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Patterns of ecosystem functioning as a 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. Incorporating 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. This article aims 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 a 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 southern tropical zone, with a desert transition area between them. However, differences between the functional characterization and some ecoregions were detected in ecoregions identified as discrepancy areas between authors. In particular, some ecoregions considered Mediterranean showed a Desert character in its functioning, and others considered as Desert were Tropical functionally. EFTs remotely sensed measured at regional scales provide the basis for a more comprehensive regionalization of geographical patterns of life and, therefore, an improvement for future conservation purposes.

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

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Introduction

Understanding how geographical patterns 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 available 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 based on 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. It allows us to organize our understanding of how major terrestrial ecosystems work and 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

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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).

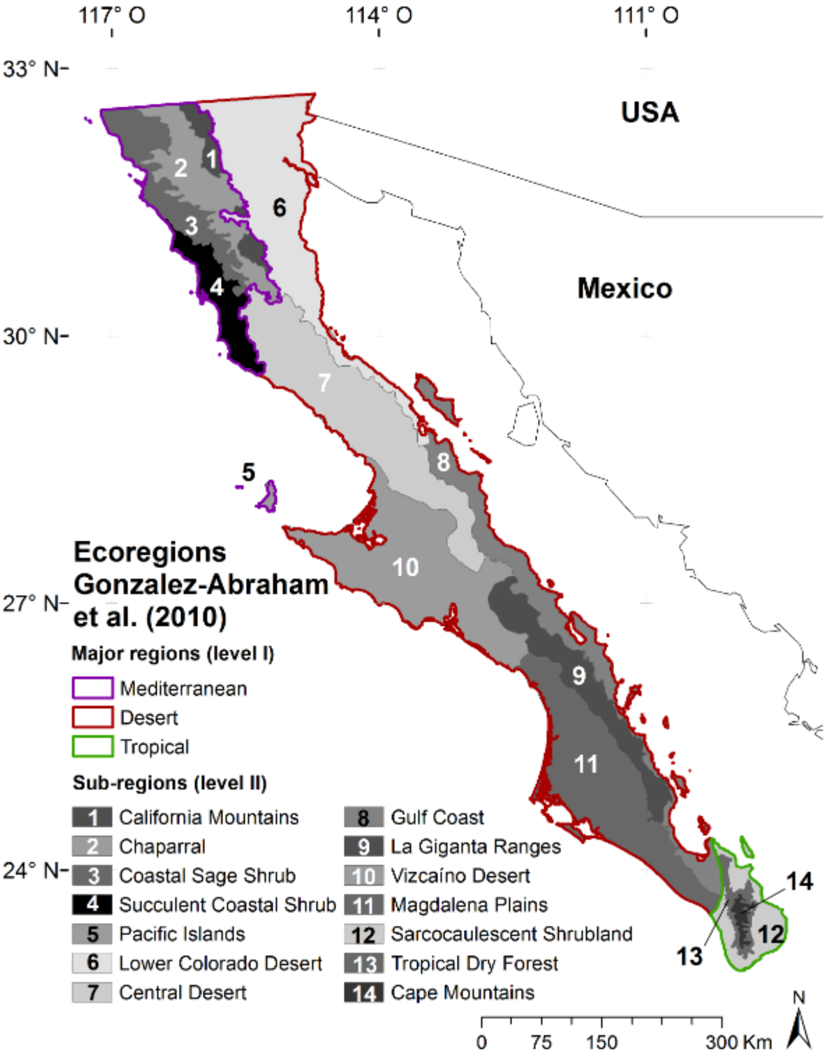

Figure 1. Study area and ecoregions by González-Abraham *et al.* (2010).

Ecologists are currently better equipped than ever before to explore 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 Functional Ecosystem 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 & Wall, 2001). Thus, EFTs are identified by three meaningful metrics derived from the annual dynamics of EVI 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 wide 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).

Materials 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).

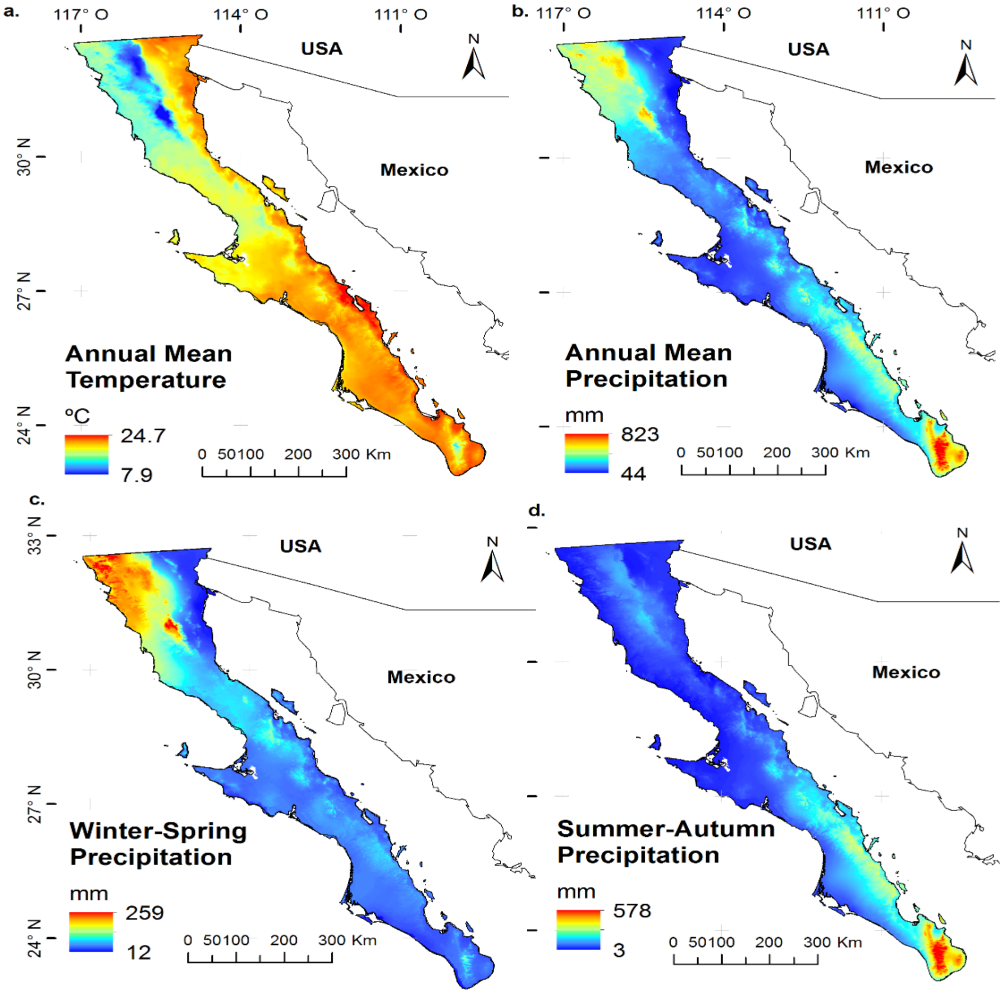

Figure 2. Climate description of the study area. a) Annual Mean Temperature in ºC; b) Annual Mean Precipitation in millimeters (mm); c) Winter-Spring Precipitation (mm); and d) Summer-autumn Precipitation (mm). Data from WorldClim version 2.1 (Fick & Hijmans, 2017).

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 asl) (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 asl–, and a long dry season (Farfán & Fogel, 2007).

Functional geography of ecosystems

We characterized the geography of a Key ecosystem function, 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. We chose as intervals the four seasons in the case of phenology, 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 those sample units from being grouped 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.

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,...).

At a 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 identify the northwestern Mediterranean area, the southern tropical zone, and the desert transition areas between them. Despite this climate-based pattern, these three functional regions presented differences concerning 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 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 Shrub, Succulent Coastal Shrub) 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 González-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.

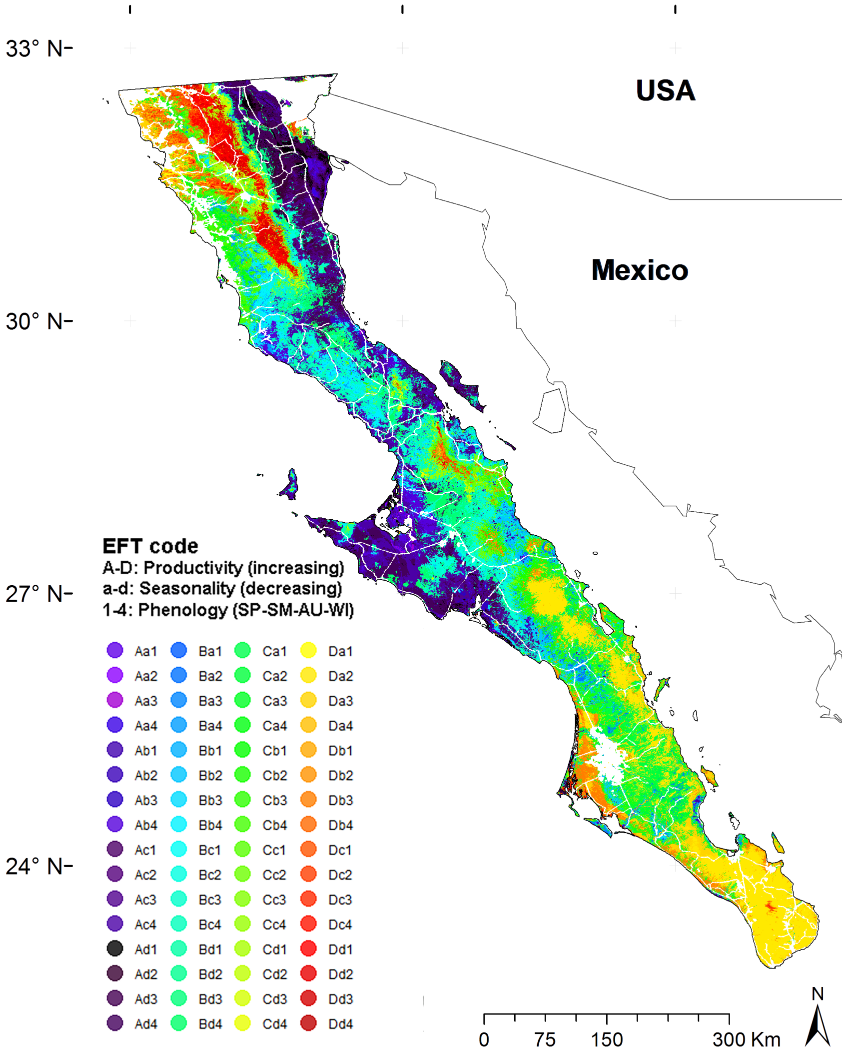

Figure 3. Ecosystem Functional Types based on EVI-MODIS dynamics for 2001–2017 period (230×230 m pixel). EFT categories were indicated in the legend. Human transformed areas appeared in white.

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 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). It 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).

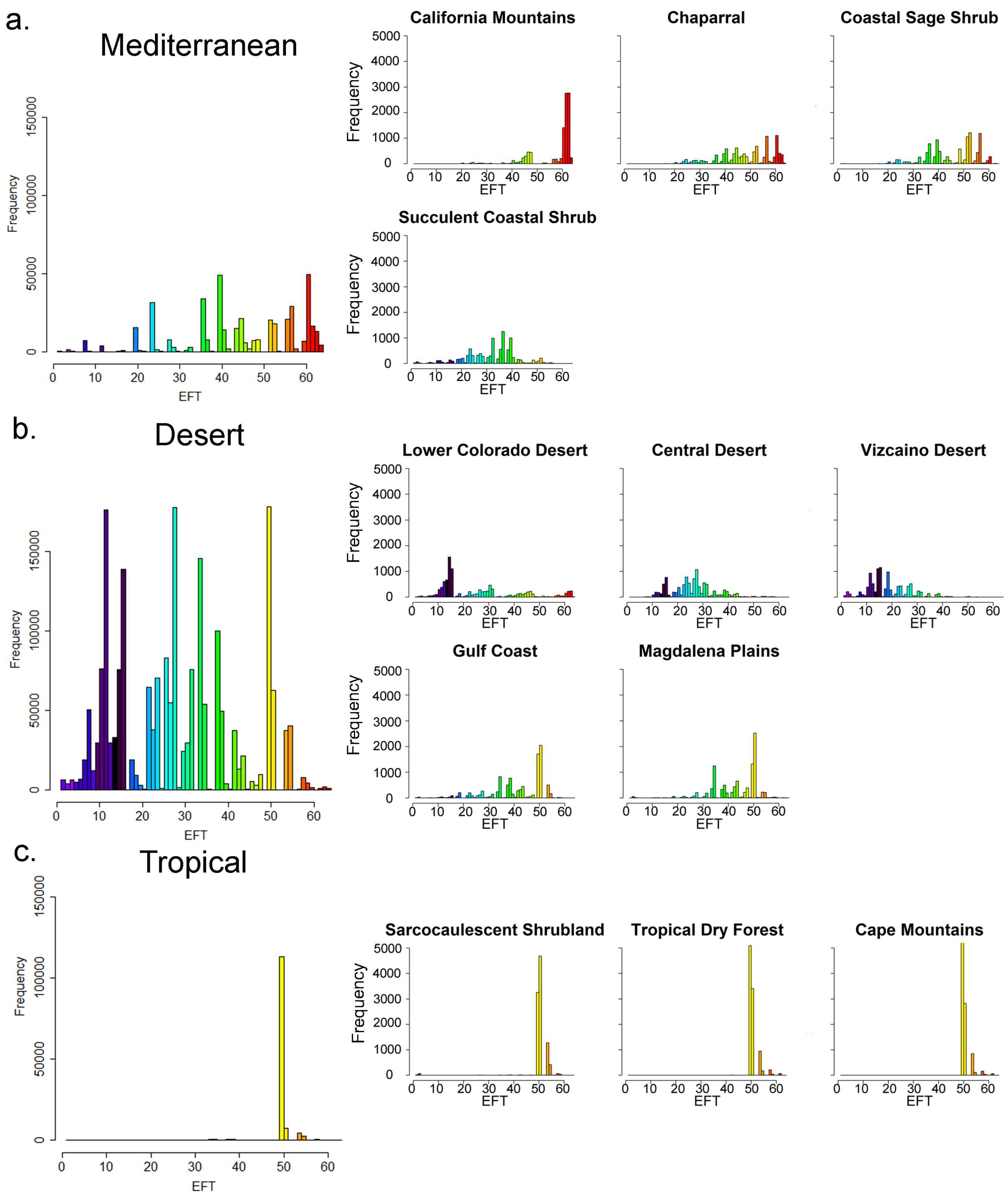

Figure 4. Functional characterization of ecoregions. EFT frequency histograms in major regions (level I) and sub-regions (level II) ordered in a latitudinal range: a, Mediterranean; b, Desert; and c, Tropical. Colours correspond to the EFTs, see legend in Figure 3.

Correspondence between geographical patterns of ecosystem functioning and ecoregions

Detrended Correspondence Analysis (DCA, Figure 5) showed that three major regions of the Peninsula were 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 the one hand, Pacific Islands appeared functionally separated from the other Mediterranean ecoregions and associated with a climatic desert. On the other hand, Succulent Coastal Shrub, 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, in the ecoregions map, the southern part of Desert region 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.

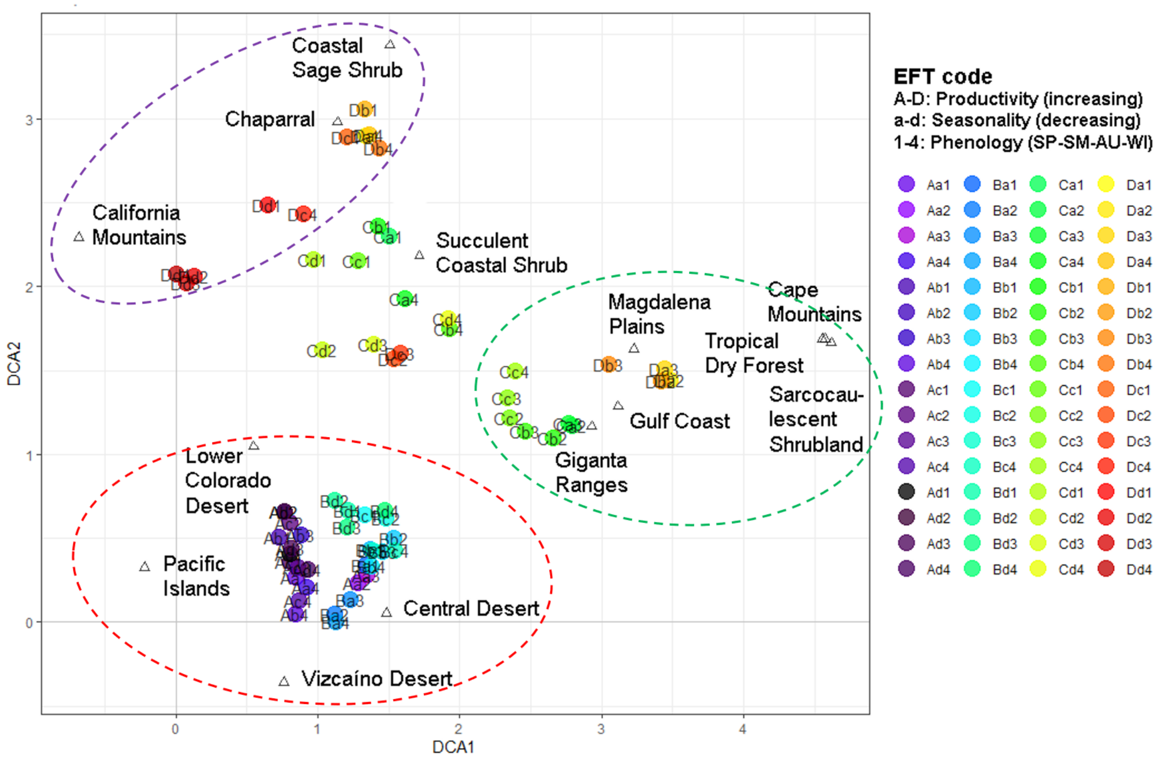

Figure 5. Ordination plot of dimension 1 and dimension 2 of the Detrended Correspondence Analysis (DCA) run with the contingency matrix between Ecosystem Functional Types, EFTs (circles) and ecoregions (triangles) in the Baja California Peninsula. See EFT codes in legend. Dotted circles represented the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

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 was 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 similar to the Tropical region than to the rest of the desert ecoregions, and ecoregions inside the Tropical region were functionally similar. These results emphasize 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 27.5ºN) (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 Vizcaíno Desert ecoregions); however, in the Gulf Coast, the Southern desert extends to reach next to 28ºN, 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. Besides the transitional climate 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) produces the high 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 León 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, 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, a climate gradient in altitude (Peinado *et al*., 2011) 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 31ºN, 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, 1999), 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 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. 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 and the more recent functional approaches based on functional traits at the 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 on land plots, 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).

Conclusion

Our work highlights those 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, also improving the future conservation purposes.

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