, 2019). Satellite-derived EFAs and EFTs have been used to describe large-scale functional biogeographical patterns (Ivits et al., 2013); to assess the representativeness of environmental observatory networks (Villarreal et al., 2018); to assess the environmental and human controls of ecosystem functional diversity (Alcaraz-Segura et al., 2013); to evaluate the effects of land-use changes on ecosystem functioning (Oki et al., 2013); to improve weather forecasting models (Lee et al., 2013; Müller et al., 2014); and to improve species distribution and abundance models (Arenas-Castro et al., 2018, 2019).

However, no study has yet assessed whether such top-down-identified EFT classes are biologically meaningful in terms of field-measured ecological processes, such as biogeochemical fluxes, which would build reliability on the concept. In addition, few studies have still formally tested the usefulness of EFTs to incorporate ecosystem functioning in ecology and conservation.

Therefore, the importance of this work relies in the strengthening of the conceptual and methodological foundations of Ecosystem Functional Types as well as in the assessment of their usefulness to incorporate ecosystem functioning as a necessary dimension of biodiversity in regional ecology and conservation biology.

2. OBJECTIVES

2. OBJECTIVES

2.1. General Objective

The overall objective of this thesis was to generate conceptual and methodological advances to incorporate the functional dimension of biodiversity at ecosystem level in regional ecology and conservation biology through the application of the Ecosystem Functional Type (EFT) concept.

To achieve this goal, we proposed the following specific objectives:

2.2. Specific Objectives (SO)

SO1. To assess whether the satellite-based methodological approach to identifying Ecosystem Functional Types, conceptually defined as land patches that show similar ecosystem functioning in terms of their exchanges of matter and energy with the atmosphere, is capable of capturing such differences in ecosystem processes as measured in the field.

SO2. To develop an approach to describe the spatial heterogeneity and temporal variability of a focal ecosystem function (i.e. primary production) by means of Ecosystem Functional Types derived from the satellite images of vegetation greenness. Such approach provides scientists and managers with valuable information of the functional heterogeneity and diversity at ecosystem level for protected areas.

SO3. To use Ecosystem Functional Types, to incorporate the spatiotemporal heterogeneity and singularity of a focal ecosystem function (i.e. primary production) in setting geographic conservation priorities, as a new complementary approach to traditional ones, which are usually based on biodiversity composition and structure.

SO4. To use the patterns of ecosystem functioning as a tool for biological regionalization, by examining the relationships between biological regionalization based on biodiversity composition and structure and patterns of ecosystem functioning revealed by the geographical distribution of EFTs.

2.3. Structure of the thesis

The thesis is organized into four chapters. Each chapter aims to respond to the objectives previously set out in section 2.2.

After the general introduction, which presents the background and need for this work, the objectives are formulated, as well as the general methodology and the results of each chapter. Moreover, a general discussion about the role of ecosystem functioning in biodiversity science and conservation, and the final general conclusions have been carried out. **CHAPTER I** aims to provide ground-based empirical evidence for the use of satellite-derived Ecosystem Functional Types (EFTs) as descriptors of the regional heterogeneity in ecosystem functioning, i.e., in the dynamics of matter and energy exchanges between the biota and the physical environment. **CHAPTER II** provides a straightforward approach to characterize the spatial heterogeneity and inter-annual variability of ecosystem functioning (i.e. EFAs and EFTs), ecosystem functional diversity (i.e. EFT richness and EFT rarity) and ecosystem functional stability (interannual variability and dissimilarity), providing to the scientific community the dataset. **CHAPTER III**, **and IV** apply the concept to conservation and regional ecology. In particular, CHAPTER III establishes EFT-based geographic conservation priorities based on EFT richness and EFT rarity, representing a new and complementary approach to long-established ones based on the compositional (e.g., species richness) and structural (e.g., vegetation types) characterizations of biodiversity. CHAPTER IV assesses the potential of EFT incorporating the functional perspective in the design of large-scale biogeographical regionalizations, by using patterns of ecosystem functioning as a means for biological regionalization.

The main road map of the thesis is presented in the following Figure 2.1.:

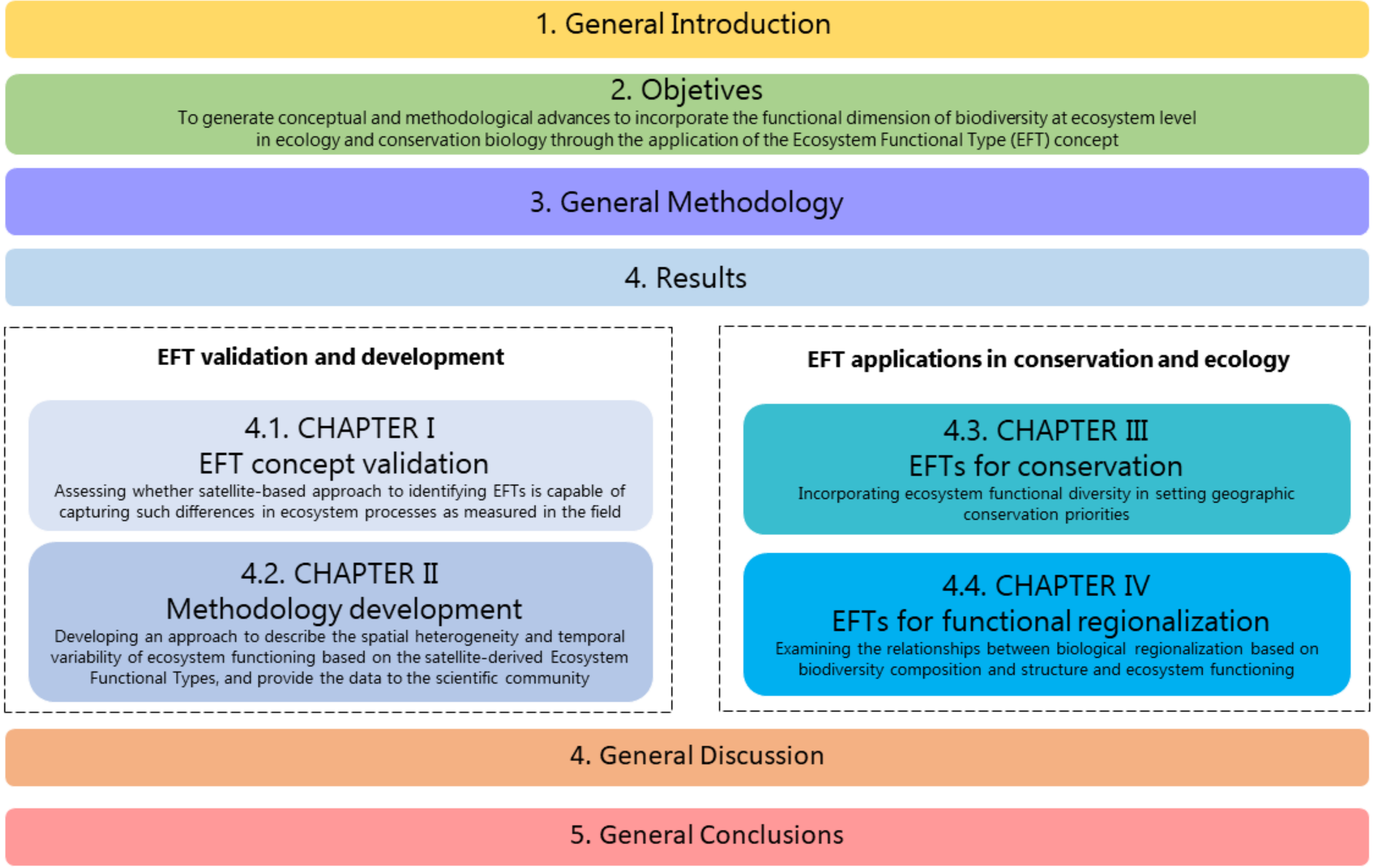

Figure 2.1. General structure of the thesis.

3. GENERAL METHODOLOGY

3. GENERAL METHODOLOGY

This section only includes general methodological aspects that were not included in the Methods sections of the different chapters that were already published or under revision as journal articles.

3.1. Characterization of ecosystem functioning by means of satellite remote sensing

In this thesis, the characterization of ecosystem functioning was based on satellite-derived attributes of primary production as focal ecosystem function. We used primary production as a focal ecosystem function because it is considered as an integrative surrogate of the stocks and fluxes of matter and energy derived from biological activity (Virginia and Wall 2001), and can be easily characterized by remote sensing.

Nowadays, the use of satellite imagery provides useful methods to produce a spatially explicit characterization of ecosystem functioning and its spatial heterogeneity (i.e., ecosystem functional diversity) from local to regional and global scales (Ustin & Gamon, 2010; Tuanmu & Jetz, 2015; Jetz et al., 2016; Asner et al., 2017; Walters and Scholes, 2017; Pettorelli et al., 2018; Anderson, 2018; Jetz et al., 2019; Gamon et al., 2019). Theoretical and empirical models support the relationship between spectral indices derived from satellite images and essential functional variables of ecosystems, such as primary production.

- **Vegetation Indices**

“A Vegetation Index (VI) is a spectral transformation of two or more bands designed to enhance the contribution of vegetation properties and allow reliable spatial and temporal inter-comparisons of terrestrial photosynthetic activity and canopy structural variations” (Huete et al., 2002). Among the most important and widely used spectral vegetation indices derived from satellite images we found the NDVI (Normalized Difference Vegetation Index) and the EVI (Enhanced Vegetation Index). The NDVI is calculated from the reflectance in the red and near-infrared wavelengths (Tucker and Sellers, 1986) while the EVI calculation also includes the reflectance in the blue band. This is an improvement over the NDVI, since EVI considers the effect of the atmosphere and the radiometric signal from the ground under the vegetation cover (Liu and Huete, 1995; Huete et al., 1999). Hence, we chose EVI instead of any other vegetation index as an indicator of carbon gains since it is supposed to be more reliable in both low and high vegetation cover situations (Huete et al., 1997). In this sense, EVI is sensitive to changes in areas having high biomass, EVI reduces the influence of atmospheric conditions on vegetation index values, and EVI corrects for canopy background signals.

EVI is computed as follows:

$$EVI = G \times \frac{(NIR - RED)}{(NIR + C1 \times RED - C2 \times Blue + L)}$$

where NIR/RED/BLUE are atmospherically-corrected (Rayleigh and ozone absorption) surface reflectances, L is the canopy background adjustment that addresses non-linear, differential NIR and red radiant transfer through a canopy, and C1, C2 are the coefficients of the aerosol resistance term, which uses the blue band to correct for aerosol influences in the red band. The coefficients adopted in the MODIS-EVI algorithm are; L=1, C1 = 6, C2 = 7.5, and G (gain factor) = 2.5.

As well as NDVI, EVI can be used as a proxy of Net Primary Production (NPP), by estimating the fraction of Photosynthetically Active Radiation absorbed by vegetation (fAPAR), which represents the main control of primary production (Monteith, 1972). Due to the linear relationship between spectral vegetation indices and fAPAR (Hatfield et al., 1984; Boschetti et al., 2011) (Figure 3.1), and that the other variables of the equation remain constant (Equation 1).

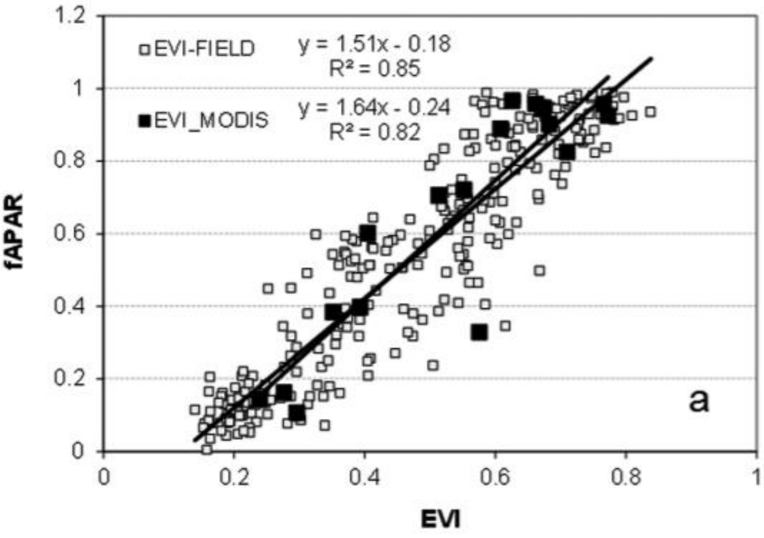

Figure 3.1. Fraction of Photosynthetically Active Radiation absorbed by vegetation (fAPAR) and Enhanced Vegetation Index (EVI) lineal relation from field data and satellite observations (from Boschetti et al., 2011).

$$\begin{array}{ccccccc} \text{NPP} & = & \text{PAR} & \text{x} & \text{fPAR} & \text{x} & \text{RUE} \\ [\text{gC m}^{-2}\ \text{year}^{-1}] & = & [\text{MJ m}^{-2}\ \text{year}^{-1}] & \text{x} & [\text{proportion}] & \text{x} & [\text{gC MJ}^{-1}] \end{array}$$

Equation 1. Monteith model to calculate the Net Primary Production (NPP) from the Photosynthetically Active Radiation (PAR), the fraction of Photosynthetically Active Radiation absorbed by vegetation (fPAR), and the Radiation-Use Efficiency by plants to transform it into organic carbon (RUE).

We obtained the spectral index EVI from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor, onboard the Earth Observing System-Terra platform. In particular, we selected the MOD13Q1.006 product (i.e. MOD13Q1 version 6) as the basis for our data since it offers a long time series (almost 20 years), and 23 EVI maximum value composite images per year (every 16 days) with an approximated pixel size of 231.65 meters at the equator, which allows for the characterization of the temporal dynamics of ecosystem functioning (Anderson, 2018).

The EVI values range from -1 to +1, where negative values generally correspond to snow, ice, or water; and values closer to +1 represent the higher density of green leaves (Huete et al., 2002). Throughout the thesis, in addition to assuming the correct native pre-processing of the data explained below, negative values (associated with snow, ice or water) were transformed into zeros.

- **MODIS-MOD13Q1 data quality**

The algorithm to produce the MOD13Q1 product from which we used EVI has several advantages over other indices in terms of data quality. MODIS EVI uses the blue band to reduce residual atmosphere contamination caused by smoke and sub-pixel thin clouds (Huete et al., 1999). Furthermore, the MODIS EVI products are computed from atmospherically corrected bi-directional surface reflectances. The algorithm used by this product (MOD13Q1.006 product) chooses the best available pixel value from all the acquisitions from the 16 day period (Maximum Value Composite, MVC). The algorithm operates on a per-pixel basis and requires multiple observations (16 days) to generate a composited EVI (Composite Value, CV). Due to orbit overlap, multiple observations may exist for one day, and a maximum of four observations per day may be collected. The MOD13Q1 algorithm separates all observations by their orbits, providing a means to filter the input data further.

Once all 16 days are collected, “the MODIS-MOD13Q1 algorithm applies a filter to the data based on quality, cloud presence, and viewing geometry (Figure 3.2). Cloud-contaminated pixels and extreme off-nadir sensor views are considered lower quality. A cloud-free, nadir view pixel with no residual atmospheric contamination represents the best quality pixel. Only the highest quality, cloud-free, filtered data are retained for compositing” (Huete et al., 1999; Didan, 2015). The goal of the compositing methodology is to extract a single value per pixel from all the retained filtered data, which is representative of each pixel over the 16-day period. The compositing technique works as follows (Figure 3.2):

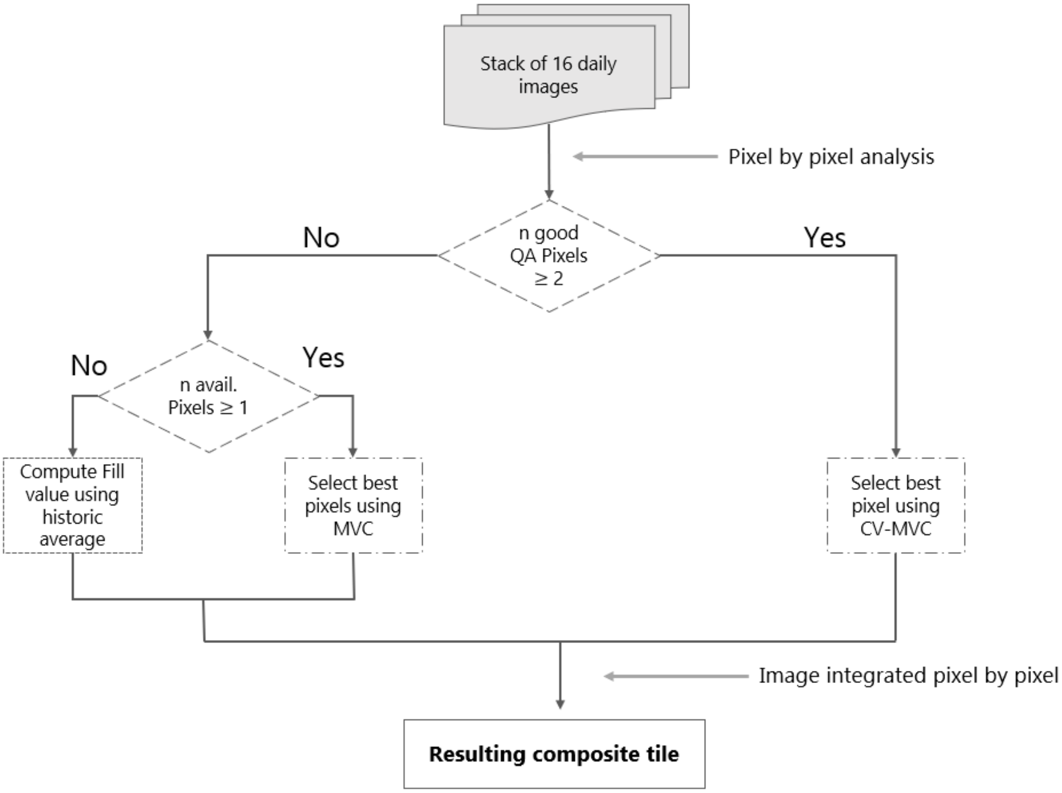

Figure 3.2. MODIS-MOD13Q1 compositing algorithm data flow (from Didan et al., 2015).

- **Advantages and disadvantages of the MOD13Q1 product over other satellite sensors to characterize ecosystem functioning**

Other satellite products could potentially be used, since they have a higher spatial resolution or more extended time series, but present some disadvantages compared to MODIS MOD13Q1.

Regarding spatial resolution, using MODIS MOD13Q1 instead of other satellites with smaller pixel size (e.g. Landsat or Sentinel 2) has several advantages in terms of data quality (e.g. presence of clouds, length of the data record) along with the time series. Since the MODIS sensor provides a daily image of the Earth, such high frequency (a maximum of four observations per day may be collected) increases the probability of finding a cloud-free image every 16-days. MODIS provides the best composite value every 16 days (i.e. chooses the best available pixel value from all the acquisitions from the 16 day period), applying an algorithm that selects the image atmospherically corrected bi-directional surface reflectances and select the image with lowest cloud presence, the lowest view angle, and the highest EVI value. Although Landsat has a lower pixel size, their images have a lower frequency (i.e., one image every 16 days). Thus, the fixed acquisition schedule makes it less probable to acquire good-quality imagery for a particular place periodically (mostly if clouds frequently occur over the area of interest, e.g. rainy seasons). Landsat 7 (1999-present) has a more extensive time series than MODIS, however, on May 31, 2003, the satellite's scan-line corrector failed. The scan-line corrector is a device on the satellite that keeps the scan lines parallel to each other. Without the Scan Line Corrector (SLC), the scan lines are misaligned, and there are wedge-shaped data gaps in the image (see sample Figure 3.3 for Sierra Nevada, Spain). Therefore, since 2003 SLC failure of Landsat 7, Landsat 8 is the only fully operational Landsat satellite in orbit, but covers a shorter time series than MODIS (Landsat8 covers from 2013 to present, while MODIS covers from 2001 to present).

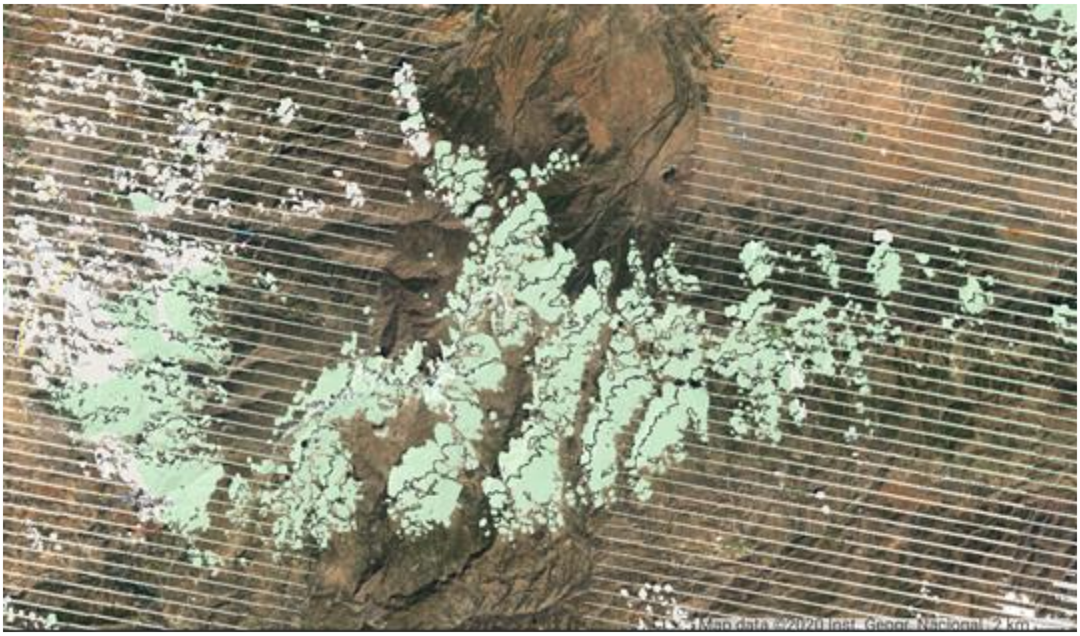

Figure 3.3. Effect of Scan Line Corrector fault on Landsat7 imagery in Sierra Nevada (Spain) and data gaps due to clouds (in green and white). Landsat-7 image courtesy of the U.S. Geological Survey.

Other satellites have also been considered for their use, as Sentinel, which also has a higher spatial resolution but the time series is still too short for long-term assessments (2014-present).

In consequence, considering the advantages and disadvantages of MOD13Q1 product over other satellite sensors to characterize ecosystem functioning, we recognize appropriate MODIS for ecological studies at regional scales, according to Anderson, (2018), which showed that the temporal resolution of MODIS is useful for characterizing the seasonal dynamics of ecosystem functioning (Figure 3.4). Furthermore, there are other works that use MODIS successfully at regional level (e.g. Lourenço et al., 2018; Requena-Mullor et al., 2018).

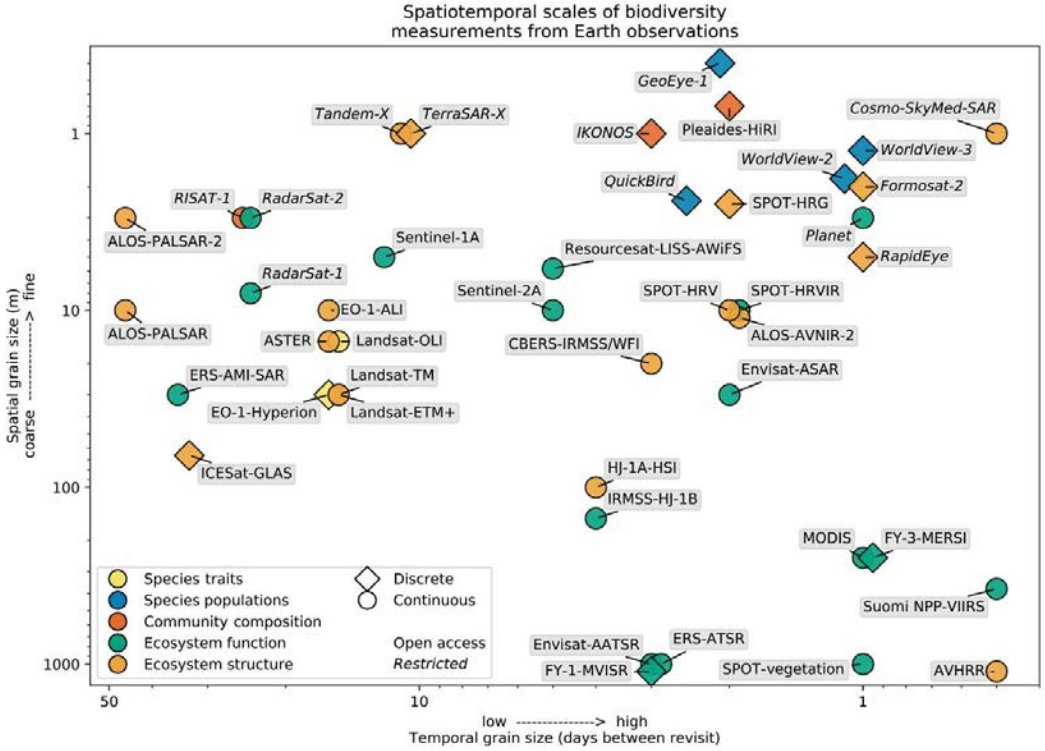

Figure 3.4. "Log–log plot of spatial and temporal and grain sizes for 44 current and historic satellite Earth observation (EO) sensors, coloured by biodiversity pattern type. Several sensors have been used to measure multiple biodiversity patterns, and the most cited or most novel were selected in these cases". From Anderson, (2018).

- **Ecosystem functioning dynamics characterization from Ecosystem Functional Attributes and Ecosystem Functional Types**

To characterize the ecosystem functioning using spectral vegetation indices we used the approach developed by Paruelo et al., (2001) and Alcaraz-Segura et al., (2006, 2013) based on Ecosystem Functional Types (EFTs), defined here as patches of the land surface that share similar primary production dynamics (i.e., Ecosystem Functional Attributes (EFAs): productivity, seasonality, and phenology). The EFT concept is analogous to the Plant Functional Type (PFT) concept that many land-cover product legends are based on, but defined at a higher level of the biological organization. As plant species can be grouped according to common functional characteristics, ecosystems can be grouped according to their common functional behavior. EFTs adopt a top-down approach to understand and map functional aspects of ecosystem heterogeneity at the regional scale, while PFTs follow a bottom-up approach to derive ecological properties at the regional scale by aggregation of species functional traits used in their classification. In practice, EFTs group ecosystems (at large scales) on the basis of shared ecosystem functioning without prior knowledge of vegetation type or canopy architecture (Fernández et al., 2010; Pérez-Hoyos et al., 2014; Villarreal et al., 2018). In other words, EFTs capture dynamics of ecosystem functioning, a different dimension to the compositional or structural vegetation types (Noss, 1990).

In this thesis, to build EFTs (workflow in Figure 3.5), we parameterized the yearly seasonal dynamics of carbon gains by using three metrics or EFAs that capture most of the variance of the EVI annual curve. Biologically, these three metrics can be interpreted as surrogates (Paruelo et al., 2001; Pettorelli et al., 2005; Alcaraz-Segura et al., 2006) of the total amount and timing (both seasonality and phenology) of primary production, one of the most integrative indicators of ecosystem functioning (Virginia and Wall, 2001). Statistically, these three metrics or EFAs are known to be highly correlated with the first two, or three axes (and hence capture most of the variance) of a Principal Component Analysis (PCA) run on the NDVI or EVI annual dynamics in different regions (Townshend et al., 1985; Paruelo and Lauenroth, 1998; Paruelo et al., 2001; Alcaraz-Segura et al., 2006, 2009; Ivits et al., 2013). In this thesis, to assess the variance explained by each metric, we examined the meaningfulness of these three EFAs for describing the vegetation dynamics with a Principal Component Analysis (PCA). We carried out it using the twelve months EVI values of the annual curve for the study area, then, we analysed the correlation between the EFAs (EVI_mean, EVI_sCV or EVI_SD and EVI_DMAX) and the first three principal axes of each PCA separately (see Appendix Chapter II). The three main descriptors or EFAs used were: annual mean (EVI_mean, surrogate of primary production), seasonal coefficient of variation or standard deviation (EVI_sCV or EVI_SD, descriptors of seasonality), and the date of maximum EVI (EVI_ DMAX, indicator of phenology). These three EVI metrics were orthogonal, since each EVI metric contributed independently to explain the variance of the EVI time series (see Appendix Chapter II).

To derive EFT classes from EFAs, the range of values of each EFA was divided into four intervals, i.e. quartiles, which were then combined, giving a potential number of (4 × 4 × 4) 64 EFTs. Following the logic of Noble and Gitay (Noble and Gitay, 1996) in developing functional classifications, we decided to start from the simplest, as long as outputs were ecologically interpretable. Our approach allows for a straightforward ecological interpretability of the legend based on four categories of productivity, seasonality, and phenology. Four intervals of each metric or EFA produced a relatively low number of potential classes (4x4x4=64) and allowed for the maintenance of the observed spatial patterns. In the case of DMAX, we wanted to reflect its ecological sense (the timing or phenology of the greatest interception of radiation by vegetation) in the final classification, so we had to group the 23 16-day MVC periods into just four classes that kept correspondence with the four seasons of the year. In the case of EVI_mean and EVI_sCV-EVI_SD, by using the first, second, and third quartiles, we also obtained four categories for each trait (as the four seasons in DMAX) with increasing values of productivity and seasonality.

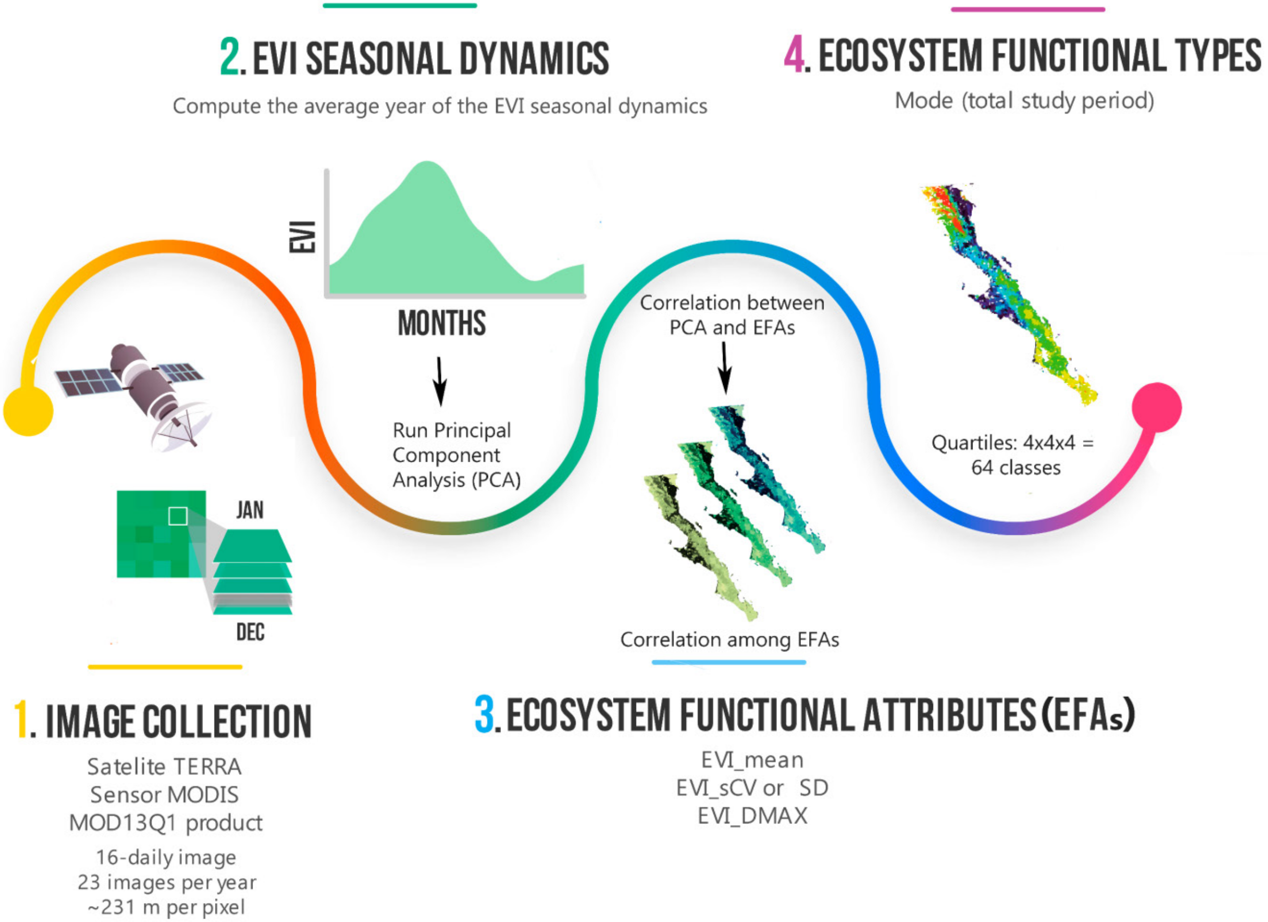

Figure 3.5. Workflow to characterize ecosystem functioning trough Ecosystem Functional Types.

Since EFTs are built from three independent descriptors of the EVI seasonal dynamics (see Appendix Chapter II), the average EVI annual cycle of the 64 EFTs show differences among each other in terms of mean annual EVI values, seasonal differences in the EVI values, and phenology of the growing season peak (see Figure 3.6).

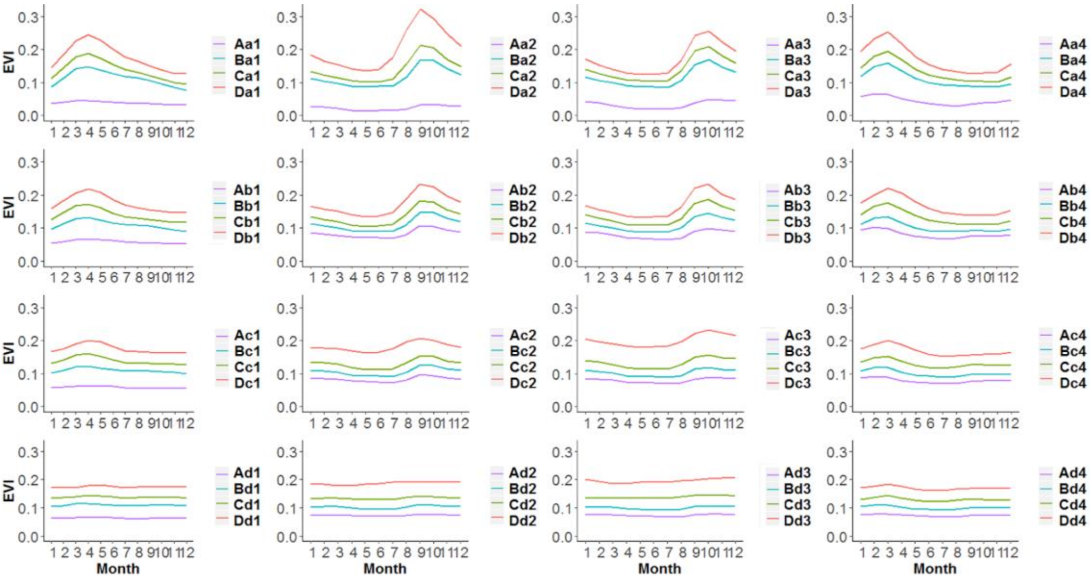

Figure 3.6. Difference in the average EVI annual cycle of the 64 EFTs. Capital letters correspond to the EVI annual mean, ranging from A to D for low to high EVI_mean. Small letters show the coefficient of variation of EVI (EVI_sCV), ranging similarly from a to d for low to high EVI_sCV. The numbers indicate the season of the date maximum of EVI (EVI_DMAX): 1-spring, 2-summer, 3-autumn, 4-winter.

In this section we only justify the use of the metrics, the methodology to build and code EFTs is explained in each of the thesis chapters (sections 4.1.2., 4.2.2., 4.2.3., 4.3.2.).

4. RESULTS

4.1.

CHAPTER I

Satellite-derived Ecosystem Functional Types capture ecosystem functional heterogeneity at regional scale

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Abstract

Describing and quantifying ecosystem functioning provides a powerful tool for the management and conservation of ecosystems and its services. Numerous ways to evaluate ecosystem functioning have been developed, such as by means of species traits, Plant Functional Types (PFTs), flux measurements with the Eddy Covariance (EC) technique, and remote sensing techniques. We propose that the spatial heterogeneity in ecosystem functioning at regional scale can be assessed and monitored by means of satellite-derived Ecosystem Functional Types (EFTs): groups of ecosystems or patches of the land surface that share similar dynamics of matter and energy exchanges. We hypothesize that, as observed for PFTs, different satellite-derived EFTs should have distinct patterns and magnitudes of Net Ecosystem Exchange (NEE) measured on ground. We derived EFTs based on the 2001-2014 time-series of satellite images of the Enhanced Vegetation Index (EVI) and compare them with NEE measurements (derived from *in situ* field observations using the EC technique) across 50 sites in Europe. Our results show that distinct EFTs classes display significantly different dynamics and magnitudes of NEE, and that EFTs perform marginally better than PFTs to explain NEE regional patterns (0.953-0.978 and 0.923-0.960, respectively). Land-cover maps based on PFTs are difficult to update at an annual basis and are not sensitive to changes in ecosystem performance (e.g. due to droughts or pests) that do involve short-term changes in PFT composition. Contrary, satellite-derived EFTs are sensitive to short-term changes in ecosystem performance and can be produced on an annual basis using the same classification rules, which provides a straightforward way to assess and monitor interannual changes in ecosystem functioning and in ecosystem functional diversity.

KEYWORDS: Functional classification; Ecosystem Functional Types; Plant Functional Types; Eddy Covariance; FLUXNET; Remote sensing.

4.1.1. Introduction

Ecosystem functioning and functional diversity are key issues of current ecological research (Jax, 2010; Violle et al., 2014, 2017; Tilman et al., 2014; Laureto et al., 2015; Pettorelli et al., 2018; Villarreal et al., 2018; Isbell et al., 2018; Malaterre et al., 2019). Quantifying, monitoring and understanding ecosystem functioning are useful to provide insights for management and conservation of ecosystems and their services (Cabello et al., 2012; Pettorelli et al., 2018). Variables capable of describing ecosystem functioning at regional to global scales are needed to define essential biodiversity variables to monitor biodiversity status (Pereira et al., 2013), to advance in the definition of this critical but still unassessed planetary boundary (Steffen et al., 2015), and to quantify their associated ecosystem services (Costanza et al., 1997; Balvanera et al., 2017). Despite the ecosystem functioning importance, its definition is unclear, and thus, multiple definitions can be found in the literature (see reviews in Jax 2010 and Pettorelli et al., 2018). Here, we adopt a holistic definition of ecosystem functioning as the information contained in magnitudes of stocks and rates of processes involving exchanges of energy and matter between the biota and the environment (Paruelo et al., 2001).

Multiple ways to evaluate ecosystem functioning have also been developed, from concepts such as species traits or Plant Functional Types (PFTs), to direct observation techniques such as Eddy Covariance (EC), and remote sensing. Traditionally, studies on ecosystem functioning were approached by grouping species into PFTs based on structural (e.g., biotypes), phylogenetic (e.g., coniferous) or functional species traits (e.g., metabolic pathway) that were linked to biological processes (Lavorel et al., 2002, 2007). These functional classifications aimed to reduce the diversity of biological entities (for instance genes, species or ecosystems) (Noss, 1990), and to allow for the identification of homogeneous categorical groups that showed a similar and coordinated responses to environmental factors and effects on ecological processes (Díaz et al., 2013). The PFT approach has been widely used, for instance in land-cover mapping and dynamic vegetation models, to simplify the continuum of species traits into a reduced number of discrete categories suitable for regional-to-global synthesis and modeling studies (Wullschleger et al., 2014). However, this simplification, although useful, can lead to information loss (Funk et al., 2017) and may not be capable of predicting the overall ecosystem functioning (Clark et al., 2016; Virtanen 2017; Thomas et al., 2019). Another more recent way to evaluate ecosystem functioning is by using direct and continuous observations of the exchanges of mass and/or energy between the land surface and the atmosphere measured. For instance, the Eddy Covariance technique (EC), a standardized method that uses high-frequency wind and scalar concentration data for calculating the Net Ecosystem CO_2 Exchange (NEE) between the land surface and the atmosphere at the ecosystem level (Baldocchi et al., 2001). This approach is widely used and regional (e.g., AmeriFlux, AsiaFlux, ICOS, NEON) and global networks of EC measurements have emerged (e.g., FLUXNET; and more recently Fluxnet-CH4) (Franz et al., 2018; Knox et al., 2019). Although FLUXNET has provided unprecedented information (Baldocchi et al., 2001), these measurements are still not enough for assessing ecosystem functioning at regional or global scales due to their small footprints (essentially considered as point-scale data) and a lack of representativity (Villarreal et al., 2018). In parallel, advances in remote sensing to measure plant traits, vegetation functions and ecosystem functional properties are providing new opportunities to measure ecosystem functioning and functional diversity from regional to global scales (Houborg et al., 2015; Huesca et al., 2015; Lausch et al., 2016; Rocchini et al., 2018). Consequently, combining field-based measurements (such as EC) with remote sensing data may allow for a better integration of information across multiple spatial and temporal scales (Running et al., 1999; Wang et al., 2017). Indeed, multiple studies aim to derive global wall-to-wall maps from fusing flux measurements with earth observation data, though challenges and limitations remain (e.g. FLUXCOM; Jung et al., 2020).

Ecosystem functioning and functional diversity at the regional scale can be assessed as the spatial heterogeneity in functions or in ecosystem functional behaviours by means of satellite-derived Ecosystem Functional Types (EFTs) (Paruelo et al., 2001). Conceptually, EFTs are defined as patches of the land surface that share similar dynamics of matter and energy exchanges between the biota and the physical environment (Alcaraz-Segura et al., 2006, 2013). The concept of EFT is equivalent to the concept of PFTs but applied to a higher level of biological organization. That is, just like plant species can be grouped based on shared functional traits (e.g. growth rates, nitrogen fixation) into PFTs, ecosystems can be grouped based on their common functional dynamics (e.g. productivity, seasonality, phenology) into EFTs (Paruelo et al., 2001). Empirically, remote sensing has been used to identify EFTs mainly through spectral indices related to the carbon dynamics (Paruelo et al., 2001; Alcaraz-Segura ant others 2006; Ivits et al., 2013) but also including other functional aspects such as evapotranspiration, surface temperature, and albedo (e.g., Fernández et al., 2010). In practical terms, EFTs classify ecosystems according to their functioning, distinguishing classes of homogeneous annual dynamics in the land surface spectral properties considered without any prior knowledge of vegetation cover (Fernández et al., 2010; Pérez-Hoyos et al., 2014). Furthermore, contrary to the static PFT classification, EFTs can be produced on an annual basis using the same classification rules, which provides a straightforward way to track interannual changes in ecosystem functioning. EFTs have been used to: describe large-scale functional biogeographical patterns (Ivits et al., 2013), assess the representativeness of environmental observatory networks (Villarreal et al., 2018, 2019), assess the environmental and human controls of ecosystem functional diversity (Alcaraz-Segura et al., 2013), evaluate the effects of land-use changes on ecosystem functioning (Oki et al., 2012), improve weather forecasting (Lee et al., 2013; Müller et al., 2014) and species distribution/abundance models (Arenas-Castro et al., 2018, 2019), and to identify geographic priorities for biodiversity conservation (Cazorla et al., 2020).

So far, EFTs have been identified from satellite remote sensing data (but see Bond-Lamberty et al., 2016; Petrakis et al., 2018). However, it still remains untested whether such top-down-identified EFT classes are biologically meaningful in terms of ecological processes measured on ground, such as biogeochemical fluxes. That is, whether satellite-derived EFT classes empirically differ in their exchanges of energy and matter measured on ground. If so, EFTs could be used as biological entities for mapping the heterogeneity of such key ecosystem processes at regional scales. Mapping EFTs as biological entities that capture the performance of whole ecosystems opens a tangible and feasible way to visualize and monitor the spatial diversity of ecosystem functions from local to global scales, which complements the traditional structural and compositional view of ecosystems (Paruelo et al., 2001; Alcaraz-Segura et al., 2006; Asner et al., 2017). Therefore, linking satellite-derived EFTs identified at large scales to biogeochemical fluxes measured at site level could help to strengthen the ecological significance of the EFT patterns for ecosystem modelling and functional diversity assessments, since it provides empirical evidence for the use of the concept in these areas.

The goal of this study is to provide field-based empirical evidence for the use of satellite-derived EFTs as descriptors of regional heterogeneity in ecosystem functioning measured on ground (i.e., seasonal dynamics of Net Ecosystem Exchange (NEE) between the biota and the physical environment). Our hypothesis was that satellite-derived EFTs should significantly differ in their exchanges of energy and matter with the atmosphere, as estimated with *in situ* field observations. That is, we propose that different satellite-derived EFTs should display significantly different NEE measured using EC technique, while sites under the same EFT should exhibit similar NEE dynamics. If proved, EFTs could serve as biologically meaningful mapping entities to characterize spatial diversity in focal ecosystem functions. To achieve our goal, we used publicly available data across continental Europe, given its high density of EC sites, 1) to characterize the regional patterns of ecosystem functioning by means of satellite-derived EFTs; 2) to assess whether different satellite-derived EFTs correspond to different NEE dynamics measured on the ground with the EC technique; and 3) to assess how EFTs perform compared to traditional PFTs to discriminate among different NEE dynamics.

4.1.2. Methods

Study area

We used NEE information of continental Europe as it has one of the largest densities of EC sites worldwide (Table 4.1.1). Sites were distributed across four biogeographical regions (EEA 2016): Mediterranean (12 sites), Continental (21 sites), Atlantic (9 sites), and Alpine (8 sites).

Only sites with a long-term (i.e., from 3 to 14 years) NEE time-series were included in the analysis (detailed below).

Satellite-derived Ecosystem Functional Types (EFTs)

To characterize the regional heterogeneity in ecosystem functioning across continental Europe, we identified Ecosystem Functional Types (EFTs) based on the 2001-2014 time-series of satellite images of the Enhanced Vegetation Index (EVI) captured by the MODIS-Terra sensor. These images (MOD13Q1.C006 product) provide a maximum composite EVI value every 16 days at a ~230 m spatial resolution. EVI is a proxy for canopy greenness and vegetation carbon gains or primary production (Huete et al., 1999). Based on the approach by Alcaraz-Segura et al., (2013), we identified EFTs using three biologically meaningful metrics of the EVI seasonal curve: the EVI annual mean (EVI_mean; an estimator of annual primary production), the EVI seasonal standard deviation (EVI_SD; a descriptor of seasonality), and the date of maximum EVI (EVI_DMAX; an indicator of phenology).

The range of values of each EVI metric was divided into four intervals, giving a potential number of 64 EFTs (4 × 4 × 4). For EVI_DMAX, the four intervals agreed with the four seasons of the year. For EVI_mean and EVI_SD, we extracted the first, second, and third quartiles for each year and then calculated their interannual average for the 14-year period. To name EFTs, we used two letters and a number: the first capital letter indicates net primary production (EVI_mean), increasing from A to D; the second small letter represents seasonality (EVI_SD), decreasing from a to d; the numbers are a phenological indicator of the growing season (EVI_DMAX), with values 1-spring, 2-summer, 3-autumn, 4-winter. To summarize the ecosystem functional diversity of the 2001–2014 period, we calculated the dominant EFT (i.e., the mode value for each pixel) of the period.

Table 4.1.1. Main characteristics of the 50 Eddy Covariance (EC) sites in the study area. Data from FLUXNET 2015 dataset

ID	Site	Country	PFT	EFT code	Ecoregion	n years (2001-2014)	Elevation (m)	Latitude	Longitude
AT-Neu	Neustift/Stubai Valley	Austria	Grasslands	Da2	Alpine	11 (2002-2013)	970	47.116	11.317
BE-Bra	Brasschaat (De Inslag Trees)	Belgium	Mixed Trees	Cc1	Atlantic	14 (2001-2014)	16	51.309	4.520
BE-Lon	Lonzee	Belgium	Croplands	Ba1	Atlantic	11 (2004-2014)	167	50.552	4.744
BE-Vie	Vielsalm	Belgium	Mixed Trees	Bc1	Continental	14 (2001-2014)	439	50.305	5.998
CH-Cha	Chamau grassland	Switzerland	Grasslands	Db1	Continental	10 (2005-2014)	393	47.210	8.410
CH-Dav	Davos-Seehorn forest	Switzerland	Evergreen Needleleaf Trees	Ac2	Alpine	14 (2001-2014)	1639	46.815	9.855
CH-Fru	Fruebuel grassland	Switzerland	Grasslands	Da2	Continental	10 (2005-2014)	982	47.115	8.537
CH-Lae	Laegeren	Switzerland	Mixed Trees	Da1	Continental	11 (2004-2014)	689	47.478	8.365
CH-Oe1	Oensingen1 grass	Switzerland	Croplands	Cb1	Continental	7 (2002-2008)	450	47.285	7.731

ID	Site	Country	PFT	EFT code	Ecoregion	n years (2001-2014)	Elevation (m)	Latitude	Longitude
CZ-BK1	Bily Kriz-Beskidy Mountains	Czech Republic	Evergreen Needleleaf Trees	Cc1	Continental	11 (2004-2014)	875	49.502	18.536
CZ-BK2	Bily Kriz-grassland	Czech Republic	Mixed Trees	Ac1	Alpine	9 (2004-2012)	855	49.494	18.542
CZ-wet	CZECHWET	Czech Republic	Croplands	Ba1	Continental	9 (2004-2012)	426	49.024	14.770
DE-Akm	Anklam	Germany	Wetlands	Ba1	Continental	5 (2010-2014)	-1	53.866	13.683
DE-Geb	Gebesee	Germany	Croplands	Ba1	Continental	14 (2001-2014)	161	51.100	10.914
DE-Gri	Grillenburg-grass station	Germany	Grassland	Da2	Continental	11 (2004-2014)	385	50.949	13.512
DE-Hai	Hainich	Germany	Mixed Trees	Ca1	Continental	12 (2001-2012)	430	51.079	10.452
DE-Kli	Klingenberg	Germany	Croplands	Ba1	Continental	11 (2004-2014)	478	50.892	13.522
DE-Lkb	Lackenberg	Germany	Evergreen Needleleaf Trees	Ab2	Continental	5 (2009-2013)	1308	49.099	13.304
DE-Lnf	Leinefelde	Germany	Deciduous Broadleaf Trees	Da1	Continental	11 (2002-2012)	451	51.328	10.367

ID	Site	Country	PFT	EFT code	Ecoregion	n years (2001-2014)	Elevation (m)	Latitude	Longitude
DE-RuR	Rollesbroich	Germany	Grasslands	Da2	Continental	4 (2011-2014)	515	50.621	6.304
DE-RuS	Selhausen Juelich	Germany	Croplands	Cb1	Atlantic	4 (2011-2014)	103	50.865	6.447
DE-Seh	Selhausen	Germany	Croplands	Cb1	Atlantic	4 (2007-2010)	103	50.870	6.449
DE-Spw	Spreewald	Germany	Mixed Trees	Ca1	Continental	5 (2010-2014)	61	51.892	14.033
DE-Tha	Tharandt-Anchor Station	Germany	Evergreen Needleleaf Trees	Bc1	Continental	14 (2001-2014)	385	50.963	13.566
DK-Eng	Enghave	Denmark	Croplands	Ca1	Continental	4 (2005-2008)	10	55.690	12.191
DK-Sor	Soroe-LilleBogeskov	Denmark	Deciduous Broadleaf Trees	Da1	Continental	14 (2001-2014)	40	55.485	11.644
ES-Amo	Amoladeras	Spain	Shrublands	Ad4	Mediterranea	6 (2007-2012)	58	36.833	-2.252
ES-LJu	Llano de los Juanes	Spain	Shrublands	Ad1	Mediterranea	10 (2004-2013)	1600	36.926	-2.752
FR-Fon	Fontainebleau	France	Deciduous Broadleaf Trees	Da1	Atlantic	10 (2005-2014)	103	48.476	2.780
FR-Gri	Grignon	France	Croplands	Cc1	Atlantic	11 (2004-2014)	125	48.844	1.951

ID	Site	Country	PFT	EFT code	Ecoregion	n years (2001-2014)	Elevation (m)	Latitude	Longitude
FR-Pue	Puechabon	France	Mixed Trees	Cd1	Mediterranea	14 (2001-2014)	270	43.741	3.595
IT-BCi	Borgo Cioffi	Italy	Croplands	Db4	Mediterranea	11 (2004-2014)	20	40.523	14.957
IT-CA1	Castel d`Asso1	Italy	Croplands	Bd1	Mediterranea	4 (2011-2014)	200	42.380	12.026
IT-CA2	Castel d`Asso2	Italy	Croplands	Cb1	Mediterranea	4 (2011-2014)	200	42.377	12.026
IT-CA3	Castel d`Asso 3	Italy	Croplands	Bd1	Mediterranea	4 (2011-2014)	197	42.380	12.022
IT-Col	Collelongo-Selva Piana	Italy	Deciduous Broadleaf Trees	Da1	Alpine	14 (2001-2014)	1560	41.849	13.588
IT-Cpz	Castelporziano	Italy	Evergreen Needleleaf Trees	Dd1	Mediterranea	9 (2001-2009)	68	41.705	12.376
IT-Lav	Lavarone (after 3/2002)	Italy	Evergreen Needleleaf Trees	Bc1	Alpine	12 (2003-2014)	1353	45.956	11.281
IT-MBo	Monte Bondone	Italy	Grasslands	Aa1	Alpine	11 (2003-2013)	1550	46.014	11.045
IT-Noe	Sardinia/Arca di Noe	Italy	Shrublands	Ad1	Mediterranea	11 (2004-2014)	25	40.606	8.151

ID	Site	Country	PFT	EFT code	Ecoregion	n years (2001-2014)	Elevation (m)	Latitude	Longitude
IT-Ro1	Roccarespampani1	Italy	Deciduous Broadleaf Trees	Da1	Mediterranea	8 (2001-2008)	235	42.408	11.930
IT-Ro2	Roccarespampani2	Italy	Deciduous Broadleaf Trees	Da1	Mediterranea	11 (2002-2012)	160	42.390	11.920
IT-SRo	San Rossore	Italy	Evergreen Needleleaf Trees	Cd3	Mediterranea	12 (2001-2012)	6	43.727	10.284
IT-Tor	Torgnon	Italy	Grassland	Aa1	Alpine	7 (2008-2014)	1260	45.844	7.578
NL-Hor	Horstermeer	Netherlands	Mixed Trees	Da1	Atlantic	8 (2004-2011)	2	52.240	5.071
NL-Loo	Loobos	Netherlands	Evergreen Needleleaf Trees	Bd2	Atlantic	14 (2001-2014)	25	52.166	5.743

Eddy covariance (EC) sites for net ecosystem exchange (NEE)

To obtain NEE fluxes, 50 EC sites were selected across our study area from the FLUXNET2015 dataset (Table 4.1.1). The FLUXNET network (Baldocchi et al., 2001) provides a high-quality, community-based globally distributed dataset of exchanges of CO_2, H_2O, and energy between the biosphere and the atmosphere measured using the EC technique (Baldocchi, 2003). We used data of NEE of CO_2 (NEE_VUT_REF, gC m^{-2} d^{-1}) from the FLUXNET2015 database, which includes NEE data using a Variable Ustar Threshold (VUT) for each year, selected on the basis of the model efficiency (MEF). The MEF analysis is repeated for each half-hourly data (Baldocchi et al., 2001). We selected sites that: (a) were located in our study area; (b) provided more than three consecutive years of data over the 2001-2014 period; (c) provided daily averages of NEE calculated from half-hourly data (DD); and (d) had quality control information (i.e. NEE_VUT_REF data with quality control flag $QC > 1$ were removed since they represent medium and poor quality gap filled data).

To assess whether different satellite-derived EFT classes correspond to different NEE dynamics and whether sites under the same EFT exhibit similar NEE dynamics, we applied discriminant analysis. Discriminant analysis allowed us to examine the homogeneity within each EFT class as well as the differences among EFT classes based on the annual dynamics of NEE as a predictor variable (Williams ,1981, 1983). We selected the EFT of the MODIS pixel where each EC site was located and its corresponding interannual average of the seasonal cycle of NEE for the available years. EC sites fluxes were regarded as the ground truth standard against which the satellite data were compared to calculate five performance metrics: Kappa, Accuracy, Precision, Recall, and F1 score (Table 4.1.2).

Table 4.1.2. Metrics, interpretations and equations used to evaluate and compare results from the discriminant analysis, Pr(a) is the relative observed agreement between observations, and Pr(e) is the hypothetical probability of agreement by chance. True Positives are the correctly classified as positive, True Negative are the correctly classified as negative, Positives are all positives including false positives (i.e. including falsely classified as positive, Type I error) and, Negatives are all negatives including false negatives (i.e. falsely classified as negative, Type II error). All performances metrics oscillate between 0 (disagreement) and 1 (maximum agreement).

Metric	Meaning	Equation
Kappa	Measures the percentage of data values in the main diagonal of the contingence table and adjusts these values for the amount of agreement that could be expected due to chance alone	K= Pr(a)-Pr(e) / 1-Pr(e)
Accuracy	Degree of closeness of measurements of a quantity to that quantity's true value	Accuracy = (True Positives + True Negatives)/ (Positives+Negatives)
Precision	Fraction of relevant instances among the retrieved instances (also called positive predictive value, i.e., how many EFTs were well discriminated)	Precision = True Positives / (True Positives+False Positives)
Recall	Fraction of relevant instances that have been retrieved over the total amount of relevant instances	Recall = True Positives / (True Positives+False Negatives)
F1	Considers both the Precision and the Recall of the test to compute the score	F1 score= 2 × (Precision × Recall) / (Precision + Recall)

Comparing how EFTs and PFTs discriminate different NEE dynamics

The PFT corresponding to each EC site was assigned by the site's principal investigators using the International Geosphere-Biosphere Programme (IGBP) legend. We verified the assigned PFTs using the MODIS MCD12Q1 land cover product. The PFT categories present in the EC sites were: cropland (15 sites), deciduous broadleaf trees (6), evergreen needleleaf trees (10), grassland (5), mixed trees (8), shrubland (3), and wetland (1) (Table 4.1.1).

During the comparison of the performance of PFTs and EFTs to discriminate the seasonal dynamics of NEE, we took into account the unbalanced sample size due to the different number of classes of EFTs (18) and PFTs (7) represented by FLUXNET2015 and to the different number of EC sites per class (which ranged between 3 and 31). To do this we considered the following steps:

First, we calculated all possible combinations without repetitions between the 18 EFT and the 7 PFT classes ($C_{(18,7)} = 31834$). Second, we discarded all combinations that had different number of EC sites in the EFT and PFT classes being combined. Third, for each combination, we applied discriminant analysis to assess how the EFT classification and the PFT classification performed to discriminate the seasonal dynamics of NEE. For each discriminant analysis, we obtained five metrics of performance (Table 4.1.2). Fourth, to assess whether there existed significant differences in the performance metrics between EFTs and PFTs, we applied the Wilcoxon non-parametric test. For each combination of number of classes and number of EC sites there was a different number of discrimant analysis in the EFT subset and in the PFT subset (Table S4.1.1). To account for such unbalanced design during the Wilcoxon test, we fixed the sample size to the smaller subset (either from the EFT or the PFT classification) and randomly bootstrapped the performance metrics from the bigger one. Fifth, for the final report, we calculated the mean and standard deviation of each metric obtained by the EFTs and PFTs classifications, the average p-value, and the percentage of times that we obtained significant differences (p-value <0.05) between EFTs and PFTs.

4.1.3. Results

Regional heterogeneity in ecosystem functioning by means of satellite-derived EFTs

The map of the EVI-derived proxies of productivity (EVI_mean), seasonality (EVI_SD) and phenology (DMAX) (Figure S4.1.1), and their integration into EFTs (Figure 4.1.1) provided a characterization of the spatial patterns of our focal ecosystem function across Europe. At continental scale, productivity decreased eastwards and southwards. Seasonality was greater in cultivated and mountainous areas, and the most frequent EVI maxima occurred in spring and summer.

The greatest EVI_mean (D) was reached in the Atlantic and Continental biogeographic regions, while the lowest EVI_mean (A) occurred in the western part of mediterranean region, corresponding to most of the Iberian Peninsula, some parts of the Italian Peninsula the mountainous areas of the Alpine region and in the eastern part of the Continental region. The greatest seasonality (a) occurred in the highest altitudes of: the Alpine region (peaks of Alps), the Continental region (southwestern, northwestern and eastern part), and eastern part of the Atlantic region. The lowest seasonality (d) was observed in the western part of mediterranean region, specifically in the Iberian Peninsula, in surroundings of the Gulf of Lion and in Coastal western places of the Atlantic region. The phenological indicator of the growing season, DMAX, showed that most areas of the mediterranean region have the EVI maxima in spring (1) and autumn (3). EVI maxima in spring (1) was also observed in the Continental and Alpine regions. Maximas in summer (2) were identified in western places of the Atlantic region and in most of the Alpine region. EVI maxima in autumn (3) also occurred in western places of the Atlantic region. Maxima in winter (4) were rare and mainly occurred in the eastern part of the Atlantic region, where all ranges of maximum greening were found.

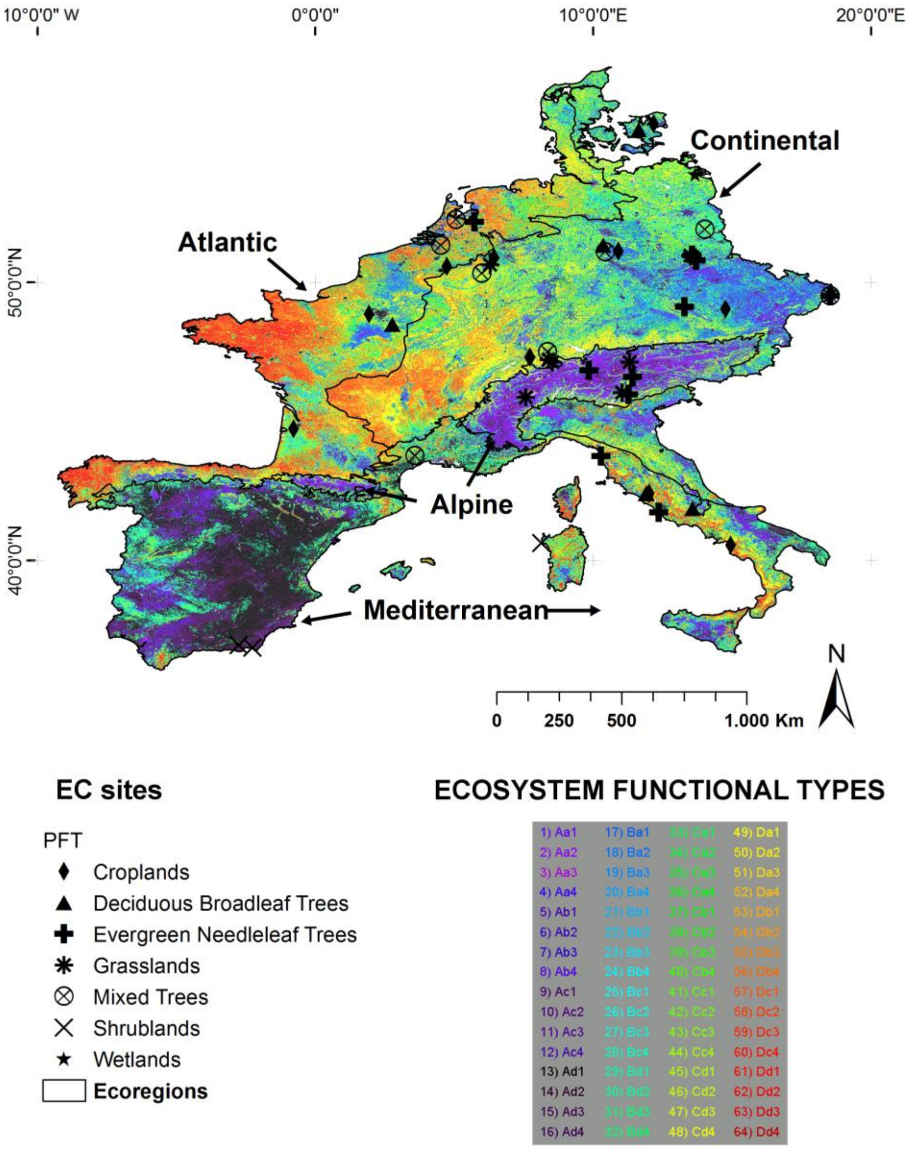

Figure 4.1.1. Ecosystem Functional Types (EFTs) based on MODIS-EVI dynamics (~230 m resolution) and Eddy Covariance (EC) sites corresponding to the 2001–2014 period. Capital letters in the legend correspond to the EVI annual mean (EVI_mean) level, ranging from A to D for low to high productivity. Small letters show the seasonal standard deviation (EVI_SD), ranging from a to d for high to low seasonality of carbon gains. The numbers indicate the season when the maximum EVI took place (DMAX): (1) spring, (2) summer, (3) autumn, (4) winter. Places with eddy covariance sites are shown with symbols, where each one represents a different plant functional type. Biogeographical regions are based on the official European biogeographical regions map (EEA, 2016).

Ground-based NEE of the satellite-derived EFTs

In total, 20 of the 64 potential EFTs, containing 73.10 % of our study area, were represented by the network of the 50 long-term EC sites that met our selection criteria (Figure 4.1.2). The most abundant EFT, Da1, showed high productivity (D) high seasonality (a) and maximum EVI in spring (1) (Figure 4.1.2). Da1 occupied 10.87% of the surface and was distributed throughout the study area, but abundantly in the western and southern extremes of the Atlantic Region). Da1 was represented by 8 EC sites that exhibited NEE with a strong seasonal variability, with a pronounced peak of carbon assimilation between -7.23 and -7.46 gC m^{-2} d^{-1} in spring (Figure 4.1.4), and corresponded with the most abundant ecosystem in Europe, the Deciduous Broadleaf and Mixed Trees (Table S4.1.2). The second most abundant EFT, Ad1, showed low productivity (A), low seasonality (d) and maximum EVI also in spring (1). Ad1 occupied 9.98% of the territory and was located mainly in the Iberian Peninsula (Figure 4.1.1). Ad1 was represented by 2 EC sites (Figure 4.1.2) that exhibited NEE dynamics with low seasonality and peak of carbon assimilation between -0.72 and -1.98 gC m^{-2} d^{-1} in spring (Figure 4.1.4) and was concentrated in areas dominated by shrub vegetation (Table S4.1.2).

In terms of abundance in EC sites, the EFT Da1 mentioned above was represented by 8 EC sites, followed by EFT Ba1 and Cb1 with 5 EC sites. The first one, EFT Ba1, was also abundant, occupying 7.4% of the total surface (Figure 4.1.2), and was located mainly in the eastern part of the study area (Atlantic and Continental regions) (Figure 4.1.1). The second one, EFT Cb1, was not as abundant as the previous one (3.61%), and was located in central areas of the Atlantic and Continental regions. NEE dynamics were characterized by high (a) and medium-high (b) seasonality and peak time of carbon assimilation between -6.40 and -7.53 gC m^{-2} d^{-1} in spring. In both cases, these places corresponded with cereal crops (Table S4.1.2), and NEE dynamics had a higher standard deviation in the annual curve, due to the variability of such crops.

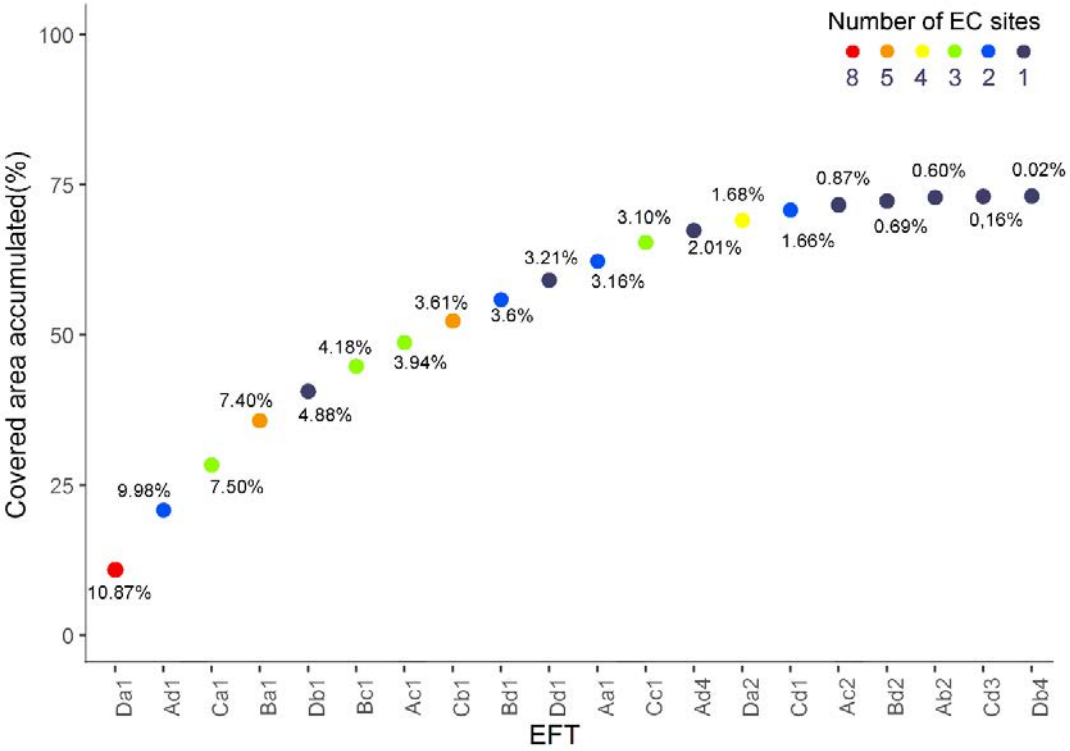

Figure 4.1.2. Accumulated covered area by the Ecosystem functional types (EFTs; in %) which are represented in the study (ordered from highest to lowest). Colours indicated the number of eddy covariance (EC) sites and the numbers indicate the area occupied by each of these EC sites (in %).

Our discriminant analysis showed that EFTs significantly differed in NEE measured *in situ* with the EC technique. The average of the performance metrics obtained from the discrimination that satellite EFTs made of EC site NEE ranged between 0.953 to 0.978 (Table 4.1.3 a). NEE dynamics significantly differed between different EFTs, but was similar within the same EFTs (Figure S4.1.2). For example, the EFT "Da1", which had high productivity, high seasonality and spring EVI maxima, also showed high average NEE values, high seasonality in NEE, and maximum carbon assimilation in spring (Figure 4.1.4, EC sites DE-Lnf, FR-Fon). The EFT "Bc1", with medium to high productivity, medium seasonality and spring EVI maxima, was also characterized by moderate seasonality in terms of NEE and maximum carbon assimilation in spring (Figure 4.1.4a for EC sites BE-Vie, DE-Tha). Contrary, the EFT "Ad1", which had low productivity, low seasonality and EVI spring maxima, also showed low average NEE, low seasonality in NEE, and a peak of maximum carbon assimilation in spring (ES-LJu, IT-Noe). As another example, the EFT "Cb1", with medium productivity, medium-high seasonality, and spring EVI maxima, also showed medium to high seasonality in terms of NEE and maximum carbon assimilation in spring (Figure 4.1.4a for EC sites DE-Seh, DE-RuS).

Table 4.1.3. Mean performances metrics, their standard deviation (SD) and differences in: Kappa, Accuracy, Precision, Recall and F1 values obtained from discriminant analysis of combinations with equal number of classes and EC sites of (a) ecosystem functional types (EFTs) and (b) plant functional types (PFTs). To assess for significant differences, we applied a Wilcoxon-test (p-values showed), and we calculated the percentage of cases in which differences between EFTs or PFTs with NEE were significant (% sig), in this case, none.

	a. EFTs		**b. PFTs**		**Difference**	
	mean	**SD**	**mean**	**SD**	**p-value**	**% sig**
Kappa	0.953	0.067	0.923	0.078	1	0
Accuracy	0.972	0.040	0.952	0.051	1	0
Precision	0.967	0.047	0.959	0.057	1	0
Recall	0.978	0.033	0.960	0.040	1	0
F1	0.972	0.040	0.959	0.048	1	0

Comparison between EFTs and PFTs to discriminate NEE measured by EC

EFTs performed marginally better than PFTs in capturing differences in NEE dynamics measured on ground (Table 4.1.3). The average across all discriminant analysis in all performance indices was marginally but not significantly higher for EFTs (e.g. mean Kappa =

0.953) than for PFTs (e.g. mean Kappa = 0.923) (Table 4.1.3, Figure 4.1.3); but, the standard deviation across all discriminant analysis was higher for PFTs (e.g. sd of Kappa = 0.078) than for EFTs (e.g. sd of Kappa = 0.067). Although performance indices showed that EFTs marginally improved the performance metrics of the analysis, no significant differences between the performance metrics of EFTs and PFTs were detected by the Wilcoxon-test in any indices (Table 4.1.3).

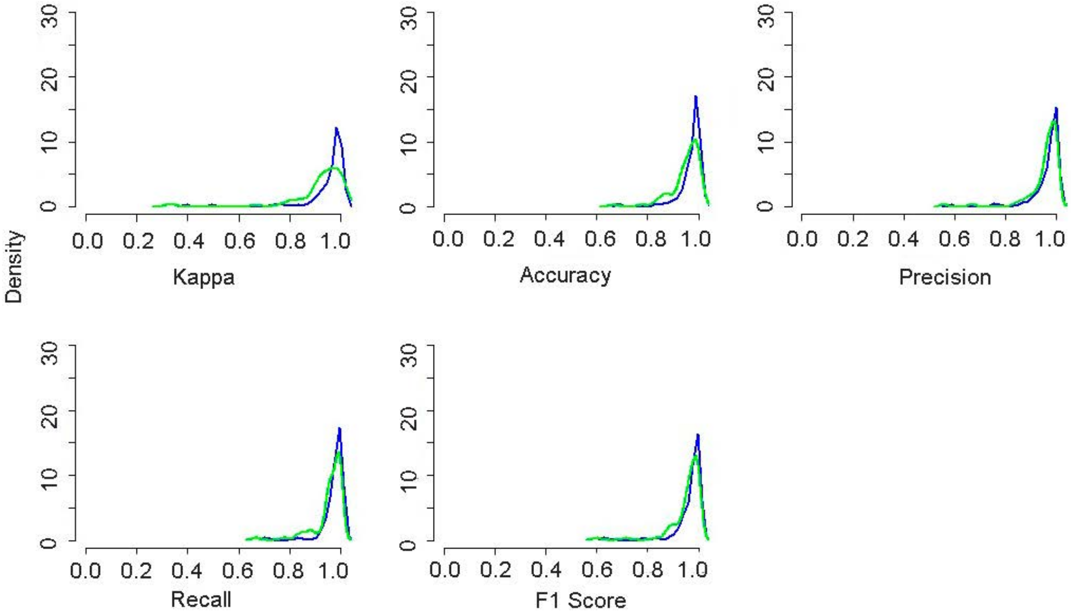

Figure 4.1.3. Histograms of performances from discriminant analysis for all combinations of Ecosystem Functional Types (EFTs) and Plant Functional Types (PFTs) with equal number of classes and EC sites. Blue lines correspond to EFTs and green lines to PFTs.

In general, NEE dynamics was similar for the same PFT or EFT across EC sites (Figure 4.1.4), though there existed some exceptions, particularly for PFTs (Figure 4.1.4b; Figure S4.1.3). For instance, sites corresponding to the PFT "deciduous broadleaf trees" or to the EFT "Da1" always showed similar NEE (Figure 4.1.4; Table 4.1.1). However, for PFTs, NEE dynamics for "evergreen needleleaf trees" exhibited a different seasonality and maximum carbon assimilation across sites (Figure 4.1.4b for EC sites CH-Dav, DE-Lkb). Differences in NEE dynamics across sites were also observed for shrublands where the ES-LJu site (EFT Ad1) was assimilating carbon throughout the year, particularly in spring, while the ES-Amo site (EFT Ad4) was mostly emitting carbon throughout the year but in the winter. Much bigger differences in NEE occurred in croplands, with maximum carbon sequestration occurring in different seasons, particularly in april and may (Figure 4.1.4b, for sites CH-Oe1 and CH-Oe2 (EFT Cb1).

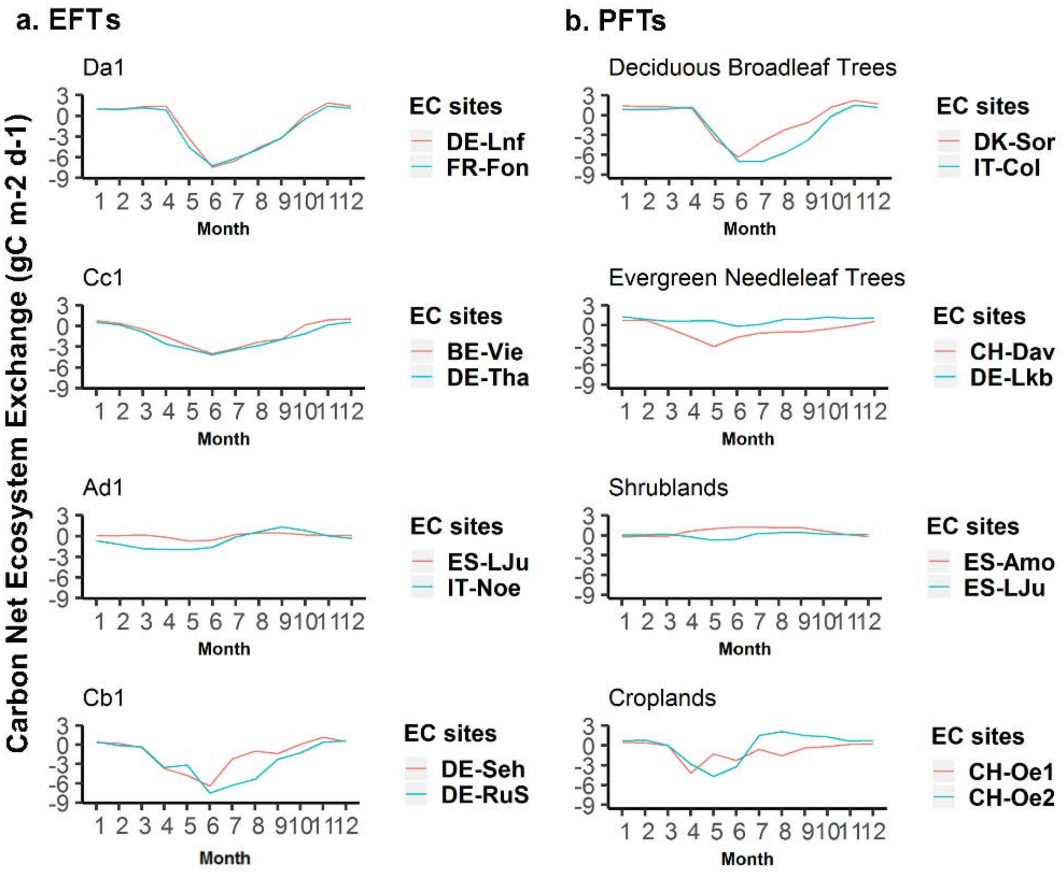

Figure 4.1.4. Comparison of the variability within and across classes of Ecosystem Functional Types (EFTs) and Plant Functional Types (PFTs) in the seasonal dynamics of NEE. a) Variability inter EFTs:

annual mean of NEE dynamics from different places with the same EFT; and b) variability inter PFTs and intra EFTs: annual mean of NEE dynamics from different places with the same PFT and different EFT.

4.1.4. Discussion

Remotely-sensed EFTs successfully mapped functionally homogeneous land patches in terms of NEE dynamics measured *in situ* with the EC technique. Furthermore, EFTs performed marginally better than the commonly used PFTs to discriminate among different NEE seasonal dynamics (Table 4.1.3), while having the advantage of being quicker and sensitive response to short-term changes in ecosystem performance than composition or structure, and can be produced on an annual basis using the same classification rules, which provides a straightforward way to track interannual changes in ecosystem functioning (Müller et al., 2014). Our focal ecosystem function was NEE dynamics, which is related to primary production, one of the most essential and integrative descriptors of ecosystem functioning (Virginia and Wall, 2010). Hence, satellite-derived EFT classifications could be used to monitor the status and changes of the regional heterogeneity or spatial diversity of the essential biodiversity variable of ecosystem production, as a surrogate of the overall ecosystem performance (Jax, 2010; Pettorelli et al., 2016).

EFTs capture differences in NEE

EFTs allowed us to characterize the regional heterogeneity of ecosystem functioning dynamics (in terms of NEE) across Europe. Twenty out of the 64 EFTs identified in Europe (corresponding to 73% of the study area) were represented by at least one EC site in the FLUXNET2015 dataset with at least three years of data. Our approach could help to the assessment of the carbon dynamics at regional scale by providing homogeneous land areas in terms of their primary production dynamics (Running et al., 2004, Zhang et al., 2015). Understanding the regional patterns and drivers of the differences in carbon dynamics at the regional scale could contribute to reduce the uncertainties on the global carbon balance between the atmosphere and the biosphere (Beer et al., 2010). Here, we quantified and mapped by means of EFTs the spatio-temporal characteristics of carbon dynamics, a crucial aspect for biodiversity conservation and ecosystem services maintenance under a global change context (Midgley et al., 2010).

EFTs captured spatial differences in NEE seasonal dynamics as good as or marginally better than mainstream approaches such as PFTs. In the real world, different areas may respond differently to environmental changes despite being dominated by the same PFT and, frequently, ecosystem-process models (parameterized for a specific PFT) may not be able to represent these differential responses (Vargas et al., 2013). Normally, the parameterization of a particular PFT is homogeneous within such PFT and does not change, for instance, according to the ecophysiological status of a particular area or its intrinsic plasticity (Müller et al., 2014). In addition, land-cover maps based on a PFT legend are static and difficult to update, while EFT are a data-driven classification, through which we can annually detect changes in exchange of matter and energy between the ecosystems and the atmosphere in response to environmental variability. In this sense, the literature (Bret-Harte et al., 2008; Suding et al., 2008; Clark et al., 2016; Saccone and Virtanen 2017; Thomas et al., 2018) has pointed out that the PFT approach is not straightforward enough to represent ecosystem functional properties at the ecosystem level.

EFT spatial patterns and environmental controls

EFTs allowed to characterize the regional heterogeneity of ecosystem functioning across Europe. In relation to the three descriptive attributes of ecosystem functioning from which the EFTs were constructed, we found general patterns determined by environmental controls. The role of environmental variables (abiotic and biotic) that control ecosystem processes is different according to the level of biological organization and the spatial scale considered (Reed et al., 1993; Pearson and Dawson, 2003). Ecosystem processes in natural areas are known to be mainly driven by precipitation (Lauenroth et al., 1978), temperature (Rosenzweig and Dickinson 1968; Jobbagy et al., 2002), soil characteristics (NoyMeir 1973) and vegetation structure (Epstein et al., 1998). In this case, EFTs productivity showed a decrease from east to west influenced by rainfall patterns determined by the Gulf Stream

(Palter 2015), which also determines changes in vegetation. Regarding seasonality of EVI, it increased in relation to two factors: 1) the altitude, having the highest values of seasonality in the mountainous areas (influenced by changes in precipitation, temperature and thus, in vegetation) and; 2) the crop areas, where management practices, harvests and crop changes are responsible of this dynamic and therefore it cannot be explained by natural environmental controls. Phenology in Europe was characterized by peaks of maximum EVI in spring and summer, when the availability of water (precipitation) and energy (temperature) for vegetation is at its optimum (Whittaker et al., 2003).

Boundaries of the biogeographical regions (EEA 2016) were consistent with the EFTs (Figure 4.1.1), but while the classification from EEA is static, EFTs provide a data-driven classification that could be better coupled to ecosystem functioning. The Alpine region was dominated by EFTs with low productivity, high seasonality and maxima in summer. In the high peaks, the vegetation is reduced to a low density of highly adapted plants which are able to tolerate extreme conditions, i.e. the short growth period and fluctuating air temperature, and therefore, has a low productivity, also detected in the global primary productivity patterns of Beer et al., (2010) and Zhang et al., (2017). In highest altitudes, snow is present over most of the year, leaving only a short time period for the development of the plants, mainly in summer, leading to a summer maximum and a high seasonality (Sundseth, 2009a).

The mediterranean region was characterized by a high heterogeneity of EFTs due to their high habitat diversity, i.e high mountains and rocky shores, thick scrub and semi-arid steppes, coastal wetlands and sandy beaches, constituting a global biodiversity hotspot (Myers et al., 2000). The main driver of ecosystem functional diversity is the climate (characterised by hot dry summers and cool winters) (Lionello et al., 2006), in combination with human influence, (i.e. livestock grazing, forest cultivation and forest fires) (Blondel and Aronson, 1999).

The Atlantic region was characterized by EFTs with high productivity, high seasonality and maximum greening in spring, due to the mild winters, cool summers and predominantly westerly winds and moderate rainfall throughout the year (Hurrel, 1995). These conditions favour the presence of non-water limited deciduous species with high productivity, resulting in a high seasonality. Due to the anthropogenic influence, agricultural landscapes are very common in this region, being one of the five major agricultural regions of Europe according to Kostrowicki (1991). Thus, the region's high productivity must be partly attributed to irrigation, and high seasonality is driven by harvest and cropping cycles.

Finally, in the Continental region the ecosystem functioning varied largely in productivity, reflecting regional climatic patterns. In the eastern part of the continental region, extremes of hot and cold temperatures, wet and dry conditions, are more frequent and have a strong impact on ecosystem functioning (dominant EFT was Aa1, low productivity, high seasonality and maximum in spring). In fact, these areas are mountainous and experience sub-alpine conditions. Moving west, climate is characterized by relatively small fluctuations of temperature due to the buffering effect of the nearby ocean and the flat landscape (Da1 and Ca1 in the transition) (Sundseth, 2009b).

Opportunities and limitations of EFTs

Since EFTs can inform at an annual basis on homogeneous patches on the land surface in terms of ecosystem functioning, they offer opportunities to be applied in ecology and conservation compared to less dynamic approaches (such as PFTs), but they also have some limitations.

The concept of EFT has been highlighted as "the first serious attempt to group ecosystems (at large scales) on the basis of shared functional behaviour" (Mucina, 2019), and its strength for being applied as a classification scheme is determined by its ability to translate ecosystem functions into discrete entities that can be mapped. EFTs are identified by remote sensing tools from aggregated measurements of ecosystem functions at the pixel level, which in practice represents information of the performance of the whole ecosystem at that grain scale. Having the possibility of mapping entities (EFTs) that reflect the performance of the whole ecosystem opens an straightforward, tangible and biologically meaningful way to measure ecosystem functions at regional scale, complementing our traditional view of ecosystems (Paruelo et al., 2001; Alcaraz-Segura et al., 2006; Butchart et al., 2010; Asner et al., 2017). In particular, satellite-derived dynamic functional classifications, such as EFTs, have several advantages over using other static approaches, such as PFTs. Satellite-derived EFAs and EFTs 1) are capable of capturing differences in ecosystem processes as measured in the field; 2) they provide a useful framework for understanding the mechanisms underlying large-scale ecological changes (Cabello et al., 2016; Alcaraz-Segura et al., 2017; Requena-Mullor et al., 2017, 2018; Arenas-Castro et al., 2018; Lourenço et al., 2018; Vaz et al., 2018); 3) they offer a faster response than compositional or structural approaches to environmental changes (McNaughton, 1989; Mouillot et al., 2013), which are are particularly noticeable at the ecosystem level (Vitousek, 1994); 4) they can be more easily monitored and updated than structural or compositional ones under a common protocol in space and time, at different spatial scales and over large extents (Paruelo et al., 2001); 5) they can complement information on vegetation structure and composition (e.g., canopy architecture, vegetation type, PFT), because they constitute complementary dimensions of biodiversity complexity (Noss 1990; Pettorelli et al., 2016); 6) they facilitate the direct assessment of ecosystem functions and services (Costanza et al., 2006; Dzikiti et al., 2016; Hellmann et al., 2017) and would link key dimensions of biodiversity to ecosystem processes including the carbon cycle, the water cycle and the provisioning of ecosystem services;7) they have already been proposed as essential variables for monitoring biodiversity (Pettorelli et al., 2016; Alcaraz-Segura et al., 2017).

However, our approach is still subjected to some challenges. First, EFTs that are represented by several EC sites could be parameterized in terms of NEE dynamics, though not all EFTs (18%) are represented yet. Second, the footprint or spatial resolution of the EC measurements oscillates between 50 m and 200 m (depending on the micrometeorological conditions and on the vegetation type, e.g. forest EC sites footprints are generally larger than in grassland EC sites), while the MODIS pixel used have a resolution of ~231 m. Such limitation could be handled in future works with the use of satellites with higher spatial resolution such as Landsat (30 m/pixel) or Sentinel-2 (10 m/pixel). Third, different ecosystems in terms of other functional aspects (e.g. evapotranspiration, heat exchange...) can be classified here as the same EFT from the primary production dynamics aspect, since we used it as our focal function. However, EFTs could also be identified to characterize the spatiotemporal heterogeneity of multiple ecosystem processes and functions at different scales, including other functional aspects (e.g. albedo, evapotranspiration, heat exchange) (Fernandez et al., 2010). Finally, the incorporation of EFTs in earth system models is difficult, since these models can use simple and small numbers of categories in a variable, and some models might not be able to run with so many (64) EFT categories, nevertheless there are works that incorporate EFTs into earth system models (Lee et al., 2013; Müller et al., 2014). The incorporation of these types of variables (dynamic and easily accessible) into the models would be useful for the monitoring and sustainable management of carbon reservoirs at time scales of in the short to medium term.

4.1.5. Conclusions

Satellite-derived EFTs are an ecosystem functional classification built from satellite observations of radiation exchanges between the land surface and the atmosphere that manage to identify homogeneous land patches in terms of an essential ecosystem function, ecosystem production measured on ground by means of NEE dynamics. EFTs performed as good as or marginally better than PFTs to discriminate different NEE dynamics, what implies two main advantages EFTs can be easily updated for any region of the world at an annual frequency based on open satellite information, and EFTs maps are more sensitive to environmental changes than vegetation composition or structure.

Our results showed the capability of using ecosystem functional attributes for grouping ecosystems at large scales according to their different carbon gains dynamics. Such classification, based on the essential biodiversity variable of ecosystem production as a focal ecosystem function opens the possibility of assessing and monitoring ecosystem functional diversity, the spatial heterogeneity in ecosystem functioning, and carbon-related ecosystem services at regional to global scales. Therefore, our study proofs that satellite-derived EFTs provide a validated tool to assess and monitor ecosystem functioning with potential applications in ecosystem monitoring and modeling, and in biodiversity and carbon managing programs.

4.1.6. References

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4.1.7. Appendices

Table S4.1.1. Number of discriminant analysis (i.e. combinations) for each number of classes and number of EC sites in the EFT and in the PFT subsets.

n EC sites	**n classes EFTs**						**n classes PFTs**					
	2	**3**	**4**	**5**	**6**	**7**	**2**	**3**	**4**	**5**	**6**	**7**
3	32						6					
4	38	56					3	3				
5	24	112					2	6				
6	26	160	392				5	2	3			
7	12	160	536				3	7	2			
8		160	585	1078				9	3	1		
9	10	126	592				1	3	9			
10		96	520	1640				2	7	3		
11	4	82	464	1668			4	3	2	5		
12	1	60	373	1655	3504		6	2	6	2	1	
13		50	320	1466	3868			12	3	3	1	
14		28	238	1312				6	6	6		
15		27	196	1112	3676			5	12	1	3	
16		12	136	922	3396			16	4	6	2	
17		8	100	746		7252		9	17	4		1
18		2	54	590	2597			2	24	6	2	
19			28	428					8	21		
20			12	267	1817				11	16	6	
21			4	160	1332				15	7	11	
22			1	78	945	4153			4	21	4	2
23				36	580	3308				13	9	2
24				10	337					5	17	
25				4	154	1610				12	4	7
26					70	958					6	5
27					20						8	
28					6	232					4	4
29						90						2
30						25						3
31						4						7

Table S4.1.2. Contingency table (in %) of EFTs and PFTs. The numbers show the percentage of EFTs classified in each PFT. EFTs are coded as follows: capital letters correspond to the EVI annual mean (EVI_mean) level, ranging from A to D for low to high productivity. Small letters show the seasonal standard deviation (EVI_SD), ranging from a to d for high to low seasonality of carbon gains. The numbers indicate the season when the maximum EVI took place (DMAX): (1) spring, (2) summer, (3) autumn, (4) winter.

%	Cropland	Deciduous broadleaf trees	Evergreen needleleaf trees	Grassland	Mixed trees	Shrubland	Wetland
Aa1				29	12		
Ab2			10				
Ac1			20				
Ac2			10				
Ad1						67	
Ad4					12	33	
Ba1	27						100
Bc1			20				
Bd1	13				25		
Bd2			10		13		
Ca1	7						
Cb1	33						
Cc1	7		10		13		
Cd1	7				25		
Cd3			10				
Da1		100					
Da2				57			
Db1				14			
Db4	6						
Dd1			10				

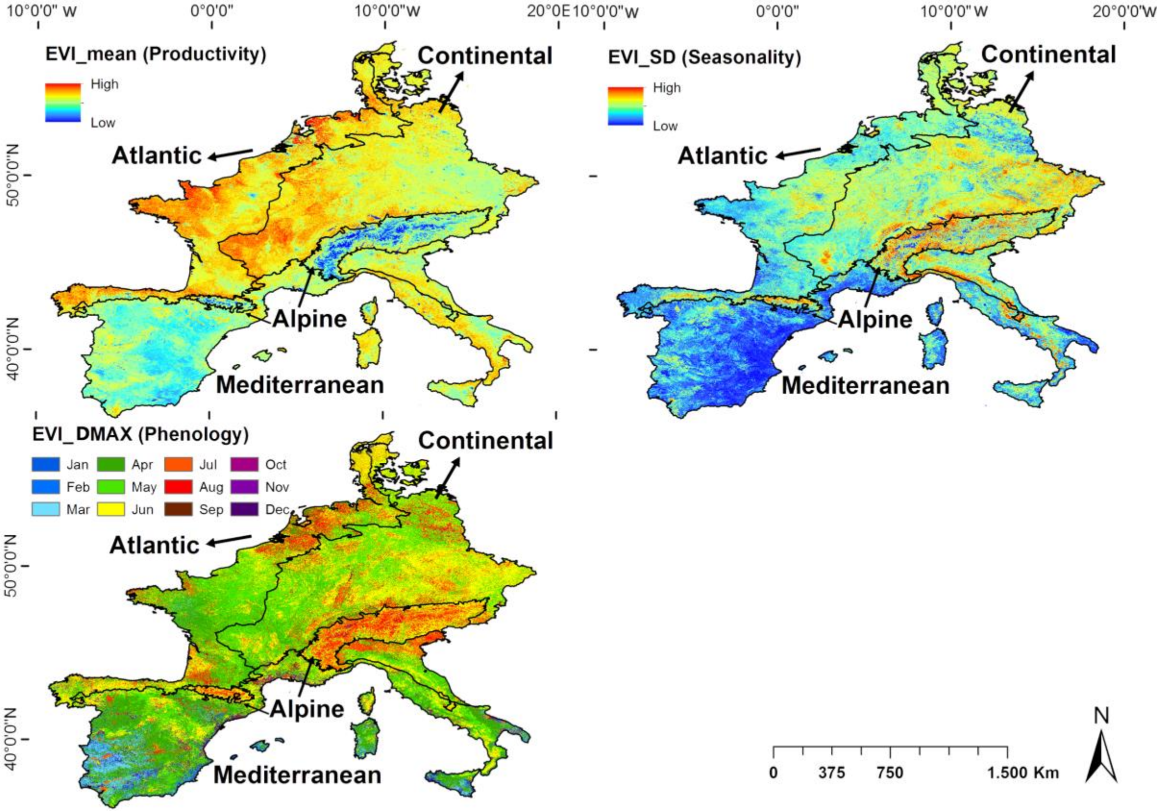

Figure S4.1.1. Ecosystem Functional Attributes based on the 2001-2014 time-series of satellite images of the Enhanced Vegetation Index (EVI) captured by the MODIS-Terra sensor (MOD13Q1.C006 product): EVI annual mean (EVI_mean; an estimator of annual primary production), the EVI seasonal standard deviation (EVI_SD; a descriptor of seasonality), and the date of maximum EVI (EVI_DMAX; an indicator of phenology). Biogeographical regions are based on the official European biogeographical regions map (EEA, 2016).

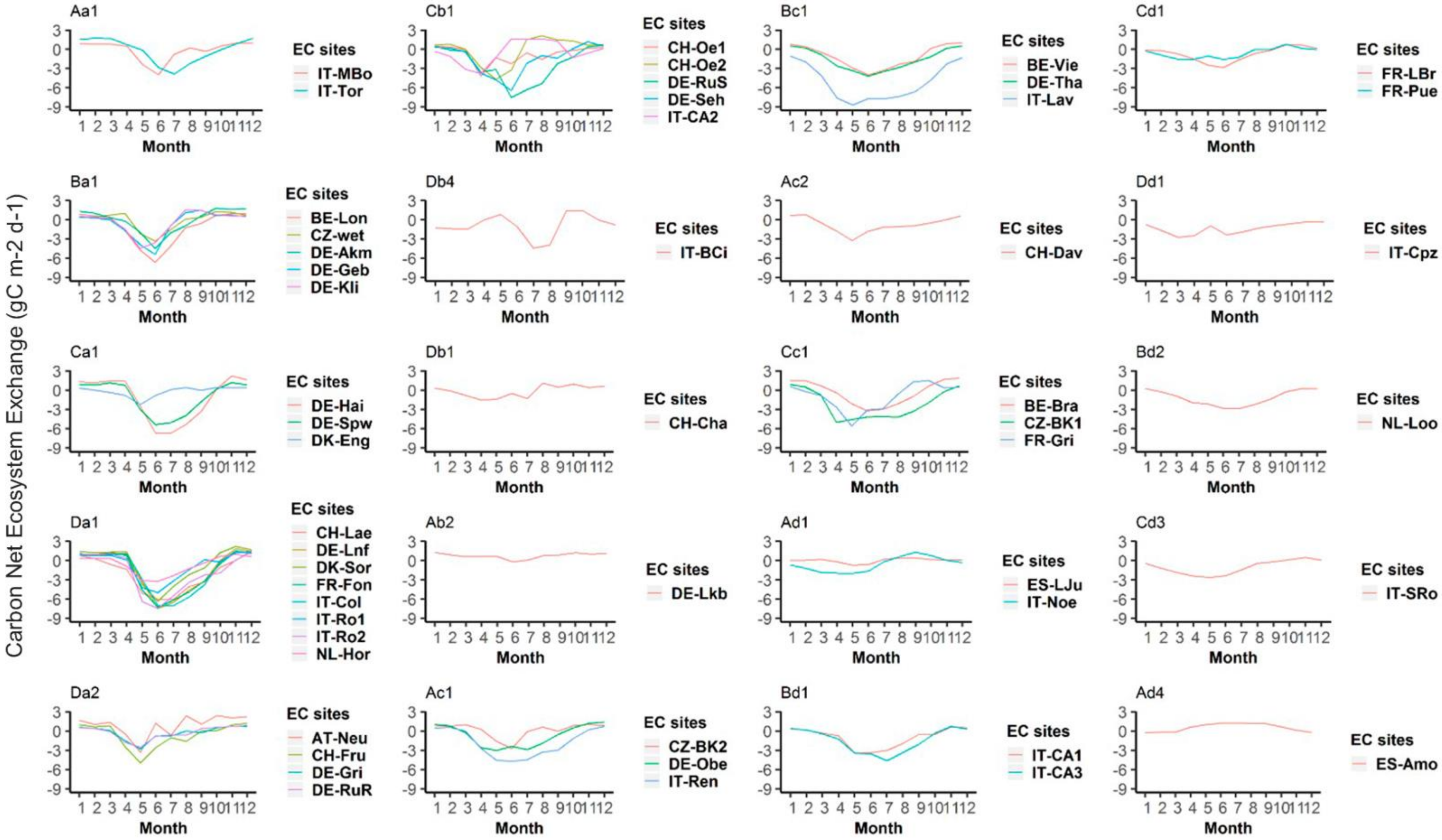

Figure S4.1.2. Variability inter EFTs: annual mean of NEE dynamics from different places with the same EFT.

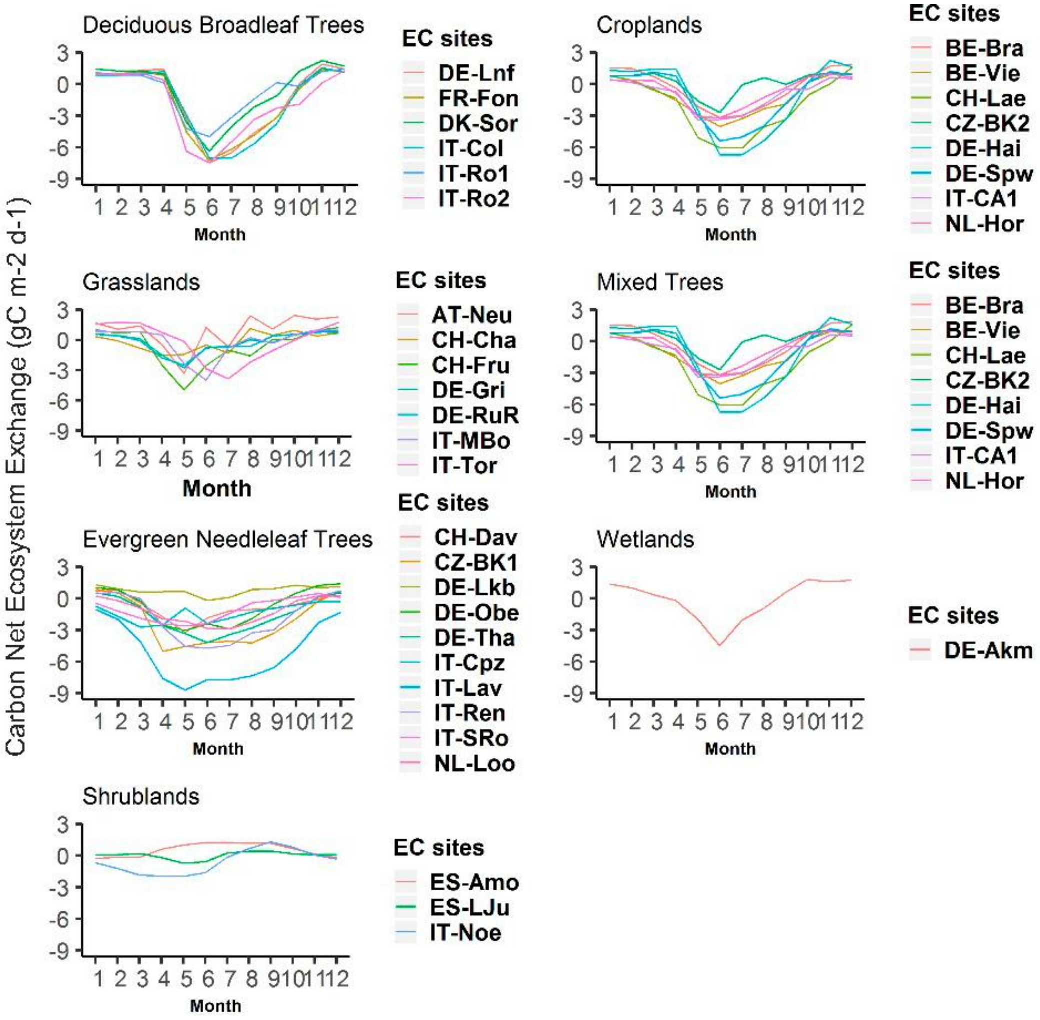

Figure S4.1.3. Variability inter PFTs and intra EFTs: Annual mean of NEE dynamics from different places with the same PFT and different EFT.

4.2.

CHAPTER II

A remote sensing-based dataset to characterize the ecosystem functioning and functional diversity

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Abstract

Conservation Biology faces the challenge of safeguarding the ecological processes and ecosystem functions that sustain the multiple facets of biodiversity. Characterization and evaluation of these processes and functions can be carried out through functional attributes or traits related to the exchanges of matter and energy between vegetation and the atmosphere. Based on this principle, satellite imagery can provide integrative spatiotemporal characterizations of ecosystem functions from local to global scales. Here, we provide a dataset at protected area level that characterizes the spatial patterns and temporal dynamics of ecosystem functioning in Sierra Nevada (Spain), captured through the spectral vegetation index EVI (Enhanced Vegetation Index) from 2001 to 2018 (product MOD13Q1.006 from MODIS sensor). First, at the annual scale, our database contains three Ecosystem Functional Attributes (EFAs) (i.e., descriptors of annual primary production, seasonality, and phenology of carbon gains), as well as their integration into a synthetic map of Ecosystem Functional Types (EFTs) classes. Second, it also includes two annual measures of ecosystem functional diversity: EFT richness and EFT rarity. Finally, it provides inter-annual summaries for all previous variables, i.e., their long-term means and inter-annual variabilities. Then, we show examples of research and management applications based on EFAs and EFTs from modelling climate, ecohydrology and species distributions to setting geographical priorities and early-warning systems in protected area networks. The datasets are available in two open-source sites (PANGAEA: https://doi.pangaea.de/10.1594/PANGAEA.904575 (Cazorla et al., 2019) and http://obsnev.es/apps/efts_SN.html), and bring to scientists, managers and the general public valuable information on the first characterization of the functional diversity based on primary production at ecosystem level developed in Sierra Nevada, a biodiversity hotspot in the Mediterranean basin. This Biosphere Reserve represents an exceptional natural laboratory for ecological research within the Long-Term Ecological Monitoring (LTER) network. The long-term data records available on biodiversity, climate, ecosystem services, hydrology, land-use changes, and management practices can now be analysed with our description of ecosystem functioning and functional diversity to explore ecological hypotheses and relationships from the landscape to the reserve scales.

KEYWORDS: Ecosystem Functional Types; Ecosystem heterogeneity; Ecosystem variability, EFT richness; EFT rarity; Sierra Nevada (Spain).

4.2.1. Introduction

A better characterization of the functional dimension of biodiversity is required to develop management approaches that ensure nature contributions to human well-being (Jax, 2010; Bennet et al., 2015). To achieve this goal, it is necessary to have a set of essential variables that allow for the characterization and monitoring of ecosystem functioning (Pereira et al., 2013). Such variables are critical to understanding the dynamics of ecological systems (Petchey and Gaston, 2006), the links between biological diversity and ecosystem services (Balvanera et al., 2006; Haines-Young and Potschin, 2010), and the mechanisms of ecological resilience (Mouchet et al., 2010). In addition, the use of ecosystem functioning variables has been demanded to assess functional diversity at large scales with the aim of measuring the Biosphere integrity (Mace et al., 2014; Steffen et al., 2015), one of the most challenging planetary boundaries to quantify (Steffen et al., 2015). Despite the importance of ecosystem functioning variables, and the conceptual frameworks developed to promote their use (Pettorelli et al., 2018), they have seldom been incorporated to ecosystem monitoring in protected areas (but see Alcaraz-Segura et al., 2009; Fernández et al., 2010; Cabello et al., 2016).

Characterization and evaluation of ecosystem functioning can be carried out through attributes or functional traits related to the exchanges of matter and energy between vegetation and the atmosphere (Mueller-Dombois and Ellenberg, 1974). Nowadays, the use of satellite imagery provides useful methods to produce a spatially explicit characterization of ecosystem functioning and its heterogeneity (i.e., functional diversity) from local (Fernández et al., 2010) to regional (Alcaraz-Segura et al., 2006, 2013) and global scales (Ivits et al., 2013). Theoretical and empirical models support the relationship between spectral indices derived from satellite images (e.g., Enhanced Vegetation Index -EVI-) and essential functional variables of ecosystems, such as primary production, evapotranspiration, surface temperature, or albedo (Running et al., 2000; Pettorelli et al., 2005; Fernández et al., 2010; Lee et al., 2013). Among them, primary production is one of the most integrative and essential descriptor of ecosystem functioning (Virginia and Wall, 2001; Pereira et al., 2013), since it has an central role in the carbon cycle (i.e., it is the energy input to the trophic web and therefore, the driving force behind many ecological processes). Moreover, primary production offers an holistic response to environmental changes and constitutes a synthetic indicator of ecosystem health (Costanza et al., 1992; Skidmore et al., 2015).

To characterize ecosystem functioning through spectral vegetation indices, we can use the approach based on Ecosystem Functional Types (EFTs), defined as patches of the land surface that share similar dynamics in the exchanges of matter and energy between the biota and the physical environment (Paruelo et al., 2001; Alcaraz-Segura et al., 2006). EFTs are derived from three Ecosystem Functional Attributes (EFAs) that describe the seasonal dynamics of carbon gains: annual mean (a surrogate of annual primary production, the most essential and integrative indicator of ecosystem functioning), annual standard deviation (a descriptor of seasonality or the differences between the growing and non-growing seasons), and the annual date of maximum (a phenological indicator of when in the year is the growing period centered). Since the concept appeared in 2001 (Paruelo et al., 2001), the EFT approach (or equivalent approaches) applications has exponentially grown to characterize functional heterogeneity from local to global scales (Alcaraz-Segura et al., 2006; Karlsen et al., 2006; Duro et al., 2007; Fernández et al., 2010; Geerken 2009; Alcaraz-Segura et al., 2013; Ivits et al., 2013; Cabello et al., 2013; Pérez-Hoyos et al., 2014; Müller et al., 2014; Wang and Huang, 2015; Villarreal et al., 2018; Coops et al., 2018; Mucina, 2019).

This article aims to provide a dataset that describes the spatial heterogeneity and temporal variability of ecosystem functioning in terms of primary production dynamics from the intra- and inter-annual variation of vegetation greenness captured through spectral vegetation indices (e.g., EVI). We introduce as a proof of concept the case of Sierra Nevada Biosphere Reserve (SE Spain), a biodiversity hotspot in the Mediterranean basin, that holds a long-term ecological monitoring program since 2010. First, for each year, we provide three Ecosystem Functional Attributes (EFAs) (i.e., annual primary production, seasonality, and phenology of carbon gains), as well as their integration into a synthetic mapping of Ecosystem Functional Types (EFTs). Second, based on these functional units, we present two measures of functional diversity: EFT richness and EFT rarity. Finally, in addition to the yearly maps, we calculated inter-annual summaries, i.e., inter-annual means and interannual variability, to show the average conditions as well as the most stable and variable zones along the period (workflow in Figure 4.2.1.).

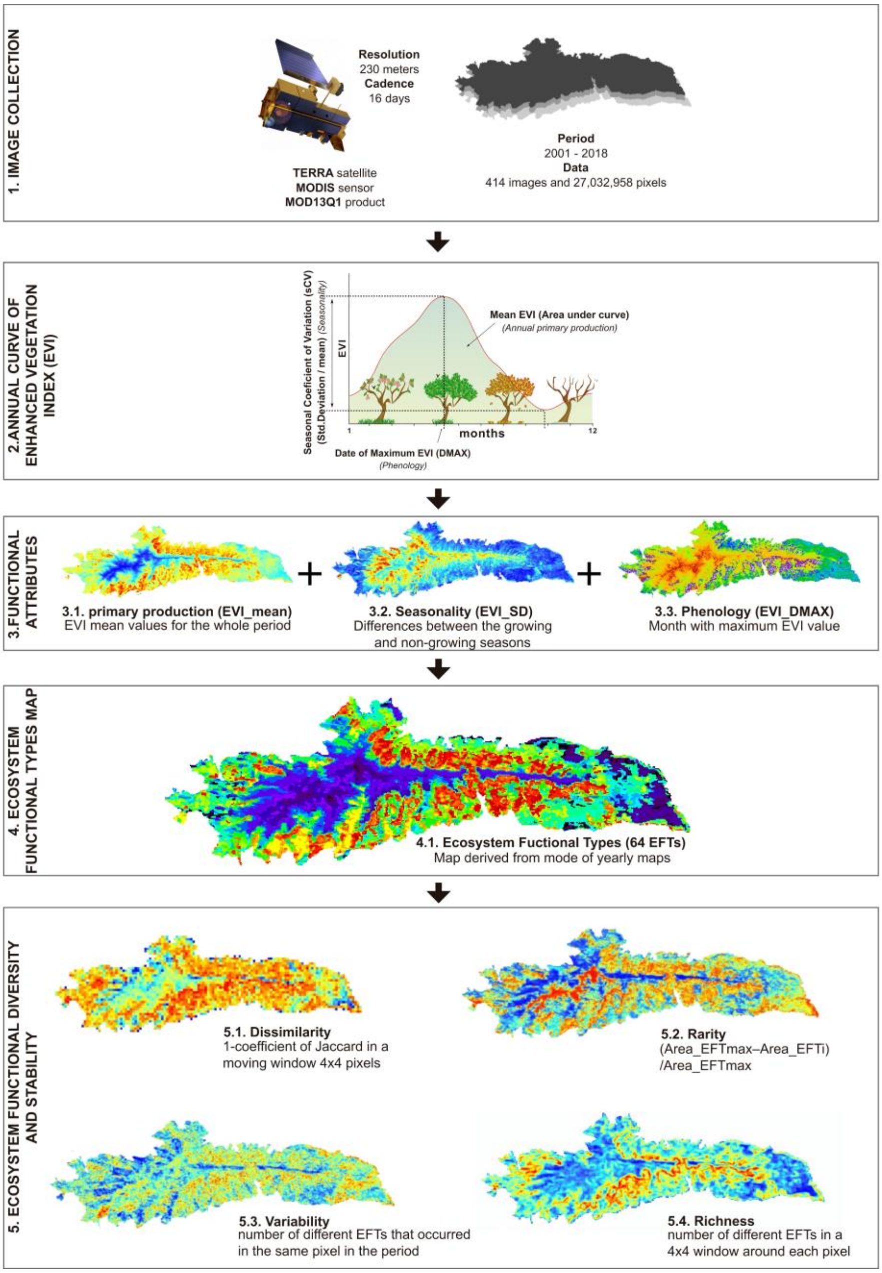

Figure 4.2.1. Workflow to characterize the ecosystem functioning and functional diversity of Sierra Nevada. MODIS (Moderate Resolution Imaging Spectroradiometer) sensor product MOD13Q1 was used aboard NASA's Terra satellite. This product contains images with 16-day temporal resolution (23 images per year) and ~231 m spatial resolution from the Enhanced Vegetation Index (EVI). The study period was from 2001 to 2018. Three functional attributes describing ecosystem functioning were

calculated from the EVI seasonal curve for each year. The range of values for each attribute was divided into four intervals, resulting in a potential number of 64 TFEs (4x4x4=64). From EFTs, we derived four metrics related to ecosystem functional diversity (EFT richness and rarity) and ecosystem functional stability (inter-annual variability and dissimilarity).

4.2.2. Methods

Site Description

Sierra Nevada (Andalusia, SE Spain) is a mountainous region covering more than 2000 km^2 with an elevation range of between 860 and 3482 m a.s.l (Figure 4.2.2.). This mountain is one of the most important 105 biodiversity hotspots in the Mediterranean region (Blanca et al., 1998; Cañadas et al., 2014), hosting endemic plant species for a total of 2353 taxa of vascular plants (33% and 20% of Spanish and European flora, respectively; Lorite 2016). Forest cover in Sierra Nevada is dominated by pine plantations (*Pinus halepensis* Mill., *Pinus pinaster* Ait., *Pinus nigra* Arnold subsp. *salzmannii* (Dunal) Franco, and *Pinus sylvestris* L.) covering approximately 40000 ha. Most of them were planted in the period 1960–1980. The main native forests of Sierra Nevada are dominated by the evergreen holm oak *Quercus ilex* subsp. *ballota* (Desf.) Samp. occupying low and medium mountain areas (8800 ha) and by the deciduous Pyrenean oak *Quercus pyrenaica* Willd ranging from 1100 to 2000 m a.s.l. (about 2000 ha). Autochthonous pine forests of *Pinus sylvestris* L. *var. nevadensis* H. Christ, characterized by low tree cover, occurs in small patches in the treeline. Above the treeline, plant communities of the Oromediterranean and Crioromediterranean belts (above 1800-2000 m a.s.l.), dominated by chamaephytes and hemicryptophytes (scrublands, grasslands, and cliff and scree communities), are the habitat to many endemic species.

Sierra Nevada receives legal protection and international recognition in multiple ways: UNESCO Biosphere Reserve (1986), Natural Park (1989), National Park (1999), Important Bird Area (2003), Special Area of Conservation in Natura 2000 network (2012), and it is in the IUCN Green List of Protected Areas (2014), a global standard of best practice for area-based conservation. Sierra Nevada is also a site within the European Long Term Ecological Research

(LTER) network, with many available ecological data records from multiple disciplines (Zamora et al., 2017, LTER_EU_ES_010). The main economic activities in this mountain region are agriculture, tourism, livestock raising, beekeeping, mining, and skiing (Bonet et al., 2010).

Vegetation studies in Sierra Nevada have mainly been developed considering a compositional (phytosociological method) or a successional perspective (vegetation dynamics). These studies have been beneficial for describing the vegetation heterogeneity at the mesoscale (Loidi, 2017), for characterizing habitats of conservation concern (EU Directive 92/43/EEC), and for developing ecological restoration actions (Valle et al., 2003). However, these traditional approaches are insufficient for monitoring the effects of environmental changes or management actions on ecosystem functions, and for assessing the role of ecosystems as providers of services and benefits to society (Cabello et al., 2019).

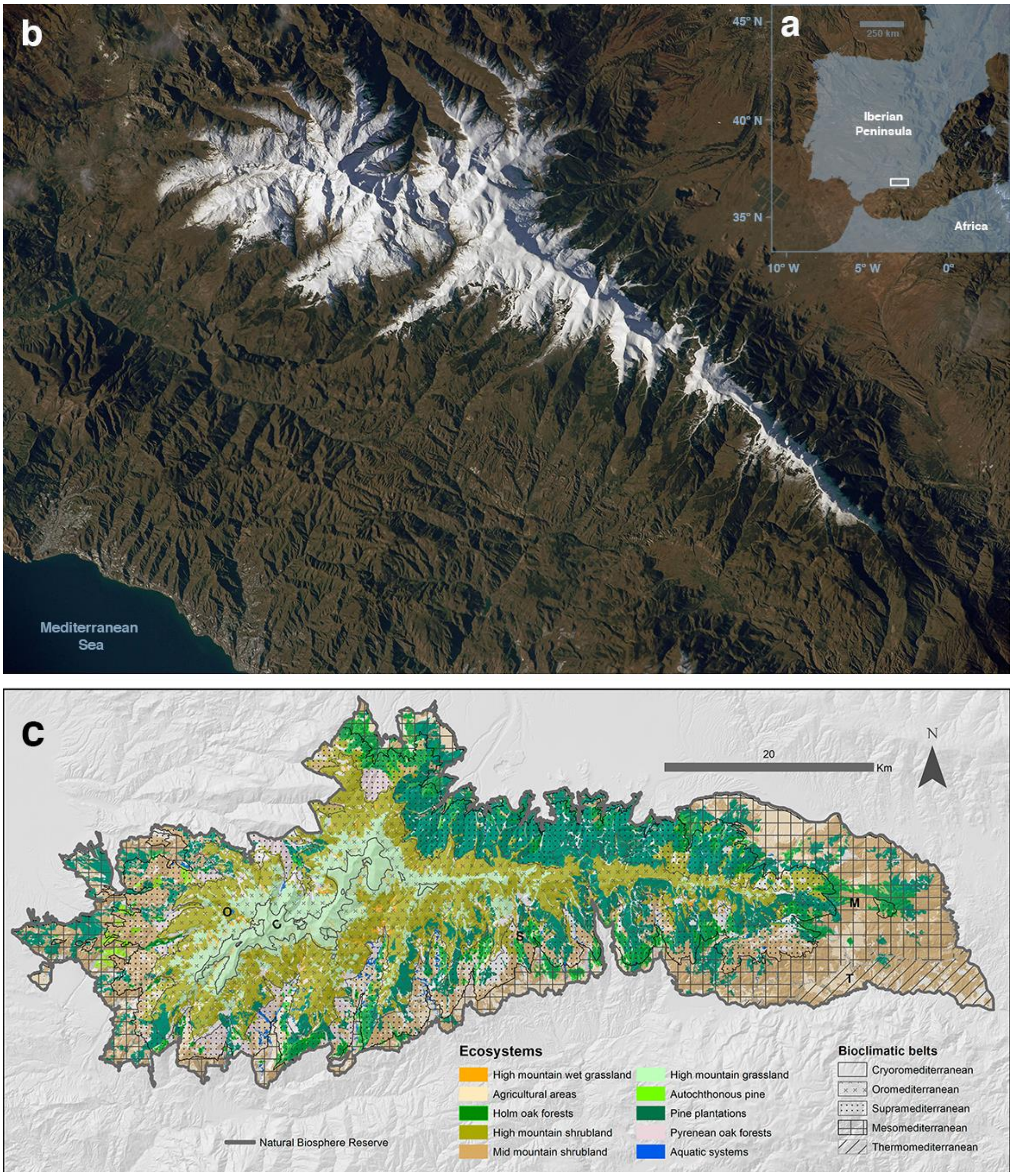

Figure 4.2.2. Study area: Sierra Nevada Biosphere Reserve. a) Location in the context of the Iberian Peninsula; b) remote view of Sierra Nevada mountain region (image from the International Space Station took in December 2014; courtesy of "Earth Science and Remote Sensing Unit, 615 NASA Johnson Space Center"); c) delimitation of the Biosphere Reserve and the distribution of the main ecosystems (Pérez-Luque et al., 2019) and thermotype bioclimatic belts (Molero-Mesa and Marfil, 2015).

Satellite images of Vegetation Indices (MOD13Q1 data product)

The characterization of ecosystem functioning in Sierra Nevada was based on the temporal dynamics of the Enhanced Vegetation Index (EVI) from 2001 to 2018. We chose EVI instead of any other vegetation index (such as SAVI, ARVI, or NDVI) as an indicator of carbon gains since it is more reliable in both low and high vegetation cover situations (Huete et al., 1997). EVI reduces the influence of atmospheric conditions on vegetation index values, and EVI corrects for canopy background signals.

EVI is computed following this equation:

$$EVI = G \times \frac{(NIR - RED)}{(NIR + C1 \times RED - C2 \times Blue + L)}$$

where NIR/red/blue are atmospherically-corrected (Rayleigh and ozone absorption) surface reflectances; L is the canopy background adjustment that addresses the non-linear and differential transfer through a canopy of the NIR and red radiations; and C1, C2 are the coefficients of the aerosol resistance term, which uses the blue band to correct for aerosol influences in the red band. The coefficients adopted in the MODIS-EVI algorithm are; L=1, C1 = 6, C2 = 7.5, and G (gain factor) = 2.5. The EVI values range from -1 to +1, where negative values generally correspond to snow, ice, or water, and values closer to +1 represent the higher density of green leaves (Huete et al., 2002).

We obtained EVI from MOD13Q1.006 product of the MODIS sensor (Moderate Resolution Imaging Spectroradiometer) onboard NASA’s Terra satellite (Didan, 2015). MOD13Q1.006 EVI product is computed from atmospherically corrected bi-directional surface reflectances by choosing the best available pixel value from all the acquisitions (4 per day) in a 16-day period based on quality, cloud presence, and viewing geometry (Huete et al., 1999, Didan et al., 2015). In addition, to further remove the potential remaining effect of snow, ice, and water in our dataset, we transformed negative EVI values into zeros. Thus, we obtained a maximum-value composite image every 16 days (23 images per year). Despite its moderate spatial resolution (~231 meters spatial resolution, though the nickname is 250 meters pixel), we chose the MOD13Q1.006 product as the basis for our data since it offers a long time series (almost 20 years) every 16 days, which allows for the characterization of the temporal dynamics of ecosystem functioning (Anderson et al., 2018).

MOD13Q1.006 images are downloadable from NASA's LP DAAC (Land Processes Distributed Active Archive Center) (https://lpdaac.usgs.gov/products/mod13q1v006/) (Didan, 2015) but we process them through the Google Earth Engine platform (https://developers.google.com/earth165_engine/datasets/catalog/MODIS_006_MOD13Q1) (Gorelick et al., 2017). EVI values are multiplied by 10000 to store them as real numbers to occupy less disk space (both in the original MOD13Q1.006 product and in our dataset).

Calculating Ecosystem Functional Attributes (EFAs)

We identified three EFAs that are known to capture most of the variance in the time series of vegetation indices and that are biologically meaningful (Paruelo et al., 2001; Alcaraz-Segura et al., 2006, 2009). These functional attributes were calculated from the EVI seasonal curve or annual dynamics (i.e., 23 measures per year): the EVI annual mean (EVI_mean; an estimator of primary production), the EVI seasonal Standard Deviation (EVI_SD; a descriptor of seasonality, i.e., the differences between the growing and non-growing seasons), and the date of maximum EVI (EVI_DMAX; a phenological indicator of the month with maximum EVI) (Figure 4.2.3.). To summarize the EFAs of the 2001-2018 period, we calculated the inter-annual mean for each attribute.

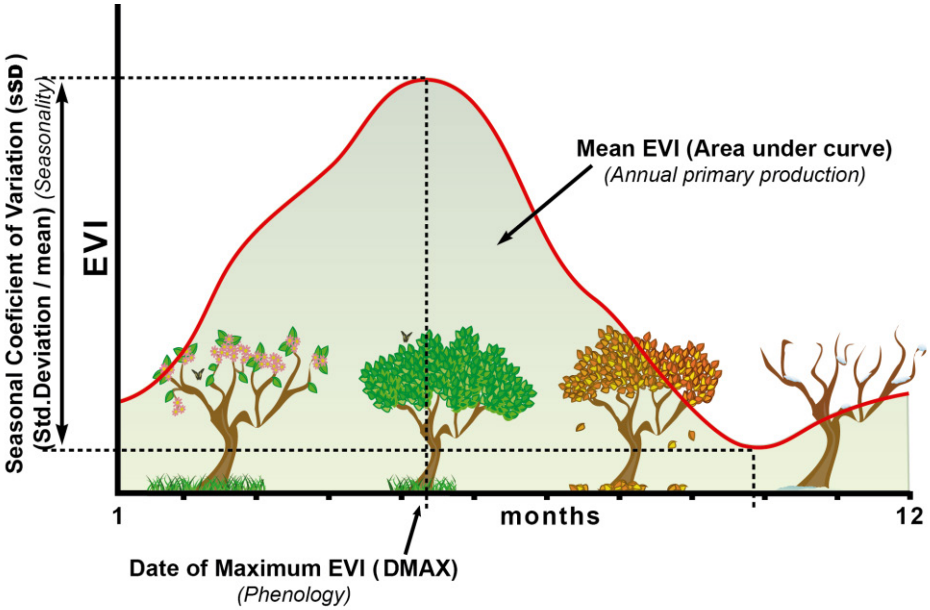

Figure 4.2.3. Seasonal dynamics of Enhanced Vegetation Index (EVI) and EVI derived metrics or Ecosystem Functional Attributes (EFAs). The axis "x" corresponds with months and the axis "y" with EVI values. EFAs were: the annual mean or the cumulative EVI, an estimator of annual productivity (EVI_mean), the EVI seasonal coefficient of variation, i.e. the differences between the minimum and the maximum EVI values, a descriptor of seasonality (EVI_SD), and the date of maximum EVI, an indicator of phenology (EVI_DMAX). We chose these three EVI metrics or EFAs since they capture most of the variance of the EVI time series.

Biologically, these three metrics can be interpreted as surrogates (Paruelo et al., 2001, Pettorelli et al., 2005, Alcaraz-Segura et al., 2006) of the total amount and timing (seasonality and phenology) of primary production, one of the most integrative indicators of ecosystem functioning (Virginia and Wall, 2001). Statistically, these three metrics are highly correlated with the first two or three axes (and hence capture most of the variance) of a Principal Component Analysis (PCA) carried out on the NDVI or EVI seasonal dynamics in different regions (Townshend et al., 1985, Paruelo and Lauenroth, 1998, Paruelo et al., 2001, Alcaraz-Segura et al., 2006, 2009, Ivits et al., 2013). To know the statistical meaningfulness of these metrics in Sierra Nevada Biosphere Reserve, we also examined their correlation with the first axes of a PCA run on the EVI annual curve of the average year (12 EVI values, i.e., the inter-annual means of the maximum value composites for each month) (see full analysis in Appendix A).

Identifying Ecosystem Functional Types (EFTs)

EFTs were identified by synthesizing in a single map the variability contained in the three EFAs following a similar approach to Alcaraz-Segura et al., (2013). The range of values of each EFA was divided into four intervals, giving a potential number of 64 EFTs (4 × 4 × 4). For EVI_DMAX, the four intervals agreed with the four seasons of the year: January to March = Winter, April to June = Spring, July to September = Summer, October to December = Autumn. For EVI_mean and EVI_SD, we extracted the first, second, and third quartiles for each year and then calculated the inter-annual mean of each quartile (means of the 18-year period) (Appendix B, Table B1). To account for the interannual variability in the quartiles and to assess how many years were necessary in the study period to get stability in the quartiles, we run a sensitivity analysis (see sections below and Appendix B). Finally, the inter-annual means of the quartiles were applied to each year as the thresholds for EVI_mean and EVI_SD to set EFT classes (Table 4.2.1.). To summarize the EFTs of the 2001–2018 period, we calculated the most frequent EFT of the period (i.e., the EFT mode for each pixel). To name EFTs, we used two letters and a number: the first capital letter indicates net primary production (EVI_mean), increasing from A to D; the second small letter represents seasonality (EVI_SD), decreasing from a to d; the numbers are a phenological indicator of the growing season (EVI_DMAX), with values 1-spring, 2-summer, 3-autumn, 4-winter (Table 4.2.1.). The EFT alphanumeric code (Aa1 to Dd4) corresponds to the numeric code (1 to 64) in the .TIF files, that is shown in the legend of Figure 4.2.4.d and in the data management plan (Appendix D).

Table 4.2.1. EFAs range used for the identification of EFTs in the Sierra Nevada Biosphere Reserve. For EVI_DMAX, the four intervals agreed with the four seasons of the year. For EVI_mean and EVI_SD, we extracted the first, second, and third quartiles for each year and then calculated the inter-annual mean of each quartile (their average over the 18-year period). The values of both EVI_mean and EVI_SD are multiplied by 10000 in the .TIF files to save disk space.

Ecosystem Functional Attribute	Character code	Digit code	Range
EVI Mean (Productivity)	A	100	0 - 0.137
	B	200	0.137 - 0.187
	C	300	0.187 – 0.241
	D	400	> 0.241
EVI SD (Seasonality)	a	10	> 0.062
	b	20	0.043 – 0.062
	c	30	0.030 – 0.043
	d	40	0 – 0.030
EVI DMAX (Phenology)	1	1	Spring
	2	2	Summer
	3	3	Autumn
	4	4	Winter

Characterizing Ecosystem Functional Diversity

To characterize ecosystem functional diversity, we used EFT richness and EFT rarity. EFT richness was calculated for each year by counting the number of different EFTs in a 4×4-pixel moving window around each pixel (top-left center pixel of a 4x4 Kernel) (modified from Alcaraz-Segura et al., 2013). Each MOD13Q1.006 pixel received a richness value derived from counting how many different EFTs there were in the surrounding 4x4 pixels. We chose a 4x4-pixel window since it offered the finest spatial resolution without saturating the number of EFT classes per Kernel (i.e., smaller Kernel sizes result in a high proportion of moving windows saturated with the maximum number of classes) (see sensitivity analysis on Kernel size in sections below and Appendix C).

EFT rarity was calculated as the extension of each EFT compared to the most abundant EFT in the study area (Equation 1) (Cabello et al., 2013). Then, the average rarity map of all years was obtained.

$$\text{Rarity of EFTi} = (\text{Area\_EFTmax} - \text{Area\_EFTi})/\text{Area\_EFTmax} \quad \text{(Equation 1)}$$

where Area_EFTmax is the area occupied by the most abundant EFT, and Area_EFTi is the area of the i EFT being evaluated, with i ranging from 1 to 64.

Once we have the rarity value of each EFT (using Equation 1), we assigned to each pixel in the EFT map such value according to its EFT class. Hence, the original spatial resolution of the EFT rarity map is the same as the resolution of the EFT map (~231 m).

Inter-annual stability in ecosystem functioning

To identify the most stable and variable areas (either due to inter-annual fluctuations or directional trends) in ecosystem functioning, we followed two approaches. First, we recorded the number of different EFTs that occurred in the same pixel in the period 2001-2018, i.e., inter-annual-variability in EFTs. Second, to consider the changes not only at the pixel but also at the landscape level, the Jaccard similarity index (Jaccard, 1901) (Equation 2) was used in 4×4-pixel moving windows (924 x 924 m).

$$\text{Jaccard Index} = (\text{the number in both sets}) / (\text{the number in either set}) * 100$$

The same formula in notation form is (Equation 3):

$$J(X,Y) = |X \cap Y| / |X \cup Y|$$

where the Jaccard index for two data sets (X = set 1; Y =set 2) is equal to the size of the intersection divided by the size of the union of the data sets. This measure represents how similar the EFT composition that occurs in each window throughout the entire time series (2001-2018) is. For each window, the Jaccard index was calculated among all possible combinations of years, and then the inter-annual average of all calculated indices was obtained.

In Steps:

1) Count the number of EFTs which are shared between both windows; 2) Count the total number of EFTs in both windows (shared and unshared); 3) Divide the number of shared EFTs 1) by the total number of EFTs 2); 4) Multiply the number found in step 3) by 100.

From there, we calculated dissimilarity as (Equation 4):

$$\text{Dissimilarity} = 1 - \text{Jaccard Index Dissimilarity}$$

values range from 0 to 1, with 1 being the highest degree of dissimilarity in composition and relative abundance of EFTs and 0 being absent.

Sensitivity analyses

Inter-annual stability in quartiles to set boundaries among EFT classes

To assess how inter-annual variability affected the quartiles of EVI_mean and EVI_SD (which set the boundaries among EFT classes), we determined the minimum number of years that were needed in a study period to get stability in all quartiles (see Appendix B). For each quartile, we plotted (Figure B1 Appendix B) the maximum inter-annual coefficient of variation observed across all possible combinations of consecutive years from 2001 to 2018 (from 17 combinations of two consecutive years to one combination of 18 years) against the number of years considered. That is, starting with two consecutive years, we plotted the maximum of 17 coefficients of variation (i.e., 2001-2002, 2002- 2003, ... 2017-2018); for three consecutive years, the maximum of 16 coefficients of variation (i.e., 2001-2002-2003, ... 2016-2017-2018); etc.

Kernel size and borderline effect on EFT richness

To assess the effect of the size of the sliding window Kernel on EFT richness, we calculated EFT richness with Kernels of 2x2, 3x3, and 4x4 pixels and compared the outputs (see analysis in Appendix C).

Since we only classified pixels within the Biosphere Reserve, external pixels with NoData values were not considered as a distinct class to compute EFT richness along the borderline of the protected area. For these reasons, it is important to note that the sliding windows along the borderline of the protected area could systematically show lower EFT richness in our dataset than in reality.

4.2.3 Results and Discussion

Available dataset

Overall, the collection of datasets provides a characterization of ecosystem functioning and ecosystem functional diversity in Sierra Nevada Biosphere Reserve (SE Spain) through remote sensing. To broaden the use of data, first, we provide data in .TIF format. Second, we have incorporated rendered versions of all layers as required by Google Earth Pro (called "filename..._forGoogleEarthVisualization.tif") for visualization. Moreover, we have also developed an ad-hoc visualization platform for the inter-annual summaries under the Sierra Nevada Global 275 Change Observatory-LTER website. All data are available yearly (2001-2018) and summarized for the period in EPSG:4326 WGS84 reference system.

The dataset is structured in three main subsets of variables: Ecosystem Functional Attributes, Ecosystem Functional Types, and Ecosystem Functional Diversity (see Table 4.2.2.). For each variable, there are two groups of data (two subfolders): one containing the yearly variables, and another one 280 containing the summaries for the 18-year period.

Data were clipped with the shapefile of the Sierra Nevada Biosphere Reserve boundaries, whose layer is available in the public database of the Andalusian regional government (REDIAM: https://descargasrediam.cica.es/07_PATRIMONIO_NATURAL/01_ESPACIOS_PROTEGIDOS).

All .TIFs files contain the following metadata: raster information (columns and rows, number of bands, cell size, uncompressed size, format, source type, pixel type, pixel depth, NoData value, pyramids, compression, status), extension (top, left, right, bottom), spatial reference (angular unit, datum) and statistics (build parameters, min, max, mean, std dev.). Furthermore, a Data Management Plan with the formal metadata of our dataset is also available in PANGAEA data repository and in Appendix D.

Table 4.2.2. Dataset description: Ecosystem Functional Attributes (EVI_mean, EVI_SD and EVI_DMAX provided yearly and summarized for the period); Ecosystem Functional Types (EFTs yearly and summarized for the period (mode, interannual variability and dissimilarity); Ecosystem Functional Diversity (EFT richness and EFT rarity, provided yearly and summarized for the period). Spatial resolution is ~231 in all cases except in the EFT dissimilarity, where it is ~231m x 4 = ~1km2. YYYY refers to year and varies from 2001 to 2018.

Filename	Variable	Definition	Biological significance	Temporal resolution
EVI_mean_YYYY_C006_MOD13Q1 _Pixel232	EVI_mean	Mean of the positive EVI values in a year	Primary production in a year	Yearly, one image per year *YYYY*
EVI_mean_InterAnnualMean_2001-2018_C006_MOD13Q1_Pixel232	EVI_mean	Inter-annual mean of the annual EVI_mean values of the period	Average annual primary production of the period	One image for the 2001-2018 period
EVI_sSD_YYYY_C006_MOD13Q1_ Pixel232	EVI_SD	Intra-annual standard deviation of the positive EVI values within a year	Seasonality in vegetation greenness. Differences in carbon gains between the growing and non-growing seasons in a year	Yearly, one image per year *YYYY*
EVI_sSD_InterannualMean_2001-2018_C006_MOD13Q1__Pixel232	EVI_SD	Inter-annual mean of the annual EVI_SD values of a period	Seasonality. Average annual of the differences in carbon gains between the growing and non-growing seasons throughout the period	Average of the 2001-2018 period

Filename	Variable	Definition	Biological significance	Temporal resolution
EVI_DMAX_YYYY_C006_MOD13Q1_Pixel232	EVI_ DMAX	Month with maximum EVI in a year	Phenology. Date of maximum greenness in a year	Yearly, one image per year YYYY
EVI_DMAX_InterannualMean_2001-2018_C006_MOD13Q1_Pixel232	EVI_ DMAX	Inter-annual mean of the month with maximum EVI of the period	Phenology. Average annual of the month with maximum greenness throughout the period	Average of the 2001-2018 period
EFTs_YYYY_C006_MOD13Q1_Pixel232	EFTs	Range of EFA's values divided into four intervals 4 × 4 × 4 = 64 potential EFTs in a year	Patches of land surface that share similar dynamics in matter and energy exchanges in a year	Yearly, one image per year YYYY
EFTs_InterannualMode_2001-2018_C006_MOD13Q1_Pixel232	EFTs	Mode of the range of EFA's values divided into four intervals 4 × 4 × 4 = 64 potential EFTs of the period	Patches of land surface that share similar dynamics in matter and energy exchanges throughout the period	Mode of the 2001-2018 period
EFT_InterannualVariability_2001-2018_C006_MOD13Q1_Pixel232	EFT interannual variability	Nº of different EFTs that occurred in the same pixel in the period	Changes in an ecosystem functioning in a period	2001-2018 period
EFT_InterannualDissimilarity_2001-2018_C006_MOD13Q1__Pixel232	EFT interannual dissimilarity	1 - *Jaccard Index*	Changes in ecosystem functioning a landscape level in a period	2001-2018 period

Filename	Variable	Definition	Biological significance	Temporal resolution
EFT_Richness_YYYY_C006_MOD13Q1_Pixel232	EFT richness	Nº of different EFTs in a 4×4-pixel moving window around each pixel in a year	Different EFTs represented in the land-surface in a year	Yearly, one image per year YYYY
EFT_Richness_InterannualMean_2001-2018_C006_MOD13Q1_Pixel232	EFT richness	Nº of different EFTs in a 4×4-pixel moving window (924 x 924 m) around each pixel in a period	Different EFTs represented in the land surface throughout the period	Average of the 2001-2018 period
EFT_Rarity_YYYY_C006_MOD13Q1_Pixel232	EFT rarity	*Rarity of EFTi = (Area_EFTmax–Area_EFTi)/Area_EFTmax (in a year)*	EFT geographical extension	Yearly, one image per year YYYY
EFT_Rarity_InterannualMean_2001-2018_C006_MOD13Q1_Pixel232	EFT rarity	*Rarity of EFTi = (Area_EFTmax–Area_EFTi)/Area_EFTmax (in a period)*	EFT geographical extension	Average of the 2001-2018 period

Ecosystem Functional Attributes patterns

Functional attributes of productivity, seasonality, and phenology showed a clear altitudinal pattern. Productivity (EVI_mean) was much lower in the high mountain bioclimatic belts (Crioro- and Oromediterranean belts) than in lower belts (Supra- and Mesomediterranean belts). Productivity also decreased from west to east (Figure 4.2.4.a). Seasonality (EVI_SD) was high in the Supramediterranean, decreasing in Meso-, and Thermomediterranean belts, and in Crioro- and Oromediterranean (Figure 4.2.4.b). Phenology (EVI_DMAX) was characterized by a dominant summer peak in vegetation greenness in the Crioro- and Oromediterranean belts, and a late spring peak in the Supra- and Mesomediterranean belts. Dry and semi-arid Thermomediterranean areas of the south and east showed greenness peaks in early autumn and winter months (Figure 4.2.4.c).

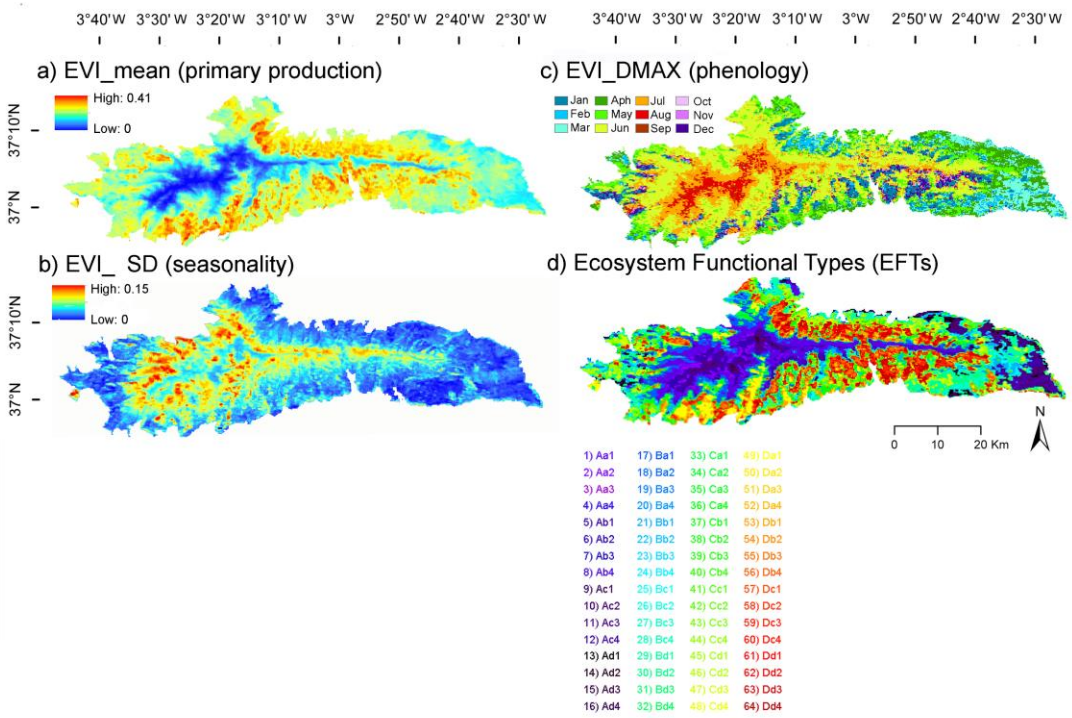

Figure 4.2.4. Ecosystem Functional Attributes (a-c) and Ecosystem Functional Types (d) describing the functioning of the canopy based on the Enhanced Vegetation Index (EVI), derived from MOD13Q1-850 TERRA (pixel ~231 m) for the period 2001-2018.

Ecosystem Functional Type patterns

As a result of the combination of the three Ecosystem Functional Attributes, productivity, seasonality, and phenology, represented in Figure 4.2.4. a-c, we obtained the EFT map (Figure 4.2.4.d) that includes a synthetic characterization of the spatial patterns of ecosystem functioning from the primary production dynamics. A total of 64 classes were observed. The most abundant EFT presented the maximum greenness in spring, with productivity values from low to intermediate and with all possible combinations of seasonality: Aa1, Ba1, Cb1, Cd1, Ba1, and Cc1 accumulated 30% of the surface. On the contrary, the rarest EFTs were Ba4, Aa4 characterized by medium or low productivity, high seasonality, and maximum greenness in winter.

Crioro- and Oromediterranean areas presented EFTs with low and intermediate productivity, high seasonality, and moments of maximum greenness mainly in summer, but also in spring. Here, extreme conditions characterized by scarce soil (Peinado et al., 2019), high solar radiation, extreme temperatures, winds, snow, and ice, give rise to a short vegetative period. Such conditions result in scarce vegetation cover, controlled by low temperatures, which can only occur in summer, being the plant growth time; hence these areas have been referred to as "cold desert" (Blanca et al., 2019). The Supra- and Mesomediterranean levels had associated EFTs of intermediate-high productivity, medium-low seasonality, and maximum green moment in spring and autumn (e.g., Cc1-3) (Figure 4.2.4.d). The Supramediterranean belt is characterized by the presence of deciduous species, e.g., oak groves associated with the most productive and seasonal ecosystem functional type of the study area, with the maximum in spring (EFT Da1). In the dry and semi-arid thermomediterranean of the eastern end, characterized by thermophilic species, which hardly suffer from frost, we detected a different functional behavior of the ecosystems. The functioning of this area showed low values of productivity, medium-low seasonality, and maximum greenness of the vegetation in spring or winter (e.g., Ac1-4). Here, the main control of ecosystem functioning is water availability, presenting plant species with a fast response to scarce water inputs (Cabello et al., 2012).

Stability in ecosystem functioning

The inter-annual variability ranged from 1 to 17 different EFTs over the 18-years period in the same pixel (Figure 4.2.5.a). The number of EFTs observed in the same pixel over 18 years was higher in the Supra- and Mesomediterranean levels, coinciding with the altitudinal range where inter-annual climate variability is most affected (e.g., they may present much snow in cold years and be affected by drought in dry and warm years). The eastern end of the semi-arid thermomediterranean also highlighted a high inter-annual variability, where there exists a more significant climate fluctuation and where small changes in precipitation produce large changes in the dynamics of primary production (Houérou et al., 1988; Cabello et al., 2012), as well as the area burned in 2005 near Lanjarón, where the fire eliminated the vegetation that has been regenerating since then. On the other hand, the most inter-annual stable areas (i.e., those that changed the least during the period) were located in the Meso-Oromediterranean and Crioromediterranean belts, specifically, the oak forests and high-mountain meadows, ecosystems that are not subject to low human pressure (e.g., low forest management and low livestock).

The results of the inter-annual dissimilarity (1 - Jaccard index) in the EFT composition (Figure 4.2.5.b), also showed an altitudinal pattern where the dissimilarity was lower in the higher mountain landscapes (Oro- and Crioromediterranean belts), as well as in the Mesomediterranean oak groves (functional stability already shown by other authors, i. e. Requena-Mullor et al, 2018). This pattern of dissimilarity increased towards lower levels, finding the highest values of dissimilarity in areas where changes in land use and management are significant (Zamora et al., 2016), such as autochthonous pine forests on dolomites, coniferous afforestation and mid-mountain (Mesomediterranean belt) holm oak forests. In addition, the eastern side of the Sierra Nevada had an area with low dissimilarity values, that is, where there were not many changes over the years.

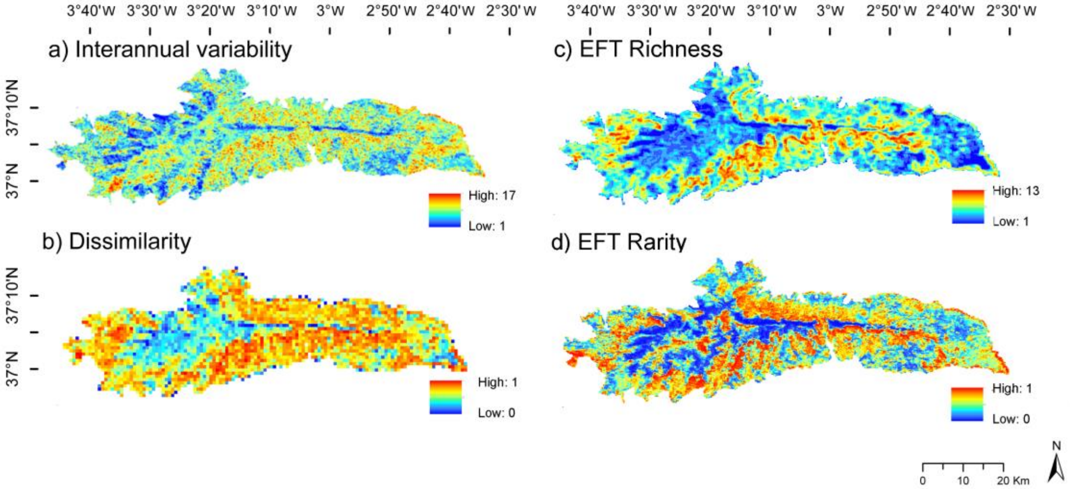

Figure 4.2.5. Functional diversity patterns based on the Enhanced Vegetation Index (EVI), derived from MOD13Q1-TERRA for the period 2001-2018. a) EFTs inter-annual variability for the period; b) EFTs inter-annual dissimilarity (1 - Jaccard index) for the period; c) Spatial EFT richness patterns from a 4x4-MODIS-pixel sliding window (∼231m x 4=∼1 km2); and d) Spatial EFT rarity patterns.

Functional diversity at the ecosystem level

Richness oscillated between 1 and 13 EFTs. Highest EFT richness was observed in the Supra- and Mesomediterranean belts, particularly in the southern face of the Sierra (Figure 4.2.5.c), where the number of vegetation series is also higher than in the rest of the bioclimatic belts (Valle et al., 2003). The presence of EFTs hotspots mainly in the mid-mountain, and particularly in the southern face, could be related to two factors. On the one hand, many Mediterranean mountains show high values of beta diversity up to 1750-1800 m a.s.l. (Wilson and Schmida, 1984), when there is an essential structural and compositional replacement of their vegetation. On the other hand, in the middle mountain and especially in its southern face, there are a very diverse mosaic of different types of natural vegetation mixed with different types of reforestation, traditional crops and uses (Camacho et al., 2002), which gives them the characteristic of multifunctional landscapes for the provision of ecosystem services (García-Nieto et al., 2013; Mastrangelo et al., 2014; Cabello et al., 2019). Molero Mesa et al., (1996) and Fernández Calzado et al., (2012) indicated that Sierra Nevada species richness decreases with altitude, while endemic taxa increases (Blanca et al., 2019). Something similar can be observed in the functional diversity of ecosystems since the maximum richness is found in areas of medium altitude. The areas with the lowest EFT richness were located in high-mountain (Oro- and Crioromediterranean belts), and in the eastern semi-arid thermomediterranean extreme, where the harsh soil and climatic conditions (Peinado et al., 2019) diminish floristic diversity although their endemicity increases (Fernández Calzado et al., 2012). The lowest values of EFT richness (richness 4-5) were found in the Supramediterranean oak groves, (as in Dionisio et al., 2012; Requena-Mullor et al., 2018) may be due to the internal homogeneity of their environmental conditions and their floristic composition (Pérez-Luque et al., 2015a, Requena-Mullor et al., 2018).

EFT rarity was highest in the highest peaks (Crioromediterranean belt) and the lowest areas of the Eastern side of Sierra Nevada (semi-arid thermomediterranean belt, both areas characterized by a high concentration of narrow endemic species. The peaks (above 2800 m a.s.l.) are landscapes with very high biodiversity values since they hold the highest concentration of local endemisms (Cañadas et al., 2014; Peñas et al., 2019) (Figure 4.2.5.d). In these areas, vegetation develops under very limiting ecological conditions that determine uncommon types of ecosystem functioning (rarity 0.6; Figure 4.2.5.d), such as, for example, in scree slopes, where the percentage of rarity or compositional endemicity rises to 80% (Blanca and Algarra, 2011). The semi-arid areas, also show a high concentration of endemic species, but in this case from the Iberian arid Southeast (Mota et al., 2004). In the high mountain areas (Oromediterranean belt), EFT rarity decreased and reached its minimum value, which reflects the fact that they are the largest (i.e., most frequent) landscapes in the Biosphere Reserve, and in consequence, broadly distributed ecosystem functional types. Mid-mountain areas (Supra- and Mesomediterranean belts) (Figure 4.2.5.d) showed medium to high EFT rarity values, corresponding the highest ones to the coniferous and oak forests (rarity 0.6). The high rarity of the ecosystem functioning in the coniferous forests of mid- and high-mountain was associated with their winter canopy phenology (e.g., Cc1, Dc1), a particular phenological behavior of these forests also identified in other areas of the Iberian

Peninsula (Aragones et al., 2019). Finally, oaks forest also showed high rarity, due to their singular deciduous habit in the context of the Mediterranean region (Dionisio et al., 2012).

Sensitivity analysis

Inter-annual stability in quartiles to set boundaries among EFT classes

The inter-annual Coefficient of Variation (CV) of the 2001-2018 period was around 5% for the EVI_mean quartiles and around 10% for the EVI_SD quartiles (Table B1, Appendix B). The quartiles of EVI_mean (our surrogate for productivity) required at least 14 years to stabilize around 5% of CV. The quartiles of EVI_SD (our surrogate for seasonality) required at least 17 years to stabilize around 10% of CV (Figure B1, Appendix B).

Despite there exists variation in the quartile values across years, we did not adopt the limits among EFT classes to such variation. Adapting the limits between classes to each year would not make it possible to compare the classification across the years. Instead, we followed a fixed-classification approach with fixed limits among EFT classes for the entire period to make the classification capable of detecting such inter-annual changes. For example, if a macro wildfire burns the entire protected area in 2020, our use of fixed limits among classes for the 2001-2018 period will allow the detection of such disturbance (most pixels would be classified as low productivity "A EFT class"). Contrary, if the limits among EFT classes were adapted to the data distribution of each year, the classification would not be able to detect the effect of wildfire and make the 2020 classification comparable to previous years.

Kernel size effect on EFT richness

The 4x4-pixel Kernel for the sliding window offered the finest spatial resolution of the EFT richness map without saturation of this variable (Figure C1, Appendix C). That is, when the size of the sliding window Kernels was 2x2 or 3x3 pixels, there was a high proportion of Kernels that reached the highest possible richness value (4 and 9 EFT classes per Kernel, respectively), so the EFT richness variable was highly saturated. The use of 5x5-pixel sliding windows never reached the maximum number of pixels in a Kernel but resulted in too coarse outputs (grain size of 5x5 MO13Q1 pixels). Hence, the 4x4-pixel Kernels offered a balance between output resolution and variable saturation, since we observed a maximum EFT richness of 13, while the maximum potential richness in a 4x4- pixel Kernel was 16.

Nevertheless, any richness assessment depends on the spatial scale. i.e., both grain and extent (Arponen et al., 2012). Regarding grain, when using species distributions to identify hotspots, the actual values of species richness reached in each cell would increase with grain size from a dataset built at 1x1 km to a dataset built at 10x10 km. However, the regional spatial patterns of species richness would not widely vary between the two datasets (Rahbek, 2005). In our analysis, the maximum number of classes per Kernel could vary depending on the Kernel size. In the future, once data records of satellite images with higher spatial resolution, such as Sentinel-2, get long enough, it will be possible to get a finer resolution picture of ecosystem functioning and functional diversity at the protected area level.

Data applications for research and conservation / Example of data usage

Ecological research based on spectral vegetation indices plays an essential role in biodiversity conservation (Cabello et al., 2012; Pettorelli, 2016, 2018) and management (Pelkey et al., 2003; Cabello et al., 2016) and for the study of biodiversity and ecosystems responses to environmental changes (Alcaraz-Segura et al., 2017; Pérez-Luque et al., 2015a). In fact, numerous studies have demonstrated the usefulness of satellite image time series to evaluate the functional changes in ecosystems at the regional scale (Alcaraz-Segura et al., 2009) and at the protected area level (AlcarazSegura et al., 2009; Lourenço et al., 2018). Recently, the use of EFAs derived from spectral indices of vegetation in species distribution models has made it possible to evaluate with high spatial and temporal precision the suitability of habitat for plant species (Arenas-Castro et al., 2018) and animals (Requena-Mullor et al., 2017; Regos et al., 2019) and may even anticipate expected changes in the distribution of plant species threatened as a consequence of climate change (Alcaraz-Segura et al., 2017). In addition, based on the EFAs, a monitoring program of the Spanish National Parks Network has been designed to identify changes and anomalies in functioning, informing managers of the health and conservation status of ecosystems (Cabello et al., 2016).

Furthermore, the EFT approach have been used to characterize spatial and temporal heterogeneity of ecosystem functioning at local and regional scales (Fernández et al., 2010; Cabello et al., 2013); to describe biogeographical patterns (Alcaraz-Segura et al., 2006; Ivits et al., 2013); to evaluate the environmental and human controls of ecosystem functional diversity (Alcaraz-Segura et al., 2013); to identify priorities for Biodiversity Conservation (Cazorla et al., 2020); to assess the representativeness environmental networks (Villarreal et al., 2018); to assess the effects of land-use changes on ecosystem functioning (Oki et al., 2013); and to improve weather forecast models (Lee et al., 2013; Müller et al., 2014).

This dataset provides the first characterization of functional diversity at the ecosystem level in Sierra Nevada. Our dataset could serve as a reference situation to track ecosystem functioning response to global change and management actions, to understand the drivers of ecosystem functioning and functional diversity, and to assess the supply of ecosystem services (Palomo et al., 2013; IniestaArandia et al., 2014; Cabello et al., 2019). The Global Change Observatory of Sierra Nevada is also a long-term ecological research site (name: ES-SNE, code: LTER_EU_ES_010) established more than a decade ago (Zamora et al., 2016, 2017). It has available data on species distributions and dynamics, climate, ecosystem services, hydrology, land-use changes, and management practices (Pérez-Luque et al., 2014, 2015b, 2015c, 2016; Ros-Candeira et al., 2019, 2020; Lorite et al., 2020). The abundance of long-term datasets from multiple disciplines constitutes an opportunity to explore the role of ecosystem functioning and functional diversity on ecohydrological and species distribution modeling, climate change mitigation and adaptation, ecological resilience, adaptive management, and ecosystem services supply.

Data availability

The datasets described in this article are available in open-access sources. To broaden their use, first, we provide data in .tif format. Second, we have incorporated rendered versions of all layers as required by Google Earth Pro (called "filename..._forGoogleEarthVisualization.tif") for visualization. Moreover, we have also developed an ad-hoc visualization platform for all the layers. Datasets are available for download in PANGAEA: https://doi.pangaea.de/10.1594/PANGAEA.904575 (Cazorla et al., 2019) and for visualization in http://obsnev.es/apps/efts_SN.html.

The MODIS database used in this work is maintained by NASA (satellite Terra, sensor MODIS, product MOD13Q1.006) and copied by Google into the Earth Engine servers (https://developers.google.com/earth-engine/datasets/catalog/MODIS_006_MOD13Q1). The Sierra Nevada Biosphere Reserve boundaries shapefile is included in the public geodatabase of the Andalusian regional government (REDIAM: https://descargasrediam.cica.es/ 07_PATRIMONIO_NATURAL/01_ESPACIOS_PROTEGIDOS.

4.2.4. Conclusions

This dataset provides a characterization of ecosystem functioning and ecosystem functional diversity patterns in terms of primary production, in the Sierra Nevada Biosphere Reserve (SE Spain), a biodiversity hotspot and a European Long Term Ecological Research (LTER) platform. We based our contribution on the identification of Ecosystem Functional Types (EFTs) through the analysis of time series of satellite images of spectral vegetation indices as surrogates of the carbon gains dynamics. First, we provided three Ecosystem Functional Attributes (EFAs) that describe the spatial and interannual variability in productivity, seasonality, and phenology of vegetation greenness. Second, we combined these EFAs into a synthetic classification, i.e., Ecosystem Functional Types (EFTs), which integrates into a single map the spatial heterogeneity of these descriptors of the seasonal dynamics of carbon gains. Finally, by using EFTs as biological entities, the spatial patterns of ecosystem functional diversity were assessed using EFT richness and EFT rarity, as well as the inter-annual variability in ecosystem functioning through EFT inter-annual variability and EFT inter-annual dissimilarity. The Ecosystem Functional Type approach improves the understanding of ecosystem processes through environmental gradients, and provides both to the scientific and managers communities with valuable information of the first characterization of the functional diversity at the ecosystem level developed in the entire protected area.

4.2.5. References

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4.2.6. Appendices

Appendix A. Identification of meaningful metrics: Ecosystem Functional Attributes

To define EFTs we use three meaningful metrics or descriptors of the EVI seasonal dynamics (i.e. of annual dynamics in primary production). Biologically, these three metrics can be interpreted as surrogates (Paruelo et al. 2001, Pettorelli et al. 2005, Alcaraz-Segura et al. 2006) of the total amount and timing (seasonality and phenology) of primary production. Statistically, these three metrics are known to be highly correlated with the first two or three axes (and hence capture most of the variance) of a Principal Component Analysis (PCA) carried out on the NDVI or EVI annual dynamics in different regions (Townshend et al. 1985, Paruelo and Lauenroth 1998, Paruelo et al. 2001, Alcaraz-Segura et al. 2006, Alcaraz-Segura et al. 2009, Ivits et al. 2013). To know the statistical meaningfulness of these metrics in the Sierra Nevada Biosphere Reserve, we examined their correlation with the first axes of a PCA run on the EVI annual curve of the average year (12 EVI values, i.e. the inter-annual means of the maximum value composites for each month). The first two axes cumulated 96.5% of the variance (PC1 87.3%, PC2 9.2%). The eigenvectors showed that the weights along the months were similar for the first PCA axis (even weights throughout the year), while for the second axis they showed a contrast between winter and summer months (Table A1). This indicated that PC1 can be related to the total or average amount of EVI, and that PC2 can be related to the intra-annual variability of EVI (Figure A1).

Table A1. Eigenvectors and cumulative variance explained by the first two components of a principal component analysis (PCA) performed on the annual curve of EVI values in Sierra Nevada.

		Scores											
PCA axis	**%[a]**	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
1	87.3	0.334	0.328	0.333	0.318	0.293	0.246	0.236	0.239	0.242	0.251	0.287	0.325
2	96.5	0.329	0.365	0.326	0.109	0.244	0.454	0.380	0.301	0.252	0.154	0.007	0.229

[a] *Cumulated variance*

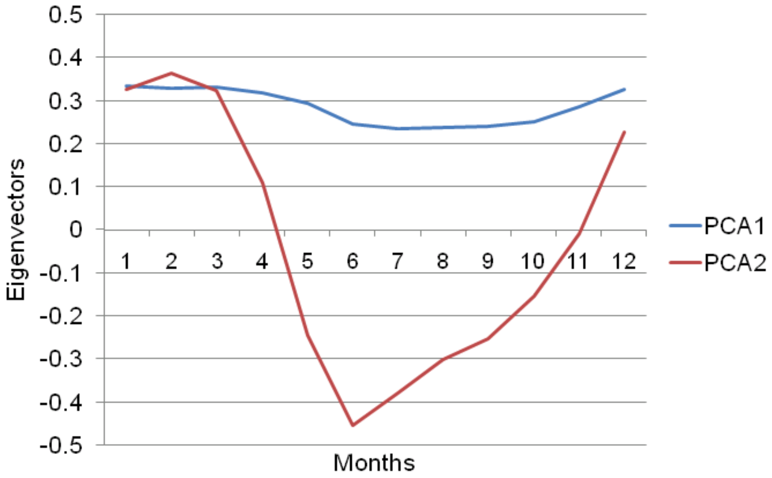

Figure A1. Eigenvectors of the first two components of a PCA performed on the annual curve of EVI values in Sierra Nevada (X axis: months; Y axis: eigenvectors values). The first PCA axis accounted for 87% of variance and showed even weights throughout the year, while the second PCA axis accounted for 9% of the variance and showed a strong contrast between seasons.

In addition, we explored the correlation between the PCA axis and the EVI metrics (i.e., EFAs). The EVI metrics showed a high correlation with the PCA axes. PC1 accounted for most of the total variance in the seasonal dynamics of the EVI (87.3%) and was strongly correlated with the EVI annual mean (PC1 vs. EVI_mean r = 0.94). PC2 accounted for 9.2% of the total variance (PC1 and PC2 cumulated 96.5% of total variance) and was related to seasonality and phenology metrics (as in Alcaraz-Segura et al. 2006, 2009) (PC2 vs. EVI_SD r = -0.75; PC2 vs DMAX_Sine = 0.67; PC2-vs DMAX_Cosine = -0.61) (Table A2). To correlate DMAX with the PC axes and keep the continuous nature of the annual period and the relative distance between months (i.e. December is as close to January as July is to June, that is, the distance between December (12) and January (1) is one month, not eleven months), we transformed months into polar coordinates. The entire circumference of a year was divided into 12 portions and each month was equated to an angle (30º for January and 360º for December). DMAX months were therefore characterized by their sine and cosine values.

In summary, PC1 was very highly correlated to EVI_mean and then can be interpreted as annual primary production. PC2 shows a high contrast in the eigenvector values between winter and summer and is highly correlated with EVI_SD and with the Sine and Cosine components of DMAX, so it can be interpreted as a combination of seasonality (SD) and phenology (DMAX). Mathematically, it could be expressed as follows: PC2 = f(a*SD + b*DMAX_Sine + c*DMAX_Cosine + d + e) (Table A1 and A2), and the r-square of this multiple regression was 0.70.

Table A2. Correlation values between PCA axis 1 and 2 and Ecosystem Functional Attributes (EFA).

EFA	**PC1**	**PC2**
EVI_mean	**0.94**	-0.01
EVI_SD	-0.14	**-0.75**
DMAX_Sine	-0.10	**0.67**
DMAX_Cosine	0.017	**-0.61**

In addition, the EVI metrics were orthogonal, since the correlation between them was low so that each EVI metric contributed independently to explain the variance of the EVI time series (Table A3).

Table A3. Pearson correlation values between metrics.

	EVI_mean	**EVI_SD**
EVI_mean	**1**	
EVI_SD	-0.14	**1**
EVI_DMAX	0.10	-0.05

Appendix B. Variability on quartile boundaries

B1. Inter-annual stability in quartiles to set boundaries among EFT classes

We determined the minimum number of years that were needed to reach stability in the quartile boundaries among EFT classes. For each quartile of EVI_mean and EVI_SD, we plotted the maximum inter-annual Coefficient of Variation (Y-axis) among the n consecutive years considered, with n ranging from n= 2 years to n=18 years against the number of years considered (X-axis) (i.e. the maximum value of the Coefficient of Variation among all possible combinations of two consecutive years, three consecutive years, four, five, etc. throughout the 2001-2018 period (Figure B1 a - f). The three EVI_mean quartiles tend to stabilize around an inter-annual Coefficient of Variation of 5%, which requires around 14 years of the study period. The three EVI_SD quartiles tend to stabilize around an inter-annual Coefficient of Variation of 10%, which requires around 17 years of the study period. Hence, the 18-year study period provided in this dataset would be enough to serve as a reference situation for this protected area. For example, if you want to show time-series of 2001-2020, it would not be necessary to derive the quartiles boundaries again for the year 2020, since our 18-year study period is representative enough to extrapolate quartiles to the new year.

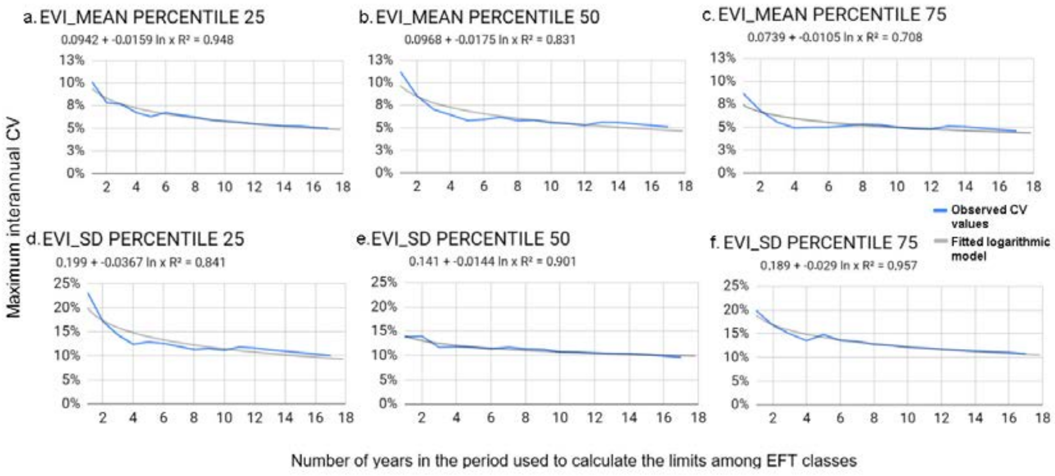

Figure B1. Stabilization of the inter-annual Coefficient of Variation (CV) of the limits (quartiles) among ecosystem functional type (EFT) classes as the number of years included in the study period increases. For each quartile, we plotted the maximum inter-annual CV (Y axis) among the n consecutive years considered, with n ranging from n=2 to n=8 (X axis). The quartiles of EVI_mean (our surrogate for productivity) required at least 14 years to stabilize around 5% of CV. The quartiles of EVI_SD (our surrogate for seasonality) required at least 17 years to stabilize around 10% of CV.

B2. Quartile boundaries variability

To know how variable the quartiles were, we obtained the quartiles of each year, their inter-annual mean, their inter-annual standard deviation, and their inter-annual Coefficient of Variation (Table B1). The variability among years or Coefficient of Variation (CV) was around 5% for EVI_mean quartiles and lower than 11% for EVI_SD quartiles, increasing in the upper quartiles (Table B1).

Table B1. Annual quartile boundaries (percentile P25, percentile P50, percentile P75) for EVI_mean and EVI_SD and summary of the period (Inter-annual mean, Standard Deviation (SD) and Coefficient of Variation (CV)).

YEAR	EVI_ mean P25	EVI_mean P50	EVI_mean P75	EVI_SD P25	EVI_SD P50	EVI_SD P75
2001	0.133	0.187	0.245	0.030	0.044	0.063
2002	0.139	0.190	0.243	0.031	0.042	0.057
2003	0.130	0.184	0.242	0.031	0.046	0.068
2004	0.142	0.197	0.251	0.032	0.047	0.068
2005	0.123	0.168	0.222	0.023	0.039	0.056
2006	0.126	0.174	0.229	0.030	0.046	0.066
2007	0.142	0.184	0.232	0.028	0.038	0.051
2008	0.133	0.176	0.229	0.029	0.042	0.062
2009	0.133	0.180	0.235	0.032	0.048	0.070
2010	0.139	0.190	0.242	0.034	0.048	0.072
2011	0.149	0.200	0.258	0.032	0.045	0.069
2012	0.139	0.187	0.238	0.027	0.037	0.052
2013	0.142	0.197	0.258	0.032	0.044	0.063
2014	0.130	0.184	0.241	0.026	0.037	0.056

2015	0.139	0.194	0.245	0.030	0.042	0.060
2016	0.134	0.182	0.233	0.024	0.036	0.054
2017	0.142	0.187	0.238	0.030	0.039	0.057
2018	0.145	0.206	0.264	0.032	0.047	0.068
Inter-annual mean	0.137	0.187	0.241	0.030	0.043	0.062
Inter-annual SD	0.007	0.009	0.011	0.003	0.004	0.006
Inter-annual CV (%)	5.001	5.103	4.593	10.040	9.597	10.745

Appendix C. Effect of Kernel size on EFT richness

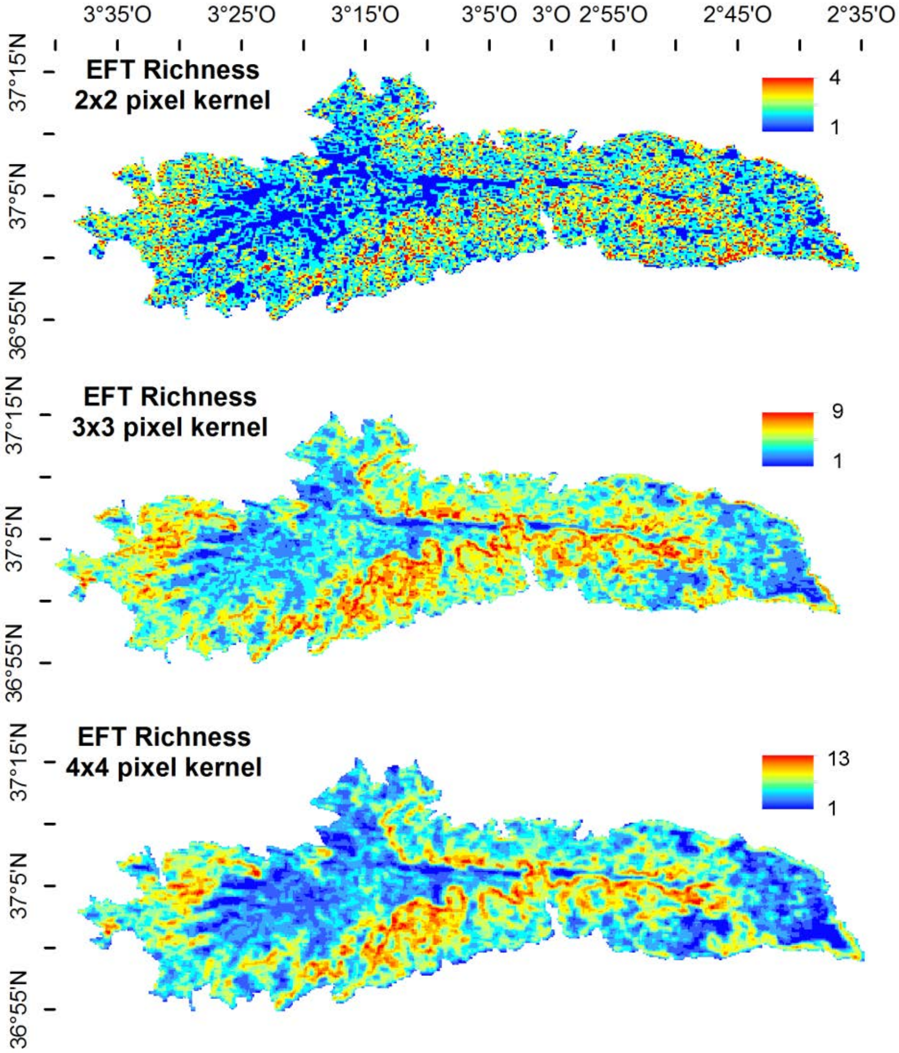

Figure C1. EFT Richness for 2x2, 3x3, and 4x4-pixel Kernel sizes. A 4x4-pixel Kernel was chosen since it offered the finest spatial resolution that did not saturate the number of EFT classes per Kernel.

4.3.

CHAPTER III

Incorporating ecosystem functional diversity into geographic conservation priorities using remotely-sensed Ecosystem Functional Types

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Abstract

Conservation biology must set geographic conservation priorities not only based on the compositional or structural but also on the functional dimensions of biodiversity. However, assessing functional diversity is challenging at the regional scale. We propose the use of satellite-derived Ecosystem Functional Types (EFTs), defined here as patches of land surface that share similar primary production dynamics, to incorporate such aspects of ecosystem functional diversity into the selection of protected areas. We applied the EFT approach to the Baja California Peninsula, Mexico, to characterize the regional heterogeneity of primary production dynamics in terms of EFTs; to set conservation priorities based on EFT richness and rarity; and to explore whether such EFT-based conservation priorities were consistent with and/or complementary to previous assessments focused on biodiversity composition and structure. EFTs were identified based on three ecosystem functional attributes derived from seasonal dynamics of the Enhanced Vegetation Index (EVI): the annual mean (proxy of primary production), the seasonal coefficient of variation (descriptor of seasonality), and the date of maximum (indicator of phenology). EFT-based priorities identified 26% of the peninsula as being of extreme or high priority and reinforced the value of the ecosystem functional diversity of areas already prioritized by traditional conservation assessments. In addition, our study revealed that biodiversity composition- and structure-based assessments had not identified the full range of important areas for EFT diversity and tended to better capture areas of high EFT rarity than those of high EFT richness. Our EFT-based assessment demonstrates how remotely sensed regional heterogeneity in ecosystem functions could reinforce and complement traditional conservation priority setting.

KEYWORDS: Ecosystem functional heterogeneity; Richness; Rarity; Ecosystem functioning; Biodiversity congruence; Holistic conservation; Geographic priorities; Remote sensing.

4.3.1. Introduction

Contemporary conservation planning faces the challenge of safeguarding the ecological processes required for the persistence of biodiversity over time (GBO4, 2014) and for the supply of ecosystem services to people (Costanza, 2012). To this end, protected areas must represent the most important areas for *in situ* global conservation effort (Watson et al., 2014). Initially, opportunism and aesthetic values drove protected area creation (Palomo et al., 2014; Baldi et al., 2017). More recently, reserve selection under systematic conservation approaches (Margules and Pressey, 2000) has mainly relied on compositional and structural dimensions of biodiversity (e.g., Rodrigues et al., 2004; Lamoreux et al., 2006). However, despite important advances to the design of more comprehensive protected area networks, geographic conservation priorities have seldom considered heterogeneity in ecosystem functions (Callicott, 1999; Mace, 2014; Turner and Gardner, 2015). The need for more representative global protected area networks (Visconti et al., 2019) that account for the three dimensions of biodiversity (composition, structure, and function; Noss, 1990) could greatly benefit from the explicit inclusion of ecosystem functions and processes that support biodiversity and ecosystem services (Meyer, 1997; Cabello et al., 2012; Pettorelli et al., 2018; Lecina-Díaz et al., 2019).

Functional diversity, ranging from gene expression to landscape processes, is an important biodiversity component to be assessed by conservation programs, as it links biological diversity with ecosystem functioning (Cadotte et al., 2011; Díaz et al., 2007; Chapin et al., 2010; Asner et al., 2017), services (Balvanera et al., 2006; Duncan et al., 2015), and resilience (Mouchet et al., 2010). Functional diversity estimates have been made by grouping species into functional types based on structural (e.g., shrubs, trees, etc.), phylogenetic (e.g., *Coniferae*, *Poaceae,* etc.) or metabolic strategies (e.g., C3, C4, etc.) related to meaningful biological processes (Lavorel et al., 2002, 2007) or by using morphofunctional species traits (Malaterre et al., 2019). However, the capacity for species functional types and traits to represent variations in ecosystem functional properties at regional scales remains a challenge (Wright et al., 2006; Pasari et al., 2013; Reichstein et al., 2014; Asner et al., 2017; Malaterre et al., 2019).

Understanding the causes and consequences of spatial heterogeneity in ecosystem functions could help protect the species and communities that they support (Meyer, 1997; Lovett et al., 2005; Turner and Gardner, 2015) and elucidate the links between ecosystem multifunctionality, ecosystem services (Manning et al., 2018) and ecological stability (Oliver et al., 2015). Environmental heterogeneity is a universal driver of taxonomic, phylogenetic, and functional diversity (Stein et al., 2014; Stark et al., 2017; Bergholz et al., 2017). However, while conserving biophysical setting variability has been suggested to preserve biodiversity against rapid environmental change (e.g., Lawler et al., 2015; Littlefield et al., 2019), variation in ecosystem functions has received less attention (Lovett et al., 2005). Developing feasible approaches to understand and account for heterogeneity in ecosystem functions could complement traditional priority settings to achieve the holistic goal of protecting all biodiversity facets.

Satellite remote sensing can guide conservation actions based on the characterization of functional diversity not only at the species trait level (Jetz et al., 2016) but also at the ecosystem level (Cabello et al., 2012; Alcaraz-Segura et al., 2013; Asner et al., 2017; Gamon et al., 2019). First, satellite-derived descriptors of ecosystem functions can be relevant as essential biodiversity variables (EBVs, Pettorelli et al., 2016, 2018; Alcaraz-Segura et al., 2017). For example, spectral indices are linked to key ecosystem functional descriptors such as primary production, evapotranspiration, surface temperature, and albedo (Paruelo et al., 1997; Fernández et al., 2010; Lee et al., 2013) (Table 4.3.1. - steps 1 and 2). Second, with these descriptors, it is possible to identify and map areas sharing similar dynamics of matter and energy exchange between biota and physical environments based on so-called satellite-derived Ecosystem Functional Types (EFTs) (Paruelo et al., 2001; Alcaraz-Segura et al., 2006, 2013).

As highlighted by Mucina, (2019), EFTs could represent ‘the first serious attempt to group ecosystems (at large scales) on the basis of shared functional behaviour’. EFTs group ecosystems on the basis of shared ecosystem functions without prior knowledge of vegetation types or canopy structure (Ivits et al., 2013). As species can be grouped into plant functional types based on common morphofunctional traits to derive ecological properties at higher biological levels (i.e., a bottom-up strategy), ecosystems can be grouped into EFTs to directly map processes and functions at larger scales (i.e., a top-down approach) (Alcaraz-Segura et al., 2006). EFTs follow a holistic approach (Naeem, 1998, 2002; Loreau 2008) to measure the overall performance of an ecosystem (see the review in Jax 2010). EFTs capture heterogeneity in ecosystem functions (e.g., primary production, evapotranspiration, or disturbance dynamics) and provide complementary information to other metrics such as those of vegetation structure and species composition to improve our understanding of the multidimensional nature of biodiversity (Noss, 1990). EFTs have already been used to characterize the spatial heterogeneity of ecosystem functioning at the global (Ivits et al., 2013), regional (Paruelo et al., 2001; Alcaraz-Segura et al., 2006; Lara et al., 2017), and protected area scales (Fernández et al., 2010; Cabello et al., 2013).

In this study, we propose the use of Ecosystem Functional Types (EFTs), defined here as patches of land surface that share similar primary production dynamics (i.e., productivity, seasonality, and phenology, Figure 4.3.1.), to incorporate the spatiotemporal heterogeneity of a focal ecosystem function into geographic conservation priorities (conceptual workflow shown in Table 4.3.1.). As a proof of concept, we applied the EFT approach to the Baja California Peninsula (Mexico): 1) to characterize the regional heterogeneity of primary production dynamics using EFTs; 2) to prioritize areas for conservation based on their EFT diversity (EFT richness and rarity); and 3) to explore whether such EFT-based priorities were congruent with and/or complementary to previous expert and systematic conservation-based assessments mainly focused on biodiversity composition and structure.

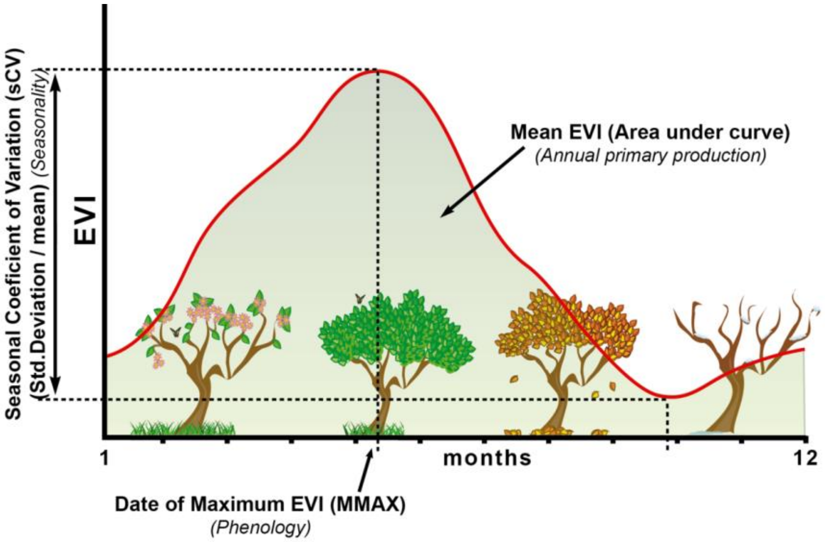


Figure 4.3.1. Seasonal dynamics of the Enhanced Vegetation Index (EVI) and of Ecosystem 793 Functional Attributes (EFAs). The X-axis corresponds to months and the Y-axis corresponds 794 to EVI values. EFAs include: the annual EVI mean, an estimator of annual productivity (EVI 795 mean); the seasonal EVI coefficient of variation (EVI_sCV), i.e., differences between 796 minimum and maximum EVI values, as a descriptor of seasonality; and the date of the 797 maximum EVI (EVI DMAX) as a phenological indicator of the growing season.

4.3.2. Methods

Study area

We chose the Baja California Peninsula as study area (Figure 4.3.2.a) because it has high environmental heterogeneity, low human influence, a large proportion of protected land (40%) (Appendix 1) and because two geographic priority assessments have been conducted on the area mainly based on biodiversity composition and structure (Arriaga et al., 2000; Koleff et al., 2009). The peninsula covers a Mediterranean-desert-tropical climatic transition area positioned along a 1400 km latitudinal gradient from 35ºN to 23ºN (González-Abraham et al., 2010). The Mediterranean Region (NW) is characterized by annual mean temperatures between 8-21ºC, dry summers and mild wet winters with annual rainfall levels ranging from 100-200 mm at sea level to 500-700 mm in the highest mountains (3100 m) (Peinado et al., 2011). The Desert Region extends from NE to S and is characterized by temperatures ranging from 20-25ºC, and very low annual rainfall (100-200 mm) concentrated in sporadic events that shift from the winter in the N to the summer in the S (Hastings and Turner 1965). The Tropical Region at the southern tip is warm year round (15-24ºC) and characterized by a nine-month dry season (November to July) followed by the tropical cyclone and storm rains with annual rainfall levels ranging from 200 mm at sea level to 700 mm in the highest mountains (at 2090 m) (Peinado et al., 2011).

Identifying Ecosystem Functional Types

Regional heterogeneity in ecosystem functions was characterized by identifying Ecosystem Functional Types (EFT) based on the seasonal dynamics of carbon gains following Alcaraz-Segura et al., (2013). We focused on primary production because it is an integrative component of ecosystem functioning (Table 4.3.1. - step 1; Virginia and Wall 2013), and its seasonal dynamics can be monitored through spectral vegetation indices. We used 2001-2017 Enhanced Vegetation Index (EVI) images from the MODIS sensor (MOD13Q1.005 product: 16-day maximum value composite images at ~231 m pixel size), as it offers a long time-series of a robust surrogate for primary production (Shi et al., 2017) (Table 4.3.1. - step 2). EFTs were derived from three meaningful metrics of the EVI seasonal curve also known as Ecosystem Functional Attributes (EFAs) (Figure 4.3.1.; Table 4.3.1. - step 3) (Pettorelli et al., 2005; Alcaraz-Segura et al., 2013): the annual mean (EVI mean; an estimate of primary production), the EVI seasonal coefficient of variation (EVI sCV; a descriptor of seasonality), and the date of the maximum EVI (EVI DMAX; an indicator of phenology). The three metrics capture most of the variance in EVI seasonal dynamics into three meaningful metrics that facilitate ecological interpretation (Paruelo et al., 2001; Alcaraz-Segura et al., 2006).

Table 4.3.1. Workflow and rationale for setting geographic conservation priorities based on Ecosystem functional Types to incorporate ecosystem functional diversity in a more holistic biodiversity conservation.

What is the goal of this step?	Why is it needed?	How did we complete it?
Step 1. To identify the targeted functional facets of biodiversity to be considered, e.g., ecosystem primary production as an essential biodiversity variable	Conservation planning based on functional dimensions of biodiversity is needed (Noss, 1990) but scarce (Cabello et al., 2012). Some facets of ecosystem functioning are more essential to biodiversity and ecosystem services, offer more available information for inventorying and monitoring, and are more relevant to particular conservation goals than others	We chose primary production, as it is the most integrative indicator of ecosystem functioning (Virginia and Wall, 2013)
Step 2. To choose surrogates for targeted functional facets, e.g., remotely sensed vegetation indices	Direct measurements of biodiversity variables are usually costly. Satellite images of the Earth can be considered biological datasets (Geller et al., 2017). Image pixels are sampling plots whose spectral information offers indirect, cost-effective estimates of matter and energy exchanges between the land surface and the atmosphere, which support ecosystem functions and services	We used the Enhanced Vegetation Index (EVI) to estimate photosynthetically active radiation absorbed by vegetation (based on the Monteith Model, 1972)
Step 3. To identify simple and biologically meaningful metrics of the ecosystem functioning surrogates, e.g., descriptors of the amount and timing of carbon gain dynamics	The dynamics of ecosystem functioning are tracked through full time-series of essential variables. Synthesizing and capturing most of the variance of these time-series into a few easy to interpret metrics reduces complexity, eases interpretability, and promotes the metrics standard use	We identified three metrics capturing most of the variance in the EVI seasonal dynamics (Ecosystem Functional Attributes, EFAs): annual production, seasonality and phenology. We parametrized yearly seasonal dynamics of the EVI for three EFAs: the annual EVI mean, seasonal EVI coefficient of variation, and the date of the maximum EVI

What is the goal of this step?	Why is it needed?	How did we complete it?
Step 4. To group patches of the land surface with similar functional behaviors by classifying continuous metrics into discrete units, e.g., Ecosystem Functional Types (EFTs)	Functional classifications synthesize continuous large-scale ecological gradients into discrete mapping units in relation to common ecosystem functions and processes. Discrete mapping units characterize ecosystem diversity at the regional scale and are needed for management and decision-making such as in systematic conservation planning	To integrate patterns of productivity, seasonality and phenology into a single map, we divided the range of values of each EFA into four intervals (quartiles), creating a potential number of 64 EFTs (4x4x4)
Step 5. To select criteria for assessing ecosystem functional diversity at the regional scale, e.g., EFT richness and rarity	Measurements of all biodiversity facets are not possible given the complex, multidimensional and hierarchical nature of biodiversity (Noss, 1990). Biodiversity indices such as richness and rarity are easy to interpret, relevant, and objective criteria frequently used in conservation assessments	We calculated EFT richness by counting the number of EFTs in a slicing window. EFT rarity was calculated as the relative extension of each EFT compared to the most abundant EFT
Step 6. To set geographic conservation priorities that capture areas of high ecosystem functional diversity, e.g., areas of high EFT richness and rarity	Landscapes of high heterogeneity in ecosystem functions are prone to contain multiple ecosystem metabolic and evolutionary pathways. Multifunctional landscapes provide more diverse ecosystem services (Manning et al., 2018), and functional diversity confers ecological stability (resistance and resilience)	We identified areas of highest (extreme and high) conservation priority as those ones with high EFT richness and high EFT composition rarity
Step 7. To compare priorities based on ecosystem functional diversity with independent assessments, e.g., complementarity and consistency between EFT-based priorities and previous assessments focused on composition and structure	Priorities based on ecosystem functioning can converge with independent priorities focused on biodiversity composition and structure so that they reinforce each other. Priorities can also be complementary, supporting decision-making by offering supplementary arguments for the holistic conservation of biodiversity	We integrated the three approaches into two synthetic maps: consistency and complementarity. To visualize agreement and disagreement between and among approaches, we used Venn diagrams

To derive EFT classes from EFAs, the range of values of each EFA was divided into four intervals that were then combined, generating a potential number of (4 × 4 × 4) 64 EFTs (Figure S1D and S2). We used this classification method with fixed boundaries between classes to maximize the biological interpretability of EFTs and to apply the same classification rules to each year. This way, the classification can be used to track interannual changes in spatial heterogeneity of ecosystem functions (Littlefield et al., 2019). As for DMAX since we wanted to maintain its ecological sense in our final classification (i.e., the timing or phenology of the interception of radiation by vegetation), the four intervals agree with the four seasons of the year: spring (April-June), summer (July-September), autumn (October-December), and winter (January-March). For EVI_mean and EVI_sCV, we extracted the first, second, and third quartiles (i.e., the 25th, 50th, and 75th percentiles, respectively) for each year. Then, we calculated the interannual means of the quartiles (average of the 17-year period), which were used as thresholds among classes (Figure S1D). The four intervals created for each variable produced a relatively low number of potential classes (64) and maintained the EFAs spatial patterns (Figure S1 and S2).

To code EFTs, we used two letters and a number (Figure S1D): the majuscule indicates primary production (EVI mean) increasing from *A* to *D*; the minuscule represents seasonality (EVI sCV) decreasing from *a* to *d*; and numbers are a phenological indicator of the growing season (EVI DMAX): 1-spring, 2-summer, 3-autumn, and 4-winter. To summarize ecosystem function patterns of the 2001–2017 period, for each pixel we calculated the most common EFT (the mode) from the 17 annual EFT maps (Table 4.3.1. - step 4). We excluded from analyses pixels with human influence according to the human footprint index (HF>0.5) (González-Abraham et al., 2015) and those including anthropogenic land-uses in the 2017-updated land-cover map (INEGI 2017).

Mapping geographic conservation priorities from EFT richness and rarity

To identify geographic conservation priorities based on spatial heterogeneity in our focal ecosystem function (i.e., primary production dynamics), we derived two diversity metrics from the EFT map: EFT richness and EFT rarity (Table 4.3.1. - step 5). Both richness and rarity are indices that are easy to interpret, objective, and commonly used in ecology and conservation (Perrin and Waldren 2020). Richness measures the different types of entities in a sample. EFT richness was calculated by counting the number of different EFTs within an 8 × 8 pixel-sliding window across the study area, serving as an indicator of spatial heterogeneity in primary production dynamics. From the EFT richness of each year, we obtained the interannual average of EFT richness (Alcaraz-Segura et al., 2013). We chose this window size because it includes 64 pixels, which is the potential maximum number of EFTs in our classification. The use of smaller window sizes resulted in many windows reaching the maximum number of classes while larger windows produced too coarse outputs (Appendix 5).

Rarity has also been a central focus in conservation (Soulé 1986). According to its abundance-based definition, rarity refers to how frequently an entity is found within an area (Kondratyeva et al., 2019). The rarity of each EFT was used as an indicator of distinctive characteristics (i.e., singularity) in primary production dynamics, which are likely to exhibit unique biodiversity features with conservation interest (Meyer 1997). EFT rarity was calculated as the extension of each EFT relative to the most abundant EFT throughout the peninsula (Equation 1) (Cabello et al., 2013).

$$Rarity\ of\ EFT_i = (Area\_EFT_{max} – Area\_EFT_i)/Area\_EFT_{max}\ (Equation\ 1)$$

where $Area\_EFT_{max}$ is the area occupied by the most abundant EFT throughout the study area, and $Area\_EFT_i$ is the area of the i EFT evaluated with i ranging from 1 (*Aa1)* to 64 (*Dd4)*. An average rarity map for all years was obtained, serving as our estimate of regional patterns of ecosystem functional singularity.

To determine EFT-based geographic conservation priorities, we searched for areas of high EFT richness and rarity (Table 4.3.1. - step 6). First, we stretched (by spatial averaging) the spatial resolution of the EFT rarity map (231 m/pixel) to match the EFT richness map resolution (i.e., an aggregated value for 8x8-pixel windows). Second, the range of values of both priority-criteria variables was divided into four intervals using quartiles. Third, a decision matrix with 4 × 4 = 16 possible combinations of richness and rarity levels was produced. Finally, the 16 combinations of richness and rarity levels were grouped into four final priority categories (Figure 4.3.3.a): extreme, high, moderate, and low for combinations that summed to 8, 7, 6, and 5, respectively. Combinations with lower sums were deemed not a priority.

Assessment of spatial congruence and complementarity between the functional approach and previous assessments

We explored the congruence and complementarity between the EFT-based geographic conservation priorities and two previous assessments based on compositional, structural, and threat features of biodiversity (Table 4.3.1. - step 7). The "systematic conservation" study by Koleff et al., (2009) used robust spatial analysis algorithms in a grid to identify four levels of "Priority Sites to Conserve" based on diversity of and threats to vertebrates, plants, and vegetation types. The "expert-based" study by Arriaga et al., (2000) identified "Terrestrial Priority Regions" through qualitative expert workshops that combined multiple biological criteria (i.e., species richness and endemicity, centers of diversification and domestication, vegetation types, etc.) with criteria for threats and opportunity (i.e., habitat loss and fragmentation, unsustainable management, threatened species, etc.).

For the congruence analysis, we overlapped the three approaches at an 8 × 8-pixel window-resolution into two synthetic maps: one that integrated congruence between the approaches (where priorities agreed) (Figure 4.3.3.C) and another that revealed complementarity (where priorities did not agree) (Figure 4.3.3.D). Congruence with other approaches was defined as the existence of a spatial overlap between EFT-based priorities and one or both of the other approaches. Complementarity with other approaches was defined as the existence of spatial discordance between EFT-based priorities and the previous priorities.

To visualize agreement and disagreement between approaches, we used Venn diagrams and the Sorensen-Dice similarity index (Figure 4.3.4.). Additionally, to show how our EFT-based approach provides useful and orthogonal conservation priority information relative to traditional approaches, we explored the characteristics of congruent and complementary areas among approaches in terms of EFT richness and rarity (Figure 4.3.5.) and of EFAs and EFT frequency (Appendix 4).

Sensitivity analyses

To assess the effect of the sliding window size (Appendix 5), we calculated EFT richness, rarity, and priorities for double and triple window-side lengths (i.e., 8 × 8-, 16 × 16-, and 24 × 24-pixels). To assess the effect of the number of EFT classes considered (Appendix 6), we calculated EFT richness, rarity, and priorities by reducing the number of EFT classes by 86% (8 classes) and 58% (27 classes). Both effects were assessed three ways: from Pearson correlations between the different output maps, from the spatial consistency among the different output maps, and from the total percentage of the peninsula prioritized by each output map. Finally, we also assessed the effects of different thresholds of EFT richness and rarity on congruence and complementarity between approaches by means of the Sorensen-Dice similarity F-1 index (Appendix 7).

4.3.3. Results

Regional patterns of focal ecosystem function by means of EFTs

All 64 potential EFTs were identified in the Baja California Peninsula (Figure 4.3.2.B) and exhibited contrasting distributions across the three main ecoregions of the peninsula (Figure 4.3.2.a; González-Abraham et al., 2010). In the Mediterranean Region to the northwest, EFTs were characterized by moderate-high primary production, moderate-low seasonality, and spring EVI maxima (Figures S1 and S2). The central and northeastern Desert Region was characterized by EFTs with low primary production, low to moderate seasonality, and winter EVI maxima in the center and in various seasons in the northeast. The southern part of the

Desert Region was characterized by slightly higher level of primary production and seasonality and by summer-autumn EVI maxima. The Tropical Region in the south was characterized by high levels of primary production and seasonality and by summer EVI maxima (Figures S1 and S2).

Conservation priorities based on EFT richness and rarity

EFT richness and rarity (Figure 4.3.2.C-D) varied across the peninsula following a combination of latitudinal, longitudinal, and topographical gradients (Figure 4.3.2.A) and were found to be partially correlated. Areas of high EFT rarity ranged from low to high EFT richness while areas of high EFT richness always showed high levels of EFT rarity (Figure S3). EFT richness levels ranged from 1 to 26 EFTs per sliding window. Most windows of the highest EFT richness (12-26 EFTs) occurred north of 30° N in the Mediterranean Region, where climatic gradients translate into high heterogeneity in EFAs, especially along the mountain divide (Figure 4.3.2.A). An intermittent fringe of high EFT richness was also found along mountains from the southern San Felipe Desert to the center of the Desert Region (from 31º N to 27° N) and continued southwards along the western desert piedmonts and around wetlands and mangroves (from 27º N to 24° N). Moderate EFT richness (7-12 EFTs) was observed in the Mediterranean mountains, San Felipe Desert, Colorado Delta, mid-mountains along the Gulf Coast (from 26º N to 30º N), and desert areas of the central peninsula. Extensive areas with the lowest EFT richness (1-3 EFTs) were found in plains and piedmonts of the Central and Vizcaíno Deserts, along the southern desert mountains (Giganta Ranges), and in the Tropical Region.

EFT rarity gradients were more pronounced than EFT richness gradients (Figure 4.3.2.D). The highest rarity (0.8-0.9) occurred in the northwestern quarter of the peninsula above 30° N (Mediterranean Region), the central-eastern desert transition, and around wetlands and mangroves. The Pacific northwestern Central and Vizcaíno Deserts (north from 27ºN) showed low rarity (0.4-0.7). The lowest rarity (below 0.3) occurred along Giganta Ranges and in the Tropical Region (south of 28ºN). This region, dominated by drought-deciduous plant functional types, was mostly occupied by one extensive EFT with high productivity and seasonality and by summer EVI maxima (*Da2*).

The highest priority areas were found in heterogeneous areas across the Mediterranean Region, the northern and central-eastern Desert Region, and around wetlands and mangroves (Figure 4.3.3.a). Extreme priority areas occupied 9.6% of the peninsula surrounded by areas of high (16.4%), moderate (18%), and low priority (16.6%). The rest of the peninsula (39.5%) was classified as a nonpriority area for EFT diversity.

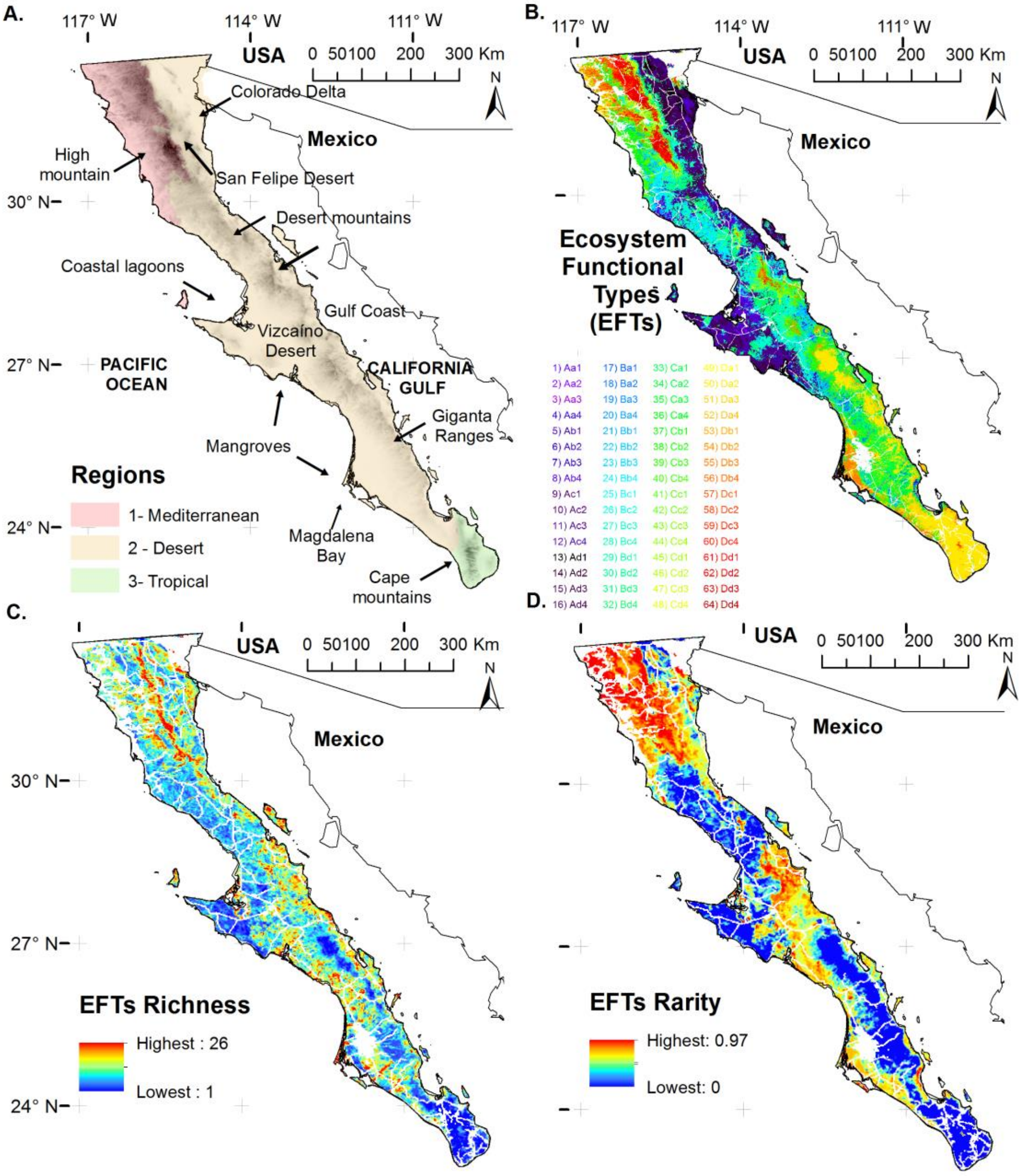
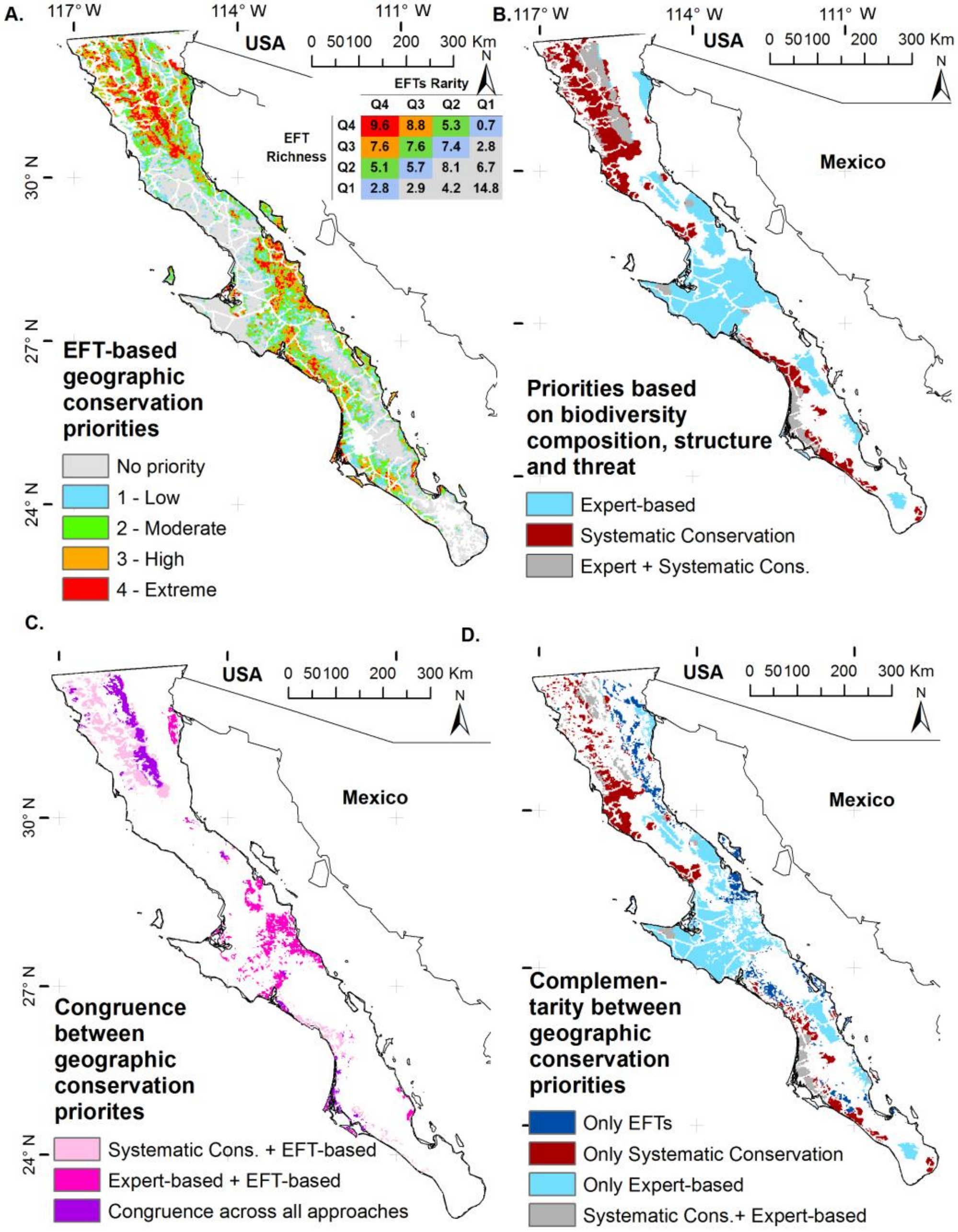


Figure 4.3.2. Spatial heterogeneity of ecosystem functioning in the Baja California Peninsula (Mexico). A) Study area showing biogeographical regions of study area and areas mentioned in the text. B) Ecosystem Functional Types (EFTs) of the 2001–2017 period (mode). EFT categories (lower left panel) are derived from three ecosystem functional attributes related to primary productivity, seasonality and the phenology of carbon gains (see maps in Appendix 2, Figure S1, S2); C) EFT richness, quantity of

EFTs occurring within 8 × 8-pixel sliding windows; and D) EFT rarity, calculated as the relative rarity of each EFT throughout the peninsula. White areas represented anthropogenic pixels removed from the analysis.

EFT-based priorities versus composition and structure-based approaches

EFT-based conservation priorities partially aligned with other approaches (Figure 4.3.3.A-B). Five percent of the peninsula was considered to be of the highest priority for all three approaches (Figure 4.3.4.) and mainly the Mediterranean Region along mountain tops and the Desert Region in isolated areas of mountains, wetlands and mangroves (Figure 4.3.3.C). An additional 14% of the peninsula was prioritized by the EFT-based approach and by either the systematic conservation approach (7%) or expert-based approach (7%) (Figures 4.3.3.C and 4.3.4.).



EFT Richness	EFTs Rarity Q4	Q3	Q2	Q1
Q4	9.6	8.8	5.3	0.7
Q3	7.6	7.6	7.4	2.8
Q2	5.1	5.7	8.1	6.7
Q1	2.8	2.9	4.2	14.8

Figure 4.3.3. Comparison of geographic conservation priorities obtained from different biodiversity conservation approaches. A) Priority areas based on ecosystem functional diversity by Ecosystem Functional Type (EFT) richness and rarity. The matrix shows the percentage of the study area of each quartile (Q) combination to obtain priority levels: extreme (red), high (orange), moderate (green), low (blue), and non-priority (gray). B) Priority areas mainly based on structural and compositional aspects

of biodiversity obtained from assessments by expert-based (Arriaga et al., 2000) and systematic conservation planning (Koleff et al., 2009) approaches. C) Congruence among geographic conservation priorities obtained by the three approaches (agreement between Figures 4.3.2A and 4.3.2B). D) Complementarity among geographic conservation priorities obtained by the three approaches (disagreement between Figures 4.3.2A and 4.3.2B). White areas were pixels where none of the categories on the map were satisfied.

The EFT-based approach also revealed complementary areas not prioritized by the two previous approaches (7% of the peninsula; Figure 4.3.4.). These areas were mainly located along mountainsides and piedmonts with riverine systems in the Desert Region: the San Felipe Desert to the northeast, the Gulf coastal desert in the center of the peninsula, and scattered areas along the southern desert (north and south of Magdalena Bay) (Figure 4.3.3.C). Conversely, some areas (5% of the peninsula) were prioritized by the two previous approaches but not by the EFT-based approach. This occurred mainly in the Mediterranean mid-mountains and in coastal plains of the central and southwestern deserts (Figures 4.3.3. and 4.3.4.).

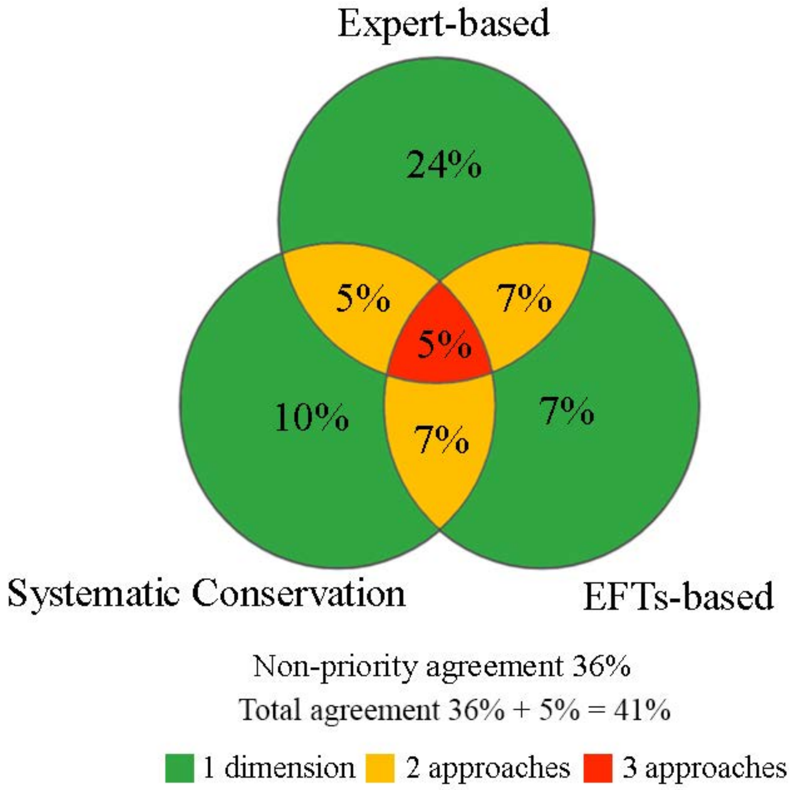


Figure 4.3.4. Agreement/disagreement between different ways to establish geographic conservation priorities for the Baja California Peninsula (Venn diagram). Numbers show the percentage of area in Baja California (not influenced by human activities) prioritized for conservation according to each approach. Our EFT-based approach focuses on two aspects of ecosystem functional diversity (Ecosystem Functional Type richness and rarity) while the two other approaches focus on biodiversity (mainly species) composition, structure and threats based on expert knowledge (Arriaga et al., 2000) and systematic conservation planning (Koleff et al., 2009).

EFAs and EFTs slightly differed among areas prioritized by each approach (Figures S6 and S7). Expert-based priorities (Arriaga et al., 2000) were biased towards EFTs with less primary production than the other approaches. Systematic conservation priorities (Koleff et al., 2009) were biased towards EFTs with higher primary production than the other approaches. In contrast, EFT-based priorities showed a more unbiased distribution of EFA values and EFT compositions than previous priorities (Figures S4 and S5).

EFT richness and EFT rarity were found to be much higher within areas consistently prioritized by the three approaches (6 and 26 EFTs per 8 × 8-pixel sliding window with most richness values from 8 to 13 EFTs and with EFT rarity ranging from 0.8 to 1) than within areas prioritized by only one of the three approaches (Figure 4.3.5.). In contrast, areas prioritized only by traditional approaches were biased towards areas of low EFT richness (less than 6) but maintained moderate to high values of EFT rarity (greater than 0.5), especially in the systematic conservation approach. Indeed, despite systematic conservation planning and the expert-based approach performing very similarly in capturing EFT richness, systematic conservation planning tended to better represent areas of high EFT rarity (Figure S6).

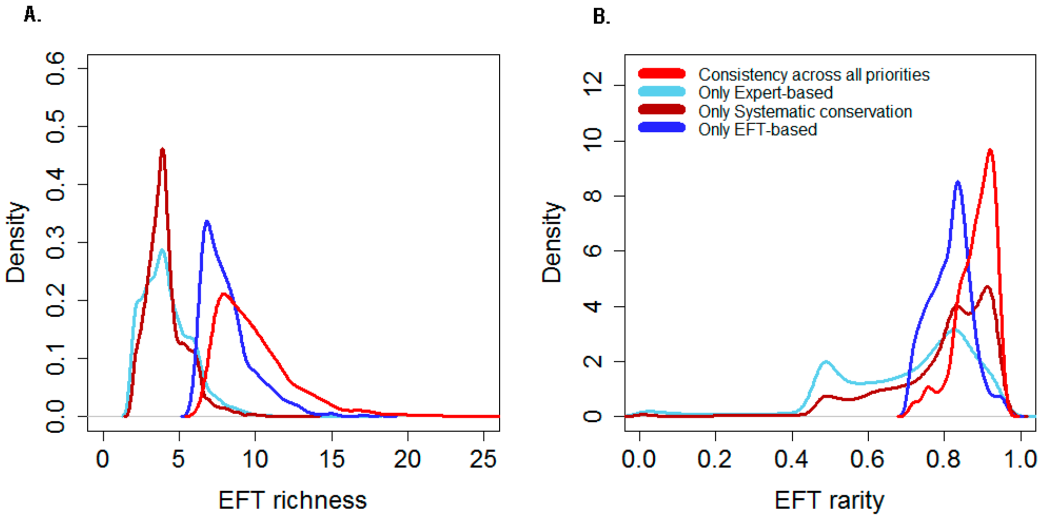


Figure 4.3.5. Congruence and complementarity among the three approaches to capture Ecosystem Functional Type (EFT) diversity. Density histograms show the frequency EFT richness (A) and rarity (B) in areas consistently prioritized by the three approaches (“congruence across all priorities”) and in areas exclusively prioritized by one of the approaches but not by the others (“complementarity across priorities”). Our EFT-based approach focuses on two aspects of ecosystem functional diversity (EFT richness and rarity) while the two other approaches focus on biodiversity composition, structure and threats based on expert knowledge (Arriaga et al., 2000) and systematic conservation planning (Koleff et al., 2009).

Robustness against window size, the number of classes, and priority thresholds

The sensitivity analyses revealed that our approach to setting priorities was robust against changes in window size and the number of EFT classes (Appendices 5 and 6). Correlations of EFT richness and EFT rarity across the 8 × 8-pixel window and coarser window sizes ranged from 0.84 to 0.98 (Table S2) and those between the 64 EFT classes and fewer classes ranged from 0.67 to 0.94 (Table S3). Regional patterns of EFT richness, rarity, and priority were largely consistent across window sizes (85% agreement among final priority maps, Figures S7 and S8) and the number of EFT classes (70% agreement among final priority maps, Figures S9 and S10). EFT-based priorities always exhibited more similarities with the more robust systematic-conservation approach than with the qualitative expert-based approach independent of thresholds of EFT richness and rarity used (Figure S11).

4.3.4. Discussion

Contemporary conservation paradigms aim to maintain all biodiversity dimensions (Noss 1990), including the ecological processes and functions that sustain ecosystem services (Meyer, 1997; Mace, 2014; Prober et al., 2019). In this study, we used satellite-derived EFTs (Paruelo et al., 2001), defined here as functionally homogeneous land patches in terms of primary production dynamics, to describe spatial patterns of a focal ecosystem function. We used this focal ecosystem function because it is considered to be an integrative surrogate of stocks and fluxes of matter and energy derived from biological activity (Virginia and Wall, 2013) and can be easily characterized by remote sensing. In essence, EFTs allowed us to map the spatial patterns of two indicators of ecosystem functional diversity at the regional scale, i.e., EFT richness and EFT rarity. From these patterns, we set geographic conservation priorities based on an ecosystem function that helped us identify important areas for the three dimensions of biodiversity (structure, composition, and function) and highlight complementary areas for this ecosystem function not prioritized by traditional approaches.

Regional patterns of ecosystem functional heterogeneity

Maps of EFAs, EFTs, and EFT richness and rarity offer a characterization of ecosystem functional heterogeneity of the Baja California Peninsula. This heterogeneity results from a combination of latitudinal, longitudinal and topographic gradients. Such gradients determine strong differences across the peninsula in terms of seasonal dynamics of radiation, temperature, precipitation, evapotranspiration, and vegetation access to groundwater (Peinado et al., 2011; Villarreal et al., 2016) and have been identified as important for plant diversity (Garcillán and Ezcurra, 2003) and endemism (Riemman and Ezcurra, 2007).

The highest levels of EFT richness were found where topography and spatiotemporal climate variability maximize ecosystem functional heterogeneity, mainly along mountains and piedmonts of the Mediterranean and Desert Regions. The Mediterranean climate imposes two limitations on plant growth: summer drought and winter cold temperatures (Hastings and Turner, 1965). These limiting factors of plant growth are strongly heterogenized by steep altitudinal and orientation gradients (Peinado et al., 2011). In the Desert Region, latitude, orientation, and access to groundwater impose varying constraints on plant growth. Such constraints include the latitudinal change in the proportion of winter and summer rains; the influence of coastal fog (Webb and Starr, 2015); and the occurrence of shallow aquifers, gullies and dry arroyos embedded within a dryland matrix (León de la Luz et al., 2015). Such high contrasts in ecosystem functions between the regional landscape matrix and its embedded ecosystems (i.e., less water-limited EFTs within a matrix of dryland EFTs) enhance ecological processes of the lateral transfer of matter and energy (Turner and Gardner 2015). For these reasons, despite being a desert, such high heterogeneity in environmental factors renders the Desert Region very diverse in EFTs, a pattern also found for plant functional types and plant communities (Webb and Turner, 2015).

The lowest levels of EFT richness were found in the tropics due to wetter and highly consistent tropical climatic conditions that homogenize vegetation (Peinado et al., 2011). In the Tropical Region, strong precipitation seasonality (summer-autumn tropical rains followed by a nine-month drought) concentrates the growing season following the cyclone season (León de la Luz et al., 2000). This high level of seasonality neutralizes even the altitudinal heterogeneity of the mountains, resulting in a spatial homogenization of primary production dynamics throughout the region. Such low EFT richness agrees with high similarities in vegetation composition along all topographic gradients, dominated by a few dry-deciduous shrubs and trees (Rascón-Ayala et al., 2018). Such an effect penetrates northwards along the Giganta Ranges with similar vegetation types to the Tropical Region (González-Abraham et al., 2010). In addition, very low EFT richness extended northwards along Central and Vizcaíno desert plains and piedmonts. EFT richness in these piedmonts, where energy and water were decoupled (winter rains dominate the Pacific northwestern Central and Vizcaíno deserts, north from 27°N), was lower than in piedmonts where energy and water were coupled (summer rains dominate the southern half of the peninsula and San Felipe Desert to the northeast; Figure S1C).

EFT rarity was found to be associated with latitude, altitude, and the presence of contrasting ecological conditions. The highest EFT rarity of the Mediterranean Region and San Felipe Desert were found to be associated with winter precipitation, which creates a rare phenological pattern in the peninsula (Peinado et al., 2011) together with the longitudinal gradient and topographical heterogeneity (e.g., the only region with areas showing EVI maxima in all seasons). In the ecological transitional zone of the center of the peninsula (28-29° N), the combined influence of summer tropical storms from the south and autumn-to-spring fronts from the north (González-Abraham et al., 2010) also results in high levels of EFT rarity. This ecotone shows singular assemblages of species from tropical and nontropical biota (González-Abraham et al., 2010) and a high diversity of distinctive lifeforms (Webb and Turner 2015). Finally, the surroundings of wetlands and mangroves in the Desert Region also showed rare EFTs, and both Mediterranean-type ecosystems and ecotones around wetlands are known to contain singular EFTs in other parts of the world (Cabello et al., 2013). The lowest EFT rarity value was measured for the Tropical Region and southern desert mountains (Giganta Ranges), where heterogeneity and singularity are only introduced by the presence of endemism-rich evergreen pine forests at the highest altitudes (León de la Luz and Domínguez-Cadena, 1989).

As found at the species level (Riemann and Ezcurra, 2007; Lamoreux et al., 2006), EFT richness and rarity were only correlated to a degree but did not always coincide in the peninsula. Such spatial aggregation between areas with both high EFT richness and rarity highlights their importance for heterogeneity and singularity in primary production.

EFTs for setting geographic conservation priorities

Three main conclusions can be drawn from our congruence analysis of the three approaches. First, our results highlight the importance of congruence areas as probable aggregated hotspots for all dimensions and scales of biodiversity, including diversity in essential ecosystem functions such as primary production dynamics. Areas with congruence reinforce their ecological and conservation value for the expansion of protected area networks (Lamoreux et al., 2006). For instance, consistently prioritized areas of the Mediterranean mountains have been historically identified as a conservation gap based on plant diversity and endemism (e.g., Garcillán and Ezcurra, 2003; Riemann and Ezcurra, 2005). This congruence of the Mediterranean Region in North America suggests that some global biodiversity hotspots stand out not only as hotspots of endemism but also as heterogeneous and singular areas of ecosystem function, even if their identification does not consider ecosystem processes (Myers et al., 2000). Second, our results indicate that traditional approaches may not identify all important areas of ecosystem functions (Meyer 1997) and may tend to better prioritize areas with rarity than those with richness in EFTs. Such an incidental focus of traditional approaches on rare EFTs could derive from the dominant role that endemicity, often related to singular conditions, plays in conservation planning (e.g., Myers et al., 2000). It is interesting that heterogeneity in ecosystem functions has played a minor role (Lovett et al., 2005) despite habitat heterogeneity fostering species adaptation and persistence (Hanson et al., 2020). Third, our results also suggest that species diversity, as in hotspots of the Tropical Region mountains (Riemann and Ezcurra, 2005, 2007), is not necessarily associated with rare or spatially heterogeneous ecosystem functions. In such areas, not high environmental heterogeneity but a long history of evolutive isolation under stable conditions has mainly driven speciation (Sundaram et al., 2019).

Conservation efforts must employ spatially explicit and parsimonious ways to incorporate heterogeneity in ecosystem functions (Turner and Chapin 2005) to develop theories and tools that complement traditional planning and management actions (Possingham et al., 2005). Our study shows how satellite-derived EFAs and EFTs of a focal ecosystem function (here primary production) offer tangible and biologically meaningful qualities of ecosystem functional heterogeneity (here EFT richness and rarity) that can complement traditional geographic priority approaches. EFAs and EFTs of focal ecosystem functions have already been used to assess the comprehensiveness and representativeness of protected areas (Cabello et al., 2012, 2013) and of environmental observatory networks (e.g., LTER, NEON, Ameriflux, and Mexflux; Villarreal et al., 2018). Previous studies have also shown how EFAs and EFTs could facilitate conservation by capturing heterogeneity in the amount and timing of key ecosystem functions to model species distributions (e.g., Tuanmu and Jetz 2015; Alcaraz-Segura et al., 2017; Arenas-Castro et al., 2018) and abundances (Arenas-Castro et al., 2019) as well as provisioning, regulating and cultural ecosystem services (Vaz et al., 2020).

Caveats and avenues for future research

The use of the EFT concept in geographic conservation is still subject to challenges. First, our satellite-derived EFT map characterizes the spatial heterogeneity of primary production dynamics. However, EFTs can also be identified from other remote sensing indices (e.g., Fernández et al., 2010) to characterize the spatiotemporal heterogeneity of multiple ecosystem processes and functions at different scales to guide biodiversity and ecosystem services policies (Pettorelli et al., 2018). Second, as the environmental observatory network expands, EFTs could be parameterized (e.g., Müller et al., 2014) and validated using ground measurements (e.g., eddy-covariance estimates of net ecosystem exchange; Villarreal et al., 2018). Third, EFT richness and rarity maps illustrate diversity and spatiotemporal heterogeneity in the occurrence of ecosystem functions, but additional landscape indices could also elucidate the spatial arrangement (Fahrig and Nuttle, 2005), connectivity, and lateral transfers (*sensu* Turner and Gardner, 2015) of energy and matter fluxes at the landscape level. Fourth, our study does not assess interannual changes in EFAs, EFTs, or EFT richness and rarity, which could help reveal areas suffering from functional diversity homogenization, which is a planetary boundary that still needs evaluation (Steffen et al., 2015). Fifth, the effects of spatial scale (grain and extent) on richness, rarity, and congruence with other biodiversity facets should be evaluated. Grain or cell size affects the magnitude, location, and spatial congruence of hotspots of species richness and endemicity (Rahbek, 2005; Arponen et al., 2012; McKerrow et al., 2018; Daru et al., 2020). The extent of the area under analysis may show that species-based priorities at one scale (e.g., global) may or not overlap with those of other scales (e.g., national or regional) (known as the parochialism effect; Pouzols et al., 2014). EFT richness, rarity, and priorities depend on the extent considered but seem to be robust against sliding window sizes and the number of EFT classes defined (Appendixes 5 and 6). Future works should explore the effect of image pixel size (e.g., with Sentinel-2 at 10 m/pixel), hierarchy in EFT classifications, and parochialism on the EFT-based approach. Finally, to test their effectiveness as ecosystem-agnostic essential biodiversity variable candidates, EFT richness, rarity, and derived priorities should be compared to robust systematic conservation-based approaches that consider multiple facets of biodiversity, i.e., compositional, structural, functional and phylogenetic, in other ecoregions of the world (Pettorelli et al., 2016).

4.3.5. Conclusions

In conclusion, the remotely sensed EFT approach can be used to incorporate the heterogeneity and singularity of ecosystem functions into geographic conservation priorities. Such an approach can support decision-making by offering supplementary arguments for the holistic conservation of biodiversity through the identification of key areas for multiple biodiversity facets (e.g., the Mediterranean Region of Baja California) and of other areas important for ecosystem function that complement existing protected area networks (e.g., mountainsides and piedmonts with riverine systems in the Desert Region). Priority assessments based on essential variables related to ecosystem function cannot replace the use of very valuable systematic conservation approaches based on field records of species distributions to assess biodiversity status and change (Pereira et al., 2013). However, our approach is useful to complement traditional priority setting, because is simple and based on only three satellite-derived meaningful descriptors of ecosystem functioning, facilitating computation and interpretation by managers and policymakers (Palumbo et al., 2017). Future conceptual and empirical development and applications of EFTs should include other ecosystem functions, field validation, temporal changes in EFT diversity, and further metrics of heterogeneity across scales.

4.3.6. References

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4.3.6. Appendices

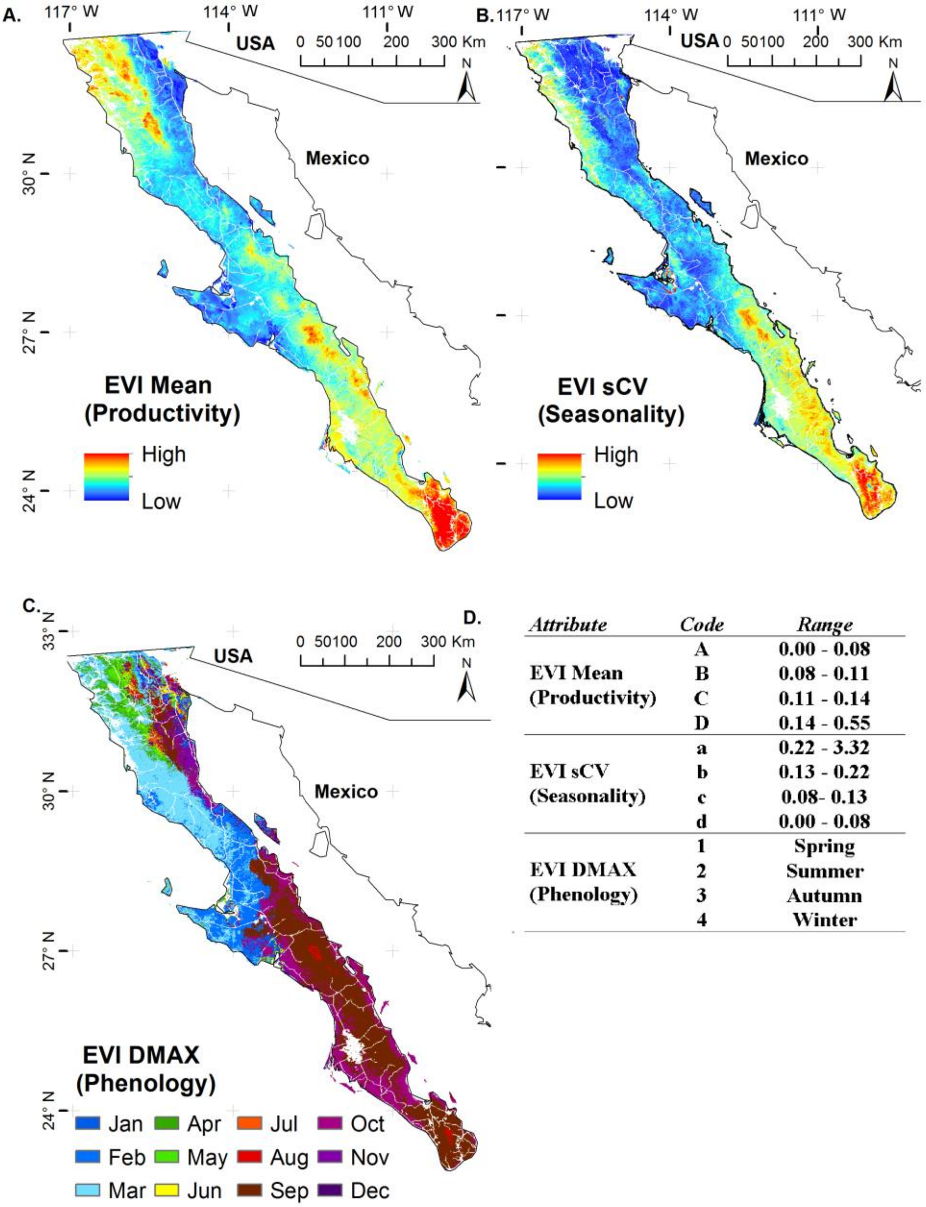
Appendix 1. Currently protected areas of the Baja California Peninsula

Protected area	Year	Terrestrial surface (ha)	Ecological region (González-Abraham et al., 2010)	Altitudinal range (m)	Vegetation type (% of surface in the protected area according to INEGI series III)	Figure protection and IUCN management category
Sierra de San Pedro Mártir	1947	72910	Mediterranean	773-2927	-Chaparral (47%) -Coniferous forest (50%) -Gallery forest (1%) -Induced grassland (2%)	National Park II
Constitución de 1857	1962	5009	Mediterranean	1522-1843	-Chaparral (22%) -Coniferous forest (67%) -Water bodies (11%)	National Park II
Valle de los Cirios	1980 and 2000	2521987	Desert	0-1799	-Sarcocaulescent scrub (13%) -Halophilic vegetation (9%) -Desert microphyll scrub (6%) -Coastal rosette vegetation (18%) -Sandy desert vegetation (3%) -Crasicaulescent scrub (43%)	Flora and Fauna Protection Area IV
Alto golfo de California y	1993	934756	Desert	0-349	-Desert microphyll scrub (13%)	Biosphere Reserve VI

Delta del Río Colorado					-Halophilic-hydrophilic vegetation (6%) -Without apparent vegetation (81%)	
Islas del Pacífico	2016	70139	Desert		-Chaparral (7%) -Mangrove (7%) -Coastal rosette vegetation (20%) -Sarcocrasicaulescent scrub (13%) -Sarcocaulescent scrub (26%) -Coastal dunes vegetation (23%) -Halophilic-xerophytic vegetation (4%)	Biosphere Reserve VI
Islas del Golfo de California	1978	374553	Desert	0-104	-Desert microphyll scrub (6%) -Halophilic-hydrophilic vegetation (2%) -Crasicaulescent scrub (45%) -Sarcocaulescent scrub (45%) -Deciduous rainforest (2%)	Flora and fauna protection area IV
El Vízcaíno	1988	2259002	Desert	0-1934	-Desert microphyll scrub (8%) -Without apparent vegetation (5%) -Halophilic-xerophytic vegetation (25%)	Biosphere Reserve Ia

					-Sandy desert vegetation (14%) -Sarcocrasicaulescent scrub (7%) -Sarcocaulescent scrub (38%) -Coastal dunes vegetation (2%) -Mangrove (1%)	
Complejo Lagunar Ojo de Liebre	1972 and 2000	79328	Desert	0-16	-Halophilic-hydrophilic vegetation (100%)	Biosphere reserve VI
Bahía de Loreto	1996 and 2000	21692	Desert	0-62	-Halophilic-xerophytic vegetation (15%) -Sarcocaulescent scrub (85%)	National Park II
Balandra	2012	1319	Tropical	0-306	-Sarcocrasicaulescent scrub (34%) -Sarcocaulescent scrub (66%)	Flora and fauna protection area IV
Sierra La Laguna	1994	112437	Tropical	116-2072	-Sarcocaulescent scrub (7%) -Quercus forest (30%) -Deciduous rainforest (63%)	Biosphere reserve VI
Cabo San Lucas	1973 and 2000	208	Tropical	0-73	-Xerophilous scrub (100%)	Flora and fauna protection area IV

Appendix 2. Ecosystem Functional Attributes of the Baja California Peninsula



Attribute	*Code*	*Range*
EVI Mean (Productivity)	**A**	**0.00 - 0.08**
	B	**0.08 - 0.11**
	C	**0.11 - 0.14**
	D	**0.14 - 0.55**
EVI sCV (Seasonality)	**a**	**0.22 - 3.32**
	b	**0.13 - 0.22**
	c	**0.08- 0.13**
	d	**0.00 - 0.08**
EVI DMAX (Phenology)	**1**	**Spring**
	2	**Summer**
	3	**Autumn**
	4	**Winter**

Figure S1. Patterns of the three key ecosystem functional attributes used to identify Ecosystem Functional Types and ecosystem functional diversity in Baja California (Mexico) derived from seasonal dynamics of the Moderate Resolution Imaging Spectroradiometer Enhanced Vegetation Index (MODIS-EVI) (230 m pixel). a) EVI annual mean (EVI Mean) as a surrogate of primary productivity; b) annual coefficient of variation (EVI sCV) as a descriptor of seasonality; c) date of the maximum EVI (EVI

DMAX) as an indicator of phenology; and d) range of functional attributes used in the definition of Ecosystem Functional Types (EFTs) for Baja California: the EVI mean, EVI sCV and EVI DMAX. Capital letters correspond to the EVI annual mean with *A* to *D* denoting low to high EVI means, respectively. Small letters show the coefficient of variation of the EVI (EVI sCV) with *a* to *d* denoting low to high EVI sCV values, respectively. Numbers indicate the season of the date of the maximum EVI (EVI DMAX). The three maps show how the peninsula is highly diverse in terms of these three key descriptors of ecosystem functioning.

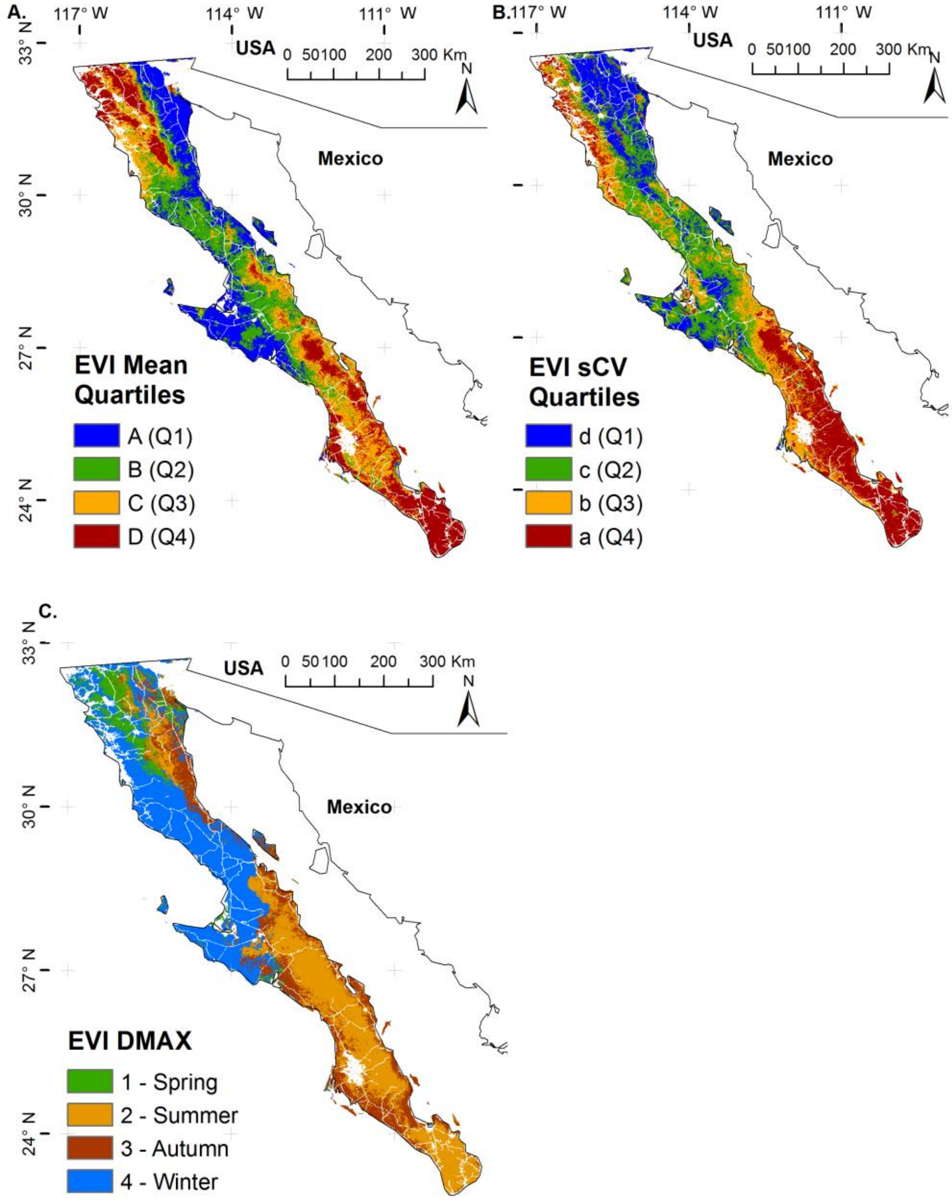


Figure S2. Quartile patterns of the three key ecosystem functional attributes used to identify Ecosystem Functional Types derived from seasonal dynamics of the Moderate Resolution Imaging Spectroradiometer Enhanced Vegetation Index (MODIS-EVI) (230 m pixel). Each attribute was divided into four ranges or quartiles (i.e., Q1, Q2, Q3 and Q4 using the 25th, 50th, 75th, and 100th percentiles, respectively). A) EVI annual mean (EVI Mean); B) annual coefficient of variation (EVI sCV); and C) date of the maximum EVI (EVI DMAX).

Appendix 3. Relationship between EFT rarity and EFT richness

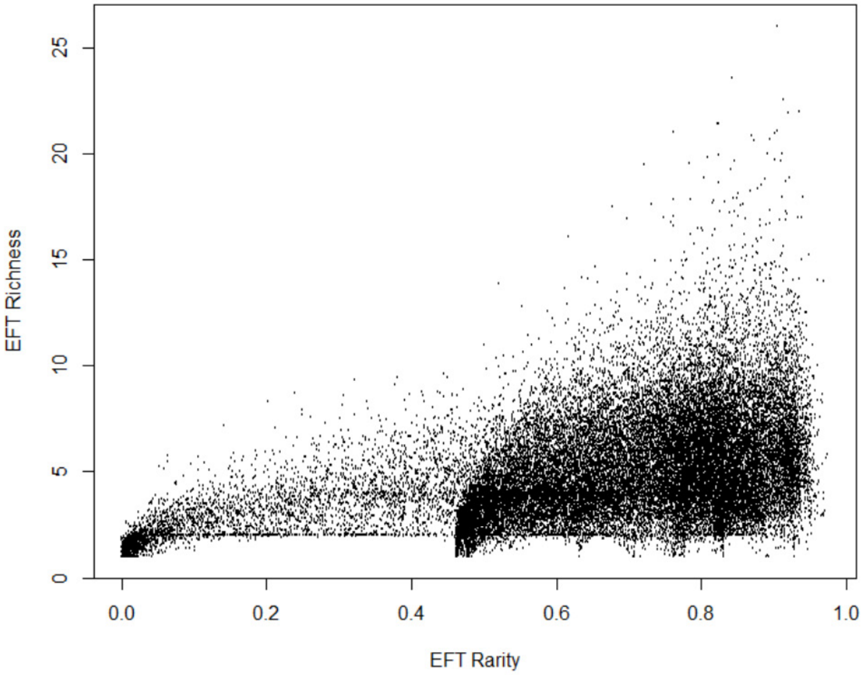


Figure S3. Scatterplot of EFT rarity (X-axis) *versus* EFT richness (Y-axis). Each point represents an 8 × 8-pixel window. Pearson correlation r = 0.45. High values of EFT richness always corresponded to high values of EFT rarity while high EFT rarity does not always imply high EFT richness values.

Appendix 4. Congruence and complementarity between EFT richness, rarity and priorities and previous methods

To demonstrate that our EFT-based approach provides useful and orthogonal conservation priority information relative to other traditional approaches, we assessed the variation in EFAs, EFTs, EFT richness and EFT rarity within the priority areas of each approach.

a) *Variation of EFAs within areas prioritized by different approaches.*

In terms of EFAs, Arriaga et al., (2001) prioritize regions with low primary productivity, low-moderate seasonality and biseasonality in the month of the maximum EVI (mainly in the spring and autumn). Systematic conservation (Koleff et al., 2009) prioritizes regions of greater primary productivity and seasonality than expert-based conservation (Arriaga et al., 2000) and with biseasonality in the month of the maximum EVI (mainly in the spring but also with peaks in the autumn). Our approach prioritizes EFA values that fall between those of other assessments with moderate values of productivity, low and moderate seasonality and biseasonality in the month of the maximum (though distributed across more months) (Figure S4).

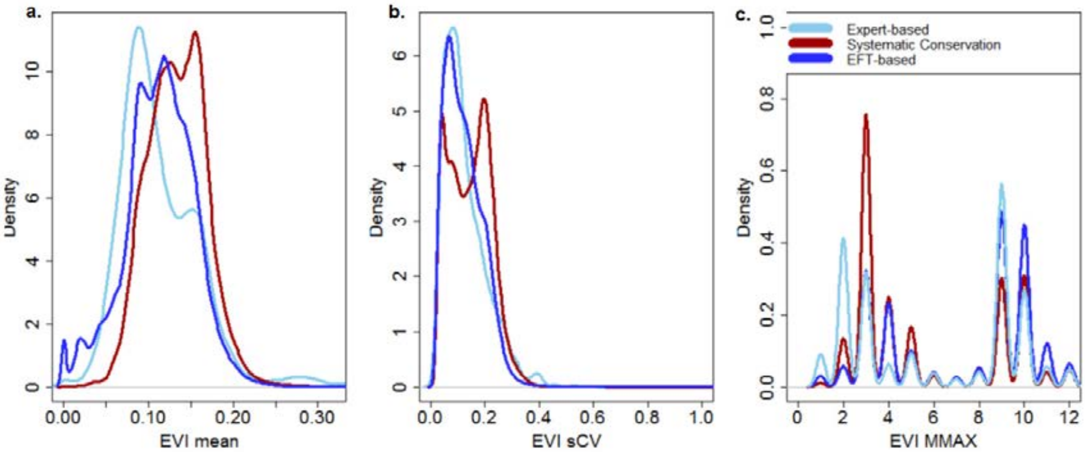


Figure S4. Variation in the three ecosystem functional attributes (EFAs) used to identify Ecosystem Functional Types (EFTs) within areas prioritized by three approaches to set geographic conservation priorities. Our approach focused on two aspects of ecosystem functional diversity (EFT rarity and richness), and two previous studies focused on biodiversity (mainly species) composition, structure and threats based on expert knowledge (Arriaga et al., 2000) and systematic conservation planning (Koleff et al., 2009). The three EFAs derived from EVI (Enhanced Vegetation Index) seasonal dynamics included: A) EVI mean or primary productivity; B) EVI sCV or seasonality; and C) EVI DMAX or phenology.

b) *Variation of EFTs in areas prioritized by different approaches.*

In terms of EFTs, all priority exercises showed a wide spectrum of different EFTs. As suggested by the EFA histograms, EFTs of expert-based (Arriaga et al., 2000) priority areas were more oriented towards low productivity EFTs, systematic conservation priorities (Koleff et al., 2009) were oriented towards high productivity EFTs, and EFT-based priorities captured the full range of EFTs (Figure S5).

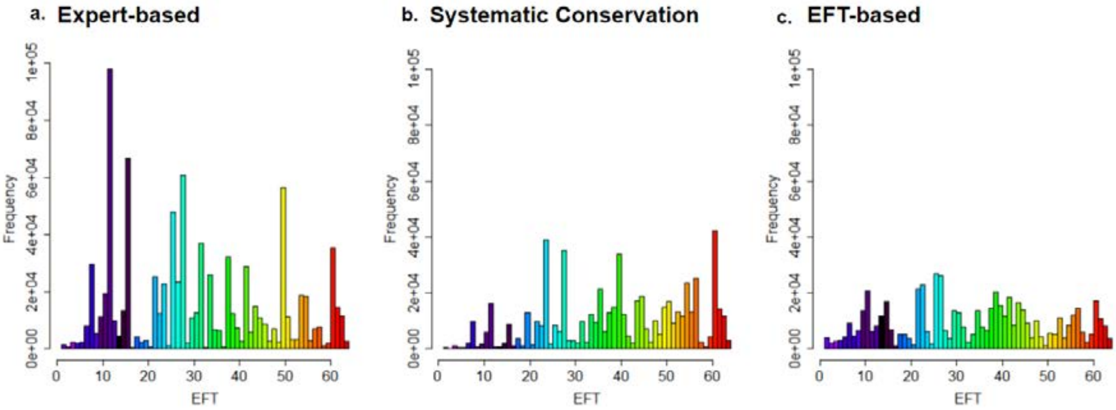


Figure S5. Variation of Ecosystem Functional Types (EFTs) within areas prioritized by three approaches to setting geographic conservation priorities. Our approach was focused on two aspects of ecosystem functional diversity (EFT rarity and richness) while those of two other studies focused on biodiversity (mainly species) composition, structure and threats based on expert knowledge (Arriaga et al., 2000) and systematic conservation planning (Koleff et al., 2009). See the color legend and EFT names in Figure 2D.

c) *Variation of EFT richness and EFT rarity in areas prioritized by different approaches*

In terms of EFT richness, the EFT-based approach was biased towards the highest EFT richness values with more than 90% of priority areas having EFT richness values of between

5 and 26. Priority areas of the two other studies showed significantly lower levels of EFT richness with more than half of the area presenting EFT richness values of lower than 5 (Figure S6).

In terms of EFT rarity, all approaches were biased towards high EFT rarity values. The EFT-based approach was more focused on the highest EFT rarity values (areas of 0.7 to 0.9 EFT rarity values) followed by those of systematic conservation (Koleff et al., 2009) (more than half of the area includes EFT rarity values of greater than 0.8) and expert-based methods (Arriaga et al., 2000) (more than half of the area includes EFT rarity values of 0.7 to 0.9) (Figure S6).

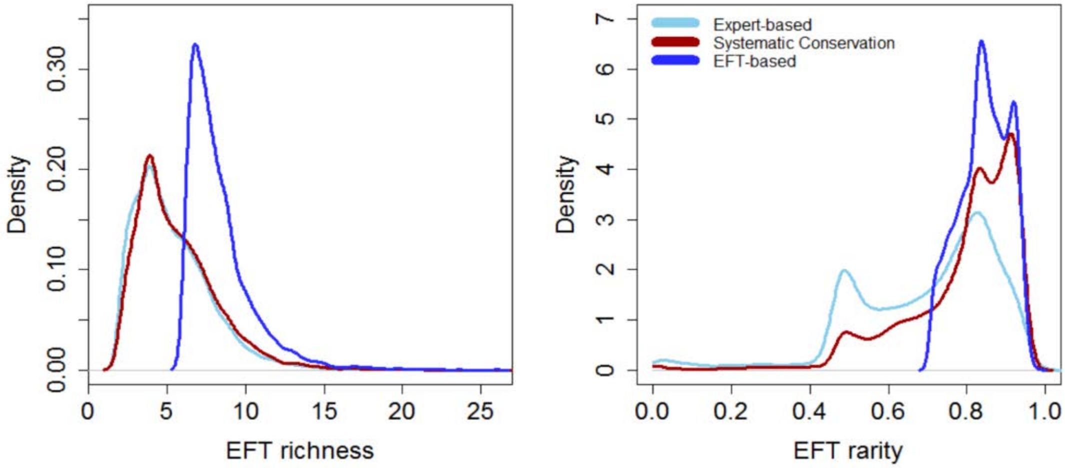


Figure S6. Variation of ecosystem functional type (EFT) richness (left) and rarity (right) in areas prioritized by three approaches to setting geographic conservation priorities. Our approach was focused on two aspects of ecosystem functional diversity (EFT rarity and richness) while those of two other studies focused on biodiversity (mainly species) composition, structure and threats based on expert knowledge (Arriaga et al., 2000) and systematic conservation planning (Koleff et al., 2009).

Appendix 5. Assessment of the effect of sliding window size on EFT richness, rarity, and priorities

To assess the effect of sliding window size on EFT richness, rarity and priorities, we doubled and tripled the size of the sliding window. First, we calculated EFT richness, rarity and priorities for 8 × 8-, 16 × 16- and 24 × 24-pixel sliding windows. Then, we compared these maps 1) visually, 2) based on Pearson correlations among them, 3) by calculating the degree of overlap between prioritized areas, and 4) by calculating the final percentage of the peninsula prioritized. Human-use pixels were masked according to each window size.

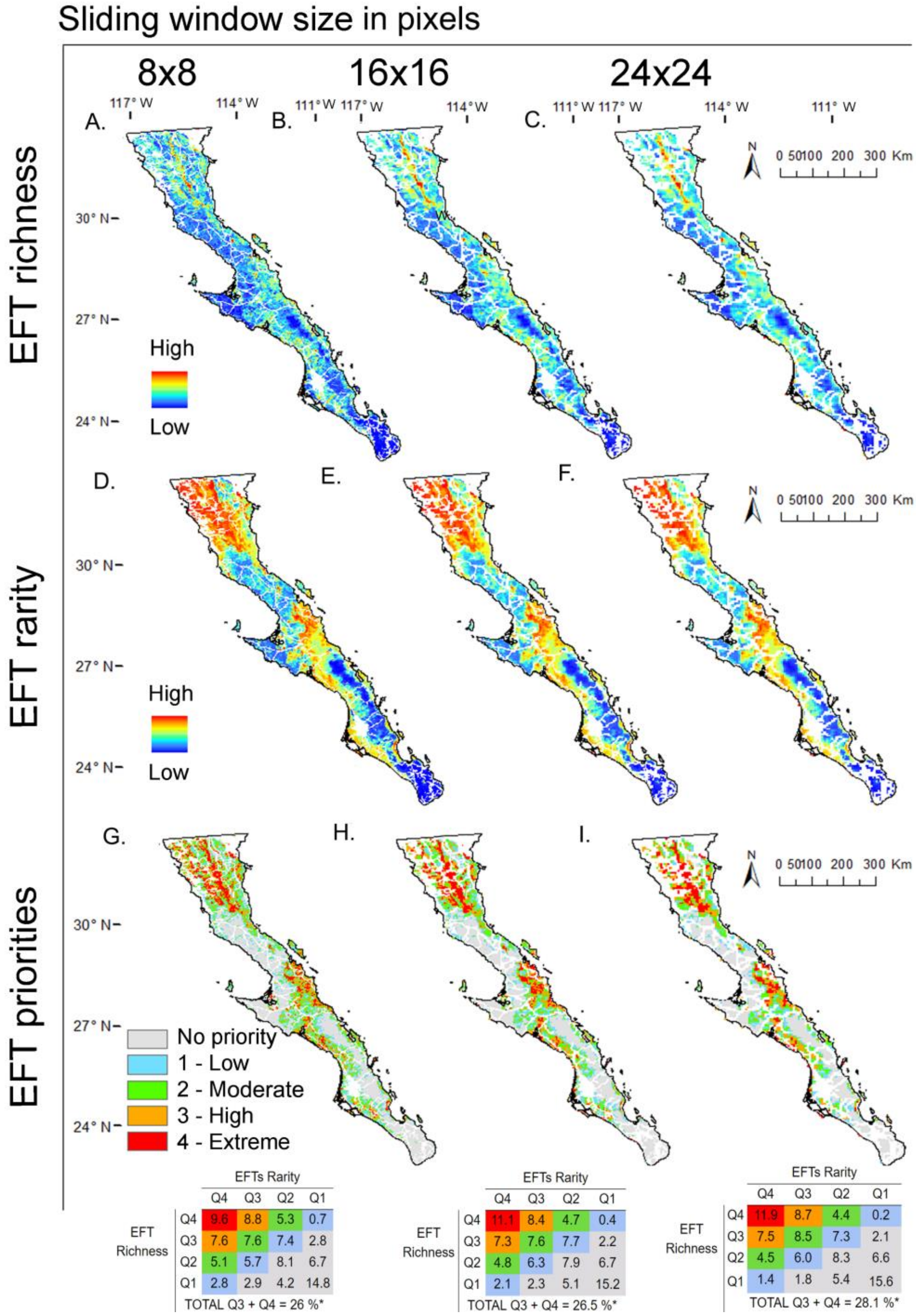
Regional patterns of EFT richness, rarity and priorities were largely consistent across the sliding windows of different sizes (Figure S7A-I). Pearson correlations among different window sizes were very high for EFT rarity (0.97-0.99) and EFT richness (0.84-0.95) and quite high for the derived priorities (0.70-0.79) (Table S2). The percentage of the peninsula of extreme and high priority was also similar across different window sizes (26-28%) (Figure S7). Regional priorities were constant in all cases and always focus on the Mediterranean area, the mountains of the central desert and mangroves of the southwestern coast (Figure S7G-I).

An overlap analysis of different windows size priorities reached 85% agreement on what is to be prioritized and or not. Specifically, all window sizes identify 66% of the peninsula as nonpriority sites and a 19% as priority sites (Figure S8A-B).

Any prioritization exercise depends on the spatial scale (i.e., both grain and extent) of assessment (Arponen et al., 2012). In any prioritization exercise, the grain size of the dataset affects the output. Regarding grain, when using species distributions to identify hotspots, actual values of species richness found in each cell will increase with grain from a dataset built at 1 × 1 km to a dataset built at 10 × 10 km. However, regional spatial patterns of species richness will not vary widely (Rahbek 2005). In our analysis, regional patterns of EFT richness, rarity and derived priorities are very robust against changes in grain size. The maximum number of EFTs found in a sliding-window can also vary by window size. When using smaller sliding-window sizes, lower EFT richness values were obtained. By contrast, when using a larger pixel size, observed patterns would get generalized while "internal" heterogeneity within each pixel was diminished.

Table S2. Pearson correlation coefficients (r) among conservation priority values given by each window size. To assess the robustness of our approach against a change in the size of the sliding window, to the original size (8x8 pixel-window) we doubled (16x16 pixel-window) and tripled (24 × 24 pixel-window) the size and we evaluated the resulting effects on EFT richness, rarity and priorities. Spatial patterns of EFT richness, rarity and priorities did not vary considerably when different sliding-window sizes were applied.

Pearson correlations among sliding window sizes	**EFT richness**		**EFT rarity**		**EFT priorities**	
	16x16	**24x24**	**16x16**	**24x24**	**16x16**	**24x24**
8x8	0.95	0.84	0.99	0.97	0.75	0.70
16x16	-	0.93	-	0.98	-	0.79



8x8

EFTs Rarity

EFT Richness	Q4	Q3	Q2	Q1
Q4	9.6	8.8	5.3	0.7
Q3	7.6	7.6	7.4	2.8
Q2	5.1	5.7	8.1	6.7
Q1	2.8	2.9	4.2	14.8

TOTAL Q3 + Q4 = 26 %*

16x16

EFTs Rarity

EFT Richness	Q4	Q3	Q2	Q1
Q4	11.1	8.4	4.7	0.4
Q3	7.3	7.6	7.7	2.2
Q2	4.8	6.3	7.9	6.7
Q1	2.1	2.3	5.1	15.2

TOTAL Q3 + Q4 = 26.5 %*

24x24

EFTs Rarity

EFT Richness	Q4	Q3	Q2	Q1
Q4	11.9	8.7	4.4	0.2
Q3	7.5	8.5	7.3	2.1
Q2	4.5	6.0	8.3	6.6
Q1	1.4	1.8	5.4	15.6

TOTAL Q3 + Q4 = 28.1 %*

Figure S7. EFT richness, rarity and priorities for each window size. The last row are shown the surface of the study area (in percentage) for each combination of quartiles (Qx) of richness and rarity. Final priorities combined Q3 and Q4, and the total area prioritized was the sum of Q3 and Q4*.

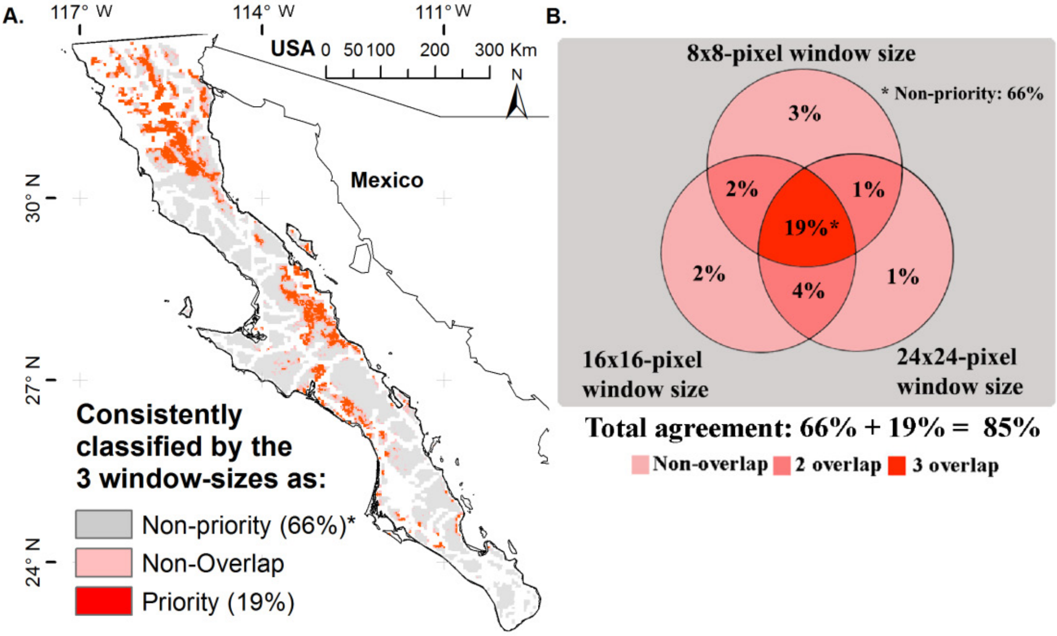


Figure S8. Proportion of the total land area with overlapping priority at different sliding windows sizes. A) Congruence between nonpriority and priority areas for different windows sizes, and B) overlap and percentage of area in Baja California Peninsula (not influenced by human activities) prioritized for conservation according to each approach: colors show where no approaches overlap, where two sliding window approaches overlapped and where all three approaches overlapped.

Appendix 6. Assessment of the effect of the number of EFT classes on EFT richness, rarity, and priorities.

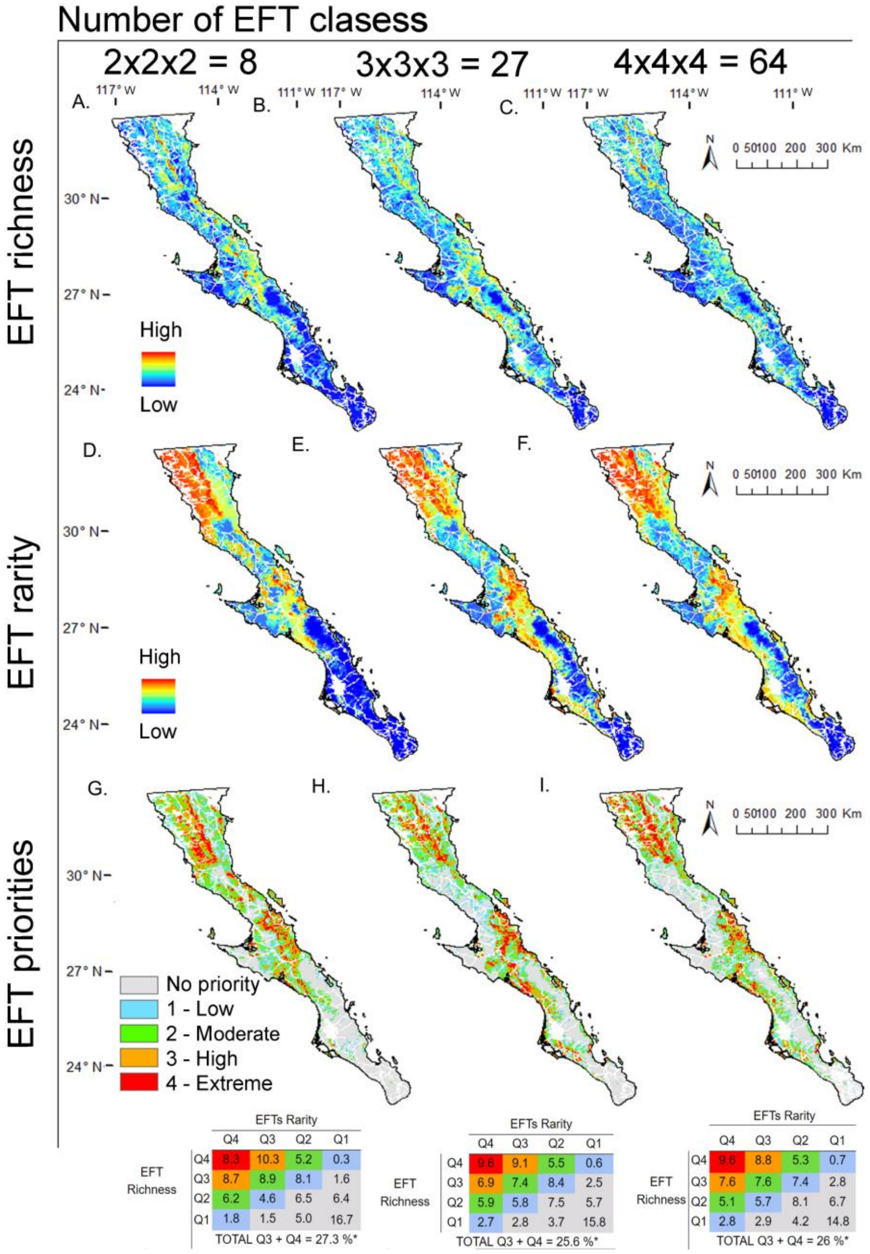
To assess the effect of the number of EFT classes on EFT richness, rarity and priorities, we reduced the number of EFT classes (64) by 58% (27 classes) and 86% (8 classes). We compare 2x2x2= 8 EFTs and 3x3x3=87 and 4x4x4=64 EFTs calculating EFT richness, rarity, and priorities for each EFT classification. We used the same method as that applied to measure the effect of window size but to measure the number of classes. We compared EFT richness, rarity and priority maps 1) visually 2) based on Pearson correlations between them, 3) by calculating the degree of prioritized area overlap, and 4) by calculating the final percentage of the peninsula prioritized.

Regional patterns of EFT richness, rarity and priorities are largely consistent among the different EFT classes (Figure S9 and Table S3). Pearson correlations among different EFT classifications were high for EFT rarity (0.72-0.74) and EFT richness (0.62-0.84) and lower for derived priority areas (max. 0.65). The percentage of the peninsula of extreme and high priority was also similar across different window sizes (25.6-27.3%) (Figure S9). Regional priorities remained constant for all approaches, always highlighting the Mediterranean area, the mountains of the central desert and mangroves of the southwest coast (Figure S9G-I).

The overlap analysis of the different approaches showed 70% agreement on what was prioritized and what was not. Specifically, all approaches identified 58% of the peninsula as nonpriority area and 12% as priority area (Figure S10A-B).

Table S3. Pearson correlation coefficients (r) between conservation priority values given by each number of Ecosystem Functional Type (EFT) classes. To assess the robustness of our approach against a change in the number of classes, we carried out a sensitivity analysis by reducing the number of EFT classes by 86% (from 64 to 8 classes) and 58% (from 64 to 27 classes) and evaluating their effects on EFT richness, rarity and priorities. Employing the same rationale adopted to build the 4x4x4 EFT classification (quartiles for the EVI mean and EVI sCV, and four seasons for EVI DMAX), we used the medians for EVI mean and EVI sCV and two seasons for the EVI peak to obtain a 2x2x2= 8 EFT classification. We also used tertiles on the EVI mean and EVI sCV and three seasons for the EVI peak to obtain a 3x3x3 = 87 EFT classification. Spatial patterns of EFT richness, rarity and priorities did not greatly vary when different EFT number of classes were applied.

Pearson correlations among different numbers of EFT classes	**EFT richness**		**EFT rarity**		**EFT priorities**	
	3x3x3	**2x2x2**	**3x3x3**	**2x2x2**	**3x3x3**	**2x2x2**
4x4x4	0.84	0.67	0.94	0.70	0.65	0.45
3x3x3	-	0.62	-	0.72	-	0.36



EFT Richness	EFTs Rarity Q4	Q3	Q2	Q1
Q4	8.3	10.3	5.2	0.3
Q3	8.7	8.9	8.1	1.6
Q2	6.2	4.6	6.5	6.4
Q1	1.8	1.5	5.0	16.7

TOTAL Q3 + Q4 = 27.3 %*

EFT Richness	EFTs Rarity Q4	Q3	Q2	Q1
Q4	9.6	9.1	5.5	0.6
Q3	6.9	7.4	8.4	2.5
Q2	5.9	5.8	7.5	5.7
Q1	2.7	2.8	3.7	15.8

TOTAL Q3 + Q4 = 25.6 %*

EFT Richness	EFTs Rarity Q4	Q3	Q2	Q1
Q4	9.6	8.8	5.3	0.7
Q3	7.6	7.6	7.4	2.8
Q2	5.1	5.7	8.1	6.7
Q1	2.8	2.9	4.2	14.8

TOTAL Q3 + Q4 = 26 %*

Figure S9. EFT richness, rarity and priorities for different numbers of Ecosystem Functional Type (EFT) classes. The last row are shown the surface of the study area (as a percentage) for each combination of quartiles (Qx) of richness and rarity. Final priorities were combinations of Q3 and Q4, and the total area prioritized was the sum of Q3 and Q4*.

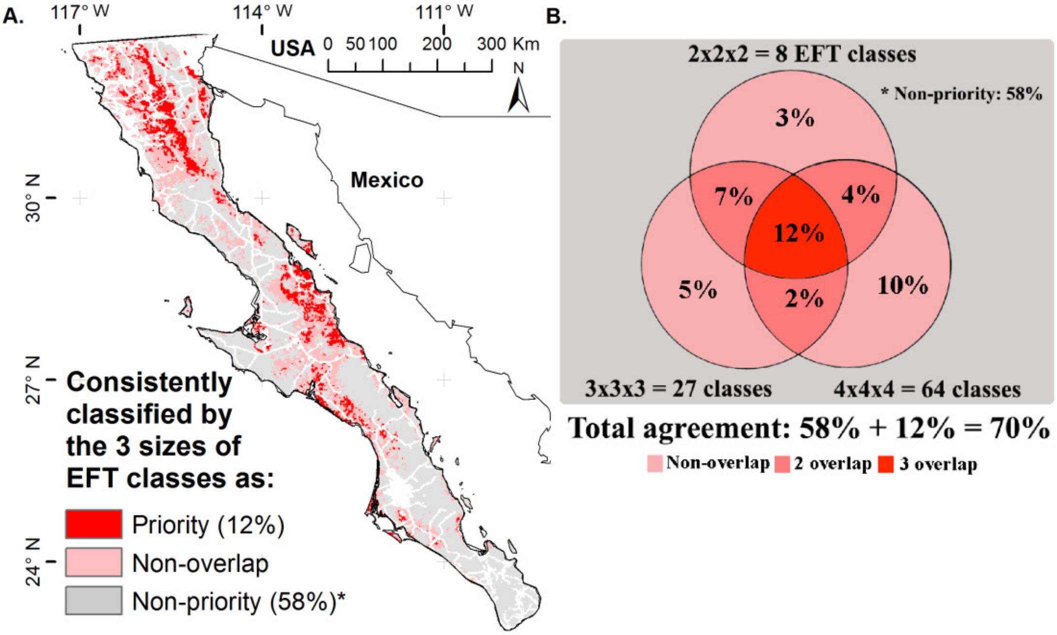
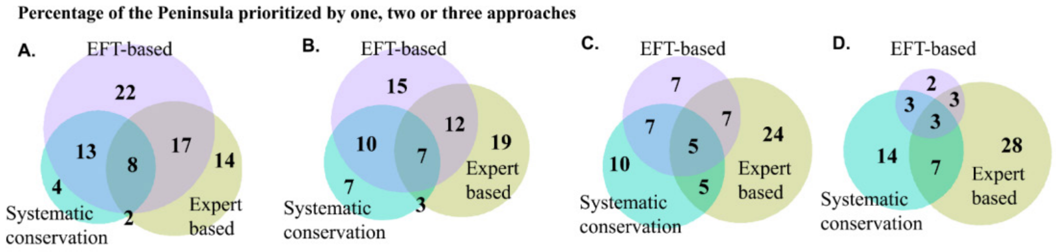


Figure S10. The proportion of the total land area with overlapping prioritization with different numbers of Ecosystem Functional Type (EFT) classes. Numbers show the percentage of area in Baja California (not influenced by human activities) prioritized for conservation according to each approach.

Appendix 7. Assessment of the effect of priority thresholds on congruence and complementarity between approaches.



Total percentage of the Peninsula prioritized by each approach

EFT-based:	60%	43%	26%	11%
Expert-based:	41%	41%	41%	41%
Systematic c.:	27%	27%	27%	27%

Sorensen-Dice similarity index between pairs of approaches:

EFT / Systematic c.:	0.48	0.48	0.45	0.32
EFT / Expert:	0.50	0.45	0.36	0.23
Expert / Systematic c.:	0.29	0.29	0.29	0.29

Figure S11. Sensitivity analysis of the EFT-based priority threshold for agreement/disagreement between the three approaches to establish geographic conservation priorities for the Baja California Peninsula (Venn Diagram). Numbers show the percentage of the peninsula to be protected by each prioritization scheme. Overlapping areas indicate the % of common surface to protect. The diagrams show congruence between the prioritized areas in Koleff (systematic conservation) and Arriaga (expert-based) with different thresholds for Cazorla's EFT-based priorities: A) our low, moderate, high and extreme priority categories, B) our moderate, high and extreme categories, C) our high and extreme categories, and D) our extreme category. Under each Venn Diagram, the Sorensen-Dice F-1 coefficient is shown for each pair of approaches using Koleff's Systematic-conservation as a reference. The three bottom rows show the total percentage of the surface of the Baja California Peninsula to be protected according to each assessment.

4.4.

CHAPTER IV

Patterns of ecosystem functioning as tool for biological regionalization: the case of the mediterranean-desert-tropical transition of Baja California

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Abstract

Large-scale ecological variations across Earth have important consequences for biodiversity and therefore, for biological conservation. Despite the widespread use of ecological maps in conservation schemes, they have been based mainly on structural and compositional features, but scarcely on functional dimensions of life. The incorporation of functional variables complements and improves the descriptions of regionalizations and offers a new understanding of biodiversity patterns. The development of remote sensing measurement allows for the description of the functional patterns of ecosystems through Ecosystem Functional Types (EFTs), opening new opportunities to analyze the geography of life. In this article, our aim was to examine the relationships between ecological regionalization based on components and structure and patterns of ecosystem functioning. As proof of case, we chose the Baja California peninsula, whose singularity has generated a rich variety of ecological and biogeographical interpretations, mainly based on ecosystem components and structure. We hypothesize that patterns in ecosystem functioning reflect ecoregionalization based on composition and structure features. We identified Ecosystem Functional Types (EFTs), from three descriptors of the seasonal curves of MODIS Enhanced Vegetation Index (EVI) from 2001 to 2017. We characterized each ecoregion in terms of ecosystem functioning and we carried out a correspondence analysis between the EFTs classification and the ecoregions. At large scale, EFTs showed a pattern with three general regions from northwest to south, capturing the north-south transition of climatic regimes shown in the ecoregions map, from the northwestern Mediterranean area to the tropical southern zone, with a desert transition area between them.

KEYWORDS: Conservation; Ecosystem Functional Types; Ecoregions; Functional biodiversity; Functional geography; Remote sensing.

4.4.1. Introduction

Understanding how geographical patterns of life and which factors are driving them have been for a long time one of the main goals of naturalists, and the foundational roots of biogeography as science (Lomolino et al., 2015, 2017). Its interest resides in that large-scale variation in vegetation across Earth has important consequences for biodiversity and resources availability to support biological conservation and human wellbeing (Olson et al., 2001). At present, the Earth system has been characterized by large ecological units whose boundaries can be defined on the basis of past or current physical and biological forces (Whittaker, 1970; Box, 1981; Dinerstein et al., 1995; Olson et al., 2001; Bailey, 2009; Kreft & Jetz, 2010). These ecological units or ecoregions can be identified at various spatial scales and/or hierarchical levels, which determines our perception of the system (Bailey, 2004). Ecoregions have been widely used for guiding management and conservation decision making, since it allows us to organize our understanding of how major terrestrial ecosystems work and to establish programs to monitor changes (Higgins et al., 2016). Despite the widespread use, these units represent human constructs derived from a boundary-setting exercise in which there is not always a consensus on how to define it and map their extent (Donoghue & Edwards, 2014; Moncrieff et al., 2016), which makes ecological maps hypotheses that can be tested and improved (Rowe & Sheard, 1981; Smith et al., 2018).

Since the pioneering work of Alexander von Humboldt, who departed from habitual taxonomic criteria and described patterns of vegetation based on physiognomic attributes and coincident climate, scientists have been analyzing geographical patterns of ecosystems based mainly on their structural and compositional features, but scarcely on the functional dimension of life. The incorporation of functional variables complements and improves the descriptions of regionalizations based on structural and compositional features (Noss, 1990) and offers a better understanding of spatial and temporal patterns of diversity (Garnier et al., 2016). In particular, understanding changes in ecosystem functioning across biogeographic gradients can benefit from a greater ability to represent and define biotic communities (Reichstein et al., 2014). This leads the functional classifications to a useful framework to understand these large-scale ecological changes in relation to ecosystem function and processes. In fact, a growing number of studies have identified the need to integrate new concepts and methodologies to connect classical regionalizations with ecosystem functioning (Violle et al., 2014).

Currently, ecologists are better equipped than ever before for exploring functional ecosystem dynamics at multiple temporal and spatial scales. Increasing large-datasets derived from remote sensing and associated development of analytic tools have opened new opportunities to explore the geography of life. A promising analytic approach in this sense is the Ecosystem Functional Types proposed by Paruelo et al., (2001) and Alcaraz-Segura *et al.,* (2006), which has been considered as the more serious attempt to characterize ecological regions from a functional perspective (Mucina, 2019). EFTs are groups or patches of land surface that share similar dynamics of matter and energy exchanges between the biota and the physical environment (Paruelo et al., 2001; Alcaraz-Segura et al., 2006). The EFT approach uses time series of spectral Vegetation Indices (VI), such as Normalized Vegetation Index (NDVI) or Enhanced Vegetation Index (EVI), to capture the spatial expression of the carbon gain dynamics, considered the most integrative indicator of ecosystem functioning (McNaughton et al., 1989; Virginia and Wall 2001). Thus, EFTs are identified by three meaningful metrics derived from the annual dynamics of EVI that reflect primary productivity, seasonality, and phenology of canopy (Paruelo et al., 2001). EFTs have been used to characterize the spatial heterogeneity of ecosystem functions at different scales, e.g., global (Ivits et al., 2013), regional (Alcaraz-Segura et al., 2006) or local (Fernández et al., 2010), but the formal comparison with regionalizations based on other dimensions of biodiversity (i.e. ecoregions) has not yet been evaluated.

In this study, our aim was to examine the relationships between biological regionalization based on the biota components and structure (species distribution, endemisms, vegetation types) and patterns of ecosystem functioning revealed by the geographical distribution of

EFTs. As proof of case, we chose the Baja California peninsula, a 1300 km-long fringe of land which contains the transition from the Californian Mediterranean region to the Tropic. This ecologically heterogeneous peninsula has captured the attention of naturalists for a long time (Garcillán et al., 2010) and has an extraordinary conservation interest (Arriaga et al., 2000; Koleff et al., 2009). This extensive history of natural exploration has generated a rich variety of ecological and biogeographical interpretations, mainly based on ecosystem components and structure, synthesized by González-Abraham et al., (2010). We hypothesize that patterns in ecosystem functioning reflect ecoregionalization based on composition and structure features, however, the spatial coincidence between these dimensions of biodiversity decreases when we compare their patterns at more detailed spatial scales, i.e. downwards in the hierarchy of ecological units, from major regions to ecoregions (sub-regions).

4.4.2. Methods

Study area and ecoregionalization

We chose the peninsula of Baja California as study area (Figure 4.4.1.) because it contains high ecological heterogeneity governed by processes at different spatial and temporal scales, from the north-south transition of mediterranean-desert-tropics to the contrasting climatic influence of its two coastal seas (Garcillán et al., 2010). Besides that, its ecological geography has been studied for more than two centuries (Garcillán et al., 2010) and recently synthesized in an ecoregional map (González-Abraham et al., 2010). Ecoregions have been identified at hierarchical levels: level I contains the three major regions, Mediterranean, Desert, and Tropical, and level II contains fourteen ecoregions (sub-regions) within the above major regions (Figure 4.4.1.).

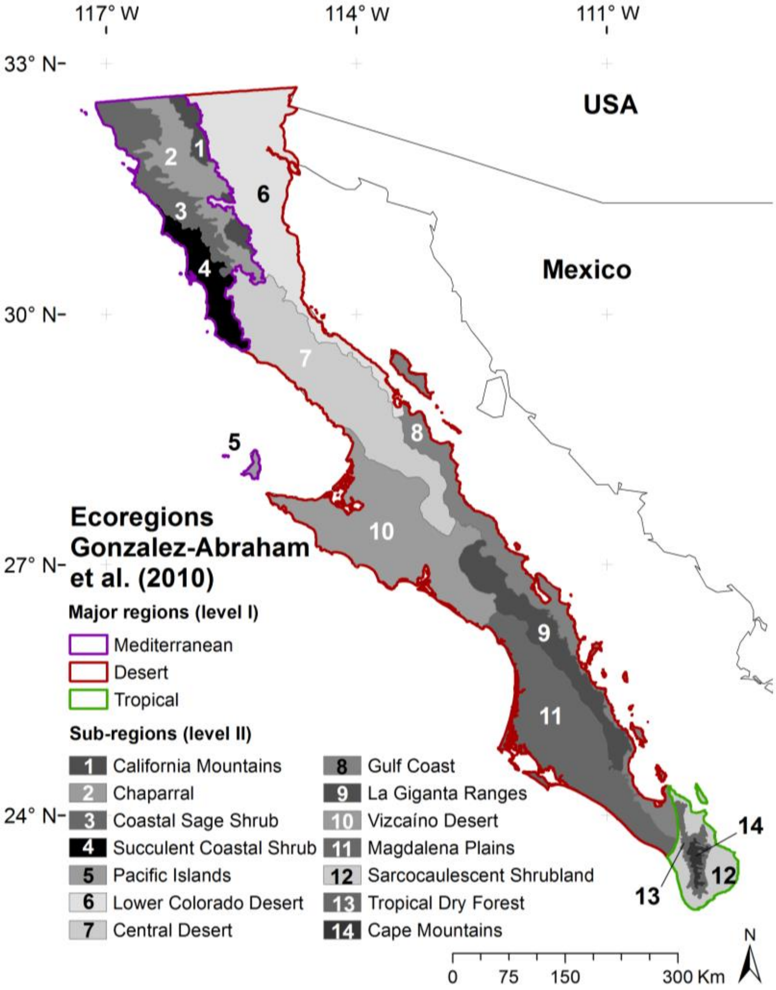

Figure 4.4.1. Study area and ecoregions by González-Abraham et al., (2010).

Regarding climatology (Figure 4.4.2.), the Mediterranean region, in the northwest, is characterized by annual mean temperatures between 8-21ºC, summer drought, and winter precipitation, with annual rainfall ranging from 100-200 mm at sea level to 500-700 mm in the highest mountains (3100 m) (Hastings & Turner, 1965). The extensive Desert region, largely distributed from northeast to south, has temperatures ranging from 20-25ºC, and very low annual rainfall (44-200 mm), concentrated in sporadic events that shift from winter in the north to summer in the south (Hastings & Turner 1965; Peinado et al., 2011). The Tropical region, in the southern tip, is warm year-round (15-24ºC) and is characterized by late summer-early autumn precipitation, mainly derived from tropical cyclones and storms (annual rainfall from 200 mm at sea level to 800 mm in the highest mountains -2090 m-, and a long dry season (Farfán & Fogel, 2007).

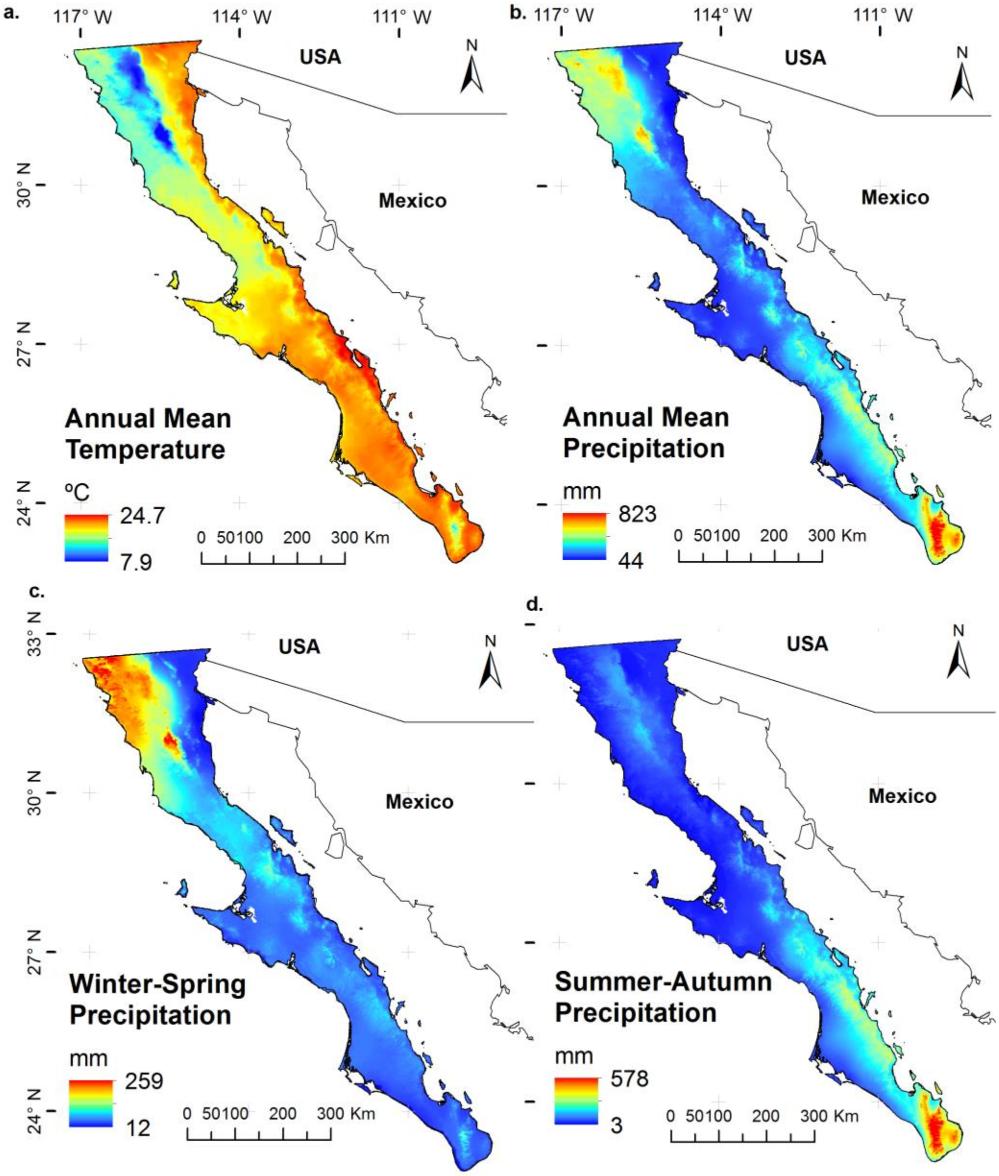

Figure 4.4.2. Climate description of the study area. a) Annual Mean Temperature in ºC; b) Annual Mean Precipitation in millimeters (mm); c) Winter-Spring Precipitation (mm); and d) Summer-autumn Precipitation. Data from WorldClim version 2.1 (Fick & Hijmans, 2017).

Functional geography of ecosystems

We characterized the geography of a key ecosystem process, terrestrial primary production dynamics, using the Ecosystem Functional Types (EFTs) approach (Paruelo et al., 2001; Alcaraz-Segura et al., 2006, 2013). For this, we used the 2001-2017 time-series of satellite images of the Enhanced Vegetation Index (EVI) obtained by the MODIS sensor, MOD13Q1.006 product (16-day maximum value composite images at 230 m pixel size). EFTs were identified from three descriptors of functional attributes from the seasonal curves of EVI, also known as Ecosystem Functional Attributes (EFAs): annual mean (EVI_surrogate of primary production), seasonal coefficient of variation (EVI_sCV, a descriptor of seasonality) and the peak of maximum EVI (EVI_DMAX, an indicator of phenology). Following Alcaraz-Segura et al., (2013), each of the three descriptors was divided into four intervals, whose potential combinations result in a total of 64 different EFTs. In the case of phenology, we chose as intervals the four seasons, and for primary production and seasonality descriptors, we used their respective quartiles. Each EFT was named using the combination of two letters and a number: A-D for each class of primary production, increasing value in alphabetic order; a-d for seasonality, decreasing value in alphabetic order; and 1-4 for phenology, starting with 1 for spring. Therefore, we obtained 17 annual maps of EFTs for the period 2001-2017. We elaborated the final map of EFTs selecting for each pixel the median of the seventeen annual values. Previously, we excluded the areas under strong anthropic transformations according to González-Abraham et al., (2015) (human footprint index>0.5), and with anthropogenic categories in the last land-use map for the year 2017 of the Peninsula (INEGI, 2017).

Structural and compositional *vs.* functional geography of ecosystems

To examine the relationship between the characterization of the ecosystem functioning geographical patterns and ecological regionalizations based on structural and compositional features of vegetation, we used the ecoregions map by González-Abraham et al., (2010). To do so, we first, characterized each ecoregion, at all levels (I and II), in terms of ecosystem functioning, showing the frequency of each EFT in each ecoregion. And second, we carried out a Detrended Correspondence Analysis (DCA) (Hill & Gauch, 1980) between EFTs and ecoregions (Alcaraz-Segura et al., 2006; Fernández et al., 2010). This analysis represents in a multidimensional space reduced the spatial relationship between the classes of both maps. DCA prevented that sample units from being grouped together at the extremes of the gradient, since it scales the axes and equalizes the variance. Similarly, we prevented the problem that rare functions influence the outcome, since it reduces their weight.

4.4.3. Results

Functional characterization across ecoregions

EFTs map provided the ecosystem functional characterization of the Baja California Peninsula in terms of three key attributes (productivity, seasonality, and phenology) related to the primary production dynamics of vegetation. All potential combinations (64 types) were present in the peninsula, although some of them were dominants (Figure 4.4.3.). Ten EFTs (16% of the total) covered approximately 50% of the total study area and twenty-five (39% of the total EFTs) 75% of the peninsula. From these results it was possible to divide the dominant ecosystem functioning into two groups: EFTs with high productivity, high seasonality and phenology in autumn (e.g. Da3, Ca3, Cb3); and EFTs with low productivity, low seasonality and phenology in winter and autumn (e.g. Ac4, Ad3, Ad4, Ba3, Bb3, Bc3...).

At large scale, EFTs geographical pattern captured roughly the north-south climatic transition in the peninsula as shown by the ecoregions map (see EFTs map (Figure 4.4.3.)) and Correspondence Analysis (Figure 4.4.5.). In this sense, we could clearly identify the northwestern Mediterranean area, the tropical southern zone, and the desert transition areas between them. Despite this climate-based pattern, these three functional regions presented differences with respect to the boundaries of major ecoregions distribution. The geographical limits between the two functional regions in the north (northwest and northeast) were very similar to those proposed in the ecoregions map for the Mediterranean and Desert structural and compositional based regions (Gonzalez-Abraham et al., 2010). In contrast, the geographical limits in ecosystem functioning of the southern half of the peninsula, between Desert and Tropical regions (EFTs map; Figure 4.4.3.) showed significant differences with the limits established in the ecoregions map. Spatial references in this section to the regions are based upon the ecoregions map by González-Abraham et al., (2010).

The Mediterranean region had the highest EFTs heterogeneity in the peninsula (Figure 4.4.4.a), showing an altitudinal and latitudinal pattern of productivity. Mountainous ecoregions were dominated by high productivity EFTs (D) (e.g. California Mountains), and as altitude and latitude decreased, a greater EFTs heterogeneity increased since more intermediate productivity EFTs (C-B) also appeared (e.g. Chaparral, Coastal Sage Shrub, and Succulent Coastal Shrub). Productivity decreased toward the desert region (i.e. southward) where we found the EFTs with the lowest values for this attribute (A) (e.g. Pacific Islands). Seasonality values were high in coastal ecoregions (a-b) (Coastal Sage Scrub, Succulent Coastal Scrub) and low (d) in the mountain (California Mountains, Chaparral). Peaks of greenness occurred mainly in spring (1) followed by autumn (3) and winter (4). This geographical pattern of EFTs coupled very well with the ecoregionalization established for the Mediterranean by Gonzalez-Abraham et al., (2010). Here was noticeable the precise functional delimitation that EFTs made between the coastal ecoregions (Coastal Sage Scrub and Succulent Coastal Sage) and mountains ecoregions (Chaparral and California Mountains) (EFTs map, Figure 4.4.3.), what suggests a clear functional boundary between these ecoregions.

Desert showed a clear latitudinal pattern of EFTs (in terms of productivity, seasonality, and phenology). Productivity was low (A) in the northern part of the region (e.g. Lower Colorado Desert, Central, Desert, and Vizaíno Desert) and increased towards the south, getting EFTs with high values for this attribute (C-D) (e.g. Gulf Coast, La Giganta Ranges, Magdalena Plains). Seasonality was also low (d) in northern ecoregions (e.g. Lower Colorado Desert) and increased southward (a-b) (e.g. La Giganta Ranges). Peaks of greening also differed along the latitudinal gradient, whereas northern desert ecoregions showed winter peak (4) (e.g. Lower Colorado, Central, and Vizaíno Desert), in the southern desert ecoregions, it occurs mainly in autumn (3) (e.g. Gulf Coast, La Giganta Ranges, and Magdalena Plains). Hence, in the Desert region, EFTs showed two functional deserts (Figures 4.4.3. and 4.4.4.b): (i) the northern part that represented the “typical” Desert (Vizcaíno Desert, Central Desert, and Lower Colorado Desert ecoregions) and (ii) the southern “tropical” Desert (that includes Gulf Coast Desert, Giganta Ranges, and Magdalena Plains ecoregions), functionally similar to the Tropical region.

Finally, the Tropical region EFTs had the highest homogeneity in ecosystem functioning (Figures 4.4.3. and 4.4.4.c) and showed a homogeneous pattern through the three altitudinal ecoregions differentiated in the ecoregions map (Sarcrocaulescent Shrubland, Tropical Dry Forest and Cape Mountains). Functional differences along the region were only appreciable in terms of phenology. High mountain showed its phenological peak in September (summer), while low mountain and lowlands showed this peak during October-November (autumn). The region had a few different EFTs with high productivity (D), high seasonality (a), and the peaks of the maximum EVI in summer (2) and autumn (3).

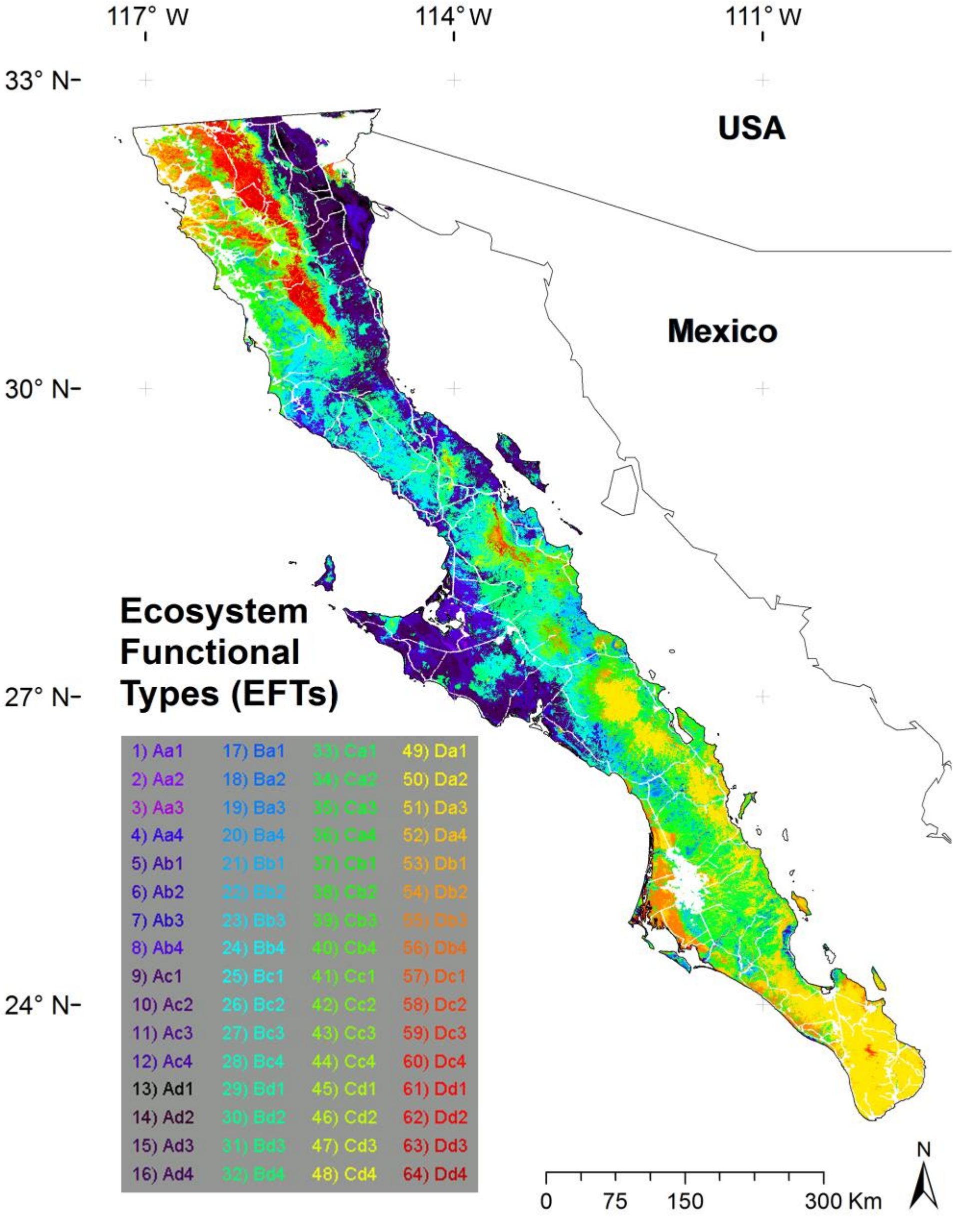

Figure 4.4.3. Ecosystem Functional Types based on EVI-MODIS dynamics for 2001-2017 period (230x230 m pixel). EFT categories were indicated in the legend. Human transformed areas appeared in

white.

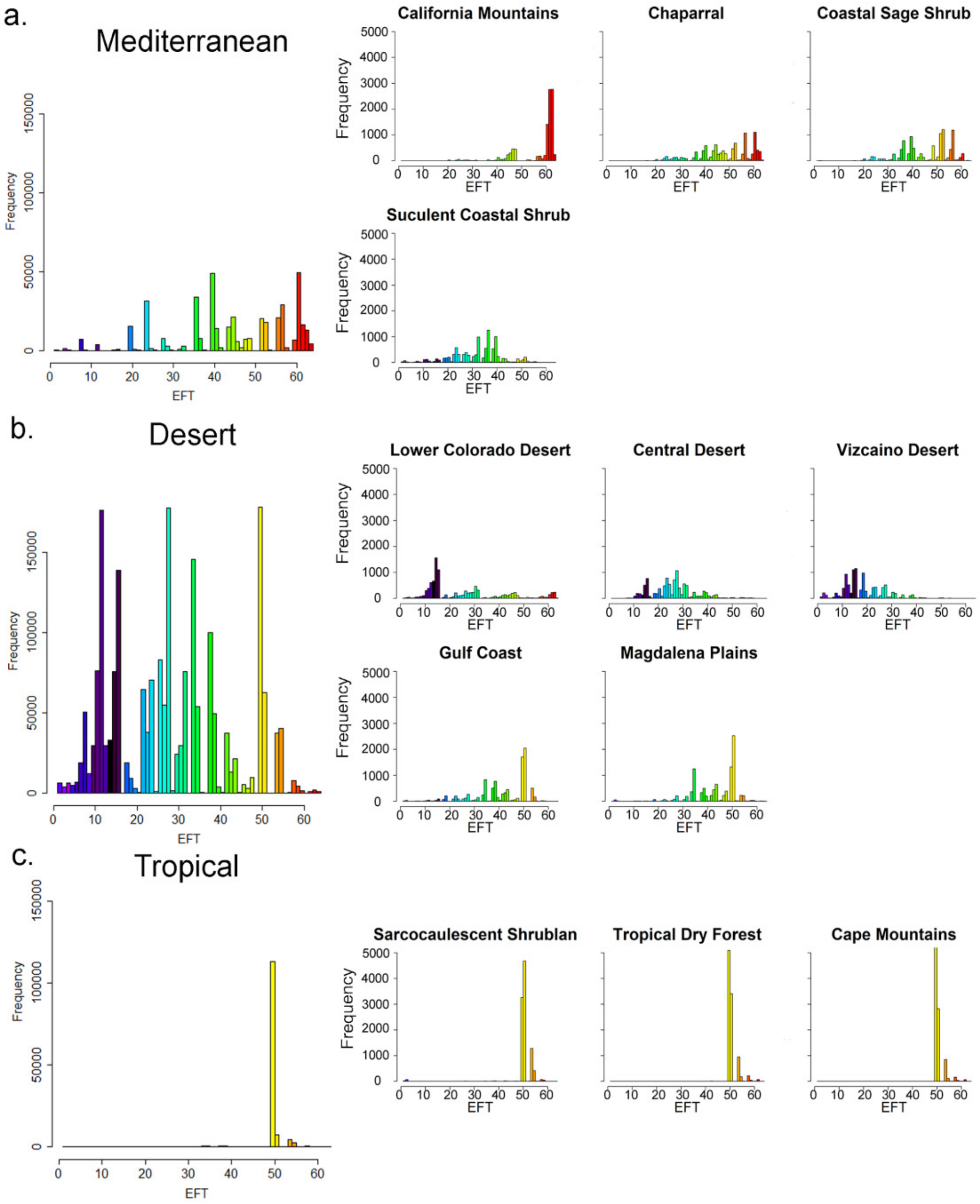

Figure 4.4.4. Functional characterization of ecoregions. EFT frequency histograms in major regions (level I) and sub-regions (level II) ordered in a latitudinal range: a) Mediterranean; b) Desert; and c) Tropical. Colours correspond to the EFTs, see legend in Figure 4.4.3.

Correspondence between geographical patterns of ecosystem functioning and ecoregions

Detrended Correspondence Analysis (DCA) (Figure 4.4.5.) showed that three major regions of the Peninsula were distributed along a marked productivity gradient (Figure 4.4.5. and Figure S1a). As a general pattern, the Mediterranean ecoregions (top left of Figure 4.4.5.), were associated with EFTs corresponding to high and intermediate productivity, low seasonality and phenology in spring (EFTs Dd1, Dc1, Cd1). However, two ecoregions considered to be Mediterranean by González-Abraham et al., (2010) did not appear in this group, being associated with other EFTs. On one hand, Pacific Islands appeared functionally separated from the other Mediterranean ecoregions and were associated with those corresponding to a climatic desert. On the other hand, Succulent Coastal Scrub, appeared in a transition zone between high productivity EFTs (typical of the Mediterranean) and low productivity EFTs (typical of the desert).

Desert ecoregions were grouped in two different places of the DCA (Figure 4.4.5. and Figure S1): (i) northern desert ecoregions (bottom right) and (ii) southern desert ecoregions (left). The group of northern desert ecoregions, had associated EFTs characterized by low productivity, in particular, Vizcaíno Desert was associated to very low productivity (A) and high seasonality (a) (EFT Aa4) and Lower Colorado Desert and Central Desert showed EFTs with low-medium productivity (B) and low or medium seasonality (c-d) (EFT Bc4). Southern desert ecoregions (i.e. Central Gulf Coast, La Giganta Ranges, and Magdalena Plains) were placed near to the tropical ecoregions, in a transition zone. Therefore, the southern part of Desert region, in the ecoregions map, is functionally more similar to the Tropical region than to the northern desert. Here, productivity was remarkably higher (C) than in the rest of desert region (A-B), and the phenological peak occurs between September to November (autumn-3), in a similar way to the tropical region and in contrast to the rest of desert region, where it occurred between February to April (mainly winter-4). Furthermore, the southern Desert region presents higher seasonality (a-b) than the rest of the Desert, and is similar to the Tropical region.

Finally, we found the group of tropical EFTs (right in Figure 4.4.5. and Figure S1) associated with EFTs of high productivity (D), high seasonality (a) and phenology in summer (2) and autumn (3) (EFT Da2, Da3). The most novel result was the functional proximity of the ecoregions of the southern desert with the tropical region.

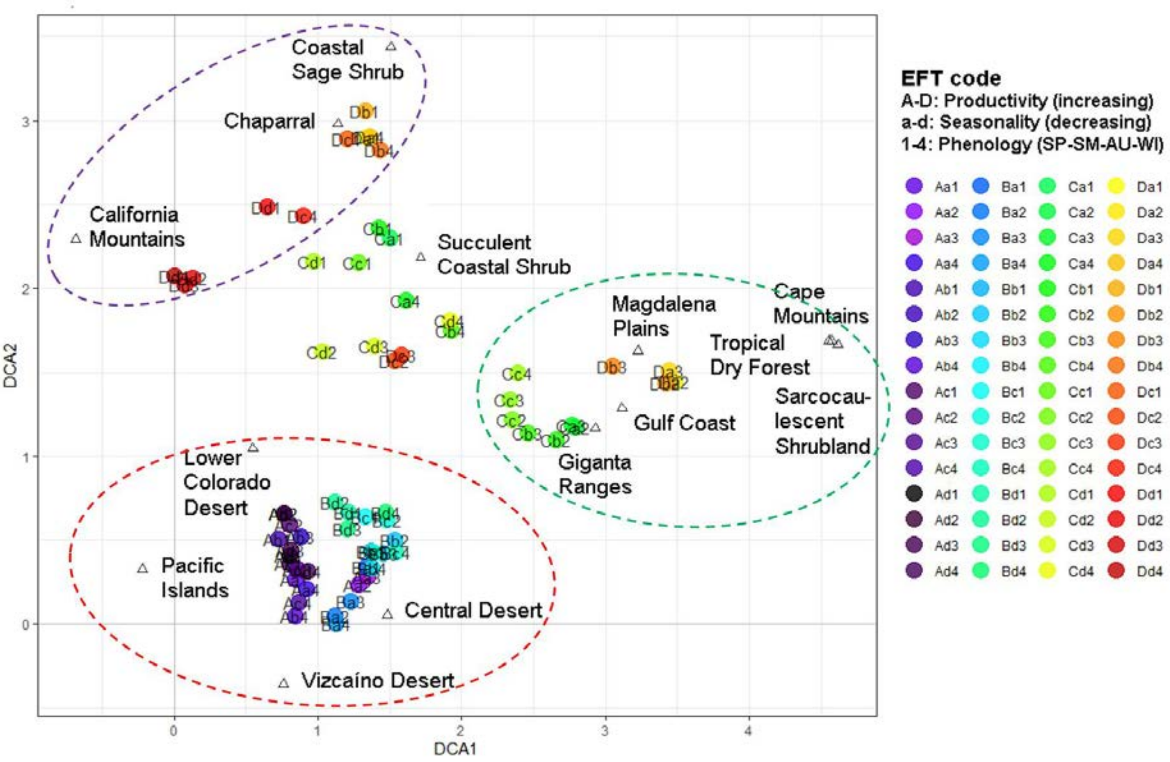

Figure 4.4.5. Ordination plot of dimension 1 and dimension 2 of the Detrended Correspondence Analysis (DCA) run with the contingency matrix between Ecosystem Functional Types, EFTs (circles) and ecoregions (triangles) in the Baja California Peninsula. See EFT codes in legend. Dotted circles represented the three major regions: Mediterranean in purple, Desert in red and Tropical in green.

4.4.4. Discussion

We found that in the Baja California Peninsula, at the broad scale, the spatial patterns in ecosystem functioning can produce different spatial patterns to the biogeographic regionalization established from structural and compositional attributes of the ecosystems.

In fact, when we focused on a more detailed scale, some disagreement between the functional patterns with ecoregions were more evident. This was particularly evident in the Desert - Tropical regions that, in contrast to the Mediterranean ecoregions, did not show spatial association with the EFTs that better represented the climatic conditions of the major region. Our analysis showed that the southern Desert ecoregions were functionally more similar to the Tropical region than to the rest of the desert ecoregions, and ecoregions inside Tropical region were functionally similar. These results emphasize the concept that functional geography provides new information about ecological systems, bringing us a new vision of another dimension of biodiversity. The knowledge of the relationship between the patterns of ecoregions and ecosystem functioning is the basis for a better understanding of spatial and temporal patterns of multidimensional biodiversity, which may guide towards a better regionalization and could aid for management and conservation purposes.

Classical regionalization and functional characterization of ecoregions: are our functional observations consistent with ecoregions?

Nature of tropics and geographical limits

We found two functional regimes with a transition around 27°-28° N: the northern half driven by winter-spring raining season and the southern half by summer-autumn rains.

There has been a long-time discussion among naturalists about the transition between the desert and tropical regions (Shreve, 1951; León de la Luz et al., 2008; González-Abraham et al., 2010). This transition has been delimited using different indices or attributes (Corlett, 2013; Feeley & Stroud, 2018), including climate variables (Hastings & Turner, 1965; Turner et al., 1995), species distribution (Garcillán et al., 2003), intra-species genetic changes (Riddle et al., 2000) or even geological features (León de la Luz et al., 2000). However, it has not been shown in terms of ecosystem functioning.

The extension of tropicality over the southern half of the peninsula, and its functioning leaves open a promising avenue for the study of the functionally tropical behavior of various parts of the desert. Something that has not been clearly explained in ecological terms before. In this sense, there are ecoregions not considered tropical until now (but desert), which although they do not have the tropicality as marked as the tropical ones (Sarcocaulescent Shrubland, Tropical Dry Forest and Cape Mountains), they also have the typical EFT of the tropics (EFT Da1) as the most abundant (Gulf Coast, La Giganta Ranges, and Magdalena Plains). Therefore, our results suggest that EFTs can help to conceptualize and define limits and dynamics of tropics or other ecological regions across different spatio-temporal scales.

Two functional deserts

One of the most remarkable results is the empirical evidence of two functionally deserts (approx. at 27.5° N) (Figure 4.4.3.). The transition between both functional deserts occurs at different latitudes depending on each peninsular coast. Here, ecosystem functioning is conditioned by the opposite thermal influence of the Gulf of California and the Pacific Ocean. The Northern desert descends southward along the Pacific coast to around 26°N characterized by low productivity, low to moderate seasonality and high dependence on winter rains (Lower Colorado Desert, Central Desert, and Vizcaíno Desert ecoregions); however, in the Gulf Coast, the Southern desert extends to reach next to 28 °N, showing higher productivity, seasonality and dependence on summer rains (Gulf Coast, La Giganta Ranges, and Magdalena Plains ecoregions). In essence, the presence of the California Current on the Pacific coast favours the southern extension along this coast of Mediterranean climate characteristics (including frequent fogging), while the high temperature of the Gulf of California prolongs the tropical influence towards the north along its coasts (Hastings & Turner, 1965; Peinado et al., 1994). On the Pacific coast, it has been shown that the ocean surface temperature (fog promoter) and the photosynthetically active radiation portion (fPAR) are directly related (Reimer et al., 2015), helping to maintain a minimum of productivity in places where precipitation is very scarce or even non-existent for long periods of time. Besides the climate transitional character of the Desert region, the scarce and high spatial and temporal variability of its precipitation (Hastings & Turner, 1965; Turner & Brown, 1982; Peinado et al., 2011) produce the elevated functional heterogeneity observed along this region.

These results can help to understand the controversy that has traditionally existed over the classification of southern desert ecoregions. Shreve (1951) considered La Giganta Ranges to be tropical, but a later study by Leon de la Luz et al., (2008) suggested that floristically it resembled the desert. In the case of Gulf Coast and Magdalena Plains, all studies since the work of Shreve (1951) have considered them to be desert ecoregions (see review in Garcillán et al., 2010; González-Abraham et al., 2010). However, our analyses showed that these three ecoregions functionally have a strong tropical character. The Gulf Coast ecoregion is a narrow strip of very long latitude (24-29° N) along the decreasing gradient of summer precipitation. These characteristics and the barrier effect of the mountains to the west, make it the most heterogeneous ecoregion in the whole Peninsula, hence its difficult classification. The Giganta Ranges was also identified as a zone of discrepancy in González-Abraham et al., (2010), but this did not happen for Magdalena Plains. Therefore, the identification of functionally tropicaloid features in this last ecoregion makes it necessary to reconsider its classification.

EFTs captured internal heterogeneity in Mediterranean ecoregions but not in tropical ecoregions

Inside the Mediterranean region, EFTs analysis showed a heterogeneous spatial pattern similar to the regionalization established in the ecoregions map, which is mainly structured by the double effect of coast and topography. In coastal ecoregions the presence of fog constitutes a climatic factor that conditions the adaptations of the organisms (Hastings & Turner, 1965; Martorell & Ezcurra, 2002). Furthermore, there exists a climate gradient in altitude (Peinado et al., 2011) that modifies the vegetation types and determines the different functional traits behaviors within the region.

Despite the similarity with the structural/compositional approaches, two ecoregions previously classified as Mediterranean were grouped with the others due to their peculiarities in ecosystem functioning. First, Succulent Coastal Scrub, located in the Pacific Coast between 29.5° and 31° N, has been long considered a transitional region (González-Abraham et al., 2010). In fact, in our CA appeared in a transition zone between EFTs characteristics of Mediterranean and Desert. Here, chaparral species extend southward to where moisture remains enough (Shreve, 1936), while the northern range of the desert species seems to depend on the absence of frost and some availability of water in summer (e.g. Shreve, 1936; Raven & Axelrod, 1978), probably associated with coastal fogs (Rundel & Mulroy, 1972; Garcillán et al., 2013). Second, Pacific Islands, which González-Abraham et al., (2010) already identified as one of the areas of discrepancy between authors. Its biological and biogeographical uniqueness is unquestionable. Most of the extension of these islands is occupied by semi-desert vegetation. However, biogeographically it is interesting that there an important proportion of Mediterranean flora (Epling & Lewis, 1942; Wallace, 1985; Smith et al., 1990; Oberbauer, 1993), which has led to consider it as a Mediterranean ecoregion in desert latitudes (González-Abraham et al., 2010). In terms of EFTs, its composition was very different from the rest of the mediterranean ecoregions (Figure 4.4.4.), showing low productivity EFTs, typical of the desert. Here, precipitation from fog condensation hybridizes the mediterranean regime of rains and allows the coexistence of these mediterranean species with the desert flora component, producing the mixed functional behavior that we observed.

The mediterranean conditions, in terms of the topographic gradient (approx. 3000 m) and coastal proximity, also occurred in the tropical region. But here EFTs did not show the heterogeneity mentioned in mediterranean, instead, they were functionally homogeneous. Although the annual precipitation variation associated with altitudinal gradient is even higher in the Tropical region (from less than 200 to 700 mm) than in Mediterranean region (from 270 to 650 mm), the homogeneity in ecosystem functioning could be due to the seasonality in the precipitation regime and the similarity in the phenological peak. Here, rain is concentrated in the summer and early autumn months (July to October) and there is an existence of a season without rain ("dry" season) of between five and eight months (Farfán & Fogel, 2007). Therefore, in this area, climatic controls are more important than altitudinal ones, which is reflected by the ecosystem functioning, i.e. in the presence of the same coastal and altitudinal factors, the ecosystem functioning is more homogeneous than mediterranean areas due to seasonality in rainfall patterns. In fact, the combination between the altitudinal range and heterogeneous distribution of precipitation and hence, phenology through the year, could be the reason for the high internal heterogeneity of EFTs in this region.

The role of ecosystem functioning in biological regionalization exercises

In the last decade, functional analysis of ecosystems has gained attention because it is a useful perspective for assessing and monitoring the effects of global change on diversity (Cabello et al., 2012; Pereira et al., 2013). Furthermore, incorporating functional aspects into regionalization practice offers a great potential for improving our understanding of spatial and temporal diversity patterns (Garnier et al., 2016); and implementing new programs for the conservation of ecological processes (Asner et al., 2017). EFT concept has been highlighted as “the first serious attempt to group ecosystems (at large scales) on the basis of shared functional behavior” (Mucina, 2019), and its strength for a better understanding of ecological systems providing new information derives from its ability to capture ecosystem functioning into discrete entities that can be mapped. Mapping such entities (EFTs) that reflect the performance of the whole ecosystem opens a straightforward, tangible and biologically meaningful way for incorporating ecosystem functioning in regionalizations, based on the regional heterogeneity of functional attributes at ecosystem level. EFT represents a new and complementary approach to long-established ones based on the compositional (e.g. species richness) and structural (e.g. vegetation types) characterizations of biodiversity, but also to the more recent functional approaches based on functional traits at species level.

The differences with these approaches derive both from the attributes of biodiversity reported by EFTs and the method used to do so. First, EFT considers ecosystem attributes related to the stocks and flows of matter and energy derived from biological activity taking place on plots of land, providing integrative information on the functional facets of biodiversity living on those plots. Second, EFTs capture temporal dynamics that are difficult to map through compositional or structural regionalization approaches, since they are a static measure with a fixed time interval (i.e. they measure conditions through the legacy of geological and evolutionary history). Third, EFTs are identified by remote sensing tools from aggregated measurements of ecosystem functions at the pixel level, which in practice represents information of the performance of the whole ecosystem. Remote sensing tools can offer more integrative functional measures of the whole ecosystem performance (productivity, evapotranspiration, etc.) that complement our traditional view of ecosystems (Butchart et al., 2010; Asner et al., 2017).

4.4.5. Conclusions

Our work highlights that differences between the proposals, rather than being a disadvantage, is the result of diverse approaches based on the different levels of ecological and biogeographical organization in the region, and their differences are highly informative. Ecosystem Functional Types allowed us to understand the relationship between different dimensions of biodiversity in regionalization exercises, i.e. between biological regionalization based on the biota components and structure (species distribution, endemisms, vegetation types) and patterns of ecosystem functioning (EFTs). The regionalization schemes have been widely used for guiding management and conservation decision-making since it allows us to organize our understanding of how major terrestrial ecosystems work. In this sense, due to the development of new techniques based on remote sensing, functional features measured at regional scales could be incorporated, allowing us to complement our traditional view of ecosystems, providing the basis for a more comprehensive regionalization of geographical patterns of life and therefore, improving also the future conservation purposes.

4.4.6. References

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4.4.7. Appendices

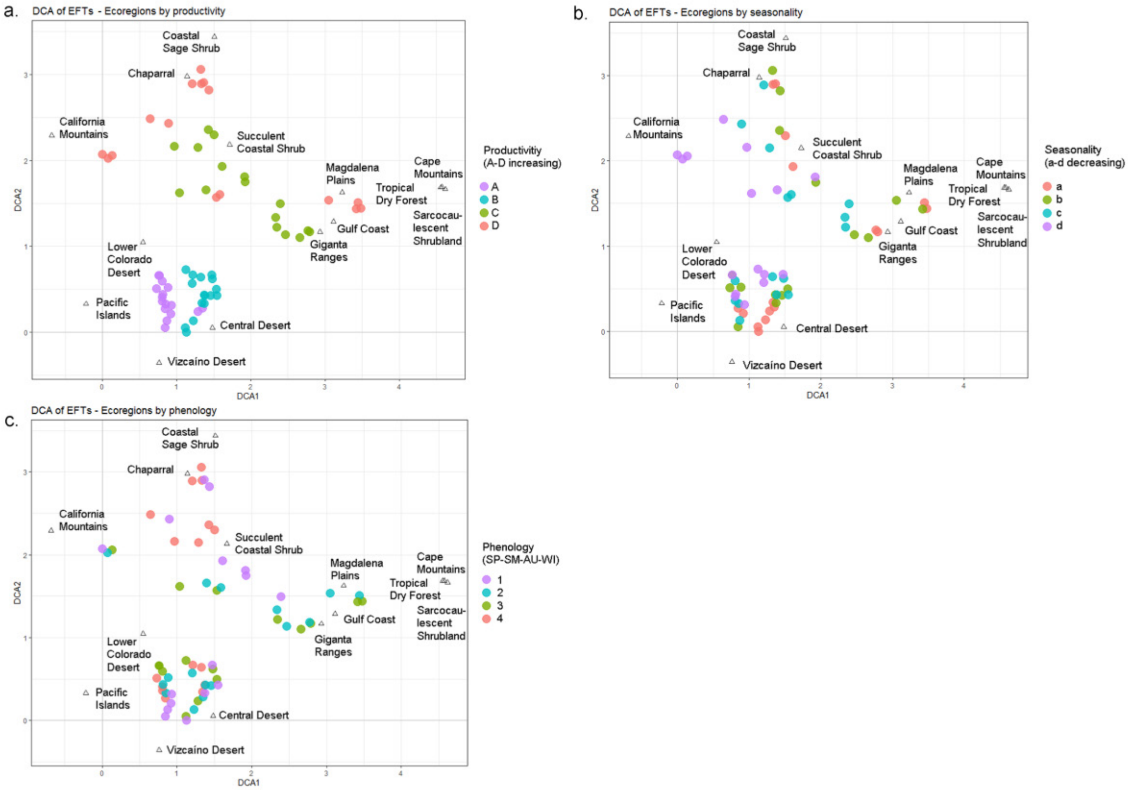

Figure S1. Ordination plot of dimension 1 and dimension 2 of the Detrended Correspondence Analysis (DCA) run with the contingency matrix between Ecosystem Functional Types, EFTs (circles) and ecoregions (triangles) in the Baja California Peninsula and colored by the three ecosystem functional attributes from which EFTs are derived. a) DCA colored by EVI mean, as surrogate of productivity, from A to D increasing; b) DCA colored by EVI sCV, indicator of seasonality from a to d decreasing and; c) DCA colored by EVI DMAX, indicating the peak of maximum EVI (SP-Spring, SU-Summer, AU-Autumn, WI-Winter).

5. GENERAL DISCUSSION

5. GENERAL DISCUSSION

This PhD thesis provides a remote-sensing based conceptual and methodological advance to incorporate the functional dimension of biodiversity at ecosystem level in ecology and conservation biology through the application of the Ecosystem Functional Type (EFT) concept. The results have provided new ways for the regional assessment of ecosystem functional patterns, ecological regionalization and setting geographic conservation priorities. Here, we discuss three main issues that have emerged along the study: 1) the role of ecosystem functioning in ecology and biodiversity science; 2) the conservation paradigm of ecosystem functioning, and 3) challenges and future research on EFT.

5.1. The role of ecosystem functioning in ecology and biodiversity science

This thesis aims to incorporate ecosystem functioning in biodiversity science and conservation and to facilitate the understanding of the relationship among the compositional, structural and functional facets of biodiversity, a central issue in ecological and environmental sciences during the last decades. Here, Ecosystem Functional Types have been proved to be a useful tool for assessing patterns of ecosystem heterogeneity (Chapter I), for identifying relevant areas in terms of ecosystem functioning (Chapter II and III), and for enhancing ecological regionalizations (Chapter IV). Ecosystem Functional Types have also been proved to be homogeneous groups that share common matter and energy dynamics (Chapter I), and therefore could show a similar and coordinated response to environmental factors. Developing a functional classification for ecosystems is relevant since it aims to reduce the diversity of biological entities (for instance genes, species or ecosystems) (Noss 1990), and to allow for the identification of homogeneous categorical groups that showed a similar and coordinated responses to environmental factors and effects on ecological processes (Díaz et al., 2013). Thus, functional classifications for ecosystems provide a useful framework for understanding the large-scale ecological changes (Alcaraz-Segura et al., 2017; Requena-Mullor et al., 2017, 2018; Arenas-Castro et al., 2018; Lourenço et al., 2018), since effects of global change are particularly noticeable at the ecosystem level (Vitousek, 1994), and have a faster influence on functional than on structural or compositional characteristics of ecosystems (McNaughton et al., 1989). Furthermore, functional classifications for ecosystems allow the assessment of global change impacts on ecosystem functioning and their associated services (Díaz et al., 2013; Hellmann et al., 2017).

No scientific consensus has been reached on how to track ecosystem functions at regional scales (Pettorelli et al., 2018). Although several efforts have focused on monitoring ecosystems over the past decades, including ecosystems functions (Oliver et al., 2015), e.g. Red List of Ecosystems assessment (Keith et al., 2015), or Essential Biodiversity Variables (Pereira et al., 2013), these efforts have not been made in a common way. Hence, this lack of clarity has hampered progress in terms of identifying opportunities for ecosystem functioning monitoring globally (Pettorelli et al., 2018). A well-known example of this lack of consensus that can be found in the framework of Planetary Boundaries (Steffen et al., 2015), where the two main dimensions to assess Biosphere Integrity are genetic diversity (for which there are targets) and functional diversity (for which there are no targets). Not having functional diversity or ecosystem functioning is a potential gap in the framework.

To address these gaps, we propose the use of the remotely sensed-Ecosystem Functional Type concept, which we have demonstrated throughout the thesis, that it is a powerful tool to assess and contribute to conserving the ecosystem functioning heterogeneity, i.e. to incorporate ecosystem functional diversity dimension in ecology and conservation. To ensure and facilitate the incorporation of such functioning, all the metrics developed to measure ecosystem functioning, as well as the database with the resulting maps, have been provided to the scientific community and managers (Chapter II). Moreover, one essential aspect of the concept should be highlighted as a major advantage: according to Pettorelli et al., (2018), currently, "remote sensing is the only methodology able to provide global coverage and continuous measures at relatively high spatial and temporal resolutions (Skidmore et al., 2015; Pettorelli et al., 2016, 2018)". Additionally, EFTs are defined with a top-down strategy, which makes use of functional characters of ecosystems identifiable at the regional scale, seeking to emphasize the overall performance of the system, and complementing our traditional structural view of ecosystems, since it facilitates the incorporation of ecosystem functioning into biodiversity science (Chapter III and IV).

Hence, EFTs provide a measurement of ecosystem functioning that could play an important role in the assessment of functional biodiversity at global scale and present improvements with respect to other methodologies. Literature has pointed out that other approaches to evaluating ecosystem functioning, such as the Plant Functional Types (PFT) approach, is not straightforward and accurate enough to represent ecosystem functional properties at the ecosystem level (Clark, 2016; Saccone et al., 2017; Thomas et al., 2019). In particular, several studies demonstrated that it is inadequate to use data from a single site to estimate the parameters of a given PFT for regional applications (Xiao et al., 2011). Jetz et al., 2016 pointed out that "scaling up processes from fine-grained local studies to larger regions (and ultimately the entire globe) is an urgent challenge for all of the Earth sciences". Thus, EFTs observations from space have the potential to provide a global assessment for functional biodiversity, with the advantage of being a quicker and sensitive response to short-term changes in ecosystem performance than composition or structure, and can be produced on an annual basis providing a straightforward way to track interannual changes in ecosystem functioning (Müller and others 2014).

5.2. Conservation paradigm of ecosystem functioning

Contemporary conservation schemes face the challenge of safeguarding the ecological processes required for the persistence of biodiversity over time (GBO4, 2014; CBD-Target 11; Visconti et al., 2019; Prober et al., 2019) and for the supply of ecosystem services to people (Costanza, 2012, 2014; Lavorel et al., 2020). In this sense, conservation efforts need to include spatially explicit and parsimonious ways to incorporate heterogeneity in ecosystem functions (Turner and Chapin, 2005; Harvey et al., 2017) in order to develop theory and tools that complement traditional planning and management actions (Possingham et al., 2005). The strength of EFTs for being applied in conservation biology derives from their ability to capture ecosystem functioning into discrete entities that can be mapped (Chapter II and III). Mapping such entities (EFTs) that reflect the performance of the whole ecosystem opens a straightforward, tangible and biologically meaningful way for conservation based on the regional heterogeneity of functional attributes at ecosystem level (Turner and Gardner, 2015). The identification of areas with high functional diversity at the ecosystem level can help to expand currently protected area networks using complementary arguments to the species richness and ecosystem structure more focused on ecosystem multifunctionality, resilience and ecosystem services (Manning et al., 2018; Lecina-Díaz et al., 2019).

EFTs applied in conservation represent a complementary approach to long-established ones based on the compositional (e.g., species richness) and structural (e.g., vegetation types) characterizations of biodiversity, but also to the more recent functional approaches based on functional traits at species level. The differences with these approaches derive both from the attributes of biodiversity reported by EFTs and the method used to do so. First, EFT-based priorities consider ecosystem attributes related to the stocks and flows of matter and energy derived from biological activity taking place on plots of land, providing integrative information on the functional facets of biodiversity living on those plots. Second, EFTs are identified by remote sensing tools from aggregated measurements of ecosystem functions at the pixel level, which in practice represents information of the performance of the whole ecosystem (Butchart et al., 2010; Asner et al., 2017).

In essence, an agreed methodology for the assessment of ecosystem functions, using satellite remote sensing, i.e. EFTs, could offer many opportunities to advance ecosystem functions conservation, allowing, for example, to identify hotspots in functional diversity and functional stability (Chapter II), to incorporate ecosystem functional diversity into geographic conservation priorities (Chapter III), and to guide management and decision making actions since it allows us to organize our understanding of how major terrestrial ecosystem works (Chapter IV).

Henceforth, providing effective tools for measuring functions is the initial stage in carrying out the policies and management required to safeguard the processes that support biodiversity and the services necessary for human well-being (Steffen et al., 2015; Naidoo et al., 2019). However, according to Pettorelli et al., (2018), "information on the state of ecosystem functions and services available remains scarce from the Biodiversity Indicators Partnership, a global initiative to promote and coordinate the development and delivery of biodiversity indicators for use by the CBD and other biodiversity-related conventions, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, the Sustainable Development Goals and national and regional agencies". While satellite remote sensing EFTs could help track progress towards the CBD targets, since it allows yearly systematic monitoring across all important sites which could help to determine whether the current management regime is effective for conservation or in retaining or restoring a site biodiversity value (according to CBD post-2020 targets, Visconti et al., 2019). In this sense, efforts of Chapter II are focused on providing both to the scientific and managers communities with valuable information of the first characterization of the functional diversity at the ecosystem level. In particular, we provide the information and data sources to reproduce the methodology in any area of the world.

5.3. Challenges and future research of EFTs

The use of the EFT concept in ecology and conservation is still subjected to some challenges. First, our satellite-derived EFT map characterizes the spatial heterogeneity of primary production dynamics. However, EFTs could also be identified from other remote sensing indices (e.g. Fernández et al., 2010), to characterize the spatiotemporal heterogeneity of multiple ecosystem processes and functions (e.g. albedo, evapotranspiration or surface temperature) at different scales to guide biodiversity and ecosystem services policies (Pettorelli et al., 2018). Second, the EFT richness and rarity maps inform on the diversity and spatiotemporal heterogeneity in the occurrence of an ecosystem function, but additional landscape indices could also inform on the spatial arrangement (Fahrig and Nuttle, 2005), connectivity, and lateral transfers (*sensu* Turner and Gardner, 2015) of energy and matter fluxes at the landscape level. Third, the incorporation of EFTs in earth system models is difficult, since these models can use simple and small numbers of categories in a variable and 64 are too many, nevertheless it is possible to incorporate it, see Lee et al., (2013) and Müller et al., (2014).

Future works should explore the effect of image pixel size (e.g. with Sentinel-2 at 10 m/pixel), hierarchy in the EFT classification, and parochialism (Pouzols et al., 2014) on the EFT-based approach, include other ecosystem functions (e.g. albedo, surface temperature), temporal changes in EFT diversity, and further metrics of heterogeneity across scales. Another challenge for future works is to demonstrate that EFTs show a homogeneous response to environmental changes and determine whether patterns remain stable with changes in spatial scale.

6. GENERAL CONCLUSIONS

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1. Ecosystem functioning descriptors, such as Ecosystem Functional Attributes (EFAs) and Ecosystem Functional Types (EFTs), derived from satellite spectral indices (e.g. Enhanced Vegetation Index, EVI), demonstrated to be useful and innovative tools to incorporate ecosystem functioning at regional scales into ecology and conservation. In particular, EFTs are a straightforward approach that builds just on three satellite-derived meaningful descriptors of ecosystem functioning, which facilitates computation and interpretation by scientists, managers and policymakers. EFTs open a new way for the regional assessment of ecosystem functional patterns, heterogeneity and diversity that can be used in ecological regionalizations and in setting geographic conservation priorities.

2. EFTs, an ecosystem functional classification built from satellite observations of radiation exchanges between the biosphere and the atmosphere, can inform on homogeneous patches on the land surface in terms of their NEE dynamics measured on ground. Given that NEE dynamics is related to primary production, one of the most essential and integrative descriptors of ecosystem functioning, satellite-derived EFTs can then be used (as essential variables) to describe, assess and monitor the regional heterogeneity and spatial diversity of ecosystem functioning.

3. EFTs allowed us to map the regional spatial patterns of two indicators of ecosystem functional diversity, i.e., EFT richness and EFT rarity and two indicators of ecosystem functional stability, i.e. EFT interannual variability and dissimilarity at the protected area level, providing both scientists and managers with valuable information of the functional diversity and their stability at ecosystem level.

4. The EFT approach can be used to incorporate the heterogeneity and singularity of ecosystem functions into geographic conservation priority setting. Such functional approach

can complement compositional and structural assessments of biodiversity to support decision-making by offering supplementary arguments for the holistic conservation of biodiversity. Important areas for ecosystem functional diversity were sometimes congruent with areas of interest for biodiversity composition and structure, which highlights their relevance for the conservation of multiple biodiversity facets, but some other times they were not congruent. That lack of congruence highlights that traditional approaches may not identify all the important areas for ecosystem functions, and may tend to better prioritize areas with rarity than with richness in EFTs.

5. EFTs allowed us to understand the relationship between different dimensions of biodiversity in regionalization exercises, i.e. between biological regionalizations based on biodiversity composition and structure (species distribution, endemisms, vegetation types) and regional patterns of ecosystem functioning (EFTs). In ecological regionalization, EFTs bring a new and complementary vision of the functional dimension of biodiversity. The knowledge of the relationship between the patterns of ecoregions and ecosystem functioning opens new ways for a better understanding the spatial and temporal patterns of multidimensional biodiversity facets, which may help towards more comprehensive and operational regionalizations that could serve management and conservation purposes of biodiversity and ecosystem services.

6. Future conceptual and empirical development and applications of EFTs should include other ecosystem functions, further field validation and EFT parameterization, hierarchy in the EFT classification, and parochialism effect on the EFT-based approach, temporal changes in EFT diversity, and further metrics of heterogeneity across scales.

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8. GENERAL APPENDICES

General Appendix 1.

Journals copies of the scientific publications derived from the thesis

Scientific publication from CHAPTER II.

Cazorla, P.B., Cabello, J., Guirado, E., Reyes, A., Peñas, J., Pérez-Luque, A., Alcaraz-Segura D.(2020) A remote sensing-based dataset to characterize the ecosystem functioning and functional diversity of a Biosphere Reserve: Sierra Nevada (SE Spain). Earth System Science Data. Discuss., https://doi.org/10.5194/essd-2019-198, in review.

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Open Access Earth System Science Data Discussions

A remote sensing-based dataset to characterize the ecosystem functioning and functional diversity of a Biosphere Reserve: Sierra Nevada (SE Spain)

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Abstract

Conservation Biology faces the challenge of safeguarding the ecological processes that sustain biodiversity. Characterization and evaluation of these processes can be carried out through attributes or functional traits related to the exchanges of matter and energy between vegetation and the atmosphere. Nowadays, the use of satellite imagery provides useful methods to produce a spatially continuous characterization of ecosystem functioning and processes at regional scales. Our dataset characterizes the patterns of ecosystem functioning in Sierra Nevada (Spain) from the vegetation greenness dynamics captured through the spectral vegetation index EVI (Enhanced Vegetation Index) since 2001 to 2018 (product MOD13Q1.006 from MODIS sensor). First, we provided three Ecosystem Functional Attributes (EFAs) (i.e., descriptors of annual primary production, seasonality, and phenology of carbon gains), as well as their integration into a synthetic mapping of Ecosystem Functional Types (EFTs). Second, we provided two measures of functional diversity: EFT richness and EFT rarity. Finally, in addition to the yearly maps, we calculated interannual summaries, i.e., means and inter-annual variabilities. Examples of research and management applications of these data sets are also included to highlight the value of EFAs and EFTs to improve the understanding and monitoring ecosystem processes across environmental gradients. The datasets are available in two open-source sites (PANGAEA: https://doi.pangaea.de/10.1594/PANGAEA.904575 (Cazorla et al. 2019) and http://obsnev.es/apps/efts_SN.html), and bring to scientists, managers and the general public valuable information on the first characterization of the functional diversity at ecosystem level developed in a Mediterranean hotspot. Sierra Nevada represents an exceptional ecology laboratory of field conditions, where a long-term monitoring (LTER) program was established 10 years ago. The data availability on biodiversity, climate, ecosystem services, hydrology, land-use changes and management practices from Sierra Nevada, will allow to explore the relationships between these other environmental data and ecosystem functional data that we provide in this work.

1 Introduction

A better characterization of the functional dimension of biodiversity is required to develop management approaches that ensure nature contributions to human well-being (Jax, 2010). To achieve this goal, it is necessary to have a set of essential variables that characterize and monitor ecosystem functioning (Pereira et al., 2013). Such variables are basic to understand the dynamics of ecological systems (Petchey and Gaston, 2006), the links

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between biological diversity and ecosystem services (Balvanera et al., 2006; Haines-Young and Potschin, 2010), and the mechanisms of ecological resilience (Mouchet et al., 2010). In addition, the use of ecosystem functioning variables has been demanded to assess functional diversity at large scales with the aim of measuring the Biosphere integrity (Mace et al., 2014; Steffen et al., 2015), one of the most challenging planetary boundaries to quantify (Steffen et al., 2015). Despite the importance of ecosystem functioning variables, and the conceptual frameworks developed to promote their use (Pettorelli et al., 2018), they have seldom been incorporated to ecosystem monitoring in protected areas (but see Alcaraz-Segura et al., 2009; Fernández et al., 2010; Cabello et al., 2016).

Characterization and evaluation of ecosystem functioning can be carried out through attributes or functional traits related to the exchanges of matter and energy between vegetation and the atmosphere (Mueller-Dombois and Ellenberg, 1974). Nowadays, the use of satellite imagery provides useful methods to produce a spatially continuous characterization of ecosystem functioning and functional diversity at local (Fernández et al., 2010), regional (Alcaraz-Segura et al., 2006, 2013) or global scales (Ivits et al., 2013). Theoretical and empirical models support the relationship between spectral indices derived from satellite images (*e.g.* Enhanced Vegetation Index, EVI) and essential functional variables of ecosystems, such as primary production, evapotranspiration, surface temperature, or albedo (Running et al., 2000; Pettorelli et al., 2005; Fernández et al., 2010; Lee et al., 2013). Among them, primary production is considered the most integrative and essential indicator of ecosystem functioning (Virginia and Wall, 2001; Pereira et al., 2013), since it has an important role in the carbon cycle (i.e., it is the energy input to the trophic web and therefore, the driving force behind many ecological processes). Moreover, primary production offers a comprehensive response to environmental changes, and constitutes a synthetic indicator of ecosystem health (Costanza et al., 1992; Skidmore et al., 2015).

To characterize ecosystem functioning through spectral vegetation indices, we can use the approach based on Ecosystem Functional Types (EFTs), defined as patches of the land surface that share similar dynamics in the exchanges of matter and energy between the biota and the physical environment (Paruelo et al., 2001; Alcaraz-Segura et al., 2006). EFTs are derived from three Ecosystem Functional Attributes (EFAs) that describe the seasonal dynamics of carbon gains: annual mean (a surrogate of annual primary production, the most essential and integrative indicator of ecosystem functioning), annual standard deviation (a descriptor of seasonality or the differences between the growing and non-growing seasons), and the annual date of maximum (a phenological indicator of when in the year is the growing period centered). Since the concept appeared in 2001 (Paruelo et al., 2001), the EFT approach (or equivalent approaches) has exponentially grown to characterize functional heterogeneity from local to global scales (Alcaraz-Segura et al., 2006; Karlsen et al., 2006; Duro et al., 2007; Fernández et al., 2010; Geerken 2009; Alcaraz-Segura et al., 2013; Ivits et al., 2013; Cabello et al., 2013; Pérez-Hoyos et al., 2014; Müller et al., 2014; Wang and Huang, 2015; Villarreal et al., 2018; Coops et al., 2018; Mucina, 2019).

This article aims to illustrate how EFAs and EFTs can be used to assess the spatio-temporal heterogeneity and inter-annual variability of ecosystem functioning in protected areas based on the vegetation dynamics captured through spectral vegetation indices (e.g. EVI). We introduce as a proof of concept the case of Sierra Nevada Biosphere reserve (SE Spain) from 2001 to 2018. First, for each year, we provide three Ecosystem Functional Attributes (EFAs) (i.e., annual primary production, seasonality and phenology of carbon gains), as well as their integration into a synthetic mapping of Ecosystem Functional Types (EFTs). Second, we present two measures of functional diversity: EFT richness and EFT rarity. Finally, in addition to the yearly maps, we calculated interannual summaries, i.e., inter-annual means and inter-annual variability, to show the average conditions as well as the most stable and variable zones along the period (workflow in Fig. 2).

2 Methods

2.1 Site Description

Sierra Nevada (Andalusia, SE Spain) is a mountainous region covering more than 2,000 km^2 with an elevation range of between 860 and 3,482 m a.s.l (Fig. 1). It is considered one of the most important biodiversity hotspots in the Mediterranean region (Blanca et al., 1998; Cañadas et al., 2014), hosting 105 endemic plant species for a total of 2,353 taxa of vascular plants (33% and 20% of Spanish and European flora, respectively; Lorite 2016). Forest cover in Sierra Nevada is dominated by pine plantations (*Pinus halepensis* Mill., *Pinus pinaster* Ait., *Pinus nigra* Arnold subsp. *salzmannii* (Dunal) Franco, and *Pinus sylvestris* L.) covering approximately 40,000 ha. Most of them were planted in the period 1960–1980. The main native forests of Sierra Nevada are dominated by the evergreen holm oak *Quercus ilex* subsp. *ballota* (Desf.) Samp. occupying low and medium mountain areas (8,800 ha.), and by the deciduous Pyrenean oak *Quercus pyrenaica* Willd ranging from 1,100 to 2,000 m a.s.l. (about 2,000 ha). Autochthonous pine *Pinus sylvestris* L. var. *nevadensis* H. Christ forests can also be found in small patches with low tree cover in the treeline. Above the treeline, plant communities of the Oromediterranean and Crioromediterranean belts (above 1,800-2,000 m.) are dominated by chamaephytes and hemicryptophytes (scrublands, grasslands, and cliff and scree communities), being the habitat to many endemic species. Sierra Nevada receives legal protection and international recognition in multiple ways: MAB Biosphere Reserve (1986), Natural Park (1989),National Park (1999), Important Bird Area (2003), Special Area of Conservation (Natura 2000 network, 2012), and it is included in the IUCN Green List of Protected Areas (2014) and in the Spanish LTER network (Zamora et al. 2017). The main economic activities in this mountain region are agriculture, tourism, livestock raising, beekeeping, mining, and skiing (Bonet et al., 2010).

In Sierra Nevada, vegetation studies have mainly been developed considering a compositional perspective (phytosociological method) or successional perspective (vegetation series). These studies have been very useful for describing the vegetation heterogeneity at mesoscale (Loidi, 2017), for characterizing habitats of conservation importance (EU Directive 92/43/EEC), and for developing forest restoration policies (Valle et al., 2003). However, these approaches are difficult to monitor the effects of environmental changes and management actions, to understand the environmental gradients at protected area scale that drive biodiversity patterns, and to evaluate the role of ecosystems as suppliers of benefits to society (Cabello et al., 2019).

2.2 Satellite images of Vegetation Indices (MOD13Q1 data product)

The characterization of ecosystem functioning in Sierra Nevada was based on the temporal dynamics of the Enhanced Vegetation Index (EVI) from 2001 to 2018. Specifically, we used the MOD13Q1.006 product of the MODIS sensor (Moderate Resolution Imaging Spectroradiometer) on board NASA's Terra satellite (Didan 2015). This product provides maximum value composite images every 16 days (23 images per year) at 231 meters spatial resolution and are downloadable from NASA's LP DAAC (Land Processes Distributed Active Archive Center) (http://lpdaac.usgs.gov/lpdaac/get_data) and in Google Earth Engine (DOI: https://doi.org/10.5067/MODIS/MOD13Q1.006). Values of EVI*10,000 are given as real numbers between 0 and 10,000.

2.3 Calculating Ecosystem Functional Attributes (EFAs)

We identified three EFAs that are known to capture most of the variance in the time series of vegetation indices and that are biologically meaningful (Paruelo et al., 2001; Alcaraz-Segura et al., 2006, 2009). These attributes were calculated from the EVI seasonal curve or annual dynamics. From the EVI seasonal curve of each year, we identified three functional attributes: the EVI annual mean (EVI_mean; an estimator of primary production), the EVI seasonal Standard Deviation (EVI_sSD; a descriptor of seasonality, i.e., the differences between the growing and non-growing seasons), and the date of maximum EVI (EVI_DMAX; a phenological indicator of the month with maximum EVI) (Fig.3). To summarize the EFAs of the 2001-2018 period, we calculated the inter-annual mean and the inter-annual variability for each attribute.

2.4 Identifying Ecosystem Functional Types (EFTs)

EFTs were identified by synthesizing in a single map the variability contained in the three EFAs following a similar approach to Alcaraz-Segura et al. (2013). The range of values of each EFA was divided into four intervals, giving a potential number of 64 EFTs (4 × 4 × 4). For EVI_DMAX, the four intervals agreed with the four seasons of the year. For EVI_mean and EVI_sSD, we extracted the first, second, and third quartiles for each year and then calculated the inter-annual mean of each quartile (means of the 18-year period) (Table 1). These fixed limits between EFT classes were applied to each year. To summarize the EFTs of the 2001–2018 period, we calculated the most frequent EFT of the period (i.e., the EFT mode for each pixel). To name EFTs, we used two letters and a number: the first capital letter indicates net primary production (EVI_mean), increasing from A to D; the second small letter represents seasonality (EVI_SD), decreasing from a to d; the numbers are a phenological indicator of the growing season (EVI_DMAX), with values 1-spring, 2-summer, 3-autumn, 4-winter.

2.5 Characterizing Ecosystem Functional Diversity

To characterize ecosystem functional diversity, we used EFT richness and EFT rarity. EFT richness was calculated for each year by counting the number of different EFTs in a 4×4-pixel moving window (924 x 924 m) around each pixel (top-left center pixel of the 4x4 Kernel) (modified from Alcaraz-Segura et al., 2013). Then, the average richness map of all years was obtained. EFT rarity was calculated for each year as the relative extension of each EFT compared to the most abundant EFT (Equation 1) (Cabello et al., 2013). Then, the average rarity map of all years was obtained.

$$\text{Rarity of EFTi} = (\text{Area\_EFTmax}–\text{Area\_EFTi})/\text{Area\_EFTmax} \quad \text{(Equation 1)}$$

where Area_EFTmax is the area occupied by the most abundant EFT and Area_EFT*i* is the area of the *i* EFT being evaluated, with *i* ranging from 1 to 64.

2.6 Stability in ecosystem functioning

To identify the most stable and variable areas (either due to inter-annual fluctuations or to directional trends) in ecosystem functioning, we provide three approaches. First, we calculated the inter-annual variability of each EFA (coefficient of variation for EVI_mean and EVI_sSD, and circular standard deviation for EVI_DMAX). Second, we recorded the number of different EFTs that occurred in the same pixel in the period 2001-2018. Third, to consider the changes not only at the pixel but also at the landscape level, the Jaccard similarity index (Jaccard, 1901) (Equation 2) was used in 4×4-pixel moving windows (924 x 924 m).

$$\text{Jaccard Index} = (\text{the number in both sets}) / (\text{the number in either set}) * 100$$

The same formula in notation is (Equation 3):

$$J(X,Y) = |X \cap Y| / |X \cup Y|$$

In Steps:

1) Count the number of EFTs which are shared between both windows; 2) Count the total number of EFTs in both windows (shared and unshared); 3) Divide the number of shared EFTs 1) by the total number of EFTs 2); 4) Multiply the number found in 3) by 100.

This measure represents how similar is the EFT composition that occurs in each window throughout the entire time series (2001-2018). For each window, the Jaccard index was calculated among all possible combinations of years and then the interannual average of all calculated indices was obtained. Dissimilarity was calculated as (Equation 4):

$$\text{Dissimilarity} = 1 - \text{Jaccard Index}$$

Dissimilarity values range from 0 to 1, with 1 being the highest degree of dissimilarity in composition and relative abundance of EFTs and 0 being absent.

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3 Results and Discussion

3.1 Available dataset

Overall, the collection of datasets provides a characterization of ecosystem functioning and ecosystem functional diversity in Sierra Nevada Biosphere Reserve (SE Spain) through remote sensing. To broaden the use of data, first, we provide data in .tif format. Second, we have incorporated rendered versions of all layers as required by Google Earth Pro (called “filename..._forGoogleEarthVisualization.tif”) for visualization. And third, we have also developed an ad-hoc visualization platform for all the layers.
All data are available yearly (2001-2018) and summarized for the period, in EPSG:4326 WGS84.

The dataset is structured in three main subsets of variables: Ecosystem Functional Attributes, Ecosystem Functional Types, and Ecosystem Functional Diversity (see Table 2). For each variable there are two groups of data (two subfolders): one containing the yearly variables, and another one containing the summaries for the 18-year period.

3.2 Ecosystem Functional Attributes patterns

Functional attributes of productivity, seasonality and phenology showed a clear altitudinal pattern. Productivity (EVI_mean) was much lower in the Crioro- and Oromediterranean bioclimatic belts than in the Supra- and Mesomediterranean belts. Productivity also decreased from west to east (Fig. 4a). Seasonality (EVI_sSD) was high in the Supramediterranean, decreasing in Meso-, and Thermomediterranean belts, and in Crioro- and Oromediterranean (Fig. 4b). Phenology (EVI_DMAX) was characterized by a dominant summer peak in vegetation greenness in the Crioro- and Oromediterranean belts, and a late spring peak in the Supra- and Mesomediterranean belts. Dry and semi-arid thermomediterranean areas of the south and east showed greeness peaks in early autumn and winter months (Fig. 4c).

3.3 Ecosystem Functional Type patterns

As a result of the combination of the three functional attributes of the canopy, productivity, seasonality and phenology, represented in Fig. 4 a-c, we obtained the EFTs map (Fig. 4d) that includes a synthetic characterization of the spatial patterns of ecosystem functioning. A total of 64 classes were observed. The most abundant EFT presented the maximum greenness in spring, with productivity values from low to intermediate and with all possible combinations of seasonality: Aa1, Ba1, Cb1, Cd1, Ba1, and Cc1 accumulated 30% of the surface. On the contrary, the rarest EFTs were Ba4, Aa4 characterized by medium or low productivity, high seasonality and maximum greenness in winter.

Crioro and oromediterranean areas presented EFTs with low and intermediate productivity, high seasonality and moments of maximum greenness mainly in summer, but also in spring. Here, extreme conditions characterized by scarce soil (Peinado et al., 2019), high solar radiation, extreme temperatures, winds, snow and ice, give rise to a short vegetative period. This results in scarce vegetation cover, controlled by low temperatures, which can only occur in summer, being the plant growth time, hence these areas have been referred to as "cold desert" (Blanca et al., 2019). The supra- and mesomediterranean levels had associated EFTs of intermediate-high productivity, medium-low seasonality and maximum green moment in spring and autumn (e.g., Cc1-3) (Fig. 4d). The supramediterranean is characterized by the presence of deciduous species, e.g., oak groves associated with the most productive and seasonal ecosystem functional type of the study area, with maximum in spring (EFT Da1). In the dry and semi-arid thermomediterranean of the eastern end, characterized by thermophilic species, which hardly suffer from frost, a different functional behaviour of the ecosystems was detected. The functioning of this area showed low values of productivity, medium-low seasonality and maximum greenness of the vegetation in spring or winter (e.g., Ac1-4). Here, the main control of ecosystem functioning is water availability, presenting plant species with a fast response to scarce water inputs (Cabello et al., 2012).

3.4 Stability in ecosystem functioning

The interannual variability ranged from 1 to 17 different EFTs over the 18-year period in the same pixel (Fig. 5a). The number of EFTs observed in the same pixel over 18 years was higher in the supra- and mesomediterranean levels, coinciding with the altitudinal range where interannual climate variability is most affected (e.g., they may present a lot of snow in cold years and be affected by drought in dry and warm years). The eastern end of the semi-arid thermomediterranean also highlighted with high inter-annual variability, where there exists a greater climate fluctuation and where small changes in precipitation produce large changes in the dynamics of primary production (Houérou et al., 1988; Cabello et al., 2012), as well as the area burned in 2005 near Lanjarón, where the fire eliminated the vegetation that has been regenerating since then. On the other hand, the most stable vegetation types interannual, i.e., those that changed the least during the period, were located in the meso-oromediterranean and crioromediterranean levels, specifically, the oak and borreguil vegetation types, ecosystems that are not subject to anthropic presence (e.g., low forest management and low presence of livestock).

The results of the inverse of the Jaccard coefficient to obtain the dissimilarity or functional changes between years in the composition of EFTs over the 2001-2018 period (Fig. 5b), showed an altitudinal pattern where the dissimilarity between EFTs was lower in the oro and cryoromediterranean levels, as well as in the mesomediterranean oak groves (functional stability already shown by other authors, i. e. Requena-Mullor et al, 2018). This pattern of dissimilarity increased towards lower levels, finding the highest values of dissimilarity (or greater change) in areas where changes in land use and management are major (Zamora et al., 2016), such as autochthonous pine forests on dolomites, coniferous repopulations and meso- and thermomediterranean holm oaks. In addition, the eastern end of the Sierra Nevada had an area with low dissimilarity values, that is, where there were not many changes over the years and when they occurred they were towards very similar EFTs.

3.5 Functional diversity at ecosystem level

Richness oscillated between 1 and 13 EFTs. Highest EFT richness was observed in the supra- and mesomediterranean, particularly in the southern face of the Sierra (Fig. 5c), where the number of vegetation series is also greater than in the rest of the bioclimatic floors (Valle et al., 2003). The presence EFTs hotspots mainly in the mid-mountain, and particularly in the southern face, could be related to two factors. On the one hand, many Mediterranean mountains show high values of beta diversity up to 1750-1800 m (Wilson and Schmida, 1984), when there is an important structural and compositional replacement of their vegetation. On the other hand, in the middle mountain and especially in its southern face, there is a very diverse mosaic of different types of natural vegetation mixed with different types of reforestation, traditional crops and uses (Camacho et al., 2002), which gives them the characteristic of multifunctional landscapes from the point of view of the provision of ecosystem services (García-Nieto et al., 2013; Mastrangelo et al., 2014; Cabello et al., 2019). Molero Mesa et al., (1996) and Fernández Calzado et al., (2012) indicated that Sierra Nevada species richness decreases with altitude, while endemic taxa increases (Blanca et al., 2019). Something similar can be observed in the functional diversity of ecosystems, since the maximum richness is found in areas of medium altitude. The areas with the lowest EFT richness were located in the oro and crioromediterranean levels, and in the eastern semi-arid thermomediterranean extreme, where the harsh soil and climatic conditions (Peinado et al., 2019) diminish floristic diversity although their endemicity increases (Fernández Calzado et al., 2012). The lowest values of EFT richness (richness 4-5) were found in the supramediterranean oak groves, (as in Dionisio et al., 2012; Requena-Mullor et al., 2018) maybe due to the internal homogeneity of their environmental conditions and their floristic composition (Pérez-Luque et al., 2015, Requena-Mullor et al., 2018).

EFT rarity was highest in the crioromediterranean level, overlapping the area with the highest concentration of endemisms (Cañadas et al., 2014; Peñas et al., 2019) (Fig. 5d). Crioromediterranean vegetation develops under a very particular ecological conditions that determine uncommon types of ecosystem functioning (rarity 0.6; Fig. 5d), such as, for example, in relatively mobile rocks and canchales located on steep slopes, where the percentage of rarity or compositional endemicity rises to 80% (Blanca and Algarra, 2011). EFT rarity was also high in the eastern end of the semi-arid thermomediterranean level, located in the biogeographic sector of Almeria (Peñas et al., 2019) with a high concentration of endemisms typical of the Desert of Tabernas (Mota et al., 2004). In the oromediterranean, EFT rarity decreased and reached its minimum, due to the great extension in the Sierra Nevada of this bioclimatic level, which made its functioning not appear as rare, and increasing again in the supra- and mesomediterranean (Fig. 5d). The most rare supra- and mesomediterranean vegetation types corresponded to coniferous and holm oak repopulations (rarity 0.6). The high rarity of coniferous repopulations may be due to disturbances or management interventions that give rise to unique functions in the different masses of conifers. On the other hand, the rarity in holm oaks may be due to their exclusive functioning, i.e. they have very specific associated EFTs (e.g., Cc1, Dc1). However, the rarity of the different vegetation types (between 0.45 and 0.64) was far from the maximum possible (1).

4 Data applications for research and conservation / Example of data usage

Ecological research based on spectral vegetation indices plays an important role in biodiversity conservation (Cabello et al., 2012; Pettorelli, 2016, 2018) and management (Pelkey et al., 2003; Cabello et al., 2016) and for the study of biodiversity and ecosystems responses to environmental changes (Alcaraz-Segura et al., 2017; Pérez-Luque et al. 2015). In fact, numerous studies have demonstrated the usefulness of satellite image time series to evaluate the functional changes in ecosystems at regional scale (Alcaraz-Segura et al., 2010) and at the protected area level (Alcaraz-Segura et al., 2009; Lourenço et al., 2018). Recently, the use of EFAs derived from spectral indices of vegetation in species distribution models, has made it possible to evaluate with great spatial and temporal precision the suitability of habitat for plant species (Arenas-Castro et al., 2018) and animals (Requena-Mullor et al., 2017; Regos et al., 2019) and may even anticipate expected changes in the distribution of plant species threatened as a consequence of climate change (Alcaraz-Segura et al., 2017). In addition, based on the EFAs, a monitoring programme of the Spanish National Parks Network has been designed to identify changes and anomalies in functioning, informing managers of the health and conservation status of ecosystems (Cabello et al., 2016).

Furthermore, EFTs have been used to characterize spatial and temporal heterogeneity of ecosystem functioning at local and regional scales (Fernández et al., 2010; Cabello et al., 2013); to describe biogeographical patterns (Alcaraz-Segura et al., 2006; Ivits et al., 2013); to evaluate the environmental and human controls of ecosystem functional diversity (Alcaraz-Segura et al., 2013); to identify priorities for Biodiversity Conservation (Cazorla et al., 2019); to assess the representativeness environmental networks (Villarreal et al., 2018); to assess the effects of land-use changes on ecosystem functioning (Oki et al., 2013); or to improve weather forecast models (Lee et al., 2013; Müller et al., 2014).

The data sets that we are providing give to the scientific community valuable information of the first characterization of the functional diversity at ecosystem level developed in the entire protected area. We provided a detailed characterization of the functional diversity at ecosystem level for Sierra Nevada, that could be useful to monitor the response of ecosystems to global change and management actions, to understand the ecosystem functioning and functional diversity across the environmental gradients at protected area scale, and to evaluate the role of ecosystems in providing ecosystem services (Cabello et al., 2019). Sierra Nevada is also a long-term ecological laboratory established 10 years ago (Zamora et al. 2016, 2017), that have available data on biodiversity, climate, ecosystem services, hydrology, land-use changes and management practices from Sierra Nevada. This will allow to explore the relationships between these other environmental data with the ecosystem functional data that we provide.

5 Data availability

The datasets described in this article are available in open-access sources. To broaden their use, first, we provide data in .tif format. Second, we have incorporated rendered versions of all layers as required by Google Earth Pro (called "filename..._forGoogleEarthVisualization.tif") for visualization. And third, we have also developed an ad-hoc visualization platform for all the layers. Datasets available for download in PANGAEA:

https://doi.pangaea.de/10.1594/PANGAEA.904575 (Cazorla et al. 2019) and for visualisation in http://obsnev.es/apps/efts_SN.html.

The MODIS database used in this work are maintained by NASA (satellite Terra, sensor MODIS, product MOD13Q1.006), and the geospatial datasets of Sierra Nevada Park are included in public database of the Andalusian regional government (REDIAM).

6 Conclusion

This dataset provides a characterization of ecosystem functioning and ecosystem functional diversity in Sierra Nevada Biosphere Reserve (SE Spain) through the analysis of time series of satellite images of spectral vegetation indices as surrogates of the carbon gains dynamics. First, three Ecosystem Functional Attributes (EFAs) describe the spatial and inter-annual variability in productivity, seasonality and phenology of vegetation photosynthetic activity. Second, the combination of these EFAs into a synthetic classification, i.e. Ecosystem Functional Types (EFTs), integrates in a single map the spatial heterogeneity of these descriptors of the seasonal dynamics of carbon gains. Finally, by using EFTs as biological entities, the spatial patterns of ecosystem functional diversity were assessed by means of EFT richness and EFT rarity, as well as the inter-annual variability in ecosystem functioning through EFT inter-annual variability and EFT inter-annual dissimilarity.

Ecosystem Functional Types approach improve the understanding of ecosystem processes through environmental gradients and provide both the scientific community with valuable information of the first characterization of the functional diversity at ecosystem level developed in the entire protected area.

Author contributions

DAS, JC, JP and BPC designed the study, and DAS, JC, JP coordinated it. BPC, AR and EG processed data and produced the associated data sets presented in this paper. BPC prepared the manuscript with contributions from all authors. BPC and EG prepared the final figures. AJPL design and made the application to visualize the data.

Competing interests. The authors declare that they have no conflict of interest.

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Figures

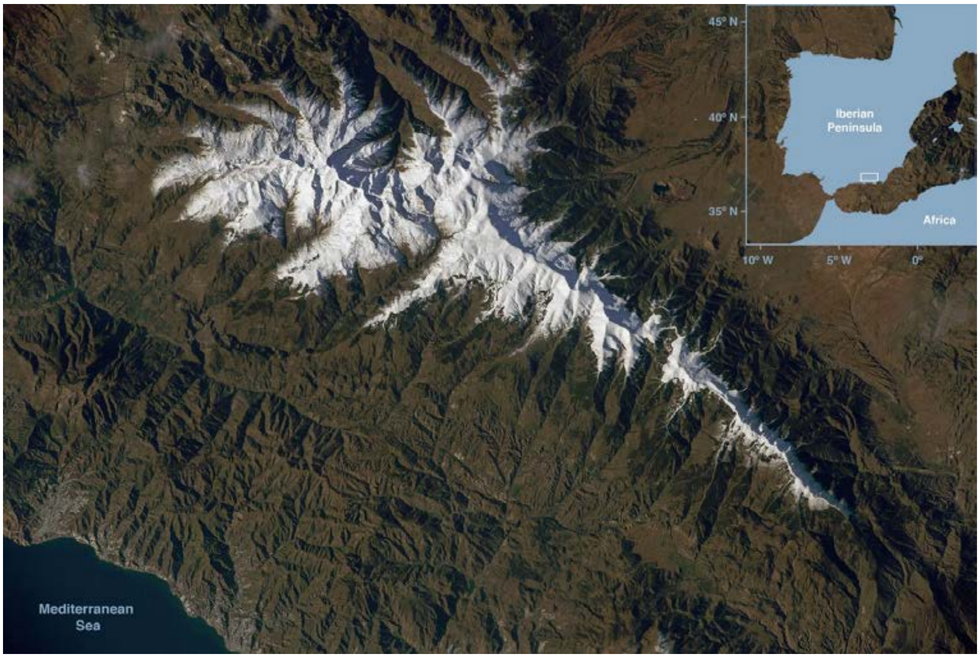

Figure 1. Location (top-right) and remote view of Sierra Nevada mountain region (image from the International Space Station took in December 2014; courtesy of "Earth Science and Remote Sensing Unit, NASA Johnson Space Center").

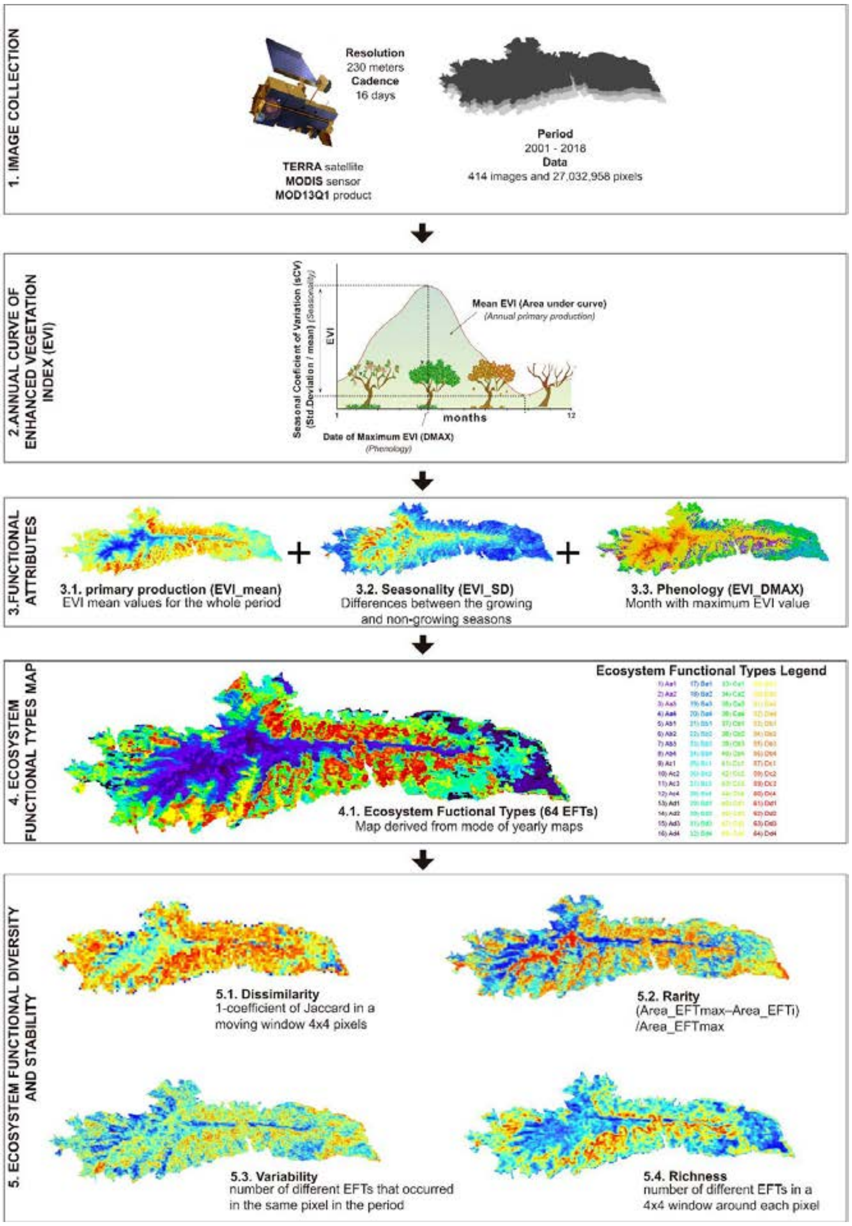

Figure 2. Workflow to characterize the ecosystem functioning and functional diversity of Sierra Nevada. MODIS (Moderate Resolution Imaging Spectroradiometer) sensor product MOD13Q1 was used aboard NASA's Terra satellite. This product contains images with 16-day temporal resolution (23 images per year) and ~232 m spatial resolution from the Enhanced Vegetation Index (EVI). The study period was from 2001 to 2018. Three functional attributes describing ecosystem functioning were calculated from the EVI seasonal curve for each year. The range of values for each attribute was divided into four intervals, resulting in a potential number of 64 TFEs (4x4x4=64). From EFTs, we derived fourth metric related to ecosystem functional diversity (EFT richness and rarity) and ecosystem functional stability (interannual variability and dissimilarity).

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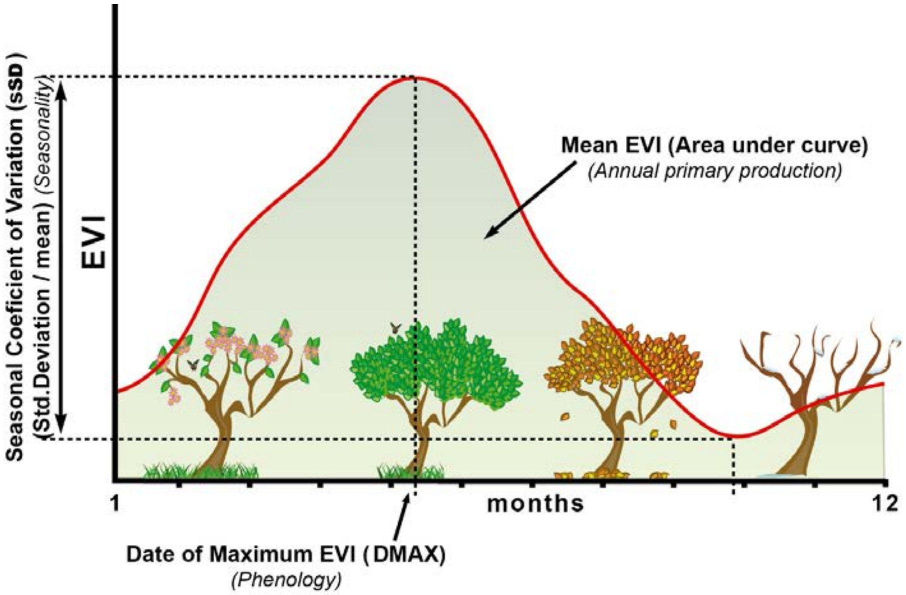

Figure 3: Seasonal dynamics of Enhanced Vegetation Index (EVI) and EVI derived metrics or Ecosystem Functional Attributes (EFAs). The axis "x" corresponds with months and the axis y with EVI values. EFAs were: the annual mean or the area under curve, an estimator of annual productivity (EVI_mean), the EVI seasonal coefficient of variation, i.e. the differences between the minimum and the maximum EVI values, a descriptor of seasonality (EVI_sSD), and the date of maximum EVI, an indicator of phenology (EVI_DMAX). We chose this three EVI metrics or EFAs due to they capture most of the variance of the EVI time series

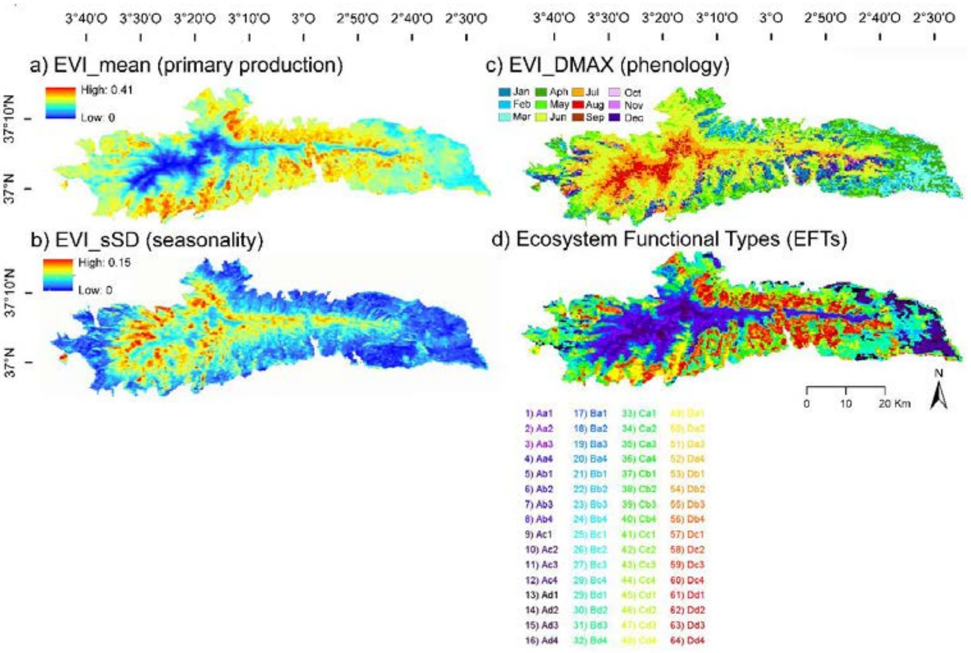

Figure 4. Ecosystem Functional Attributes (a-c) and Ecosystem Functional Types (d) describing the functioning of the canopy based on the Enhanced Vegetation Index (EVI), derived from MOD13Q1-TERRA (pixel ~232 m) for the period 2001-2018.

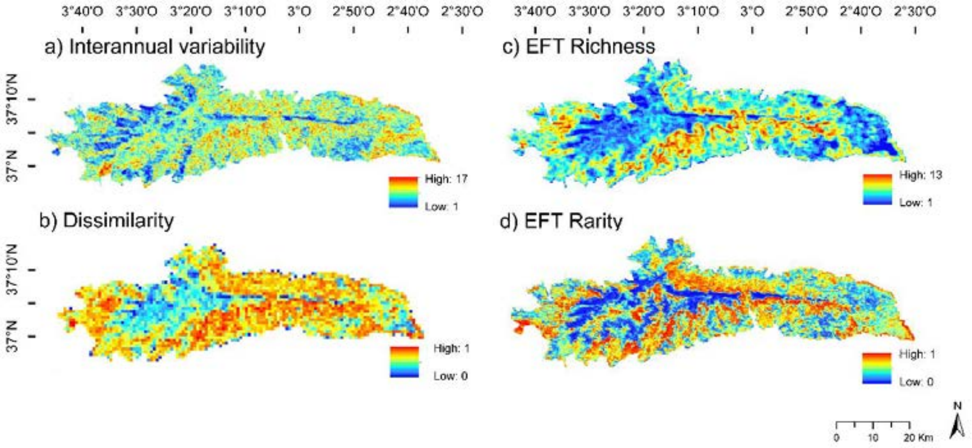

Figure 5. Functional diversity patterns based on the Enhanced Vegetation Index (EVI), derived from MOD13Q1-TERRA for the period 2001-2018. a) EFTs interannual variability for the period; b) EFTs interannual dissimilarity or 1 - Jaccard coefficient for the period; c) Spatial EFT richness patterns from a 4x4 pixel MODIS mobile window (∼1 km2); and d) Spatial EFT rarity patterns.

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Table 1. EFAs range used for identification of EFTs in Sierra Nevada. For EVI_DMAX, the four intervals agreed with the four seasons of the year. For EVI_mean and EVI_sSD, we extracted the first, second, and third quartiles for each year and then calculated the inter-annual mean of each quartile (means of the 18-year period).

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Ecosystem Functional Attribute	Character code	Digit code	Range
EVI Mean (Productivity)	A	100	0 - 0,137
	B	200	0,137 - 0,187
	C	300	0,187 – 0,241
	D	400	> 0,241
EVI SD (Seasonality)	a	10	> 0,062
	b	20	0,043 – 0,062
	c	30	0,030 – 0,043
	d	40	0 – 0,030
EVI MMAX (Phenology)	1	1	Spring
	2	2	Summer
	3	3	Autumn
	4	4	Winter

Table 2. Dataset description: Ecosystem Functional Attributes (EVI_Mean, EVI_sSD and EVI_MMAX provided yearly and summarized for the period); Ecosystem Functional Types (EFTs yearly and summarized for the period (mode, interannual variability and dissimilarity); Ecosystem Functional Diversity (EFT richness and EFT rarity, provided yearly and summarized for the period). Spatial resolution is ~232 in all cases except in the EFT dissimilarity, where it is ~298. YYYY refers to year and varies from 2001 to 2018.

Filename	Variable	Definition	Biological significance	Temporal resolution
EVI_Mean_YYYY_C006_MOD13Q1 _Pixel232	EVI_mean	Mean of the positive EVI values in a year	Primary production in a year	Yearly, one image per year *YYYY*
EVI_Mean_InterAnnualMean_2001-2018_C006_MOD13Q1_Pixel232	EVI_mean	Inter-annual mean of the annual EVI_mean values of the period	Average annual primary production of the period	One image for the 2001-2018 period
EVI_sSD_YYYY_C006_MOD13Q1_Pixel232	EVI_sSD	Intra-annual standard deviation of the positive EVI values within a year	Seasonality in vegetation greenness. Differences in carbon gains between the growing and non-growing seasons in a year	Yearly, one image per year *YYYY*
EVI_sSD_InterannualMean_2001-2018_C006_MOD13Q1__Pixel232	EVI_sSD	Inter-annual mean of the annual EVI_sSD values of a period	Seasonality. Average annual of the differences in carbon gains between the growing and non-growing seasons throughout the period	Average of the 2001-2018 period
EVI_MMAX_YYYY_C006_MOD13Q1_Pixel232	EVI_MMAX	Month with maximum EVI in a year	Phenology. Date of maximum greenness in a year	Yearly, one image per year YYYY
EVI_MMAX_InterannualMean_2001-2018_C006_MOD13Q1_Pixel232	EVI_MMAX	Inter-annual mean of the month with maximum EVI of the period	Phenology. Average annual of the month with maximum greenness throughout the period	Average of the 2001-2018 period
EFTs_YYYY_C006_MOD13Q1_Pixel232	EFTs	Range of EFA's values divided into four intervals 4 × 4 × 4 = 64 potential EFTs in a year	Patches of land surface that share similar dynamics in matter and energy exchanges in a year	Yearly, one image per year YYYY

EFTs_InterannualMode_2001-2018_C006_MOD13Q1_Pixel232	EFTs	Mode of the range of EFA's values divided into four intervals 4 × 4 × 4 = 64 potential EFTs of the period	Patches of land surface that share similar dynamics in matter and energy exchanges throughout the period	Mode of the 2001-2018 period
EFT_InterannualVariability_2001-2018_C006_MOD13Q1_Pixel232	EFT interannual variability	Nº of different EFTs that occurred in the same pixel in the period	Changes in an ecosystem functioning in a period	2001-2018 period
EFT_InterannualDissimilarity_2001-2018_C006_MOD13Q1_Pixel232	EFT interannual dissimilarity	1 - *Jaccard Index*	Changes in ecosystem functioning a landscape level in a period	2001-2018 period
EFT_Richness_YYYY_C006_MOD13Q1_Pixel232	EFT richness	Nº of different EFTs in a 4×4-pixel moving window around each pixel in a year	Different EFTs represented in the land-surface in a year	Yearly, one image per year YYYY
EFT_Richness_InterannualMean_2001-2018_C006_MOD13Q1_Pixel232	EFT richness	Nº of different EFTs in a 4×4-pixel moving window (924 x 924 m) around each pixel in a period	Different EFTs represented in the land surface throughout the period	Average of the 2001-2018 period
EFT_Rarity_YYYY_C006_MOD13Q1_Pixel232	EFT rarity	*Rarity of EFTi = (Area_EFTmax–Area_EFTi)/Area_EFTmax (in a year)*	EFT geographical extension	Yearly, one image per year YYYY
EFT_Rarity_InterannualMean_2001-2018_C006_MOD13Q1_Pixel232	EFT rarity	*Rarity of EFTi = (Area_EFTmax–Area_EFTi)/Area_EFTmax (in a period)*	EFT geographical extension	Average of the 2001-2018 period

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ECOSYSTEMS

Incorporating Ecosystem Functional Diversity into Geographic Conservation Priorities Using Remotely Sensed Ecosystem Functional Types

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ABSTRACT

Conservation biology must set geographic conservation priorities not only based on the compositional or structural but also on the functional dimensions of biodiversity. However, assessing functional diversity is challenging at the regional scale. We propose the use of satellite-derived Ecosystem Functional Types (EFTs), defined here as patches of land surface that share similar primary production dynamics, to incorporate such aspects of ecosystem functional diversity into the selection of protected areas. We applied the EFT approach to the Baja California Peninsula, Mexico, to characterize the regional heterogeneity of primary production dynamics in terms of EFTs; to set conservation priorities based on EFT richness and rarity; and to explore whether such EFT-based conservation priorities were consistent with and/or complementary to previous assessments focused on biodiversity composition and structure. EFTs were identified based on three ecosystem functional attributes derived from seasonal dynamics of the Enhanced Vegetation Index: the annual mean (proxy of primary production), the seasonal coefficient of variation (descriptor of seasonality), and the date of maximum (indicator of phenology). EFT-based priorities identified 26% of the peninsula as being of extreme or high priority and reinforced the value of the ecosystem functional diversity of areas already prioritized by traditional conservation assessments. In addition, our study revealed that biodiversity composition- and structure-based assessments had not identified the full range of important areas for EFT diversity and tended to better capture areas of high EFT rarity than those of high EFT richness. Our EFT-based assessment demonstrates how remotely sensed regional heterogeneity in ecosystem functions could reinforce and complement traditional conservation priority setting.

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Key words: Ecosystem functional heterogeneity; Richness; Rarity; Ecosystem functioning; Biodiversity congruence; Holistic conservation; Geographic priorities; Remote sensing.

HIGHLIGHTS

- Satellite-based Ecosystem Functional Types capture primary production heterogeneity.
- Ecosystem Functional Type richness and rarity as estimates of functional diversity.
- Functional conservation priorities reinforce and complement traditional approaches.

INTRODUCTION

Contemporary conservation planning faces the challenge of safeguarding the ecological processes required for the persistence of biodiversity over time (GBO4 2014) and for the supply of ecosystem services to people (Costanza 2012). To this end, protected areas must represent the most important areas for in situ global conservation effort (Watson and others 2014). Initially, opportunism and aesthetic values drove protected area creation (Palomo and others 2014; Baldi and others 2017). More recently, reserve selection under systematic conservation approaches (Margules and Pressey 2000) has mainly relied on compositional and structural dimensions of biodiversity (for example, Rodrigues and others 2004; Lamoreux and others 2006). However, despite important advances to the design of more comprehensive protected area networks, geographic conservation priorities have seldom considered heterogeneity in ecosystem functions (Callicott and others 1999; Mace 2014; Turner and Gardner 2015). The need for more representative global protected area networks (Visconti and others 2019) that account for the three dimensions of biodiversity (composition, structure, and function; Noss 1990) could greatly benefit from the explicit inclusion of ecosystem functions and processes that support biodiversity and ecosystem services (Meyer 1997; Cabello and others 2012; Pettorelli and others 2018; Lecina-Díaz and others 2019).

Functional diversity, ranging from gene expression to landscape processes, is an important biodiversity component to be assessed by conservation programs, as it links biological diversity with ecosystem functioning (Cadotte and others 2011; Díaz and others 2007; Chapin and others 2010; Asner and others 2017), services (Balvanera and others 2006; Duncan and others 2015), and resilience (Mouchet and others 2010). Functional diversity estimates have been made by grouping species into functional types based on structural (for example, shrubs, trees, and so on), phylogenetic (for example, *Coniferae*, *Poaceae*, and so on), or metabolic strategies (for example, C3, C4, and so on) related to meaningful biological processes (Lavorel and Garnier 2002, Lavorel and others 2007) or by using morphofunctional species traits (Malaterre and others 2019). However, the capacity for species functional types and traits to represent variations in ecosystem functional properties at regional scales remains a challenge (Wright and others 2006; Pasari and others 2013; Reichstein and others 2014; Asner and others 2017; Malaterre and others 2019).

Understanding the causes and consequences of spatial heterogeneity in ecosystem functions could help protect the species and communities that they support (Meyer 1997; Lovett and others 2005; Turner and Gardner 2015) and elucidate the links between ecosystem multifunctionality, ecosystem services (Manning and others 2018) and ecological stability (Oliver and others 2015). Environmental heterogeneity is a universal driver of taxonomic, phylogenetic, and functional diversity (Stein and others 2014; Stark and others 2017; Bergholz and others 2017). However, although conserving biophysical setting variability has been suggested to preserve biodiversity against rapid environmental change (for example, Lawler and others 2015; Littlefield and others 2019), variation in ecosystem functions has received less attention (Lovett and others 2005). Developing feasible approaches to understand and account for heterogeneity in ecosystem functions could complement traditional priority settings to achieve the holistic goal of protecting all biodiversity facets.

Satellite remote sensing can guide conservation actions based on the characterization of functional diversity not only at the species trait level (Jetz and others 2016) but also at the ecosystem level (Cabello and others 2012; Alcaraz-Segura and others 2013; Asner and others 2017; Gamon and others 2019). First, satellite-derived descriptors of ecosystem functions can be relevant as essential biodiversity variables (EBVs, Pettorelli and others 2016, 2018; Alcaraz-Segura and others 2017). For example, spectral indices are linked to key ecosystem functional descriptors such as primary production, evapotranspiration, surface temperature, and albedo (Paruelo and others 1997; Fernández and others 2010; Lee and others 2013) (Table 1—steps 1 and 2). Second, with these descriptors, it is possible to identify and map areas sharing similar dynamics of matter and energy exchange between biota and physical environments based on so-called satellite-derived Ecosystem Functional Types (EFTs) (Paruelo and others 2001; Alcaraz-Segura and others 2006, 2013).

As highlighted by Mucina (2019), EFTs could represent ''the first serious attempt to group ecosystems (at large scales) on the basis of shared functional behavior.'' EFTs group ecosystems on the basis of shared ecosystem functions without prior knowledge of vegetation types or canopy structure (Ivits and others 2013). As species can be grouped into plant functional types based on common morphofunctional traits to derive ecological properties at higher biological levels (that is, a bottom-up strategy), ecosystems can be grouped into EFTs to directly map processes and functions at larger scales (that is, a top-down approach) (Alcaraz-Segura and others 2006). EFTs follow a holistic approach (Naeem 1998, 2002; Loreau 2008) to measure the overall performance of an ecosystem (see the review in Jax 2010). EFTs capture heterogeneity in ecosystem functions (for example, primary production, evapotranspiration, or disturbance dynamics) and provide complementary information to other metrics such as those of vegetation structure and species composition to improve our understanding of the multidimensional nature of biodiversity (Noss 1990). EFTs have already been used to characterize the spatial heterogeneity of ecosystem functioning at the global (Ivits and others 2013), regional (Paruelo and others 2001; Alcaraz-Segura and others 2006; Lara and others 2017), and protected area scales (Fernández and others 2010; Cabello and others 2013).

In this study, we propose the use of Ecosystem Functional Types (EFTs), defined here as patches of land surface that share similar primary production dynamics (that is, productivity, seasonality, and phenology, Figure 1), to incorporate the spatiotemporal heterogeneity of a focal ecosystem function into geographic conservation priorities (conceptual workflow shown in Table 1). As a proof of concept, we applied the EFT approach to the Baja California Peninsula (Mexico): (1) to characterize the regional heterogeneity of primary production dynamics using EFTs; (2) to prioritize areas for conservation based on their EFT diversity (EFT richness and rarity); and (3) to explore whether such EFT-based priorities were congruent with and/or complementary to previous expert and systematic conservation-based assessments mainly focused on biodiversity composition and structure.

MATERIALS AND METHODS

Study Area

We chose the Baja California Peninsula as study area (Figure 2A) because it has high environmental heterogeneity, low human influence, a large proportion of protected land (40%) (Table S1) and because two geographic priority assessments have been conducted on the area mainly based on biodiversity composition and structure (Arriaga and others 2000; Koleff and others 2009). The peninsula covers a Mediterranean desert tropical climatic transition area positioned along a 1400 km latitudinal gradient from 35°N to 23°N (González-Abraham and others 2010). The Mediterranean Region (NW) is characterized by annual mean temperatures between 8 and 21°C, dry summers and mild wet winters with annual rainfall levels ranging from 100 to 200 mm at sea level to 500–700 mm in the highest mountains (3100 m) (Peinado and others 2011). The Desert Region extends from NE to S and is characterized by temperatures ranging from 20 to 25°C, and very low annual rainfall (100–200 mm) concentrated in sporadic events that shift from the winter in the N to the summer in the S (Hastings and Turner 1965). The Tropical Region at the southern tip is warm year round (15–24°C) and characterized by a nine-month dry season (November–July) followed by the tropical cyclone and storm rains with annual rainfall levels ranging from 200 mm at sea level to 700 mm in the highest mountains (at 2090 m) (Peinado and others 2011).

Identifying Ecosystem Functional Types

Regional heterogeneity in ecosystem functions was characterized by identifying Ecosystem Functional Types (EFTs) based on the seasonal dynamics of carbon gains following Alcaraz-Segura and others (2013). We focused on primary production because it is an integrative component of ecosystem functioning (Table 1—step 1; Virginia and Wall 2013), and its seasonal dynamics can be monitored through spectral vegetation indices. We used 2001–2017 Enhanced Vegetation Index (EVI) images from the MODIS sensor (MOD13Q1.005 product: 16-day maximum value composite images at ~ 230 m pixel size), as it offers a long time-series of a robust surrogate for primary production (Shi and others 2017) (Table 1—step 2). EFTs were derived from three meaningful metrics of the EVI seasonal curve also known as Ecosystem Functional Attributes (EFAs) (Figure 1; Table 1—step 3) (Alcaraz-Segura and others 2013; Pettorelli and others 2005): the annual mean (EVI mean; an estimate of

Table 1. Workflow for Setting Geographic Conservation Priorities Based on Ecosystem Functional Types

What is the goal of this step?	Why is it needed?	How did we complete it?
Step 1. To identify the targeted functional facets of biodiversity to be considered, for example, ecosystem primary production as an essential biodiversity variable	Conservation planning based on functional dimensions of biodiversity is needed (Noss 1990) but scarce (Cabello and others 2012). Some facets of ecosystem functioning are more essential to biodiversity and ecosystem services, offer more available information for inventorying and monitoring, and are more relevant to particular conservation goals than others	We chose primary production, as it is the most integrative indicator of ecosystem functioning (Virginia and Wall 2013)
Step 2. To choose surrogates for targeted functional facets, for example, remotely sensed vegetation indices	Direct measurements of biodiversity variables are usually costly. Satellite images of the Earth can be considered biological datasets (Geller and others 2017). Image pixels are sampling plots whose spectral information offers indirect, cost-effective estimates of matter and energy exchanges between the land surface and the atmosphere, which support ecosystem functions and services	We used the Enhanced Vegetation Index (EVI) to estimate photosynthetically active radiation absorbed by vegetation (based on the Monteith Model, 1972)
Step 3. To identify simple and biologically meaningful metrics of the ecosystem functioning surrogates, for example, descriptors of the amount and timing of carbon gain dynamics	The dynamics of ecosystem functioning are tracked through full time-series of essential variables. Synthesizing and capturing most of the variance of these time-series into a few easy to interpret metrics reduce complexity, ease interpretability, and promote the metrics standard use	We identified three metrics capturing most of the variance in the EVI seasonal dynamics (Ecosystem Functional Attributes, EFAs): annual production, seasonality, and phenology. We parameterized yearly seasonal dynamics of the EVI for three EFAs: the annual EVI mean, seasonal EVI coefficient of variation, and the date of the maximum EVI
Step 4. To group patches of the land surface with similar functional behaviors by classifying continuous metrics into discrete units, for example, Ecosystem Functional Types (EFTs)	Functional classifications synthesize continuous large-scale ecological gradients into discrete mapping units in relation to common ecosystem functions and processes. Discrete mapping units characterize ecosystem diversity at the regional scale and are needed for management and decision-making such as in systematic conservation planning	To integrate patterns of productivity, seasonality, and phenology into a single map, we divided the range of values of each EFA into four intervals (quartiles), creating a potential number of 64 EFTs (4 × 4 × 4)
Step 5. To select criteria for assessing ecosystem functional diversity at the regional scale, for example, EFT richness and rarity	Measurements of all biodiversity facets are not possible given the complex, multidimensional, and hierarchical nature of biodiversity (Noss 1990). Biodiversity indices such as richness and rarity are easy to interpret, relevant, and objective criteria frequently used in conservation assessments	We calculated EFT richness by counting the number of EFTs in a slicing window. EFT rarity was calculated as the relative extension of each EFT compared to the most abundant EFT

Table 1. continued

What is the goal of this step?	Why is it needed?	How did we complete it?
Step 6. To set geographic conservation priorities that capture areas of high ecosystem functional diversity, for example, areas of high EFT richness and rarity	Landscapes of high heterogeneity in ecosystem functions are prone to contain multiple ecosystem metabolic and evolutionary pathways. Multifunctional landscapes provide more diverse ecosystem services (Manning and others 2018), and functional diversity confers ecological stability (resistance and resilience)	We identified areas of the highest (extreme and high) conservation priority as those ones with high EFT richness and high EFT composition rarity
Step 7. To compare priorities based on ecosystem functional diversity with independent assessments, for example, complementarity and consistency between EFT-based priorities and previous assessments focused on composition and structure	Priorities based on ecosystem functioning can converge with independent priorities focused on biodiversity composition and structure so that they reinforce each other. Priorities can also be complementary, supporting decision-making by offering supplementary arguments for the holistic conservation of biodiversity	We integrated the three approaches into two synthetic maps: consistency and complementarity. To visualize agreement and disagreement between and among approaches, we used Venn diagrams

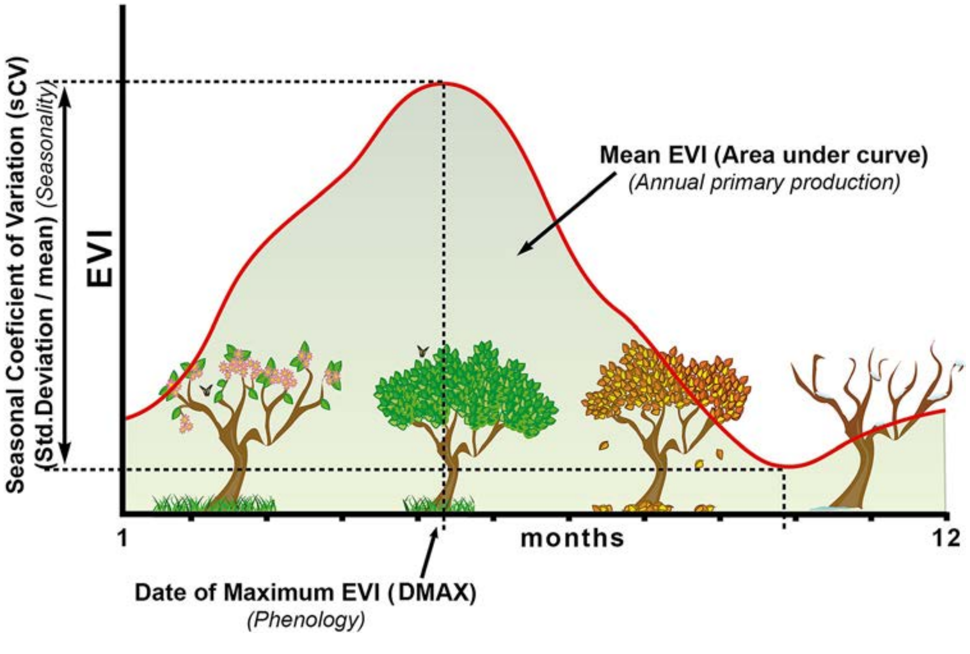

Figure 1. Seasonal dynamics of the Enhanced Vegetation Index (EVI) and of Ecosystem Functional Attributes (EFAs). The *X* axis corresponds to months, and the *Y* axis corresponds to EVI values. EFAs include: the annual EVI mean, an estimator of annual productivity (EVI mean); the seasonal EVI coefficient of variation (EVI sCV), that is, differences between minimum and maximum EVI values, as a descriptor of seasonality; and the date of the maximum EVI (EVI DMAX) as a phenological indicator of the growing season.

primary production), the EVI seasonal coefficient of variation (EVI sCV; a descriptor of seasonality), and the date of the maximum EVI (EVI DMAX; an indicator of phenology). The three metrics capture most of the variance in EVI seasonal dynamics into three meaningful metrics that facilitate ecological interpretation (Paruelo and others 2001; Alcaraz-Segura and others 2006).

To derive EFT classes from EFAs, the range of values of each EFA was divided into four intervals that were then combined, generating a potential number of (4 × 4 × 4) 64 EFTs (Figure S1D and S2). We used this classification method with fixed boundaries between classes to maximize the biological interpretability of EFTs and to apply the same classification rules to each year. This way, the classification can be used to track interannual changes in spatial heterogeneity of ecosystem functions (Littlefield and others 2019). As for DMAX since we wanted to maintain its ecological sense in our final classification (that is, the timing or phenology of the interception of radiation by vegetation), the four intervals agree with the four seasons of the year: spring (April–June), summer (July–September), autumn (October–December), and winter (January–March). For EVI_Mean and EVI_sCV, we extracted the first, second, and third quartiles (that is, the 25th, 50th, and 75th percentiles, respectively) for each year. Then, we calculated the interannual means of the quartiles (average of the 17-year period), which were used as thresholds among classes (Figure S1D). The four intervals created for each variable produced a relatively low number of potential classes (64) and maintained the EFAs spatial patterns (Figure S1 and S2).

To code EFTs, we used two letters and a number (Figure S1D): the majuscule indicates primary production (EVI mean) increasing from *A* to *D*; the minuscule represents seasonality (EVI sCV) decreasing from *a* to *d*; and numbers are a phenological indicator of the growing season (EVI DMAX): 1—spring, 2—summer, 3—autumn, and 4—winter. To summarize ecosystem function patterns of the 2001–2017 period, for each pixel we calculated the most common EFT (the mode) from the 17 annual EFT maps (Table 1—step 4). We excluded from analyses pixels with human influence according to the human footprint index ($HF > 0.5$) (González-Abraham and others 2015) and those including anthropogenic land uses in the 2017-updated land cover map (INEGI 2017).

Mapping Geographic Conservation Priorities from EFT Richness and Rarity

To identify geographic conservation priorities based on spatial heterogeneity in our focal ecosystem function (that is, primary production dynamics), we derived two diversity metrics from the EFT map: EFT richness and EFT rarity (Table 1—step 5). Both richness and rarity are indices that are easy to interpret, objective, and commonly used in ecology and conservation (Perrin and Waldren 2020). Richness measures different types of entities in a sample. EFT richness was calculated by counting the number of different EFTs within an 8 × 8 pixel sliding window across the study area, serving as an indicator of spatial heterogeneity in primary production dynamics. From the EFT richness of each year, we obtained the interannual average of EFT richness (Alcaraz-Segura and others 2013). We chose this window size because it includes 64 pixels, which is the potential maximum number of EFTs in our classification. The use of smaller window sizes resulted in many windows reaching the maximum number of classes while larger windows produced too coarse outputs (Appendix 5).

Rarity has also been a central focus in conservation (Soulé 1986). According to its abundance-based definition, rarity refers to how frequently an entity is found within an area (Kondratyeva and others 2019). The rarity of each EFT was used as an indicator of distinctive characteristics (that is, singularity) in primary production dynamics, which are likely to exhibit unique biodiversity features with conservation interest (Meyer 1997). EFT rarity was calculated as the extension of each EFT relative to the most abundant EFT throughout the peninsula (Eq. 1) (Cabello and others 2013).

$$\text{Rarity of EFT}_i = (\text{Area\_EFT}_{\max} - \text{Area\_EFT}_i)/\text{Area\_EFT}_{\max} \tag{1}$$

where $\text{Area\_EFT}_{\max}$ is the area occupied by the most abundant EFT throughout the study area and Area_EFT_i is the area of the *i* EFT evaluated with *i* ranging from 1 (*Aa1*) to 64 (*Dd4*). An average rarity map for all years was obtained, serving as our estimate of regional patterns of ecosystem functional singularity.

To determine EFT-based geographic conservation priorities, we searched for areas of high EFT richness and rarity (Table 1—step 6). First, we stretched (by spatial averaging) the spatial resolution of the EFT rarity map (230 m/pixel) to match the EFT richness map resolution (that is, an aggregated value for 8 × 8-pixel windows). Second, the range of values of both priority criteria variables was divided into four intervals using quartiles. Third, a decision matrix with 4 × 4 = 16 possible combinations of richness and rarity levels was produced. Finally, the 16 combinations of richness and rarity levels were grouped into four final priority categories (Figure 3A): extreme, high, moderate, and low for combinations that summed to 8, 7, 6, and 5, respectively. Combinations with lower sums were deemed not a priority.

Assessment of Spatial Congruence and Complementarity Between the Functional Approach and Previous Assessments

We explored the congruence and complementarity between the EFT-based geographic conservation priorities and two previous assessments based on compositional, structural, and threat features of biodiversity (Table 1—step 7). The ''systematic conservation'' study by Koleff and others (2009) used robust spatial analysis algorithms in a grid to identify four levels of ''Priority Sites to Conserve'' based on diversity of and threats to vertebrates, plants, and vegetation types. The ''expert-based'' study by Arriaga and others (2000) identified ''Terrestrial Priority Regions'' through qualitative expert workshops that combined multiple biological criteria (that is, species richness and endemicity, centers of diversification and domestication, vegetation types, and so on) with criteria for threats and opportunity (that is, habitat loss and fragmentation, unsustainable management, threatened species, and so on).

For the congruence analysis, we overlapped the three approaches at an 8 × 8-pixel window resolution into two synthetic maps: one that integrated congruence between the approaches (where priorities agreed) (Figure 3C) and another that revealed complementarity (where priorities did not agree) (Figure 3D). Congruence with other approaches was defined as the existence of a spatial overlap between EFT-based priorities and one or both of the other approaches. Complementarity with other approaches was defined as the existence of spatial discordance between EFT-based priorities and the previous priorities.

To visualize agreement and disagreement between approaches, we used Venn diagrams and the Sorensen-Dice similarity index (Figure 4). Additionally, to show how our EFT-based approach provides useful and orthogonal conservation priority information relative to traditional approaches, we explored the characteristics of congruent and complementary areas among approaches in terms of EFT richness and rarity (Figure 5) and of EFAs and EFT frequency (Appendix 4).

Sensitivity Analyses

To assess the effect of the sliding window size (Appendix 5), we calculated EFT richness, rarity, and priorities for double and triple window side lengths (that is, 8 × 8-, 16 × 16-, and 24 × 24-pixels). To assess the effect of the number of EFT classes considered (Appendix 6), we calculated EFT richness, rarity, and priorities by reducing the number of EFT classes by 86% (8 classes) and 58% (27 classes). Both effects were assessed three ways: from Pearson correlations between different output maps, from the spatial consistency among different output maps, and from the total percentage of the peninsula prioritized by each output map. Finally, we also assessed the effects of different thresholds of EFT richness and rarity on congruence and complementarity between approaches by means of the Sorensen-Dice similarity F-1 index (Appendix 7).

RESULTS

Regional Patterns of Focal Ecosystem Function by Means of EFTs

All 64 potential EFTs were identified in the Baja California Peninsula (Figure 2B) and exhibited contrasting distributions across the three main ecoregions of the peninsula (Figure 2A; González-Abraham and others 2010). In the Mediterranean Region to the northwest, EFTs were characterized by moderate–high primary production, moderate–low seasonality, and spring EVI maxima (Figures S1 and S2). The central and northeastern Desert Region was characterized by EFTs with low primary production, low to moderate seasonality, and winter EVI maxima in the center and in various seasons in the northeast. The southern part of the Desert Region was characterized by slightly higher level of primary production and seasonality and by summer–autumn EVI maxima. The Tropical Region in the south was characterized by high levels of primary production and seasonality and by summer EVI maxima (Figures S1 and S2).

Conservation Priorities Based on EFT Richness and Rarity

EFT richness and rarity (Figure 2C, D) varied across the peninsula following a combination of latitudinal, longitudinal, and topographical gradients (Figure 2A) and were found to be partially correlated. Areas of high EFT rarity ranged from low to high EFT richness while areas of high EFT richness always showed high levels of EFT rarity (Figure S3). EFT richness levels ranged from 1 to 26 EFTs per sliding window. Most windows of the highest EFT richness (12–26 EFTs) occurred north

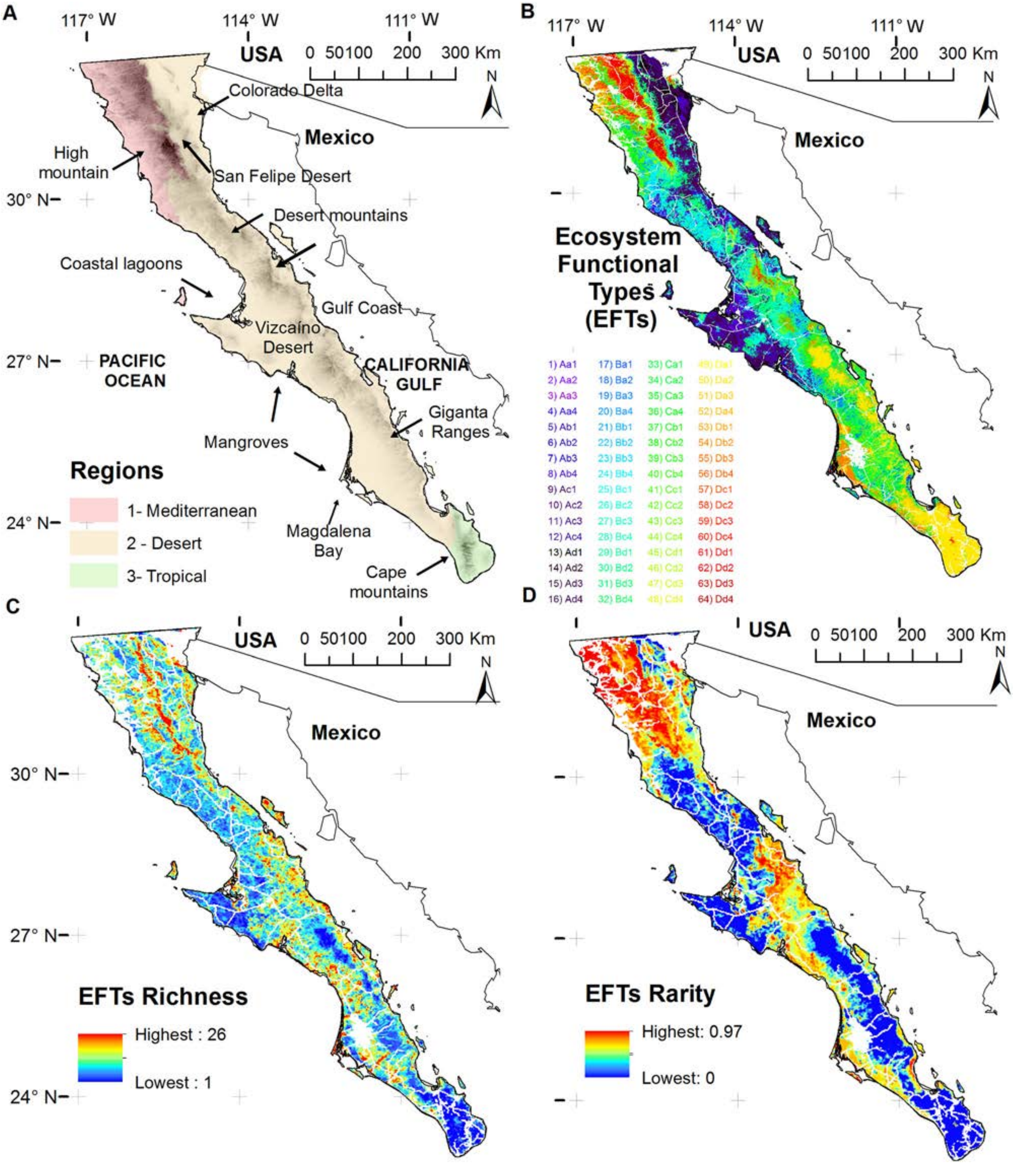

Figure 2. Spatial heterogeneity of ecosystem functioning in the Baja California Peninsula (Mexico). (A) Study area showing biogeographical regions of study area and areas mentioned in the text; (B) Ecosystem Functional Types (EFTs) of the 2001–2017 period (mode). EFT categories (lower left panel) are derived from three ecosystem functional attributes (Figure 1) related to primary productivity, seasonality, and the phenology of carbon gains (see maps in Appendix 2, Figure S1, S2); (C) EFT richness, quantity of EFTs occurring within 8 × 8-pixel sliding windows; and (D) EFT rarity, calculated as the relative rarity of each EFT throughout the peninsula. White areas represented anthropogenic pixels removed from the analysis.

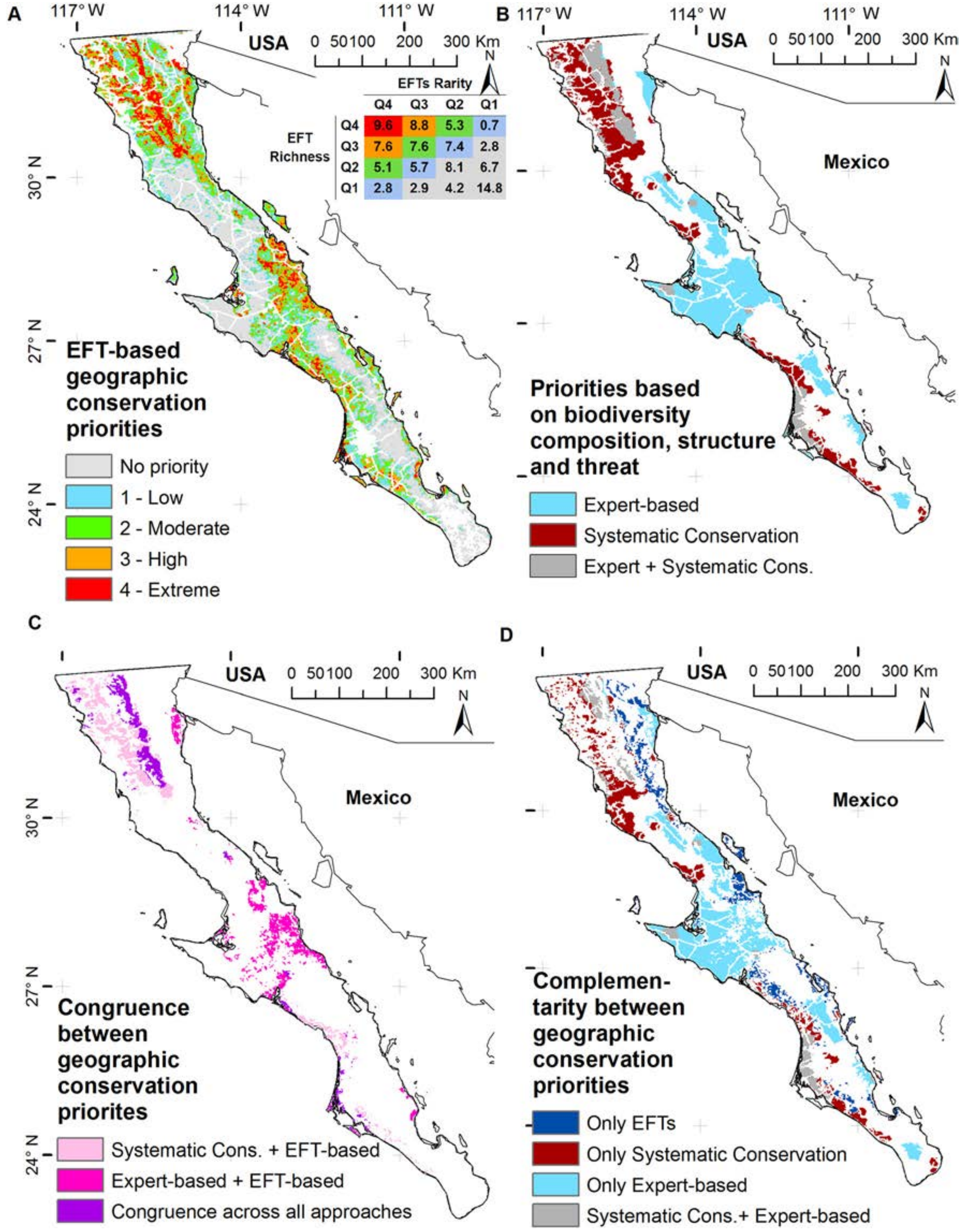

Figure 3. Comparison of geographic conservation priorities obtained from different biodiversity conservation approaches. (A) Priority areas based on ecosystem functional diversity by Ecosystem Functional Type (EFT) richness and rarity. The matrix shows the percentage of the study area of each quartile (Q) combination to obtain priority levels: extreme (red), high (orange), moderate (green), low (blue), and nonpriority (gray). (B) Priority areas mainly based on structural and compositional aspects of biodiversity obtained from assessments by expert-based (Arriaga and others 2000) and systematic conservation planning (Koleff and others 2009) approaches. (C) Congruence among geographic conservation priorities obtained by the three approaches (agreement between Figure 2A, B). (D) Complementarity among geographic conservation priorities obtained by the three approaches (disagreement between Figure 2A, B). White areas were pixels where none of the categories on the map were satisfied.

of 30° N in the Mediterranean Region, where climatic gradients translate into high heterogeneity in EFAs, especially along the mountain divide (Figure 2A). An intermittent fringe of high EFT richness was also found along mountains from the southern San Felipe Desert to the center of the Desert Region (from 31° N to 27° N) and continued southwards along the western desert piedmonts and around wetlands and mangroves (from 27° N to 24° N). Moderate EFT richness (7–12 EFTs) was observed in the Mediterranean mountains, San Felipe Desert, Colorado Delta, mid-mountains along the Gulf Coast (from 26° N to 30° N), and desert areas of the central peninsula. Extensive areas with the lowest EFT richness (1–3 EFTs) were found in plains and piedmonts of the Central and Vizcaíno Deserts, along the southern desert mountains (Giganta Ranges), and in the Tropical Region.

EFT rarity gradients were more pronounced than EFT richness gradients (Figure 2D). The highest rarity (0.8–0.9) occurred in the northwestern quarter of the peninsula above 30° N (Mediterranean Region), the central eastern desert transition, and around wetlands and mangroves. The Pacific northwestern Central and Vizcaíno Deserts (north from 27° N) showed low rarity (0.4–0.7). The lowest rarity (below 0.3) occurred along Giganta Ranges and in the Tropical Region (south of 28° N). This region, dominated by drought deciduous plant functional types, was mostly occupied by one extensive EFT with high productivity and seasonality and by summer EVI maxima (*Da2*).

The highest priority areas were found in heterogeneous areas across the Mediterranean Region, the northern and central eastern Desert Region, and around wetlands and mangroves (Figure 3A). Extreme priority areas occupied 9.6% of the peninsula surrounded by areas of high (16.4%), moderate (18%), and low priority (16.6%). The rest of the peninsula (39.5%) was classified as a nonpriority area for EFT diversity.

EFT-Based Priorities Versus Composition and Structure-Based Approaches

EFT-based conservation priorities partially aligned with other approaches (Figure 3A, B). Five percent of the peninsula was considered to be of the highest priority for all three approaches (Figure 4) and mainly the Mediterranean Region along mountain tops and the Desert Region in isolated areas of mountains, wetlands, and mangroves (Figure 3C). An additional 14% of the peninsula was prioritized by the EFT-based approach and by either the systematic conservation approach (7%) or expert-based approach (7%) (Figs. 3C and 4).

The EFT-based approach also revealed complementary areas not prioritized by the two previous approaches (7% of the peninsula; Figure 4). These areas were mainly located along mountainsides and piedmonts with riverine systems in the Desert Region: the San Felipe Desert to the northeast, the Gulf coastal desert in the center of the peninsula, and scattered areas along the southern desert (north and south of Magdalena Bay) (Figure 3C). Conversely, some areas (5% of the peninsula) were prioritized by the two previous approaches but not by the EFT-based approach. This occurred mainly in the Mediterranean mid-mountains and in coastal plains of the central and southwestern deserts (Figs. 3 and 4).

EFAs and EFTs slightly differed among areas prioritized by each approach (Figures S6 and S7).

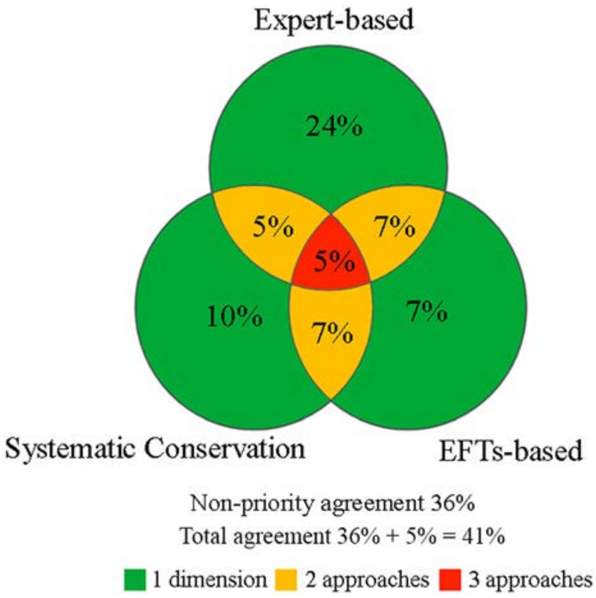

Figure 4. Agreement/disagreement between different ways to establish geographic conservation priorities for the Baja California Peninsula (Venn diagram). Numbers show the percentage of area in Baja California (not influenced by human activities) prioritized for conservation according to each approach. Our EFT-based approach focuses on two aspects of ecosystem functional diversity (Ecosystem Functional Type richness and rarity) while the two other approaches focus on biodiversity (mainly species) composition, structure, and threats based on expert knowledge (Arriaga and others 2000) and systematic conservation planning (Koleff and others 2009).

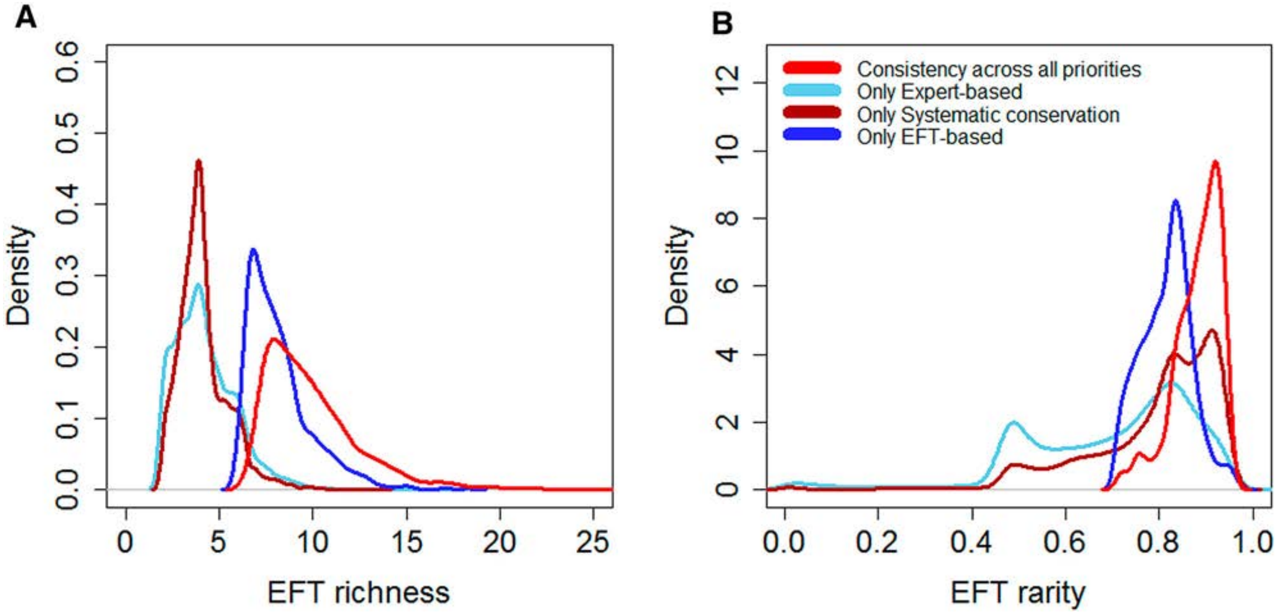

Figure 5. Congruence and complementarity among the three approaches to capture Ecosystem Functional Type (EFT) diversity. Density histograms show the frequency of EFT richness (A) and rarity (B) in areas consistently prioritized by the three approaches (''congruence across all priorities'') and in areas exclusively prioritized by one of the approaches but not by the others (''complementarity across priorities''). Our EFT-based approach focuses on two aspects of ecosystem functional diversity (EFT richness and rarity, i.e. heterogeneity and singularity) while the two other approaches focus on biodiversity composition, structure, and threats based on expert knowledge (Arriaga and others 2000) and systematic conservation planning (Koleff and others 2009).

Expert-based priorities (Arriaga and others 2000) were biased toward EFTs with less primary production than the other approaches. Systematic conservation priorities (Koleff and others 2009) were biased toward EFTs with higher primary production than the other approaches. In contrast, EFT-based priorities showed a more unbiased distribution of EFA values and EFT compositions than previous priorities (Figures S4 and S5).

EFT richness and EFT rarity were found to be much higher within areas consistently prioritized by the three approaches (6 and 26 EFTs per 8 × 8-pixel sliding window with most richness values from 8 to 13 EFTs and with EFT rarity ranging from 0.8 to 1) than within areas prioritized by only one of the three approaches (Figure 5). In contrast, areas prioritized only by traditional approaches were biased toward areas of low EFT richness (less than 6) but maintained moderate to high values of EFT rarity (greater than 0.5), especially in the systematic conservation approach. Indeed, despite systematic conservation planning and the expert-based approach performing very similarly in capturing EFT richness, systematic conservation planning tended to better represent areas of high EFT rarity (Figure S6).

Robustness Against Window Size, the Number of Classes, and Priority Thresholds

The sensitivity analyses revealed that our approach to setting priorities was robust against changes in window size and the number of EFT classes (Appendixes 5 and 6). Correlations of EFT richness and EFT rarity across the 8 × 8-pixel window and coarser window sizes ranged from 0.84 to 0.98 (Table S2) and those between the 64 EFT classes and fewer classes ranged from 0.67 to 0.94 (Table S3). Regional patterns of EFT richness, rarity, and priority were largely consistent across window sizes (85% agreement among final priority maps, Figures S7 and S8) and the number of EFT classes (70% agreement among final priority maps, Figures S9 and S10). EFT-based priorities always exhibited more similarities with the more robust systematic conservation approach than with the qualitative expert-based approach independent of thresholds of EFT richness and rarity used (Figure S11).

DISCUSSION

Contemporary conservation paradigms aim to maintain all biodiversity dimensions (Noss 1990), including the ecological processes and functions that sustain ecosystem services (Meyer 1997; Mace 2014; Prober and others 2019). In this study, we used satellite-derived EFTs (Paruelo and others 2001), defined here as functionally homogeneous land patches in terms of primary production dynamics, to describe spatial patterns of a focal ecosystem function. We used this focal ecosystem function because it is considered to be an integrative surrogate of stocks and fluxes of matter and energy derived from biological activity (Virginia and Wall 2013) and can be easily characterized by remote sensing. In essence, EFTs allowed us to map the spatial patterns of two indicators of ecosystem functional diversity at the regional scale, that is, EFT richness and EFT rarity. From these patterns, we set geographic conservation priorities based on an ecosystem function that helped us identify important areas for the three dimensions of biodiversity (structure, composition, and function) and highlight complementary areas for this ecosystem function not prioritized by traditional approaches.

Regional Patterns of Ecosystem Functional Heterogeneity

Maps of EFAs, EFTs, and EFT richness and rarity offer a characterization of ecosystem functional heterogeneity of the Baja California Peninsula. This heterogeneity results from a combination of latitudinal, longitudinal and topographic gradients. Such gradients determine strong differences across the peninsula in terms of seasonal dynamics of radiation, temperature, precipitation, evapotranspiration, and vegetation access to groundwater (Peinado and others 2011; Villarreal and others 2016) and have been identified as important for plant diversity (Garcillán and Ezcurra 2003) and endemism (Riemann and Exequiel 2007).

The highest levels of EFT richness were found where topography and spatiotemporal climate variability maximize ecosystem functional heterogeneity, mainly along mountains and piedmonts of the Mediterranean and Desert Regions. The Mediterranean climate imposes two limitations on plant growth: summer drought and winter cold temperatures (Hastings and Turner 1965). These limiting factors of plant growth are strongly heterogenized by steep altitudinal and orientation gradients (Peinado and others 2011). In the Desert Region, latitude, orientation, and access to groundwater impose varying constraints on plant growth. Such constraints include the latitudinal change in the proportion of winter and summer rains; the influence of coastal fog (Webb and Starr 2015); and the occurrence of shallow aquifers, gullies and dry arroyos embedded within a dryland matrix (León de la Luz and others 2015). Such high contrasts in ecosystem functions between the regional landscape matrix and its embedded ecosystems (that is, less water-limited EFTs within a matrix of dryland EFTs) enhance ecological processes of the lateral transfer of matter and energy (Turner and Gardner 2015). For these reasons, despite being a desert, such high heterogeneity in environmental factors renders the Desert Region very diverse in EFTs, a pattern also found for plant functional types and plant communities (Webb and Turner 2015).

The lowest levels of EFT richness were found in the tropics due to wetter and highly consistent tropical climatic conditions that homogenize vegetation (Peinado and others 2011). In the Tropical Region, strong precipitation seasonality (summer–autumn tropical rains followed by a nine-month drought) concentrates the growing season following the cyclone season (León de la Luz and others 2000). This high level of seasonality neutralizes even the altitudinal heterogeneity of the mountains, resulting in a spatial homogenization of primary production dynamics throughout the region. Such low EFT richness agrees with high similarities in vegetation composition along all topographic gradients, dominated by a few dry deciduous shrubs and trees (Rascón-Ayala and others 2018). Such an effect penetrates northwards along the Giganta Ranges with similar vegetation types to the Tropical Region (González-Abraham and others 2010). In addition, very low EFT richness extended northwards along Central and Vizcaíno desert plains and piedmonts. EFT richness in these piedmonts, where energy and water were decoupled (winter rains dominate the Pacific northwestern Central and Vizcaíno deserts, north from 27° N), was lower than in piedmonts where energy and water were coupled (summer rains dominate the southern half of the peninsula and San Felipe Desert to the northeast; Figure S1C).

EFT rarity was found to be associated with latitude, altitude, and the presence of contrasting ecological conditions. The highest EFT rarity of the Mediterranean Region and San Felipe Desert was found to be associated with winter precipitation, which creates a rare phenological pattern in the peninsula (Peinado and others 2011) together with the longitudinal gradient and topographical heterogeneity (for example, the only region with areas showing EVI maxima in all seasons). In the ecological transitional zone of the center of the peninsula (28–29° N), the combined influence of summer tropical storms from the south and autumn-to-spring fronts from the north (González-

Abraham and others 2010) also results in high levels of EFT rarity. This ecotone shows singular assemblages of species from tropical and nontropical biota (González-Abraham and others 2010) and a high diversity of distinctive lifeforms (Webb and Turner 2015). Finally, the surroundings of wetlands and mangroves in the Desert Region also showed rare EFTs, and both Mediterranean-type ecosystems and ecotones around wetlands are known to contain singular EFTs in other parts of the world (Cabello and others 2013). The lowest EFT rarity value was measured for the Tropical Region and southern desert mountains (Giganta Ranges), where heterogeneity and singularity are only introduced by the presence of endemism-rich evergreen pine forests at the highest altitudes (León de la Luz and Domínguez-Cadena 1989).

As found at the species level (Riemann and Exequiel 2007; Lamoreux and others 2006), EFT richness and rarity were only correlated with a degree but did not always coincide in the peninsula. Such spatial aggregation between areas with both high EFT richness and rarity highlights their importance for heterogeneity and singularity in primary production.

EFTs for Setting Geographic Conservation Priorities

Three main conclusions can be drawn from our congruence analysis of the three approaches. First, our results highlight the importance of congruence areas as probable aggregated hotspots for all dimensions and scales of biodiversity, including diversity in essential ecosystem functions such as primary production dynamics. Areas with congruence reinforce their ecological and conservation value for the expansion of protected area networks (Lamoreux and others 2006). For instance, consistently prioritized areas of the Mediterranean mountains have been historically identified as a conservation gap based on plant diversity and endemism (for example, Garcillán and Ezcurra 2003; Riemann and Ezcurra 2005). This congruence of the Mediterranean Region in North America suggests that some global biodiversity hotspots stand out not only as hotspots of endemism but also as heterogeneous and singular areas of ecosystem function, even if their identification does not consider ecosystem processes (Myers and others 2000). Second, our results indicate that traditional approaches may not identify all important areas of ecosystem functions (Meyer 1997) and may tend to better prioritize areas with rarity than those with richness in EFTs. Such an incidental focus of traditional approaches on rare EFTs could derive from the dominant role that endemicity, often related to singular conditions, plays in conservation planning (for example, Myers and others 2000). It is interesting that heterogeneity in ecosystem functions has played a minor role (Lovett and others 2005) despite habitat heterogeneity fostering species adaptation and persistence (Hanson and others 2020). Third, our results also suggest that species diversity, as in hotspots of the Tropical Region mountains (Riemann and Ezcurra 2005, 2007), is not necessarily associated with rare or spatially heterogeneous ecosystem functions. In such areas, not high environmental heterogeneity but a long history of evolutive isolation under stable conditions has mainly driven speciation (Sundaram and others 2019).

Conservation efforts must employ spatially explicit and parsimonious ways to incorporate heterogeneity in ecosystem functions (Turner and Chapin 2005) to develop theories and tools that complement traditional planning and management actions (Possingham and others 2005). Our study shows how satellite-derived EFAs and EFTs of a focal ecosystem function (here primary production) offer tangible and biologically meaningful qualities of ecosystem functional heterogeneity (here EFT richness and rarity) that can complement traditional geographic priority approaches. EFAs and EFTs of focal ecosystem functions have already been used to assess the comprehensiveness and representativeness of protected areas (Cabello and others 2012, 2013) and of environmental observatory networks (for example, LTER, NEON, Ameriflux, and Mexflux; Villarreal and others 2018). Previous studies have also shown how EFAs and EFTs could facilitate conservation by capturing heterogeneity in the amount and timing of key ecosystem functions to model species distributions (for example, Tuanmu and Jetz 2015; Alcaraz-Segura and others 2017; Arenas-Castro and others 2018) and abundances (Arenas-Castro and others 2019) as well as provisioning, regulating, and cultural ecosystem services (Vaz and others 2020).

Caveats and Avenues for Future Research

The use of the EFT concept in geographic conservation is still subject to challenges. First, our satellite-derived EFT map characterizes the spatial heterogeneity of primary production dynamics. However, EFTs can also be identified from other remote sensing indices (for example, Fernández and others 2010) to characterize the spatiotemporal heterogeneity of multiple ecosystem processes and functions at different scales to guide biodiversity and ecosystem services policies (Pettorelli and others 2018). Second, as the environmental observatory network expands, EFTs could be parameterized (for example, Müller and others 2014) and validated using ground measurements (for example, eddy covariance estimates of net ecosystem exchange; Villarreal and others 2018). Third, EFT richness and rarity maps illustrate diversity and spatiotemporal heterogeneity in the occurrence of ecosystem functions, but additional landscape indices could also elucidate the spatial arrangement (Fahrig and Nuttle 2005), connectivity, and lateral transfers (sensu Turner and Gardner 2015) of energy and matter fluxes at the landscape level. Fourth, our study does not assess interannual changes in EFAs, EFTs, or EFT richness and rarity, which could help reveal areas suffering from functional diversity homogenization, which is a planetary boundary that still needs evaluation (Steffen and others 2015). Fifth, the effects of spatial scale (grain and extent) on richness, rarity, and congruence with other biodiversity facets should be evaluated. Grain or cell size affects the magnitude, location, and spatial congruence of hotspots of species richness and endemicity (Rahbek 2005; Arponen and others 2012; McKerrow and others 2018; Daru and others 2020). The extent of the area under analysis may show that species-based priorities at one scale (for example, global) may or not overlap with those of other scales (for example, national or regional) (known as the parochialism effect; Pouzols and others 2014). EFT richness, rarity, and priorities depend on the extent considered but seem to be robust against sliding window sizes and the number of EFT classes defined (Appendixes 5 and 6). Future works should explore the effect of image pixel size (for example, with Sentinel-2 at 10 m/pixel), hierarchy in EFT classifications, and parochialism on the EFT-based approach. Finally, to test their effectiveness as ecosystem agnostic essential biodiversity variable candidates, EFT richness, rarity, and derived priorities should be compared to robust systematic conservation-based approaches that consider multiple facets of biodiversity, that is, compositional, structural, functional, and phylogenetic, in other ecoregions of the world (Pettorelli and others 2016).

In conclusion, the remotely sensed EFT approach can be used to incorporate the heterogeneity and singularity of ecosystem functions into geographic conservation priorities. Such an approach can support decision-making by offering supplementary arguments for the holistic conservation of biodiversity through the identification of key areas for multiple biodiversity facets (for example, the Mediterranean Region of Baja California) and of other areas important for ecosystem function that complement existing protected area networks (for example, mountainsides, and piedmonts with riverine systems in the Desert Region). Priority assessments based on essential variables related to ecosystem function cannot replace the use of very valuable systematic conservation approaches based on field records of species distributions to assess biodiversity status and change (Pereira and others 2013). However, our approach is useful to complement traditional priority setting, because is simple and based on only three satellite-derived meaningful descriptors of ecosystem functioning, facilitating computation and interpretation by managers and policymakers (Palumbo and others 2017). Future conceptual and empirical development and applications of EFTs should include other ecosystem functions, field validation, temporal changes in EFT diversity, and further metrics of heterogeneity across scales.

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EDICIONES COMPLUTENSE

Patterns of ecosystem functioning as tool for biological regionalization: the case of the mediterranean-desert-tropical transition of Baja California

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Abstract. Large-scale ecological variations across Earth have important consequences for biodiversity and therefore, for biological conservation. Despite the widespread use of ecological maps in conservation schemes, they have been based mainly on structural and compositional features, but scarcely on functional dimensions of life. The incorporation of functional variables complements and improves the descriptions of regionalizations and offers a new understanding of biodiversity patterns. The development of remote sensing measurement allows for the description of the functional patterns of ecosystems through Ecosystem Functional Types (EFTs), opening new opportunities to analyze the geography of life. In this article, our aim was to examine the relationships between ecological regionalization based on components and structure and patterns of ecosystem functioning. As proof of case, we chose the Baja California peninsula, whose singularity has generated a rich variety of ecological and biogeographical interpretations, mainly based on ecosystem components and structure. We hypothesize that patterns in ecosystem functioning reflect ecoregionalization based on composition and structure features. We identified Ecosystem Functional Types (EFTs), from three descriptors of the seasonal curves of MODIS Enhanced Vegetation Index (EVI) from 2001 to 2017. We characterized each ecoregion in terms of ecosystem functioning and we carried out a correspondence analysis between the EFTs classification and the ecoregions. At large scale, EFTs showed a pattern with three general regions from northwest to south, capturing the north-south transition of climatic regimes shown in the ecoregions map, from the northwestern Mediterranean area to the tropical southern zone, with a desert transition area between them.

Keywords: Conservation; Ecosystem Functional Types; Ecoregions; Functional biodiversity; Functional geography; Remote sensing.

Patrones de funcionamiento ecosistémico como instrumento de regionalización biológica: el caso de la transición mediterráneo-desértico-tropical de Baja California

Resumen. Las variaciones ecológicas a gran escala en la Tierra tienen importantes consecuencias para la biodiversidad y por tanto, para la conservación biológica. A pesar del uso generalizado de los mapas ecológicos en los planes de conservación, éstos se han basado principalmente en características estructurales y de composicionales, pero apenas en las dimensiones funcionales de la vida. La incorporación de variables funcionales complementa y mejora las descripciones de las regionalizaciones y ofrece una nueva comprensión de los patrones de la diversidad biológica. El desarrollo de técnicas de teledetección permite la descripción de los patrones del funcionamiento ecosistémico a través del concepto de Tipos Funcionales de Ecosistemas (TFEs), abriendo nuevas oportunidades para analizar la geografía de la vida. En este artículo, nuestro objetivo fue examinar las relaciones entre la regionalización ecológica basada composición y estructura y los patrones de funcionamiento ecosistémico. Para ello, elegimos la Península de Baja California, cuya singularidad ha generado una rica variedad de interpretaciones ecológicas y biogeográficas, principalmente basadas en la composición y la estructura del ecosistema. Nuestra hipótesis guía, fue que de que los patrones de funcionamiento del ecosistema reflejan la ecorregionalización basada en las características composicionales y estructurales de la biodiversidad. Identificamos los Tipos Funcionales de Ecosistemas (TFEs), a partir de tres descriptores de las curvas estacionales del Índice de Vegetación Mejorado (EVI – Enhanced Vegetation Index) de MODIS de 2001 a 2017. Caracterizamos cada ecorregión en términos de funcionamiento ecosistémico y realizamos un análisis de correspondencia segmentado (DCA – Detrended Correspondence Analysis) entre la clasificación de TFEs y las ecorregiones. A gran escala, los TFEs mostraron un patrón con tres regiones generales desde el noroeste hasta el sur, representando la transición norte-sur de los regímenes climáticos mostrados en el mapa de las ecorregiones, desde la zona Mediterránea noroccidental a la zona Tropical meridional, con una zona de transición desértica entre ellas. Sin embargo, se identificaron diferencias entre las ecorregiones y la caracterización funcional, en aquellas ecorregiones identificadas como áreas de discrepancia entre autores. En particular, algunas ecorregiones consideradas Mediterráneas, mostraron un carácter desértico en su funcionamiento, y otras consideradas como Desérticas, resultaron Tropicales desde la perspectiva del funcionamiento. Los TFEs obtenidos mediante teledetección a escala regional, constituyen la base de una regionalización más integral de los patrones geográficos de la vida y por tanto, una mejora para futuros propósitos de conservación.

Palabras clave: Biodiversidad Funcional; Conservación; Ecorregiones; Geografía Funcional; Teledetección; Tipos Funcionales de Ecosistemas.

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Introduction

Understanding how geographical patterns of life and which factors are driving them have been for a long time one of the main goals of naturalists, and the foundational roots of biogeography as science (Lomolino *et al.,* 2015, 2017). Its interest resides in that large-scale variation in vegetation across Earth has important consequences for biodiversity and resources availability to support biological conservation and human wellbeing (Olson *et al.,* 2001). At present, the Earth system has been characterized by large ecological units whose boundaries can be defined on the basis of past or current physical and biological forces (Whittaker, 1970; Box 1981; Dinerstein *et al.,* 1995; Olson *et al.,* 2001; Bailey, 2009; Kreft & Jetz, 2010). These ecological units or ecoregions can be identified at various spatial scales and/or hierarchical levels, which determines our perception of the system (Bailey, 2004). Ecoregions have been widely used for guiding management and conservation decision making, since it allows us to organize our understanding of how major terrestrial ecosystems work and to establish programs to monitor changes (Higgins *et al.,* 2016). Despite the widespread use, these units represent human constructs derived from a boundary-setting exercise in which there is not always a consensus on how to define it and map their extent (Donoghue & Edwards, 2014; Moncrieff *et al.,* 2016), which makes ecological maps hypotheses that can be tested and improved (Rowe & Sheard, 1981; Smith *et al.,* 2018).

Since the pioneering work of Alexander von Humboldt, who departed from habitual taxonomic criteria and described patterns of vegetation based on physiognomic attributes and coincident climate, scientists have been analyzing geographical patterns of ecosystems based mainly on their structural and compositional features, but scarcely on the functional dimension of life. The incorporation of functional variables complements and improves the descriptions of regionalizations based on structural and compositional features (Noss, 1990) and offers a better understanding of spatial and temporal patterns of diversity (Garnier *et al.,* 2016). In particular, understanding changes in ecosystem functioning across biogeographic gradients can benefit from a greater ability to represent and define biotic communities (Reichstein *et al.,* 2014). This leads the functional classifications to a useful framework to understand these large-scale ecological changes in relation to ecosystem function and processes. In fact, a growing number of studies have identified the need to integrate new concepts and methodologies to connect classical regionalizations with ecosystem functioning (Violle *et al.,* 2014).

Currently, ecologists are better equipped than ever before for exploring functional ecosystem dynamics at multiple temporal and spatial scales. Increasing large-datasets derived from remote sensing and associated development of analytic tools have opened new opportunities to explore the geography of life. A promising analytic approach in this sense is the Ecosystem Functional Types proposed by Paruelo *et al., (*2001) and Alcaraz-Segura *et al.*, (2006), which has been considered as the more serious attempt to characterize ecological regions from a functional perspective (Mucina, 2019). EFTs are groups or patches of land surface that share similar dynamics of matter and energy exchanges between the biota and the physical environment (Paruelo *et al.,* 2001; Alcaraz-Segura *et al.,* 2006). The EFT approach uses time series of spectral Vegetation Indices (VI), such as Normalized Vegetation Index (NDVI) or Enhanced Vegetation Index (EVI), to capture the spatial expression of the carbon gain dynamics, considered the most integrative indicator of ecosystem functioning (McNaughton *et al.,* 1989; Virginia and Wall 2001). Thus, EFTs are identified by three meaningful metrics derived from the annual dynamics of EVI that reflect primary productivity, seasonality, and phenology of canopy (Paruelo *et al.,* 2001). EFTs have been used to characterize the spatial heterogeneity of ecosystem functions at different scales, e.g., global (Ivits *et al.,* 2013), regional (Alcaraz-Segura *et al.,* 2006) or local (Fernández *et al.,* 2010), but the formal comparison with regionalizations based on other dimensions of biodiversity (i.e. ecoregions) has not yet been evaluated.

In this study, our aim was to examine the relationships between biological regionalization based on the biota components and structure (species distribution, endemisms, vegetation types) and patterns of ecosystem functioning revealed by the geographical distribution of EFTs. As proof of case, we chose the Baja California peninsula, a 1300 km-long fringe of land which contains the transition from the Californian Mediterranean region to the Tropic. This ecologically heterogeneous peninsula has captured the attention of naturalists for a long time (Garcillán *et al.,* 2010) and has an extraordinary conservation interest (Arriaga *et al.,* 2000; Koleff *et al.,* 2009). This extensive history of natural exploration has generated a rich variety of ecological and biogeographical interpretations, mainly based on ecosystem components and structure, synthesized by González-Abraham *et al.*, (2010). We hypothesize that patterns in ecosystem functioning reflect ecoregionalization based on composition and structure features, however, the spatial coincidence between these dimensions of biodiversity decreases when we compare their patterns at more detailed spatial scales, i.e. downwards in the hierarchy of ecological units, from major regions to ecoregions (sub-regions).

Material and Methods

Study area and ecoregionalization

We chose the peninsula of Baja California as study area (Figure 1) because it contains high ecological heterogeneity governed by processes at different spatial and temporal scales, from the north-south transition of mediterranean-desert-tropics to the contrasting climatic influence of its two coastal seas (Garcillán *et al.,* 2010). Besides that, its ecological geography has been studied for more than two centuries (Garcillán *et al.,* 2010) and recently synthesized in an ecoregional map (González-Abraham *et al.,* 2010). Ecoregions have been identified at hierarchical levels: level I contains the three major regions, Mediterranean, Desert, and Tropical, and level II contains fourteen ecoregions (sub-regions) within the above major regions (Figure 1).

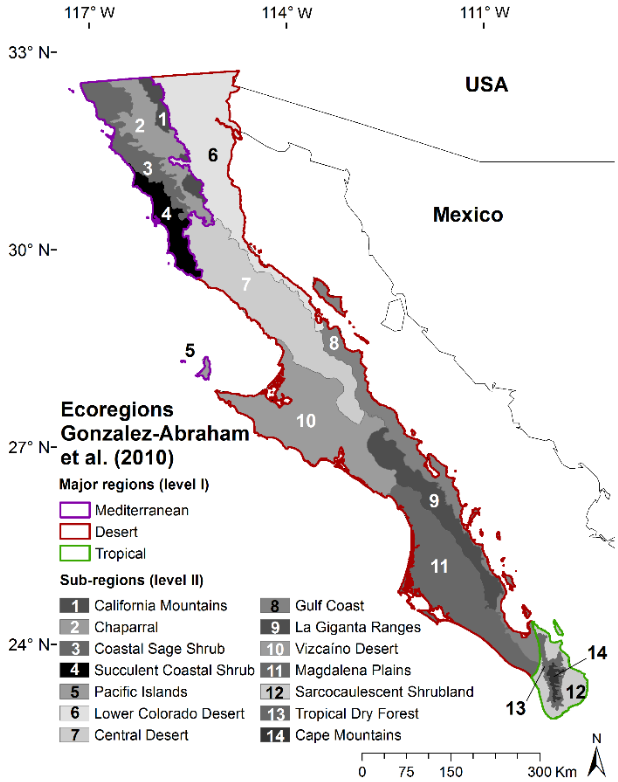

Figure 1. Study area and ecoregions by González-Abraham *et al.* (2010).

Regarding climatology (Figure 2), the Mediterranean region, in the northwest, is characterized by annual mean temperatures between 8-21ºC, summer drought, and winter precipitation, with annual rainfall ranging from 100-200 mm at sea level to 500-700 mm in the highest mountains (3100 m) (Hastings & Turner, 1965). The extensive Desert region, largely distributed from northeast to south, has temperatures ranging from 20-25ºC, and very low annual rainfall (44-200 mm), concentrated in sporadic events that shift from winter in the north to summer in the south (Hastings & Turner 1965; Peinado *et al.,* 2011). The Tropical region, in the southern tip, is warm year-round (15-24ºC) and is characterized by late summer-early autumn precipitation, mainly derived from tropical cyclones and storms (annual rainfall from 200 mm at sea level to 800 mm in the highest mountains -2090 m-, and a long dry season (Farfán & Fogel, 2007).

Functional geography of ecosystems

We characterized the geography of a key ecosystem process, terrestrial primary production dynamics, using the Ecosystem Functional Types (EFTs) approach (Paruelo *et al.,* 2001; Alcaraz-Segura *et al.,* 2006, 2013). For this, we used the 2001-2017 time-series of satellite images of the Enhanced Vegetation Index (EVI) obtained by the MODIS sensor, MOD13Q1.006 product (16-day maximum value composite images at 230 m pixel size). EFTs were identified from three descriptors of functional attributes from the seasonal curves of EVI, also known as Ecosystem Functional Attributes (EFAs): annual mean (EVI_surrogate of primary production), seasonal coefficient of variation (EVI_sCV, a descriptor of seasonality) and the peak of maximum EVI (EVI_DMAX, an indicator of phenology). Following Alcaraz-Segura *et al.*, (2013), each of the three descriptors was divided into four intervals, whose potential combinations result in a total of 64 different EFTs. In the case of phenology, we chose as intervals the four seasons, and for primary production and seasonality descriptors, we used their respective quartiles. Each EFT was named using the combination of two letters and a number: A-D for each class of primary production, increasing value in alphabetic order; a-d for seasonality, decreasing value in alphabetic order; and 1-4 for phenology, starting with 1 for spring. Therefore, we obtained 17 annual maps of EFTs for the period 2001-2017. We elaborated the final map of EFTs selecting for each pixel the median of the seventeen annual values. Previously, we excluded the areas under strong anthropic transformations according to González-Abraham *et al.,* (2015) (human footprint index>0.5), and with anthropogenic categories in the last land-use map for the year 2017 of the Peninsula (INEGI, 2017).

Structural and compositional vs. functional geography of ecosystems

To examine the relationship between the characterization of the ecosystem functioning geographical patterns and ecological regionalizations based on structural and compositional features of vegetation, we used the ecoregions map by González-Abraham *et al.*, (2010). To do so, we first, characterized each ecoregion, at all levels (I and II), in terms of ecosystem functioning, showing the frequency of each EFT in each ecoregion. And second, we carried out a Detrended Correspondence Analysis (DCA) (Hill & Gauch, 1980) between EFTs and ecoregions (Alcaraz-Segura *et al.,* 2006; Fernández *et al.,* 2010). This analysis represents in a multidimensional space reduced the spatial relationship between the classes of both maps. DCA prevented that sample units from being grouped together at the extremes of the gradient, since it scales the axes and equalizes the variance. Similarly, we prevented the problem that rare functions influence the outcome, since it reduces their weight.

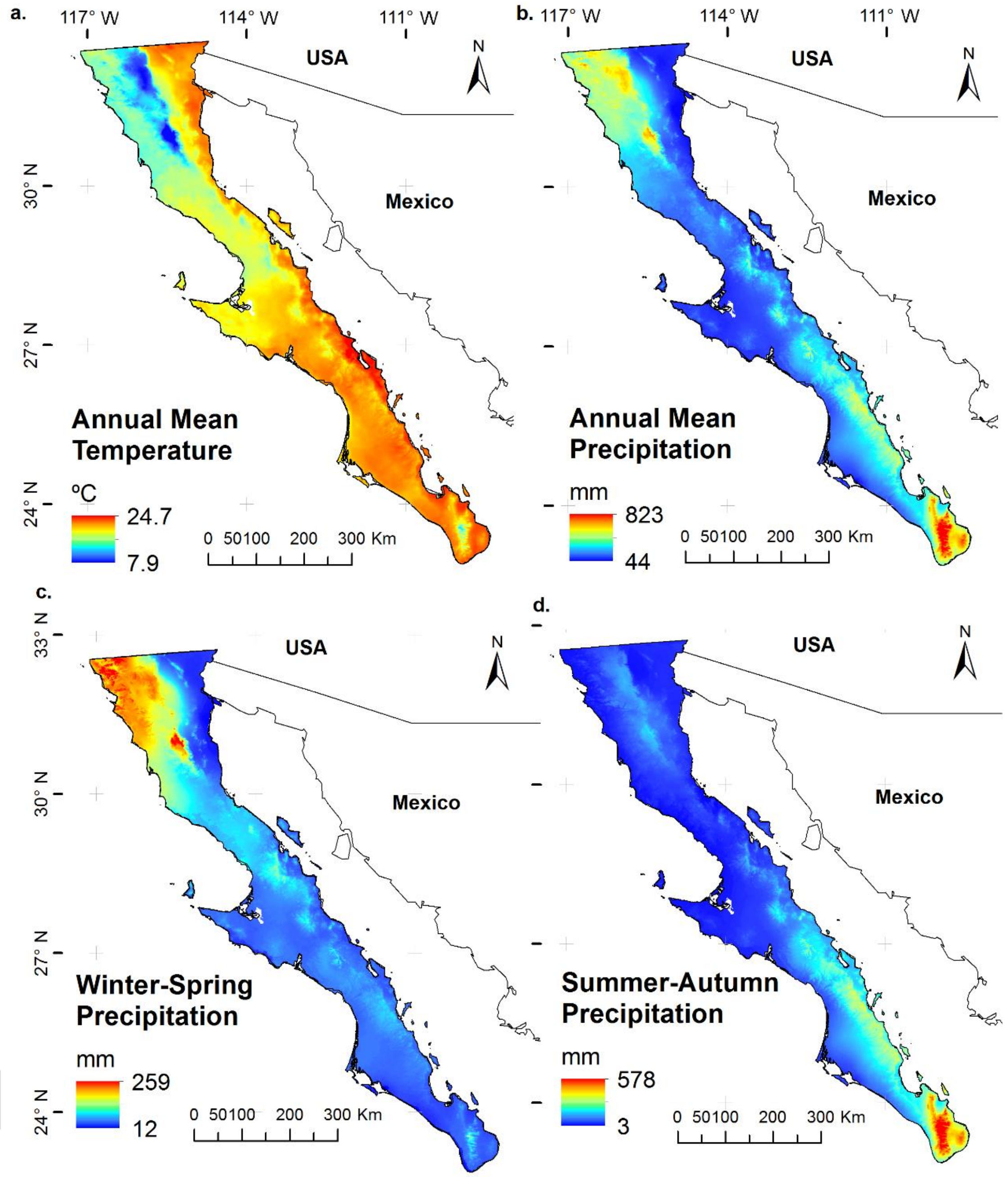

Figure 2. Climate description of the study area. a) Annual Mean Temperature in ºC; b) Annual Mean Precipitation in millimeters (mm); c) Winter-Spring Precipitation (mm); and d) Summer-autumn Precipitation. Data from WorldClim version 2.1 (Fick & Hijmans, 2017).

Results

Functional characterization across ecoregions

EFTs map provided the ecosystem functional characterization of the Baja California Peninsula in terms of three key attributes (productivity, seasonality, and phenology) related to the primary production dynamics of vegetation. All potential combinations (64 types) were present in the peninsula, although some of them were dominants (Figure 3). Ten EFTs (16% of the total) covered approximately 50% of the total study area and twenty-five (39% of the total EFTs) 75% of the peninsula. From these results it was possible to divide the dominant ecosystem functioning into two groups: EFTs with high productivity, high seasonality and phenology in autumn (e.g. Da3, Ca3, Cb3); and EFTs with low productivity, low seasonality and phenology in winter and autumn (e.g. Ac4, Ad3, Ad4, Ba3, Bb3, Bc3...).

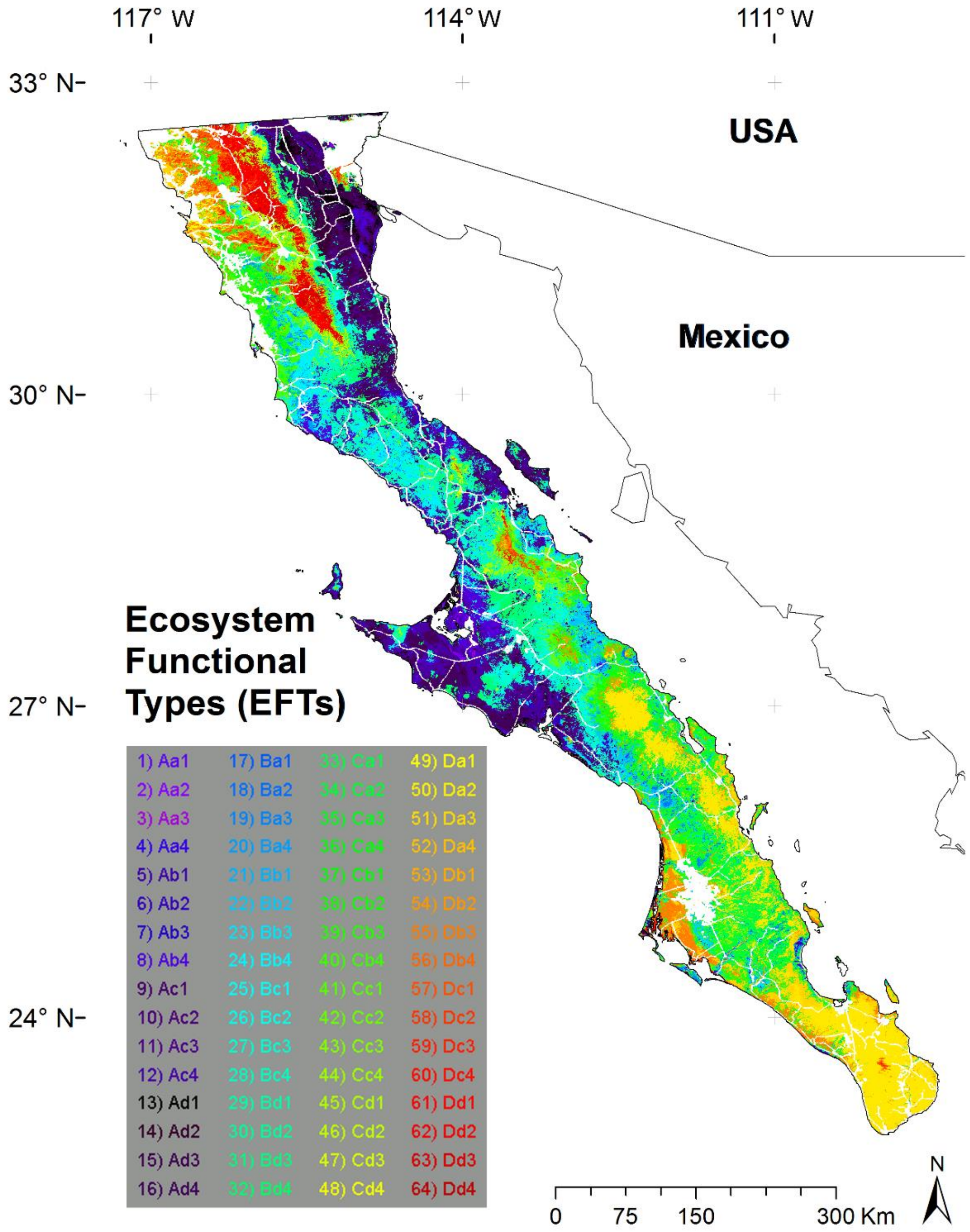

Figure 3. Ecosystem Functional Types based on EVI-MODIS dynamics for 2001-2017 period (230x230 m pixel). EFT categories were indicated in the legend. Human transformed areas appeared in white.

At large scale, EFTs geographical pattern captured roughly the north-south climatic transition in the peninsula as shown by the ecoregions map (see EFTs map (Figure 3)) and Correspondence Analysis (Figure 5). In this sense, we could clearly identify the northwestern Mediterranean area, the tropical southern zone, and the desert transition areas between them. Despite this climate-based pattern, these three functional regions presented differences with respect to the boundaries of major ecoregions distribution. The geographical limits between the two functional regions in the north (northwest and northeast) were very similar to those proposed in the ecoregions map for the Mediterranean and Desert structural and compositional based regions (Gonzalez-Abraham *et al.,* 2010).

In contrast, the geographical limits in ecosystem functioning of the southern half of the peninsula, between Desert and Tropical regions (EFTs map; Figure 3) showed significant differences with the limits established in the ecoregions map. Spatial references in this section to the regions are based upon the ecoregions map by González-Abraham *et al.,* (2010).

The Mediterranean region had the highest EFTs heterogeneity in the peninsula (Figure 4a), showing an altitudinal and latitudinal pattern of productivity. Mountainous ecoregions were dominated by high productivity EFTs (D) (e.g. California Mountains), and as altitude and latitude decreased, a greater EFTs heterogeneity increased since more intermediate

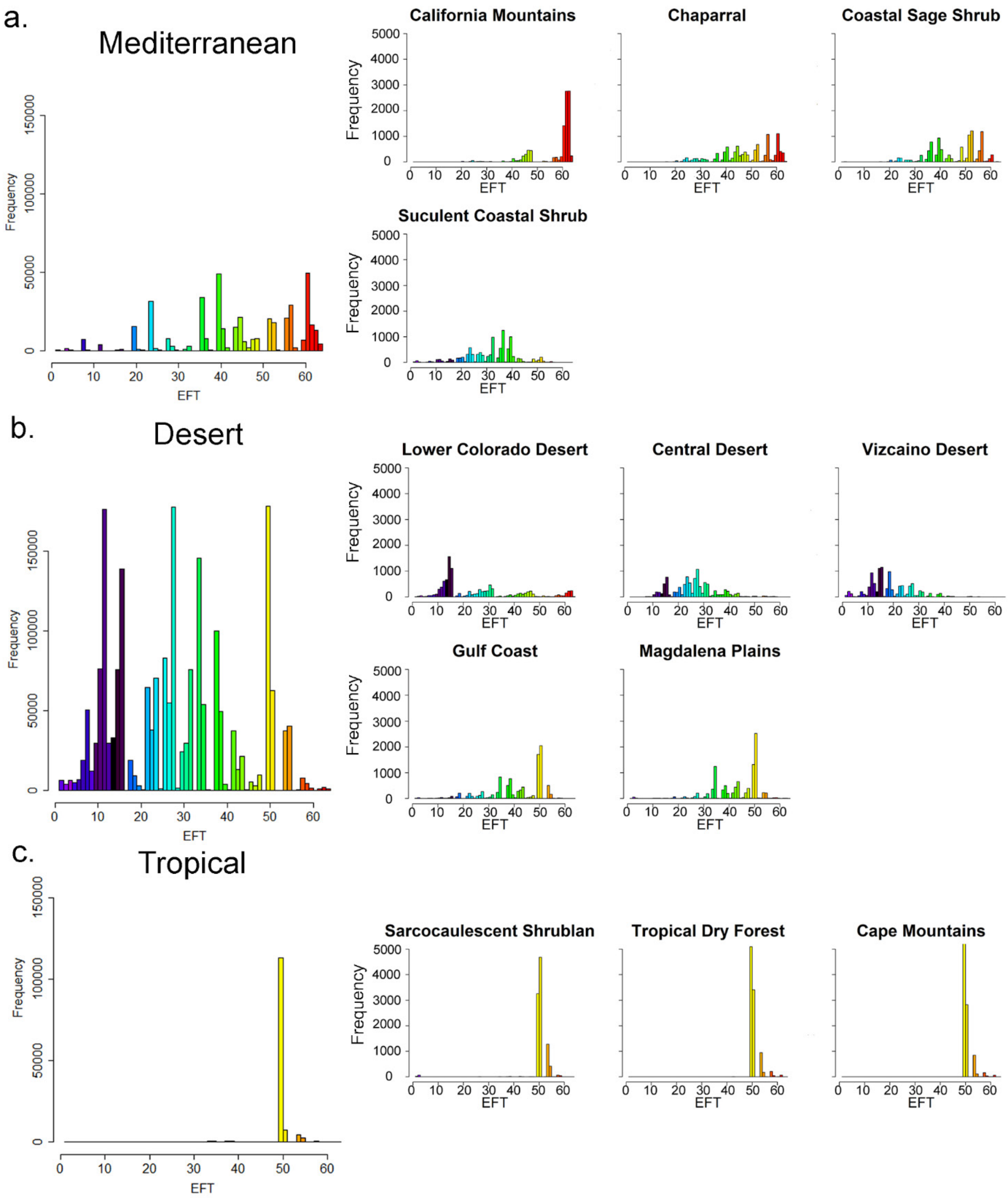

Figure 4. Functional characterization of ecoregions. EFT frequency histograms in major regions (level I) and sub-regions (level II) ordered in a latitudinal range: a) Mediterranean; b) Desert; and c) Tropical. Colours correspond to the EFTs, see legend in Figure 3.

Productivity EFTs (C-B) also appeared (e.g. Chaparral, Coastal Sage Shrub, and Succulent Coastal Shrub). Productivity decreased toward the desert region (i.e. southward) where we found the EFTs with the lowest values for this attribute (A) (e.g. Pacific Islands). Seasonality values were high in coastal ecoregions (a-b) (Coastal Sage Scrub, Succulent Coastal Scrub) and low

(d) in the mountain (California Mountains, Chaparral). Peaks of greenness occurred mainly in spring (1) followed by autumn (3) and winter (4). This geographical pattern of EFTs coupled very well with the ecoregionalization established for the Mediterranean by Gonzalez-Abraham *et al.,* (2010). Here was noticeable the precise functional delimitation that EFTs made between the coastal ecoregions (Coastal Sage Scrub and Succulent Coastal Sage) and mountains ecoregions (Chaparral and California Mountains) (EFTs map, Figure 3), what suggests a clear functional boundary between these ecoregions.

Desert showed a clear latitudinal pattern of EFTs (in terms of productivity, seasonality, and phenology). Productivity was low (A) in the northern part of the region (e.g. Lower Colorado Desert, Central, Desert, and Vizaíno Desert) and increased towards the south, getting EFTs with high values for this attribute (C-D) (e.g. Gulf Coast, La Giganta Ranges, Magdalena Plains). Seasonality was also low (d) in northern ecoregions (e.g. Lower Colorado Desert) and increased towards the south, getting EFTs with high values for this attribute (C-D) (e.g. Gulf Coast, La Giganta Ranges, Magdalena Plains). Seasonality was also low (d) in northern ecoregions (e.g. Lower Colorado Desert) and increased southward (a-b) (e.g. La Giganta Ranges). Peaks of greening also differed along the latitudinal gradient, whereas northern desert ecoregions showed winter peak (4) (e.g. Lower Colorado, Central, and Vizaíno Desert), in the southern desert ecoregions, it occurs mainly in autumn (3) (e.g. Gulf Coast, La Giganta Ranges, and Magdalena Plains). Hence, in the Desert region, EFTs showed two functional deserts (Figures 3 and 4b): (i) the northern part that represented the "typical" Desert (Vizcaíno Desert, Central Desert, and Lower Colorado Desert ecoregions) and (ii) the southern "tropical" Desert (that includes Gulf Coast Desert, Giganta Ranges, and Magdalena Plains ecoregions), functionally similar to the Tropical region.

Finally, the Tropical region EFTs had the highest homogeneity in ecosystem functioning (Figure 3 and 4c) and showed a homogeneous pattern through the three altitudinal ecoregions differentiated in the ecoregions map (Sarcrocaulescent Shrubland, Tropical Dry Forest and Cape Mountains). Functional differences along the region were only appreciable in terms of phenology. High mountain showed its phenological peak in September (summer), while low mountain and lowlands showed this peak during October-November (autumn). The region had a few different EFTs with high productivity (D), high seasonality (a), and the peaks of the maximum EVI in summer (2) and autumn (3).

Correspondence between geographical patterns of ecosystem functioning and ecoregions

Detrended Correspondence Analysis (DCA) (Figure 5) showed that three major regions of the Peninsula were

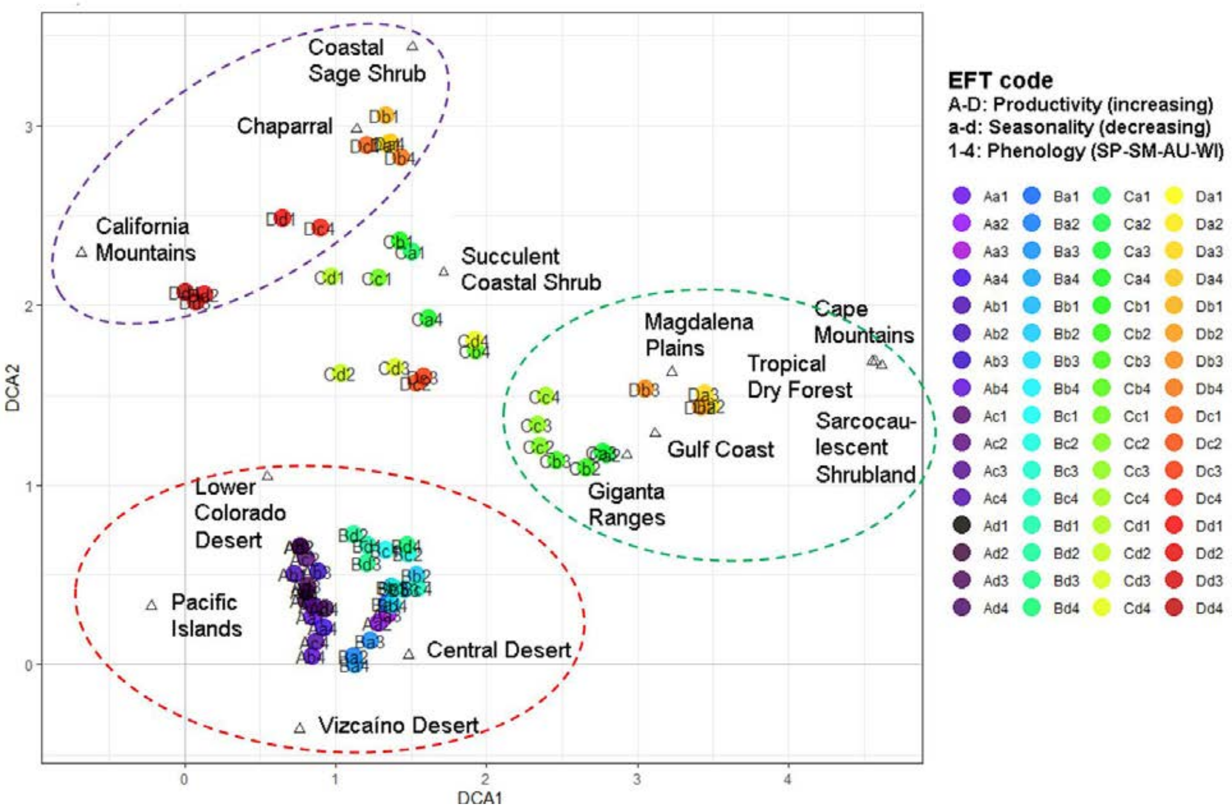

Figure 5. Ordination plot of dimension 1 and dimension 2 of the Detrended Correspondence Analysis (DCA) run with the contingency matrix between Ecosystem Functional Types, EFTs (circles) and ecoregions (triangles) in the Baja California Peninsula. See EFT codes in legend. Dotted circles represented the three major regions: Mediterranean in purple, Desert in red and Tropical in green

distributed along a marked productivity gradient (Figure 5 and Figure S1a). As a general pattern, the Mediterranean ecoregions (top left of Figure 5), were associated with EFTs corresponding to high and intermediate productivity, low seasonality and phenology in spring (EFTs Dd1, Dc1, Cd1). However, two ecoregions considered to be Mediterranean by González-Abraham *et al.,* (2010) did not appear in this group, being associated with other EFTs. On one hand, Pacific Islands appeared functionally separated from the other Mediterranean ecoregions and were associated with those corresponding to a climatic desert. On the other hand, Succulent Coastal Scrub, appeared in a transition zone between high productivity EFTs (typical of the Mediterranean) and low productivity EFTs (typical of the desert).

Desert ecoregions were grouped in two different places of the DCA (Figure 5 and Figure S1): (i) northern desert ecoregions (bottom right) and (ii) southern desert ecoregions (left). The group of northern desert ecoregions, had associated EFTs characterized by low productivity, in particular, Vizcaíno Desert was associated to very low productivity (A) and high seasonality (a) (EFT Aa4) and Lower Colorado Desert and Central Desert showed EFTs with low-medium productivity (B) and low or medium seasonality (c-d) (EFT Bc4). Southern desert ecoregions (i.e. Central Gulf Coast, La Giganta Ranges, and Magdalena Plains) were placed near to the tropical ecoregions, in a transition zone. Therefore, the southern part of Desert region, in the ecoregions map, is functionally more similar to the Tropical region than to the northern desert. Here, productivity was remarkably higher (C) than in the rest of desert region (A-B), and the phenological peak occurs between September to November (autumn-3), in a similar way to the tropical region and in contrast to the rest of desert region, where it occurred between February to April (mainly winter-4). Furthermore, the southern Desert region presents higher seasonality (a-b) than the rest of the Desert, and is similar to the Tropical region.

Finally, we found the group of tropical EFTs (right in Figure 5 and Figure S1) associated with EFTs of high productivity (D), high seasonality (a) and phenology in summer (2) and autumn (3) (EFT Da2, Da3). The most novel result was the functional proximity of the ecoregions of the southern desert with the tropical region.

Discussion

We found that in the Baja California Peninsula, at the broad scale, the spatial patterns in ecosystem functioning can produce different spatial patterns to the biogeographic regionalization established from structural and compositional attributes of the ecosystems. In fact, when we focused on a more detailed scale, some disagreement between the functional patterns with ecoregions were more evident. This was particularly evident in the Desert - Tropical regions that, in contrast to the Mediterranean ecoregions, did not show spatial association with the EFTs that better represented the climatic conditions of the major region. Our analysis showed that the southern Desert ecoregions were functionally more similar to the Tropical region than to the rest of the desert ecoregions, and ecoregions inside Tropical region were functionally similar. These results emphasize the concept that functional geography provides new information about ecological systems, bringing us a new vision of another dimension of biodiversity. The knowledge of the relationship between the patterns of ecoregions and ecosystem functioning is the basis for a better understanding of spatial and temporal patterns of multidimensional biodiversity, which may guide towards a better regionalization and could aid for management and conservation purposes.

Classical regionalization and functional characterization of ecoregions: are our functional observations consistent with ecoregions?

- *Nature of tropics and geographical limits*

We found two functional regimes with a transition around 27o-28o N: the northern half driven by winter-spring raining season and the southern half by summer-autumn rains.

There has been a long-time discussion among naturalists about the transition between the desert and tropical regions (Shreve, 1951; León de la Luz *et al.,* 2008; González-Abraham *et al.,* 2010). This transition has been delimited using different indices or attributes (Corlett, 2013; Feeley & Stroud, 2018), including climate variables (Hastings & Turner, 1965; Turner *et al.,* 1995), species distribution (Garcillán *et al.,* 2003), intra-species genetic changes (Riddle *et al.,* 2000) or even geological features (León de la Luz *et al.,* 2000). However, it has not been shown in terms of ecosystem functioning.

The extension of tropicality over the southern half of the peninsula, and its functioning leaves open a promising avenue for the study of the functionally tropical behavior of various parts of the desert. Something that has not been clearly explained in ecological terms before. In this sense, there are ecoregions not considered tropical until now (but desert), which although they do not have the tropicality as marked as the tropical ones (Sarcocaulescent Shrubland, Tropical Dry Forest and Cape Mountains), they also have the typical EFT of the tropics (EFT Da1) as the most abundant (Gulf Coast, La Giganta Ranges, and Magdalena Plains). Therefore, our results suggest that EFTs can help to conceptualize and define limits and dynamics of tropics or other ecological regions across different spatio-temporal scales.

- *Two functional deserts*

One of the most remarkable results is the empirical evidence of two functionally deserts (approx. at 27.5º N)

(Figure 3). The transition between both functional deserts occurs at different latitudes depending on each peninsular coast. Here, ecosystem functioning is conditioned by the opposite thermal influence of the Gulf of California and the Pacific Ocean. The Northern desert descends southward along the Pacific coast to around 26ºN characterized by low productivity, low to moderate seasonality and high dependence on winter rains (Lower Colorado Desert, Central Desert, and Vizcaino Desert ecoregions); however, in the Gulf Coast, the Southern desert extends to reach next to 28 oN, showing higher productivity, seasonality and dependence on summer rains (Gulf Coast, La Giganta Ranges, and Magdalena Plains ecoregions). In essence, the presence of the California Current on the Pacific coast favours the southern extension along this coast of Mediterranean climate characteristics (including frequent fogging), while the high temperature of the Gulf of California prolongs the tropical influence towards the north along its coasts (Hastings & Turner, 1965; Peinado *et al.,* 1994). On the Pacific coast, it has been shown that the ocean surface temperature (fog promoter) and the photosynthetically active radiation portion (fPAR) are directly related (Reimer *et al.,* 2015), helping to maintain a minimum of productivity in places where precipitation is very scarce or even non-existent for long periods of time. Besides the climate transitional character of the Desert region, the scarce and high spatial and temporal variability of its precipitation (Hastings & Turner, 1965; Turner & Brown, 1982; Peinado *et al.,* 2011) produce the elevated functional heterogeneity observed along this region.

These results can help to understand the controversy that has traditionally existed over the classification of southern desert ecoregions. Shreve (1951) considered La Giganta Ranges to be tropical, but a later study by Leon de la Luz *et al*., (2008) suggested that floristically it resembled the desert. In the case of Gulf Coast and Magdalena Plains, all studies since the work of Shreve (1951) have considered them to be desert ecoregions (see review in Garcillán *et al.,* 2010; González-Abraham *et al.,* 2010). However, our analyses showed that these three ecoregions functionally have a strong tropical character. The Gulf Coast ecoregion is a narrow strip of very long latitude (24-29o N) along the decreasing gradient of summer precipitation. These characteristics and the barrier effect of the mountains to the west, make it the most heterogeneous ecoregion in the whole Peninsula, hence its difficult classification. The Giganta Ranges was also identified as a zone of discrepancy in González-Abraham *et al.,* (2010), but this did not happen for Magdalena Plains. Therefore, the identification of functionally tropicaloid features in this last ecoregion makes it necessary to reconsider its classification.

- *EFTs captured internal heterogeneity in Mediterranean ecoregions but not in tropical ecoregions*

Inside the Mediterranean region, EFTs analysis showed A heterogeneous spatial pattern similar to the regionalization established in the ecoregions map, which is mainly structured by the double effect of coast and topography. In coastal ecoregions the presence of fog constitutes a climatic factor that conditions the adaptations of the organisms (Hastings & Turner, 1965; Martorell & Ezcurra, 2002). Furthermore, there exists a climate gradient in altitude (Peinado *et al.,* 2011) that modifies the vegetation types and determines the different functional traits behaviors within the region.

Despite the similarity with the structural/compositional approaches, two ecoregions previously classified as Mediterranean were grouped with the others due to their peculiarities in ecosystem functioning. First, Succulent Coastal Scrub, located in the Pacific Coast between 29.5º and 31º N, has been long considered a transitional region (González-Abraham *et al.,* 2010). In fact, in our CA appeared in a transition zone between EFTs characteristics of Mediterranean and Desert. Here, chaparral species extend southward to where moisture remains enough (Shreve, 1936), while the northern range of the desert species seems to depend on the absence of frost and some availability of water in summer (e.g. Shreve, 1936; Raven & Axelrod, 1978), probably associated with coastal fogs (Rundel & Mulroy, 1972; Garcillán *et al.,* 2013). Second, Pacific Islands, which González-Abraham *et al.,* (2010) already identified as one of the areas of discrepancy between authors. Its biological and biogeographical uniqueness is unquestionable. Most of the extension of these islands is occupied by semi-desert vegetation. However, biogeographically it is interesting that there an important proportion of Mediterranean flora (Epling & Lewis, 1942; Wallace, 1985; Smith *et al.,* 1990; Oberbauer, 1993), which has led to consider it as a Mediterranean ecoregion in desert latitudes (González-Abraham *et al.,* 2010). In terms of EFTs, its composition was very different from the rest of the mediterranean ecoregions (Figure 4), showing low productivity EFTs, typical of the desert. Here, precipitation from fog condensation hybridizes the mediterranean regime of rains and allows the coexistence of these mediterranean species with the desert flora component, producing the mixed functional behavior that we observed.

The mediterranean conditions, in terms of the topographic gradient (approx. 3000 m) and coastal proximity, also occurred in the tropical region. But here EFTs did not show the heterogeneity mentioned in mediterranean, instead, they were functionally homogeneous. Although the annual precipitation variation associated with altitudinal gradient is even higher in the Tropical region (from less than 200 to 700 mm) than in Mediterranean region (from 270 to 650 mm), the homogeneity in ecosystem functioning could be due to the seasonality in the precipitation regime and the similarity in the phenological peak. Here, rain is concentrated in the summer and early autumn months (July to October) and there is an existence of a season without rain ("dry" season) of between five and eight months (Farfán & Fogel, 2007). Therefore, in this area, climatic controls are more important than altitudinal ones, which is reflected by the ecosystem functioning, i.e. in the presence of the same coastal and altitudinal factors, the ecosystem functioning is more homogeneous than mediterranean areas due to seasonality in rainfall patterns. In fact, the combination between the altitudinal range and heterogeneous distribution of precipitation and hence, phenology through the year, could be the reason for the high internal heterogeneity of EFTs in this region.

- *The role of ecosystem functioning in biological regionalization exercises*

In the last decade, functional analysis of ecosystems has gained attention because it is a useful perspective for assessing and monitoring the effects of global change on diversity (Cabello *et al.,* 2012; Pereira *et al.,* 2013). Furthermore, incorporating functional aspects into regionalization practice offers a great potential for improving our understanding of spatial and temporal diversity patterns (Garnier *et al.,* 2016); and implementing new programs for the conservation of ecological processes (Asner *et al.,* 2017). EFT concept has been highlighted as “the first serious attempt to group ecosystems (at large scales) on the basis of shared functional behavior” (Mucina, 2019), and its strength for a better understanding of ecological systems providing new information derives from its ability to capture ecosystem functioning into discrete entities that can be mapped. Mapping such entities (EFTs) that reflect the performance of the whole ecosystem opens a straightforward, tangible and biologically meaningful way for incorporating ecosystem functioning in regionalizations, based on the regional heterogeneity of functional attributes at ecosystem level. EFT represents a new and complementary approach to long-established ones based on the compositional (e.g. species richness) and structural (e.g. vegetation types) characterizations of biodiversity, but also to the more recent functional approaches based on functional traits at species level.

The differences with these approaches derive both from the attributes of biodiversity reported by EFTs and the method used to do so. First, EFT considers ecosystem attributes related to the stocks and flows of matter and energy derived from biological activity taking place on plots of land, providing integrative information on the functional facets of biodiversity living on those plots. Second, EFTs capture temporal dynamics that are difficult to map through compositional or structural regionalization approaches, since they are a static measure with a fixed time interval (i.e. they measure conditions through the legacy of geological and evolutionary history). Third, EFTs are identified by remote sensing tools from aggregated measurements of ecosystem functions at the pixel level, which in practice represents information of the performance of the whole ecosystem. Remote sensing tools can offer more integrative functional measures of the whole ecosystem performance (productivity, evapotranspiration, etc.) that complement our traditional view of ecosystems (Butchart *et al.,* 2010; Asner *et al.,* 2017).

Conclusions

Our work highlights that differences between the proposals, rather than being a disadvantage, is the result of diverse approaches based on the different levels of ecological and biogeographical organization in the region, and their differences are highly informative. Ecosystem Functional Types allowed us to understand the relationship between different dimensions of biodiversity in regionalization exercises, i.e. between biological regionalization based on the biota components and structure (species distribution, endemisms, vegetation types) and patterns of ecosystem functioning (EFTs). The regionalization schemes have been widely used for guiding management and conservation decision-making since it allows us to organize our understanding of how major terrestrial ecosystems work. In this sense, due to the development of new techniques based on remote sensing, functional features measured at regional scales could be incorporated, allowing us to complement our traditional view of ecosystems, providing the basis for a more comprehensive regionalization of geographical patterns of life and therefore, improving also the future conservation purposes.

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Supplementary material

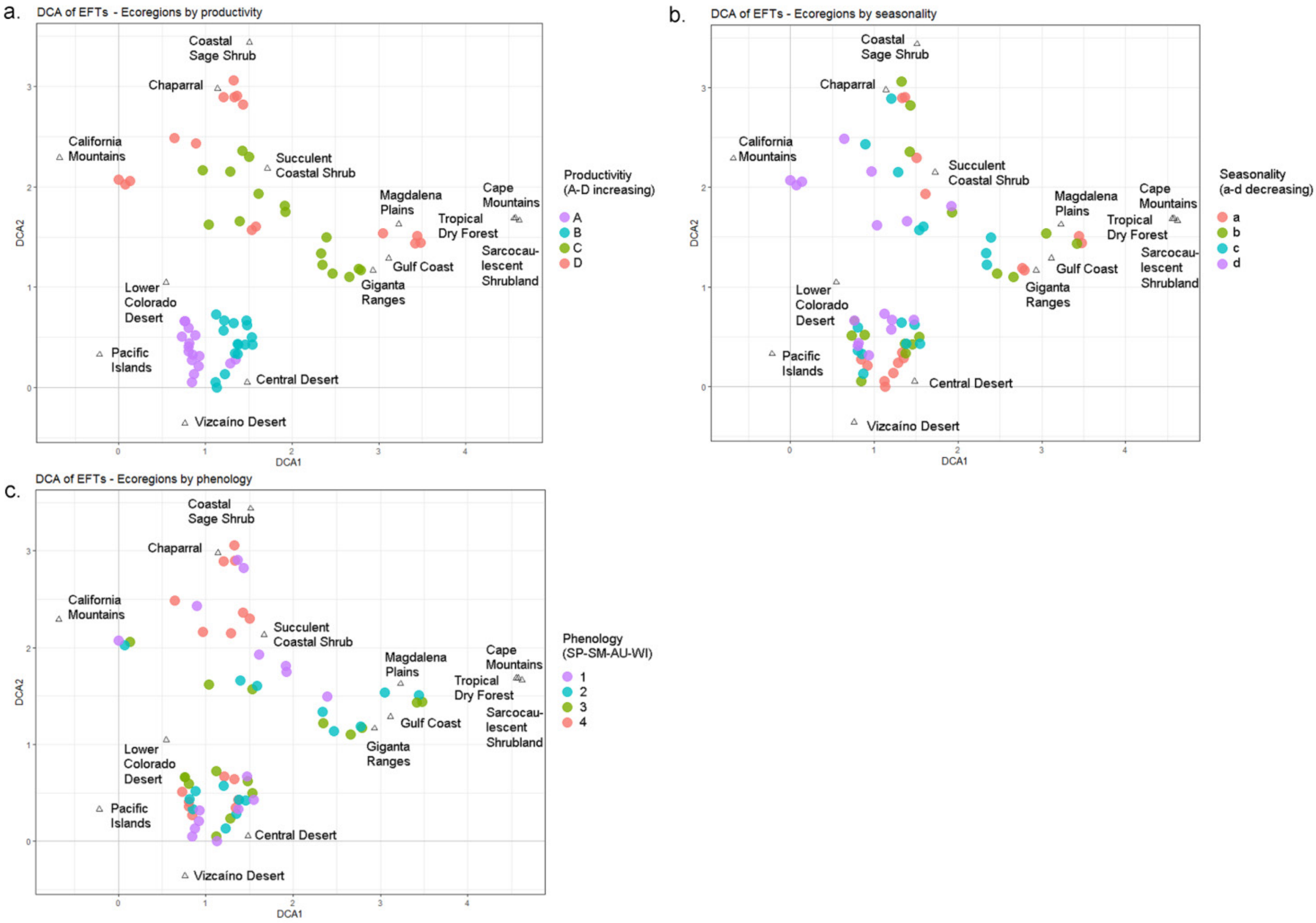

Figure S1. Ordination plot of dimension 1 and dimension 2 of the Detrended Correspondence Analysis (DCA) run with the contingency matrix between Ecosystem Functional Types, EFTs (circles) and ecoregions (triangles) in the Baja California Peninsula and colored by the three ecosystem functional attributes from which EFTs are derived. a) DCA colored by EVI mean, as surrogate of productivity, from A to D increasing; b) DCA colored by EVI sCV, indicator of seasonality from a to d decreasing and; c) DCA colored by EVI MMAX, indicating the peak of maximum EVI (SP-Spring, SU-Summer, AU-Autumn, WI-Winter).

General Appendix 2.

Other scientific publications derived from the thesis

Book Chapter:

Cazorla, B.P., Cabello, J., Peñas, J., Guirado, E., Reyes, A., Alcaraz-Segura, D. (2019). Funcionamiento de la vegetación y diversidad funcional de los ecosistemas de Sierra Nevada. In: Peñas, J. & Lorite, J. (eds.), Biología de la Conservación de plantas en Sierra Nevada. Principios y retos para su preservación. Granada: Editorial Universidad de Granada.

CAPÍTULO 15

Funcionamiento de la vegetación y diversidad funcional de los ecosistemas de Sierra Nevada

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**In memoriam:*

A Andrés Reyes, por cada momento contigo, grande en todos los sentidos. Gracias mil y una veces.

Resumen

La Biología de la Conservación se enfrenta al desafío de salvaguardar los procesos ecológicos que sustentan la biodiversidad. Este capítulo caracteriza los patrones de funcionamiento de los ecosistemas de Sierra Nevada, proporcionando además la primera caracterización de la diversidad funcional a nivel de ecosistema realizada en Sierra Nevada. Para caracterizar el funcionamiento de los ecosistemas utilizamos el enfoque basado en Tipos Funcionales de Ecosistemas (TFEs), parches de la superficie terrestre que poseen dinámicas similares en los intercambios de materia y energía entre la biota y el ambiente físico. Los TFEs se identificaron a partir de tres atributos funcionales del dosel vegetal relacionados con la producción primaria, estacionalidad y fenología del ecosistema, derivados del índice de espectral de vegetación EVI (*Enhanced Vegetation Index*) para el periodo 2001-2016. El funcionamiento de los ecosistemas nevadenses muestran un claro patrón altitudinal caracterizado por un descenso de la productividad de los ecosistemas y un aumento en la estacionalidad con la altitud. Excepto en el extremo oriental termomediterráneo, donde a pesar de ser cotas de menor

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altitud, la productividad también es baja y la estacionalidad alta. La riqueza de TFEs es mayor en la media montaña, descendiendo con la altitud, a la vez que aumenta la rareza de TFEs. El empleo de los TFEs como entidades biológicas permite analizar los patrones espaciales del funcionamiento, su diversidad funcional y la variabilidad interanual en la diversidad funcional a nivel de ecosistema, revelando la existencia de puntos calientes de riqueza y rareza funcional en Sierra Nevada.

Palabras clave: Funcionamiento ecosistémico, teledetección, Tipos Funcionales de Ecosistemas, Sierra Nevada.

Introducción

La biodiversidad de cualquier área es susceptible de ser estudiada a través sus tres dimensiones, composición, estructura y función, y a todos los niveles de la organización biológica, desde los genes, individuos, poblaciones, comunidades y ecosistemas, hasta los paisajes y ecorregiones (Noss, 1990). Mientras que el estudio de los aspectos estructurales y composicionales de la biodiversidad (como la fisionomía de la vegetación o la composición florística; (Mueller-Dombois y Ellenberg, 1974; Stephenson, 1990) han contado tradicionalmente con una gran atención, no ocurre lo mismo con la dimensión funcional, cuyo análisis es mucho más reciente y requiere aún de un mayor desarrollo metodológico (e.g., Cabello et al., 2012a). Esta dimensión de la biodiversidad engloba a los procesos ecológicos y evolutivos que tienen lugar en el ecosistema, desde los intercambios de información (por ejemplo, el flujo de genes) hasta los intercambios de materia y energía entre la biota y el ambiente (Jax, 2010). Si atendemos a los niveles más altos de la organización biológica, por ejemplo, el funcionamiento de la vegetación, vemos que este ha sido escasamente estudiado en comparación con su composición y estructura (Soulé y Wilcox, 1980). De hecho, desde los inicios de la Biología de la Conservación, se viene apelando a la necesidad de incorporar los procesos ecológicos y funciones de los ecosistemas a las prácticas de conservación tradicionales, basadas en especies individuales (Pettorelli et al., 2016).

Actualmente, al desafío de salvaguardar los procesos ecológicos necesarios para la persistencia de la biodiversidad a lo largo del tiempo (CDB, 2010; GBO4, 2014) se une la preocupación general por mantener la capacidad de los ecosistemas para sostener y regular sus funciones (Chapin et al., 2010) y servicios (Naidoo et al., 2008; Costanza, 2012). De hecho, un número creciente de compromisos internacionales, como el Convenio sobre la Diversidad Biológica o las Metas de Aichi requieren planes específicos de gestión que aborden específicamente el funcionamiento de los ecosistemas (Frid et al., 2008; CDB, 2011). Además, desde el punto de vista de la planificación y la gestión, también se señala la importancia de incorporar los procesos y funciones ecosistémicas en la planificación sistemática de la conservación, la gestión ecosistémica y la gestión adaptativa (Margules y Pressey, 2000; Jax, 2010). Finalmente, se ha constatado que desde el punto de vista de la evaluación y adaptación a los impactos de cambio global, los indicadores funcionales de la biodiversidad pueden ser especialmente relevantes gracias a su respuesta más rápida ante los cambios ambientales (Aspizua et al., 2012; Cabello et al., 2016; Alcaraz-Segura et al., 2017, Pettorelli et al., 2017).

La caracterización y evaluación del funcionamiento a nivel de ecosistema se puede llevar a cabo a través de atributos o rasgos funcionales relacionados, por ejemplo, con el intercambio de materia y energía entre la vegetación y la atmósfera (Mueller-Dombois y Ellenberg, 1974). Actualmente, el uso de imágenes de satélite proporciona métodos adecuados para producir una caracterización del funcionamiento ecosistémico, espacialmente continua y a escala regional (Alcaraz-Segura et al., 2006; 2013). Tanto modelos teóricos como empíricos apoyan la relación entre índices espectrales derivados de imágenes de satélite y atributos funcionales de los ecosistemas como la producción primaria, la evapotranspiración, la temperatura superficial, o el albedo (Running et al., 2000; Pettorelli et al., 2005). Entre ellos, la producción primaria está considerada como el indicador más integrador y esencial del funcionamiento de los ecosistemas (Virginia y Wall, 2001; Pereira et al., 2013), ya que posee un papel fundamental en el ciclo del carbono, siendo la base energética de la cadena trófica y, por tanto, el motor de inicio de muchos procesos ecológicos. Además, al presentar una respuesta integral ante los cambios ambientales, constituye un indicador sintético de la salud del ecosistema (Costanza et al., 1992; Skidmore et al., 2015).

Entre los índices espectrales derivados de imágenes de satélite más importantes y utilizados se encuentran los índices de vegetación, como el EVI (*Enhanced Vegetation Index* o Índice de Vegetación Mejorado). Este índice se puede utilizar para estimar la fracción de la radiación fotosintéticamente activa absorbida por la vegetación (fAPAR), que representa el control principal de la producción primaria (Monteith, 1972), debido a la relación lineal existente entre ambas variables (Hatfield et al.,1984).

Las investigaciones ecológicas basadas en índices espectrales de vegetación poseen un gran valor en Biología de la Conservación (Cabello et al., 2012a; Pettorelli, 2016; 2018), como apoyo a la gestión (Pelkey et al., 2003; Cabello et al., 2016) y en el estudio de respuestas de la biodiversidad frente a cambios ambientales (Alcaraz-Segura et al., 2017). Entre las numerosas ventajas que presenta el uso de estos índices para estudiar la variabilidad espacial y temporal de la dinámica de la vegetación está el empleo de protocolos comunes en toda la Tierra (Pettorelli et al., 2018), su gran sensibilidad y rápida respuesta ante los cambios ambientales (Milchunas y Lauenroth, 1995), su claro significado biológico (Pettorelli et al. 2005; Bagnato et al., 2019) y su conexión con la evaluación de las funciones y servicios de los ecosistemas (Volante et al., 2012; Paruelo et al., 2016). De hecho, numerosos trabajos han demostrado la capacidad de las series temporales de imágenes de satélite para evaluar la existencia de cambios funcionales en los ecosistemas tanto a nivel regional (Alcaraz-Segura et al., 2010) como de área protegida (Alcaraz-Segura et al., 2009a; Lourenço et al., 2018). Recientemente, el empleo de Atributos Funcionales de los Ecosistemas derivados de índices espectrales de vegetación en modelos de distribución de especies está permitiendo evaluar con gran precisión espacial y temporal la idoneidad del hábitat para especies de plantas (Arenas-Castro et al., 2018) y animales (Regos et al., 2019) pudiendo incluso anticipar los cambios esperados en la distribución de especies de plantas amenazadas como consecuencia del cambio climático (Alcaraz-Segura et al., 2017). Además, a partir los Atributos Funcionales de los Ecosistemas, se ha diseñado un programa de seguimiento de la Red de Parques Nacionales de España, que permite identificar los cambios y anomalías en el funcionamiento, informando a los gestores de la salud y estado de conservación de los ecosistemas (Cabello et al., 2016).

Para caracterizar la heterogeneidad regional en el funcionamiento de los ecosistemas mediante índices espectrales de vegetación podemos utilizar el enfoque basado en Tipos Funcionales de Ecosistemas (TFEs), desarrollado por Paruelo et al., (2001) y Alcaraz-Segura et al., (2006, 2013). Conceptualmente, los Tipos Funcionales de Ecosistemas (TFEs) fueron definidos como parches de la superficie terrestre que poseen dinámicas similares en los intercambios de materia y energía entre la biota y el ambiente físico (Alcaraz-Segura et al., 2006). Metodológicamente, el empleo de teledetección permite identificar TFEs a partir de tres descriptores sintéticos del funcionamiento ecosistémico derivados de la curva anual o dinámica estacional de índices espectrales de vegetación (Figura 1). Estos atributos funcionales, relacionados con la producción primaria anual, la estacionalidad y fenología de las ganancias de carbono, capturan la mayor parte de la varianza de la serie temporal de los índices de vegetación (Paruelo et al., 2001; Alcaraz-Segura et al., 2006; 2009b). Investigaciones recientes (Cazorla et al., 2019a) han demostrado cómo esta aproximación para identificar TFEs permite obtener clases de ecosistemas homogéneos en términos de su dinámica del inter-

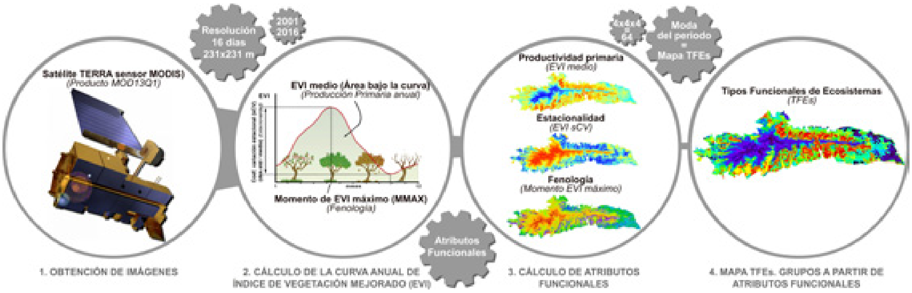

Figura 1. Flujo de trabajo para la construcción de los Tipos Funcionales de Ecosistemas. Se utilizó el producto MOD13Q1 del sensor MODIS (Moderate Resolution Imaging Spectroradiometer) a bordo del satélite Terra de la NASA. Este producto contiene imágenes con resolución temporal de 16 días (23 imágenes por año) y resolución espacial de 231 x 231 m del *Enhanced Vegetation Index* (EVI). El periodo de estudio fue de 2001 a 2016. A partir de la curva estacional del EVI para cada año se calcularon tres atributos funcionales descriptores del funcionamiento de los ecosistemas. El rango de valores de cada atributo se dividió en cuatro intervalos, que dan lugar al número potencial de 64 TFEs (4x4x4=64).

cambio neto de CO_2 medido en campo con torres de covarianza de torbellinos (*eddy covariance*), ofreciendo una separación entre distintas dinámicas ligeramente superior a la que proporciona el esquema tradicional basado en tipos funcionales de plantas. Esta capacidad de los TFEs para capturar la diversidad funcional de los ecosistemas ha sido empleada para evaluar la representatividad de redes de seguimiento ambiental (como Ameriflux y NEON en Estados Unidos; Villarreal et al., 2018) y para establecer prioridades geográficas en conservación (en la red de áreas protegidas de Baja California; Cazorla et al., 2019b).

Desde que apareció el concepto de TFE en 2001 (Paruelo et al., 2001), su implementación o la de metodologías similares no ha parado de crecer para caracterizar la heterogeneidad funcional a escala regional (Alcaraz-Segura et al., 2006; Karlsen et al., 2006; Duro et al., 2007; Fernández et al., 2010; Geerken, 2009; Alcaraz-Segura et al., 2013; Ivits et al., 2013; Pérez-Hoyos et al., 2014; Müller et al., 2014; Wang y Huang, 2015; Villarreal et al., 2018; Coops et al., 2018; Mucina, 2018).

En España, son clásicos los estudios del paisaje vegetal bajo una perspectiva composicional (método fitosociológico) o sucesional (series de vegetación). Estos estudios han sido muy útiles para describir la heterogeneidad de la vegetación a mesoescala (Valle et al., 2003; Loidi, 2017), han estado en la base de la caracterización de los hábitats de interés para la conservación (Directiva 92/43/EEC), y sirvieron para el desarrollo de políticas de restauración forestal orientadas a la recuperación de la diversidad vegetal (Valle et al., 2004). Sin embargo, estas aproximaciones son difíciles de usar para monitorear la respuesta de los ecosistemas frente al cambio global, y la caracterización y cartografía de la vegetación desde el punto de vista de la provisión de servicios ecosistémicos (Cabello et al., 2019). Este es el caso de Sierra Nevada, una montaña que cuenta con excelentes descripciones de la vegetación, pero no dispone de estudios de los patrones de funcionamiento de la vegetación. El estudio de estos patrones puede ayudar al seguimiento de los efectos de las acciones de gestión, a la comprensión de los gradientes ambientales a escala de área protegida que subyacen a la biodiversidad, y a evaluar el papel de los ecosistemas proveyendo beneficios a la sociedad.

Este capítulo persigue contribuir a la descripción de la heterogeneidad espacial y variabilidad temporal del funcionamiento de los ecosistemas de Sierra Nevada a partir de la dinámica del verdor de la vegetación, proporcionando además la primera caracterización de la diversidad funcional a nivel de ecosistema realizada como área protegida. En primer lugar, el capítulo analiza los patrones espaciales de tres atributos funcionales de los ecosistemas, como son la producción primaria anual, la estacionalidad y la fenología de las ganancias de carbono por parte de la vegetación, así como su integración en una cartografía sintética de tipos funcionales de ecosistemas (TFEs). En segundo lugar, para identificar los puntos calientes de riqueza y rareza funcional en Sierra Nevada, se muestran dos formas de describir la diversidad funcional a nivel de ecosistemas, como son la riqueza y la rareza de tipos funcionales de ecosistemas (ver fórmula utilizada más adelante). A continuación, para mostrar cuáles son las zonas más estables y más variables entre años (ya sea por cambios direccionales o por fluctuaciones) en términos del funcionamiento ecosistémico, se evaluó la variabilidad interanual en el funcionamiento de los ecosistemas a partir de dos medidas, el número de TFEs que fueron observados durante el periodo 2001-2016 a nivel de píxel, y la similitud interanual en la composición de TFEs a nivel de paisaje. En todos los casos, para facilitar al lector la interpretación de los patrones espaciales hallados, se proporciona una comparación con los tipos de vegetación natural de Sierra Nevada. Por último, se identifican las implicaciones que una evaluación funcional de los ecosistemas puede tener para la conservación y gestión del Espacio Natural protegido de Sierra Nevada.

¿Cómo abordar el estudio del funcionamiento de los ecosistemas a nivel de paisaje en Sierra Nevada?

Para caracterizar el funcionamiento de los ecosistemas de Sierra Nevada se emplearon series temporales de imágenes de satélite para el *Enhanced Vegetation Index* (EVI). Concretamente, se usó el producto MOD13Q1 del sensor MODIS (Moderate Resolution Imaging Spectroradiometer) a bordo del satélite Terra de la NASA. Este producto consiste en imágenes con resolución temporal de 16 días (23 imágenes por año) y resolución espacial de 231 x 231 m. El periodo de estudio fue de 2001 a 2016. A partir de la curva estacional del EVI para cada año se calcularon tres atributos funcionales descriptores del funcionamiento de los ecosistemas (Figura 1): el EVI medio anual como estimador de la producción primaria anual (EVI_medio), el coeficiente de variación estacional del EVI como descriptor de la estacionalidad (EVI sCV), y el momento de máximo EVI como indicador de la fenología del máximo verdor anual (EVI MMAX). Se eligieron estos tres atributos porque capturan la mayor parte de la varianza en las series temporales de índices de vegetación y guardan un claro significado biológico (Paruelo et al., 2001; Alcaraz-Segura et al., 2006; 2009a).

Los TFEs se identificaron siguiendo la metodología de Alcaraz-Segura et al. (2013) (Figura 1) a partir de los tres atributos funcionales de los ecosistemas anteriores. El rango de valores de cada atributo se dividió en cuatro intervalos, que dan lugar al número potencial de 64 TFEs (4x4x4=64). Para EVI MMAX se usaron las cuatro estaciones del año. En el caso de EVI medio y EVI sCV se empleó la mediana interanual del primer, segundo y tercer cuartiles obtenidos en cada año. Para nombrar cada TFE se utilizó la terminología sugerida por Alcaraz-Segura et al., (2013), basada en dos letras y un número. La primera letra, en mayúscula (A-D), indica la producción primaria y corresponde con el valor medio del índice de vegetación (EVI medio), incrementando en orden alfabético su valor (de menor a mayor productividad). La segunda letra, en minúscula (a-d), muestra la estacionalidad (EVI sCV), decreciendo en orden alfabético su valor (de mayor a menor estacionalidad). Los números son un indicador fenológico de la estación de crecimiento, momento del máximo EVI (1-4 para primavera, verano, otoño e invierno). Por ejemplo, el TFE Aa1 posee una baja productividad (A), elevada estacionalidad (a) y momento del máximo EVI en primavera (1). Una vez que se han fijado los límites entre los intervalos de cada variable, se aplicaron a las imágenes de los tres atributos para cada año, obteniendo así una serie temporal de 16 mapas de TFEs, uno por año (2001-2016). Para obtener un solo mapa que represente la heterogeneidad funcional característica del período se seleccionó la moda interanual de los 16 mapas anuales.

Para evaluar la correspondencia espacial entre los TFEs y los tipos de vegetación, se empleó un análisis de correspondencias sin tendencia (*Detrended Correspondence Analysis*, DCA) (Legendre y Legendre, 2012) a partir de la tabla de contingencia entre ambos mapas (Alcaraz-Segura et al., 2006; Fernández et al., 2010). El análisis de correspondencias sin tendencia representa en un espacio multidimensional reducido la relación espacial existente entre las clases de ambos mapas. Por tanto, este espacio visualiza la relación espacial entre cada TFE y un tipo de vegetación estructural. Así, si un grupo de TFEs y tipo de vegetación aparecen cercanas entre sí en el DCA, y distantes de otro grupo, es porque existe un alto grado de correspondencia espacial o solapamiento entre ellas. Usamos un DCA para evitar que las unidades muestrales se agrupen en los extremos del gradiente, ya que reescala los ejes e iguala la varianza. El mapa de tipos de vegetación que se utilizó fue elaborado a partir del mapa de vegetación de Andalucía 1:10000 (1996-2006) (Bonet et al., 2010). Los tipos de vegetación considerados fueron: pastizales, canchales y roquedos de alta montaña; borreguiles; matorral de alta montaña; pastos de media montaña; matorral de media montaña; pinares autóctonos de *Pinus sylvestris* subsp. *nevadensis* (H.Christ) Heywood; pinares autóctonos sobre dolomías; repoblaciones de coníferas; robledales; encinares; y cultivos de montaña extensivos (Figura 3 c y d).

Para caracterizar la diversidad funcional de ecosistemas y poder identificar los puntos calientes de riqueza y rareza funcional, se utilizó la riqueza y la rareza de TFEs como indicador de la diversidad de tipos de funcionamiento ecosistémico que ocurren en el paisaje. El mapa de riqueza de TFEs se calculó contando el número de TFEs que existen dentro de una ventana móvil de 4x4 píxeles MODIS (924 x 924 m; ~1 km^2) a través de toda el área de estudio. El mapa de rareza de TFEs se obtuvo calculando el valor de rareza relativa de cada TFE (Rareza_TFEi; Cabello et al., 2013) como:

Rareza_TFEi = (A_TFEmax – A_TFEi) / A_TFEmax

donde i es el TFE en cuestión, *A_TFEmax* es el área ocupada por el TFE más abundante y *A_TFEi* es el área del TFE en cuestión. Este índice de rareza posee valores entre 0 y 1, siendo 0 el tipo de funcionamiento ecosistémico más abundante, y 1 el tipo de funcionamiento ecosistémico más raro o poco común.

Para mostrar cuáles son las zonas más estables y con mayor variabilidad interanual (ya sea por cambios direccionales o por fluctuaciones) en el funcionamiento de los ecosistemas, se calculó el número de TFEs diferentes que tuvieron lugar en un mismo píxel en el periodo 2001-2016. Como medida adicional de la variación interanual que tuviera en cuenta no sólo los cambios que experimenta un píxel sino también los movimientos en el funcionamiento ecosistémico que pudieran ocurrir a nivel de paisaje, se empleó el índice de similitud de Jaccard (Jaccard, 1901) en ventanas móviles de 4x4 píxeles MODIS (924 x 924 m; ~1 km^2). Esta medida representa cómo de parecidos son los TFEs que ocurren en dicha ventana a lo largo de toda la serie temporal (2001-2016). Para cada ventana, primero se calculó el índice de Jaccard entre todas las combinaciones posibles de años y después se obtuvo la media interanual de todos los índices calculados. Para obtener una medida igual a la variabilidad interanual, se calculó la dismilitud, es decir, 1-coeficiente de Jaccard. Los valores de disimilitud oscilan entre 0 y 1, siendo 1 el mayor grado de disimilitud en la composición y abundancia relativa de TFEs y 0 ausencia de la misma.

Patrones espaciales del funcionamiento de la vegetación

ATRIBUTOS DESCRIPTORES DEL FUNCIONAMIENTO DEL DOSEL VEGETAL

Los atributos funcionales indicadores de la producción primaria anual, la estacionalidad y fenología de los ecosistemas mostraron un claro patrón altitudinal (Figura 2). Así, los valores más bajos productividad primaria se registraron en el crioro- y oromediterráneo (Figura 3 a y b), en pastizales, canchales, roquedos de alta montaña y borreguiles. Los valores más altos se observaron en el supra- y mesomediterráneo asociados a los robledales, encinares, repoblaciones de coníferas y pinares autóctonos de *Pinus sylvestris* subsp. *nevadensis*. En los extremos este y oeste del espacio protegido, en los pisos termo- y mesomediterráneos (Figura 3 a) se obtuvieron valores intermedios de productividad, siendo medio-altos en la zona occidental, y medio-bajos en la oriental, ambas dominadas por matorral, y pastos de media montaña (Figura 2 a y b).

Para la estacionalidad (Figura 2 c y d), entendida como coeficiente de variación de EVI, encontramos un patrón inverso al de la productividad, es decir, valores altos en el crioro- y oromediterráneo que disminuyen conforme bajamos en altitud hacia los pisos supra-, meso- y termomediterráneo (Figura 3 a). El crioro- y oromediterráneo se caracterizan por los ecosistemas más estacionales, como pastizales, canchales y roquedos de alta

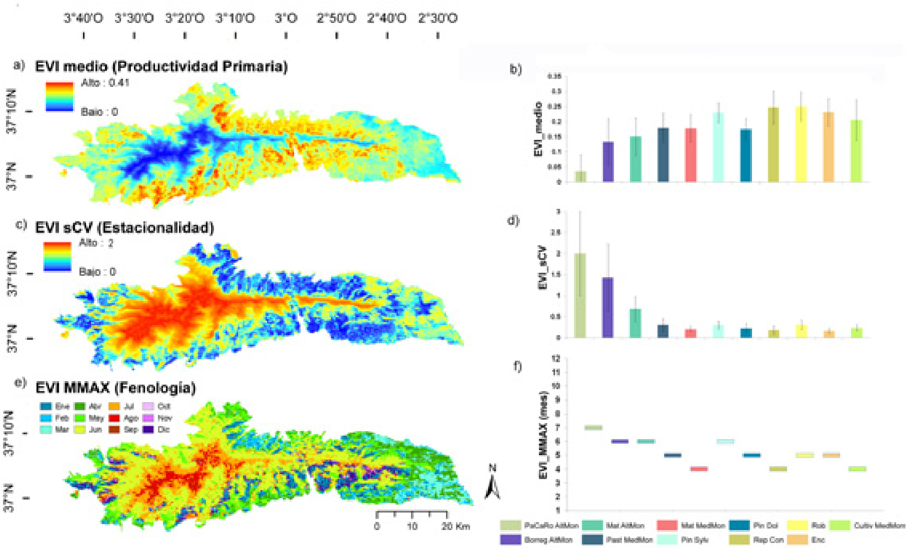

Figura 2. Atributos descriptores del funcionamiento del dosel vegetal basados en el índice de vegetación EVI (Enhanced Vegetation Index), derivado del producto MOD13Q1-TERRA (píxel 230 m) para el periodo 2001-2016. En el margen izquierdo aparecen los patrones espaciales de cada atributo funcional (EVI medio, sCV y MMAX) y en el margen derecho los valores medios de cada atributo por ecosistema. 1: PaCaRo AltMon: Pastizales, canchales y roquedos de alta montaña; Borreg: 2: Borreguiles; 3: Mat AltMon: Matorral de alta montaña; 4: Pas MedMon: Pastizal de media montaña; 5: Mat MedMon: Matorral de media montaña; 6: Pin Syl: Pinares autóctonos de *Pinus sylvestris* subsp. *nevadensis*; 7: Pin Dol: Pinares autóctonos sobre dolomías; 8: Rep Con: Repoblaciones de coníferas; 9: Rob: Robledal; 10: Enc: Encinar; 11: Cult MedMon: Cultivos de media montaña extensivos. Mapa de vegetación de Andalucía 1:10000 (1996-2006) (Bonet et al., 2010).

montaña, borreguiles, y matorral de alta montaña, donde las nevadas son el factor limitante determinante. En los pisos supra- y mesomediterráneo (Figura 3 a) encontramos también valores altos de estacionalidad debido a la presencia de robledales. Además, aparecen los pinares autóctonos de *Pinus sylvestris* subsp. *nevadensis* y los pastos de media montaña con valores medios de estacionalidad, y los encinares, las plantaciones de coníferas y los matorrales de media montaña con baja estacionalidad (Figura 2 d). Al descender más en altitud, hacia la parte oriental del espacio protegido,

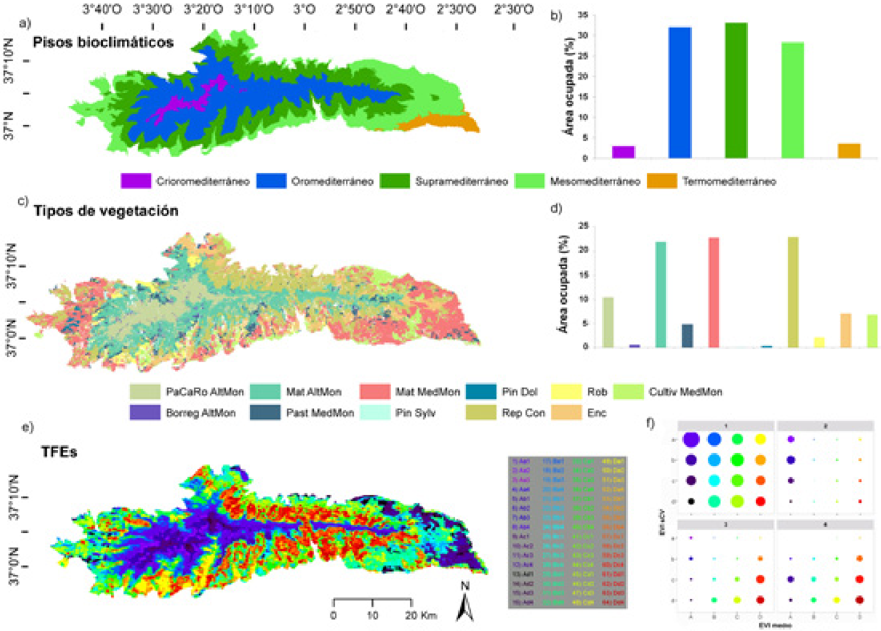

Figura 3. Clasificaciones ecológicas de Sierra Nevada. a) Pisos bioclimáticos y b) área ocupada por cada categoría; c) Tipos de vegetación y d) área ocupada por cada categoría; e) Tipos Funcionales de ecosistemas basados en el índice de vegetación EVI (Enhanced Vegetation Index), derivado del producto MOD13Q1-TERRA para el periodo 2001-2016 y d) Abundancia relativa de cada TFE. Las clases de TFEs están indicadas en la leyenda. PaCaRo AltMon: Pastizales, canchales y roquedos de alta montaña; Borreg: Borreguiles; Mat AltMon: Matorral de alta montaña; Pas MedMon: Pastizal de media montaña; Mat MedMon: Matorral de media montaña; Pin Syl: Pinares autóctonos de *Pinus sylvestris* subsp. *nevadensis*; Pin Dol: Pinares autóctonos sobre dolomías; Rep Con: Repoblaciones de coníferas; Rob: Robledal; Enc: Encinar; Cult MedMon: Cultivos de media montaña extensivos. Mapa de vegetación de Andalucía 1:10000 (1996-2006) (Bonet et al., 2010).

en los pisos meso- y termomediterráneo, los valores de estacionalidad volvieron a ser medio-altos (Figura 2 c).

Respecto a la fenología, en el crioro- y oromediterráneo, en los tipos de vegetación de pastizales, canchales, roquedos y borreguiles, dominó el momento de máximo verdor de la vegetación en verano (julio-agosto) (Figura 2 e). En el supra- y mesomediterráneo, asociados a los pastizales y matorrales de media montaña, pinares autóctonos, robledales y encinares, el momento de máximo verdor de la vegetación solía ocurrir en primavera tardía (mayo-junio). No obstante, algunos valles del oeste y del sur mostraron pequeñas zonas con máximo verdor durante los meses de otoño e invierno temprano, llegando incluso a ser de invierno en el extremo oriental termomediterráneo semiárido (Figura 2 f).

TIPOS FUNCIONALES DE ECOSISTEMAS Y SU RELACIÓN CON LOS TIPOS DE VEGETACIÓN NATURAL

Resultado de la combinación de los tres atributos funcionales del dosel vegetal, productividad media, estacionalidad y fenología, representados en la Figura 2, se obtuvo el mapa de TFEs (Figura 3 e) que recoge una caracterización sintética de los patrones espaciales del funcionamiento ecosistémico. Se observaron un total de 62 clases de las 64 posibles. Los TFEs más abundantes presentaron el máximo verdor en primavera, con valores de productividad de baja a intermedia y bajo todos los grados de estacionalidad posibles: Aa1, Ba1, Cb1, Cd1, Bb1, y Cc1 acumularon el 37% de la superficie de la Sierra. Por el contrario, los TFEs más raros fueron Bc2, Ca4 y Ba3, caracterizados por una productividad media, estacionalidad media o alta y un máximo de verano, invierno y otoño respectivamente. Por último, los que no aparecieron representados en el área de estudio correspondieron a ecosistemas poco productivos, muy estacionales y máximo de verdor en invierno: Aa4 y Ba4 (Figura 3 f).

El análisis de correspondencias sin tendencia (*Detrended Correspondence Analysis* (DCA)) (Figura 4) usado evaluar el grado de asociación entre los TFEs y los tipos de vegetación, ordenó los tipos de vegetación de Sierra Nevada con un marcado gradiente altitudinal de productividad. El primer eje (Dimensión 1) del DCA representó el 61% de la varianza de los datos y el segundo eje (Dimensión 2) el 24%. El gráfico está dividido en cuatro cuadrantes, donde los tipos de vegetación y funcionamiento de alta montaña se situaron en la margen derecha y los de media montaña en el centro y la margen izquierda. Por un lado, los tipos de vegetación del crioro- y oromediterráneo, presentaron TFEs de productividad baja e intermedia, muy estacionales y con momentos de máximo verdor principalmente en verano, pero también en primavera. En particular, los tipos de vegetación pastizales, canchales y roquedos se asociaron con los TFEs Aa2, Ab2, Ac3, mientras que los borreguiles con los TFEs Aa1, Ba1 y los matorrales de alta montaña

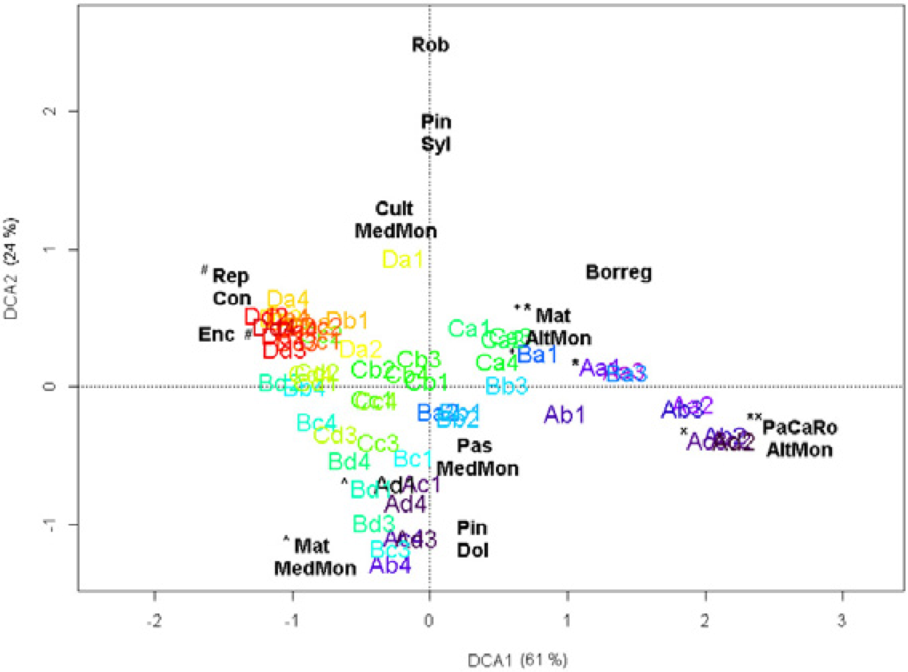

Figura 4. Análisis de correspondencias sin tendencia (Detrended Correspondece Analysis, DCA) entre funcionamiento (TFEs, ver leyenda de colores en la Figura 3) y tipos de vegetación. El primer eje (Dimensión 1) del DCA representó el 61% de la varianza de los datos y el segundo eje (Dimensión 2) el 24%. Las asociaciones significativas están marcadas con el mismo símbolo para el TFE y el tipo de vegetacion.

con Ba1, Bb3 (Figura 4). Las extremas condiciones para la vida en este ambiente, caracterizadas por escasa presencia de suelo (Martín Peinado et al., 2019), una elevada radiación solar, temperaturas extremas, fuertes vientos y precipitaciones en invierno en forma de nieve y hielo, dan lugar a un corto periodo vegetativo. Esto se traduce en la existencia de una escasa cobertura vegetal, limitada por las bajas temperaturas, que únicamente desarrolla su periodo vegetativo en verano, de ahí que estas áreas se hayan denominado como “desierto de frío” (Blanca et al., 2019). Los tipos de vegetación del supra- y mesomediterráneo, tuvieron asociados TFEs de productividad intermedia-alta, media-baja estacionalidad y momento de máximo verdor en primavera y otoño (e.g., Cc1-3) (Figura 4). El piso supramediterráneo se caracteriza por la presencia de especies de hoja caduca, e.g., robledales que fueron los tipos funcionales de ecosistemas más productivos y estacionales de la Sierra, con máximo en primavera (TFE Da1). El mesomediterráneo es donde tienen su óptimo las comunidades vegetales perennifolias (Rivas-Martínez y Arnáiz, 1984; Salazar y Valle, 2019). Ahí se diferenció un grupo de TFEs muy productivos, TFEs Cd1, Dc1, Da4, Db3, correspondientes a encinares y repoblaciones de coníferas. Además, encontramos pinares autóctonos asociados con el TFE Bb1, acompañados de pastos de media montaña y matorrales de media montaña, que se asociaron con los TFEs Bc3, Bc1, Bb1. En el termomediterráneo seco y semiárido del extremo oriental, caracterizado por especies termófilas, que apenas sufren heladas, se detectó un comportamiento funcional de los ecosistemas diferente. Este área presentó valores bajos de productividad, estacionalidad medio-baja y máximo verdor de la vegetación en primavera o invierno (e.g., Ac1-4). Aquí, el principal control de funcionamiento ecosistémico es la disponibilidad de agua, con especies vegetales que presentan una rápida respuesta a los escasos aportes hídricos (Cabello et al., 2012b) (Figura 4).

Diversidad funcional a nivel de ecosistema

La riqueza osciló entre 1 y 12 TFEs por ventana móvil de ~1 km^2. La mayor riqueza de TFEs se observó en los pisos supra- y mesomediterráneo, particularmente en la cara sur de la Sierra (Figura 5 a), donde el número de series de vegetación también es mayor que en otros pisos bioclimáticos (Valle et al., 2003). La presencia de puntos calientes de riqueza de TFEs principalmente en la media montaña, y en particular en la cara sur, podría estar relacionada con dos factores. Por un lado, muchas montañas mediterráneas muestran altos valores de diversidad beta hasta los 1750-1800 m (Wilson y Schmida, 1984; Peñas et al., 1995), y a partir de estas cotas existe un importante reemplazamiento en la estructura y composición de la vegetación. Por otro lado, en la media montaña y especialmente en su cara sur existe un mosaico muy diverso de distintos tipos de vegetación natural mezclada con diferentes tipos de repoblaciones forestales, cultivos y aprovechamientos tradicionales (Camacho et al., 2002), lo que les confiere el calificativo de paisajes multifuncionales desde el punto de vista del suministro de servicios ecosistémicos (García-Nieto et al., 2013; Mastrangelo et al., 2014; Cabello et al., 2019).

Molero Mesa et al. (1996) y Fernández Calzado et al. (2012) señalaron que la riqueza florística de Sierra Nevada decrece con la altitud, al tiempo que se incrementa el porcentaje de taxones endémicos (Blanca et al., 2019).

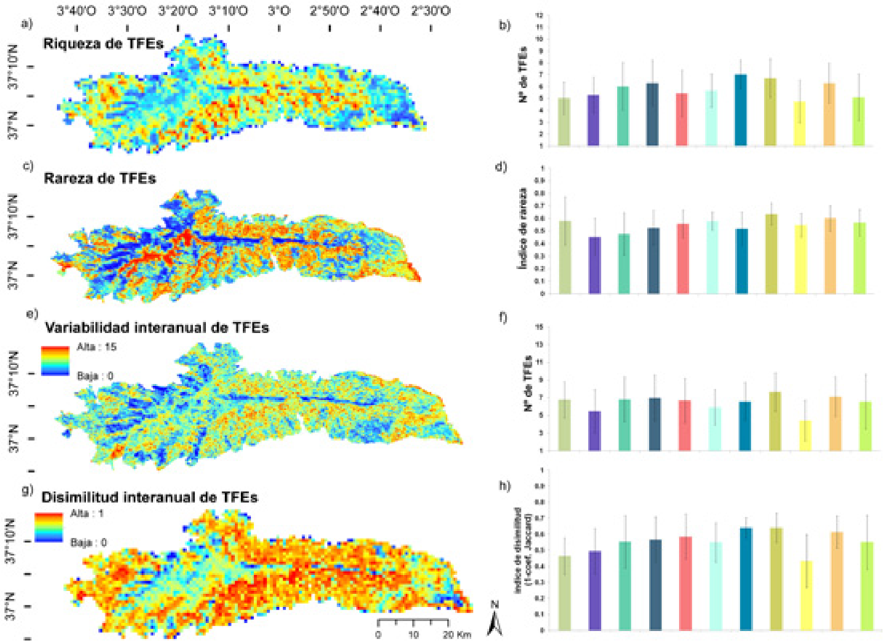

Figura 5. Patrones de diversidad funcional basados en el índice de vegetación EVI (Enhanced Vegetation Index), derivado del producto MOD13Q1-TERRA para el periodo 2001-2016. a) Patrones espaciales de riqueza de TFEs a partir de una ventana móvil de 4x4 píxeles MODIS (~ 1 km2) y b) valores de riqueza por ecosistema; c) Patrones espaciales de rareza de TFEs y d) valores por ecosistema; e) Variabilidad interanual de TFEs para el periodo y f) valores por ecosistema; g) Disimilitud interanual de TFEs o 1 - coeficiente de Jaccard para el periodo y h) valores por ecosistemas. PaCaRo AltMon: Pastizales, canchales y roquedos de alta montaña; Borreg: Borreguiles; Mat AltMon: Matorral de alta montaña; Pas MedMon: Pastizal de media montaña; Mat MedMon: Matorral de media montaña; Pin Syl: Pinares autóctonos de *Pinus sylvestris* subsp. *nevadensis*; Pin Dol: Pinares autóctonos sobre dolomías; Rep Con: Repoblaciones de coníferas; Rob: Robledal; Enc: Encinar; Cult MedMon: Cultivos de media montaña extensivos. Mapa de vegetación de Andalucía 1:10000 (1996-2006) (Bonet et al., 2010).

En la diversidad funcional de ecosistemas se observa algo similar, ya que la máxima riqueza se encuentra en pisos de altitud media. Concretamente, como tipos de vegetación con alta riqueza funcional, aparecen los pinares autóctonos sobre dolomías (riqueza 7), que también han sido identificados como zonas de elevada riqueza de especies endémicas (Mota et al., 1996; 2019). También muestran alta riqueza funcional los pinares de repoblación (riqueza 6-7), lo que se explica porque las masas de coníferas de Sierra Nevada funcionan de maneras muy distinta entre ellas (Cabello et al., 2016; Reyes et al., 2016). Esto muestra que pese a la alta densidad, monoespecificidad y coetaneidad de las repoblaciones de coníferas (Zamora et al., 2015), las distintas especies utilizadas (Aragonés et al., 2019), las condiciones locales (e.g., el suelo), las perturbaciones (e.g., plagas, incendios, decaimiento forestal) (Hódar et al., 2012), y con total seguridad las acciones de gestión (e.g., naturalización y diversificación de las masas de pinares durante la última década) (Bonet et al., 2009; Gómez-Aparicio et al., 2009) han modificado el funcionamiento de estas manchas de forma diferente en distintos lugares, consiguiendo que, al menos a nivel de funcionamiento ecosistémico, sean bastante heterogéneas a escala regional (Figura 5 b).

Los matorrales de alta montaña, y los pastizales de media montaña también estuvieron entre los tipos de vegetación más ricos en TFEs diferentes (riqueza 6). Los primeros son zonas con gran riqueza de flora endémica (Lorite, 2001; 2016), mientras que los segundos se han utilizado tradicionalmente para la actividad ganadera, cuya intensidad ha cambiado en los últimos años (Camacho et al., 2002), lo que podría reflejarse en los distintos tipos de funcionamiento observados.

Las zonas con menor riqueza de TFEs se situaron en los pisos oro- y crioromediterráneo, y en el extremo oriental termomediterráneo semiárido, donde las duras condiciones edafoclimáticas (Martín Peinado et al., 2019) causan una disminución en la diversidad florística, aunque promuevan una alta endemicidad (Fernández Calzado et al., 2012). Por ecosistemas, los valores más bajos de riqueza de TFEs (riqueza 4-5), se dieron en los robledales supramediterráneos. La baja heterogeneidad espacial observada en el funcionamiento ecosistémico de cada una de las manchas de robledal, observada también por Dionisio et al., (2012) y Requena-Mullor et al., (2018), puede deberse tanto a la homegeneidad interna de sus condiciones ambientales, como de su composición florística (Pérez-Luque et al., 2015; Requena-Mullor et al., 2018).

La rareza de TFEs fue máxima en el crioromediterráneo, coincidiendo con el área con mayor concentración de endemismos nevadenses (Cañadas et al., 2014; Peñas et al., 2019) (Figura 5 c). La vegetación crioromediterránea se desarrolla bajo unas condiciones ecológicas muy particulares que determinan unos tipos de funcionamiento ecosistémico poco comunes (rareza 0,6; Figura 4 d), como por ejemplo, en los roquedos y canchales relativamente móviles situados en fuertes pendientes, donde el porcentaje de rareza o endemicidad de especies se eleva hasta un 80% (Blanca y Algarra, 2011). La rareza de TFEs también fue muy alta en el extremo oriental termomediterráneo semiárido, situado ya en el sector biogeográfico Almeriense (Peñas et al., 2019), con alta concentración de endemismos propios del Desierto de Tabernas (Mota et al., 2004) (Figura 5 c). En el oromediterráneo la rareza de TFEs disminuyó bruscamente, alcanzando su mínimo, debido a la gran extensión en Sierra Nevada de este piso bioclimático (Figura 3 a y b), que hizo que su funcionamiento no apareciese como raro, y volviendo a aumentar en el supra- y mesomediterráneo (Figura 5 c). Los tipos de vegetación supra- y mesomediterráneas de mayor rareza se correspondieron con repoblaciones de coníferas y encinares (rareza 0,6), las cuales también se diferenciaron del resto en el análisis de correspondencias sin tendencia (Figura 4, Figura 5 d). La elevada rareza promedio de las repoblaciones de coníferas puede deberse a que, en el contexto del espacio natural protegido, las perturbaciones o intervenciones de gestión dan lugar a funcionamientos singulares en las distintas masas de coníferas, por los motivos mencionados anteriormente. Por otro lado, la rareza en los encinares puede deberse a que su funcionamiento es muy exclusivo, es decir, tienen TFEs muy concretos asociados (e.g., Cc1, Dc1). No obstante, la rareza promedio de los distintos tipos de vegetación (entre 0,45 y 0,64) quedó lejos del máximo posible de rareza (1).

Estabilidad en el funcionamiento de los ecosistemas

La variabilidad interanual osciló entre 1 y 15 TFEs diferentes a lo largo del periodo de 16 años para un mismo píxel (Figura 5 e y f). El número de TFEs que se observó en un mismo píxel a lo largo de los 16 años fue mayor en los pisos supra- y mesomediterráneos, coincidiendo con el rango altitudinal donde más afecta la variabiliadad climática interanual (e.g., pueden presentar mucha nieve en años fríos y verse afectados por sequía en años secos y cálidos). En estas zonas, los tipos de vegetación que más variaron su funcionamiento durante el periodo de estudio fueron los encinares, las repoblaciones de coníferas (quizá por las mismas razones explicadas anteriormente en relación a la riqueza y rareza de TFEs, como las perturbaciones y las acciones de gestión), los pastos de media montaña y el matorral de alta montaña (ecosistemas sometidos a importantes cambios en los usos y manejo del suelo, especialmente drásticos en el caso de la ganadería durante las últimas décadas). Alcaraz-Segura et al., (2015) ya identificaron las plantaciones de coníferas y los encinares como zonas con tendencias significativas en el índice de vegetación, lo que también produciría una mayor variabilidad interanual relacionada con ese cambio direccional. También destaca la gran variabilidad interanual del extremo oriental termomediterráneo semiárido, donde existe una mayor fluctuación del clima y donde pequeños cambios en la precipitación producen grandes cambios en la dinámica de la producción primaria (Houérou et al., 1988; Cabello et al., 2012b), al igual que el área incendiada en 2005 cerca de Lanjarón, donde el incendio eliminó la vegetación que se viene regenerando desde entonces. Por otro lado, los tipos de vegetación más estables interanualmente, es decir, los que menos cambiaron durante el periodo, se situaron en los pisos meso- oromediterráneo y crioromediterráneo, concretamente robledales y borreguiles, ecosistemas sometidos a una baja presión antrópica (e.g., baja gestión forestal y baja presencia de ganado).

Los resultados de la inversa del coeficiente de Jaccard para obtener la disimilitud o los cambios funcionales entre años en la composición de TFE a lo largo del periodo 2001-2016 (Figura 5 g y h), mostraron un patrón altitudinal donde la disimilitud entre TFEs fue menor en el piso oro- y crioromediterráneo (pastizales, canchales y roquedos de alta montaña junto con borreguiles), así como en los robledales del mesomediterráneo (estabilidad funcional ya mostrada por otros autores, i.e. Requena-Mullor et al., 2018). Dicho patrón de disimilitud aumentó hacia pisos inferiores, encontrando los valores más altos de disimilitud (o mayores de cambio) en zonas donde los cambios de uso y manejo del suelo son más importantes (Zamora et al., 2015). Como ocurre en los pinares autóctonos sobre dolomías, las repoblaciones de coníferas y los encinares meso- y termomediterráneos. Además, el extremo Este del Sierra Nevada tuvo un área con bajos valores de disimilitud, es decir, no existieron cambios significativos a lo largo de los años.

Conclusión

Este estudio proporciona una caracterización del funcionamiento de los ecosistemas de Sierra Nevada mediante el análisis de series temporales de imágenes de satélite de índices espectrales que recogen la actividad fotosintética de la vegetación. La combinación de los atributos funcionales en una clasificación sintética de Tipos Funcionales de Ecosistemas, integra en un solo mapa la heterogeneidad espacial y temporal de las ganancias de carbono por parte de la vegetación. Por otro lado, el empleo de los TFEs como entidades biológicas permitió analizar los patrones espaciales y la variabilidad interanual en la diversidad funcional a nivel de ecosistema y reveló la existencia de puntos calientes de riqueza y rareza funcional en la Sierra, así como de zonas más estables y otras con mayor variabilidad entre años.

Conocer y describir las dinámicas del funcionamiento ecosistémico del conjunto de Sierra Nevada sienta las bases para poder conservar y gestionar la biodiversidad funcional de manera eficaz y para incorporar los procesos ecológicos a escala de ecosistema en la gestión del área protegida. De hecho, ya existen programas de seguimiento basados en índices de vegetación, derivados de imágenes de satélite, (e.g., sistema REMOTE, Cabello et al., 2016) cuyo objetivo es informar a los tomadores de decisiones y gestores de la Red de Parques Nacionales de España de la salud y estado de conservación de los ecosistemas de cada parque, entre los que se incluye Sierra Nevada.

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Incorporating ecosystem functioning in ecology and conservation is key to promote sustainability and a safe operating space for humanity. Actually, variables describing ecosystem functioning are widely demanded to define essential biodiversity variables, a framework to coordinate biodiversity monitoring programmes worldwide. This PhD Thesis provides remote-sensing based conceptual and methodological advances to incorporate the functional dimension of biodiversity at ecosystem level in ecology and conservation biology through the application of the Ecosystem Functional Type (EFT) concept, i.e., groups of ecosystems or patches of the land surface with similar dynamics of matter and energy exchanges between the biota and the physical environment