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Interactions of past human disturbance and aridity trigger abrupt shifts in the functional state of Mediterranean holm oak woodlands

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ABSTRACT

Empirical evidence of the vulnerability of dryland ecosystems to suffer abrupt changes in response to global change is highly needed to assess the applicability of threshold models, understand the underlying mechanisms and anticipate the onset of abrupt shifts.

We study the onset of abrupt changes in Mediterranean holm oak (*Quercus ilex*) woodlands, by analyzing the combined effect of past human disturbance (mainly deforestation) and aridity on the functional state of these ecosystems. We determine ecosystem state in terms of herbaceous/woody species ratio, species richness and soil properties related to carbon and nitrogen cycling and microbial activity. The influence of both drivers was determined along spatial gradients of past human disturbance (from lightly to highly disturbed areas) and aridity (three levels: sub-humid, dry-transition, semi-arid).

Our results show a strong interaction between aridity and past human disturbance on soil and vegetation properties. As disturbance increased, soil function decreased linearly in semi-arid and dry-transition conditions, but the trend was non-linear in sub-humid conditions. The latter showed a sharp decline at low-to-moderate disturbance intensity followed by a gentle recovery at higher intensities. These patterns were consistent for all soil properties. Structural changes in vegetation along the disturbance gradient, from open woodlands to shrublands in semi-arid and dry-transition conditions and from dense woodlands to grasslands in sub-humid conditions accompanied the linear vs non-linear patterns in soil function, respectively. Our results evidenced the existence of a critical climatic threshold in the boundary between sub-humid and dry-transition conditions, where the ecosystem switched from a fertile grassland to a highly degraded shrubland at moderate-to-high levels of disturbance (shrub encroachment), losing its capacity to buffer the effects of increasing disturbance. We propose a conceptual model illustrating the ecological mechanisms that may be underlying the onset of such abrupt shift.

1. Introduction

Ecosystems are experiencing major changes at an unprecedented rate due to complex interactions between climatic fluctuations and disturbances caused by human activities (MEA, 2005). Future global change scenarios forecast a reduction of ecosystem functionality associated with desertification processes in sub-humid to arid climatic conditions (D'Odorico et al., 2013; Scheffers et al., 2016). Understanding how ecosystems undergo environmental change has become a question of considerable interest that needs to be deeply explored to improve our ability to predict the impact of global change on natural ecosystems and the services they provide (Trumbore et al., 2015).

According to theoretical models, the loss of ecosystem functionality in response to environmental change and human disturbance may be gradual and linear, or it may display non-linear dynamics with the onset of a single (Scheffer et al., 2001, 2009) or a series (Whisenant, 1999) of

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abrupt changes in the functional state of the ecosystem. Recent models suggest that drylands (i.e. arid, semi-arid and dry sub-humid ecosystems), and more particularly those in arid and semi-arid climatic conditions, are prone to such non-linear functional changes and critical transitions (Scheffer et al., 2001; Rietkerk et al., 2004; Lohmann et al., 2012; D'Odorico et al., 2013). Arid and semi-arid ecosystems are spatially self-organized by a series of scale-dependent feedbacks between plant growth and resource availability (short-range facilitation and long-range competition) that make them particularly vulnerable to non-linear functional changes, because increasing external pressure may imbalance the feedback mechanisms underlying self-organized patchiness and ecosystem stability (Schlesinger et al., 1990; Rietkerk et al., 2004; Kéfi, 2019). However, empirical evidence of such abrupt changes has been lacking (Scheffer et al., 2009), albeit with a few exceptions providing evidence of abrupt shifts in the transition zone between semi-arid and arid conditions (Kéfi et al., 2007; Berdugo et al., 2017, 2020). This information is critical, because drylands cover up to 41% of the Earth's terrestrial surface and host more than one-third of the global population (MEA, 2005; Reynolds et al., 2007).

The Mediterranean region is projected to be one of the most vulnerable regions to global change (Schröter et al., 2005; Giorgi and Lionello, 2008). Human-induced degradation and climatic alterations are major global drivers of change in the functioning of Mediterranean ecosystems, including forests (Sala et al., 2000). The long history of land use in the Mediterranean region, particularly intense in the last 3500 years (Stevenson, 2000), has led to a significant loss of forest area, an increase of landscape fragmentation, a rapid decline of remnant forests, and a reduction of functionality which might be irreversible in some cases (Valladares et al., 2014). Recent studies highlight the long-term impact of former land use on the current state and dynamics of Mediterranean forest ecosystems through functional changes in vegetation and soil properties (Lloret et al., 2009; Navarro-González et al., 2013). Moreover, future climate change scenarios for the Mediterranean region forecast an increase in aridity during the 21st century, with a reduction in water availability for plants and an increase in evapotranspiration (Giorgi and Lionello, 2008; IPCC, 2013). Numerous studies have evidenced that aridity negatively impacts forest productivity and tree growth (Ogaya et al., 2003, FAO and Plan Bleu, 2018), enhances tree mortality and limits plant recruitment (Lloret et al., 2004, 2009). Aridity also decreases soil biological activity and organic matter decomposition rate and, as a consequence, affects belowground biogeochemical cycles and soil nutrient availability (Curiel Yuste et al., 2007). Although the interaction of multiple drivers may speed up ecosystem degradation or enhance the onset of critical transitions (Moreno-de las Heras et al., 2018), recent studies have mainly focused until now on the effects of single drivers, rather than multiple drivers, on the state of Mediterranean forest ecosystems (Doblas-Miranda et al., 2015; Valladares et al., 2014). In line with this, Doblas-Miranda et al. (2015) emphasize among the challenging research priorities for Mediterranean terrestrial ecosystems in the face of global change the current influence of historical land use in forest ecosystems susceptible to increases in aridity.

Holm oak (*Quercus ilex* L.) forests are among the most representative ecosystems in the Mediterranean basin and the Iberian Peninsula (Terradas, 1999). They are biologically, economically, and culturally significant ecosystems that provide essential ecosystem services to human population (Marañón et al., 2012). As a result of the long history of human use during the last millennia (mainly deforestation for fuel, domestic livestock and agricultural demand, Aranbarri et al., 2014), holm oak forests have undergone a significant reduction of their range and changes in their structure (Terradas, 1999). In many instances, dense forests have changed to grasslands or shrublands with few scattered holm oak trees, resulting in a wide variety of degradation levels that are visible in our current landscapes (Terradas, 1999).

In this study, we aim at (1) analyzing the interacting effect of past human disturbance (mainly deforestation) and aridity on the state of holm oak woodlands in terms of herbaceous/woody species ratio, species richness and soil properties related to carbon and nitrogen cycling and microbial activity, and (2) identifying the onset of abrupt functional changes in holm oak woodlands along a past human disturbance gradient under different climate aridity levels. For this purpose, we used spatial gradients of past human disturbance (from lightly to highly disturbed areas) and aridity (three levels: sub-humid: SH, dry-transition: DR, semi-arid: SA).

According to models that predict arid and semi-arid drylands are particularly prone to abrupt changes, we hypothesize dense holm oak woodlands in sub-humid conditions would show a linear decrease of their functional state in response to increasing past human disturbance, whereas in semi-arid conditions, opened holm oak woodlands would undergo non-linear trends with abrupt changes in their functionality at critical thresholds of past human disturbance. In dry-transition conditions, an intermediate behavior would be expected.

2. Materials and methods

2.1. Study area

The study was conducted in a large 20,000 km^2 region of Eastern Spain, in the eastern part of the Iberian System that includes areas of the Tajo, Ebro, Turia and Mijares river basins (Fig. 1; see Moreno-de-las-Heras et al., 2018 for a detailed description of the study area). The Iberian System is a northwest-southeast oriented mountain range between the Ebro valley and the central Plateau. The climate is Mediterranean with mean annual precipitation (MAP) and temperature ranging, respectively, from 350 to 700 mm and 9.0 °C to 12.5 °C. Evapotranspiration (PET) varies between 850 and 950 mm and resulting aridity (Ar), defined as (1-MAP/PET), ranges from 0.25 to 0.65 (from sub-humid to semi-arid conditions, respectively). Ar is a function of the UNEP aridity index (Ai = MAP/PET; Middleton and Thomas, 1992) and its value increases as conditions get drier. Ar values were calculated using mean annual precipitation data from the digital climatic Atlas of the Iberian Peninsula (Ninyerola et al., 2005, http://opengis.uab.es/wms/iberia/, 1951–1999 period) and potential evapotranspiration data from the world Global Potential Evapo-Transpiration (Potential-PET) Dataset of the CGIAR-Consortium for Spatial Information (Trabucco and Zomer, 2009, https://cgiarcsi.community/data/global-aridity-and-pet-database/, 1950–2000 period).

Holm oak woodlands in the study area suffered from a long history of human land use during the last 3500 years, mainly wood consumption for fuel, timber and charcoal production, livestock and agriculture (Aranbarri et al., 2014). Historical studies point out that land use pattern was homogeneous in the whole study area, in terms of types and intensities of human activities, at least from the Middle Ages to the present (Pascua Echegaray, 2012).

2.2. Plot selection criteria and characteristics

Plots used in this study were a subset of a large set of 138 plots (231 × 231 m) from a previous study that were selected within the study area through large-scale GIS exploration and met the following homogeneous criteria: holm oak woodlands, located on high (between 1025 and 1420 m a.s.l.), flat (slope $< 5°$ with no signs of erosion) areas on calcareous parent materials (i.e. limestones and dolomites from Cretaceous or Jurassic origin) (see Moreno-de las Heras et al., 2018 for a detailed description of plot selection procedure). This imposed homogeneity in the selection criteria aimed to minimize the influence of environmental factors others than the factors of interest under study (i.e. aridity and past human disturbance) on the variables studied (here, vegetation and soil properties).

Under these homogeneous conditions, soils in the selected plots were red Mediterranean soils with high amounts of calcareous coarse fragments, a silty-clay/clay texture (53 ± 15% clay), red/reddish colors, high organic matter contents (5–15%) and neutral to alkaline *pH* (7–8.2 in H_2O). Surface organic/organic-mineral horizons varied in depth

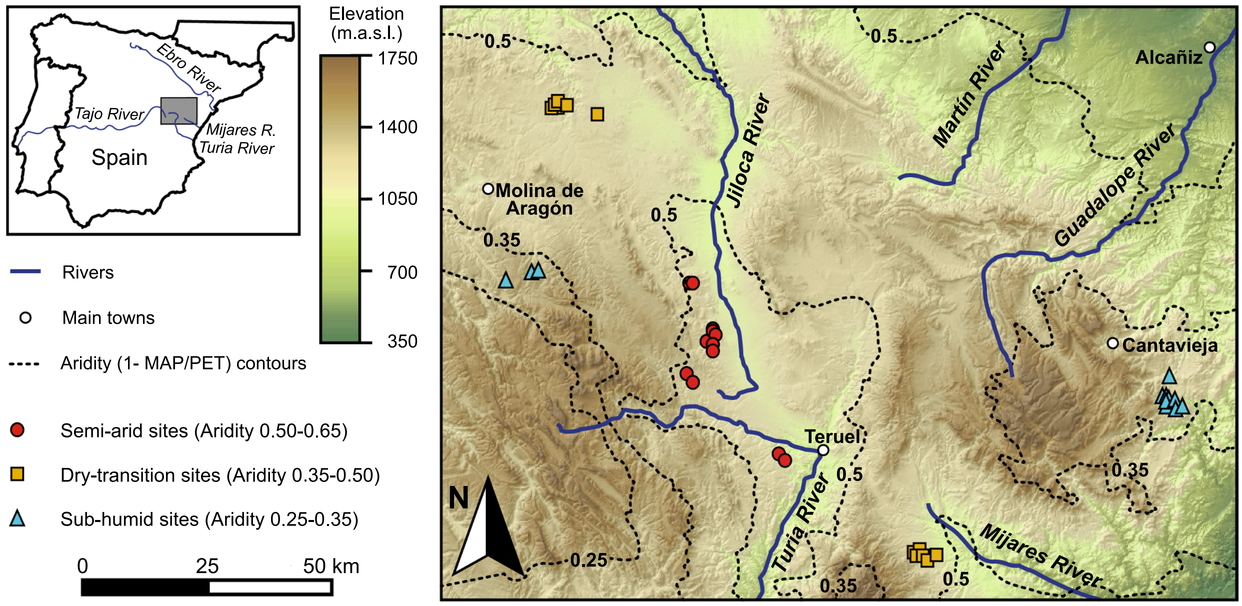

Fig. 1. Map of plot location. Within the approximately 20,000 km^2 study area, total number of plots is 36, with 12 plots per climate aridity level (semi-arid, dry-transition and sub-humid) distributed along a past human disturbance gradient. Aridity, Ar = 1- MAP/PET (where MAP is mean annual precipitation and PET is potential evapotranspiration).

(0–30 cm), and subsurface clay red-colored argillic horizons were embedded in rock cracks and distributed between outcrops of the parent material.

Holm oak woodlands in the selected plots were dominated mainly by *Q. ilex* trees with, in some cases, an anecdotal presence of other tree species (e.g. *Pinus nigra, Quercus faginea, Juniperus thurifera*).

Plot selection was validated in the field by visiting the plots and confirming that *Q. ilex* was the dominant tree species. We also checked that plots included at least one single *Q. ilex* tree, and when there were only a few individuals of *Q. ilex* in the plots, we confirmed *Q. ilex* dominance in the adjoining plots. Finally, we confirmed that selected plots showed no evident signs of agriculture (absence of terraces and regular patterns) or fire (absence of burnt trunks, that usually decompose slowly in such environments).

2.3. Climate aridity classes and past human disturbance gradient

We selected a total of 36 plots among the above-mentioned more extensive set of plots, equally divided in three climate aridity levels (Ar: 0.25–0.35, 0.35–0.50 and 0.50–0.65, for sub-humid, dry-transition and semi-arid, respectively; Fig. 1). Within each aridity level, the 12 selected plots were distributed along a gradient of cover and forest structure, from plots with practically zero cover of holm oaks to plots covered by holm oak woodlands. This gradient is closely related to the intensity of human deforestation in the past, as verified in a previous study in the same study area based on a large number of holm oak woodlands selected according to the same homogeneous selection criteria used for plot selection and showing different forest structures and *Q. ilex* covers at the plot scale (N = 138, Moreno-de las Heras et al., 2018). These authors found no effect of geomorphological site conditions (such as slope aspect and angle) on *Q. ilex* tree cover because of the gentle and homogeneous topographic conditions in the selected woodlands. On the contrary, they reported a significant decrease in tree cover with site proximity to the nearest human settlements. This effect results from the well-described traditional land use patterns in the Mediterranean Basin, where human activities (such as wood consumption for fuel, timber and charcoal production, domestic livestock and agriculture) and their effects on tree cover development (mainly deforestation) are typically nucleated near human settlements (e.g. Grove and Rackham, 2001; Millington et al., 2008; Barton et al., 2010). These results support the idea that actual tree cover is a legacy of the historical alterations suffered by the vegetation during more than 3500 years in this region.

In line with these results, we used the DI index of disturbance intensity developed by Moreno-de las Heras et al., 2018 to describe the intensity of past human disturbance in the study area. This index expresses the level of historical forest cover reduction suffered by a landscape as regard the maximum forest cover development this landscape may achieve, given its climatic conditions:

$$DI = (TCmax - TC)/TCmax$$

where TC (%) represents tree cover of a given plot and TCmax (%) is the maximum tree cover for the corresponding climate aridity level in the study area. We applied supervised classification to recent high resolution (50-cm pixel size) aerial photographs provided by the IGN-Iberpix Platform (http://www.ign.es/iberpix2/visor/) to determine tree cover (TC) (see Moreno-de las Heras et al., 2018 for a detailed description of photograph analysis procedure). Maximum tree cover values in each climate aridity level were set on the basis of tree cover determinations from a large set of 917 plots (208, 373 and 336 explored plots, 231 × 231 m, in semi-arid, dry-transition and sub-humid conditions, respectively) within the 20,000 km^2 study area that met the same environmental criteria used for plot selection. Maximum tree cover (TCmax) was 53, 75 and 87% in semi-arid, dry-transition and sub-humid conditions, respectively. The similar TCmax values obtained in a one order of magnitude larger area (100,000 km^2), which included our study area and covered 5274 explored plots of identical dimensions, supported the use of TCmax as a surrogate of maximum tree cover (Curo Rosales, 2020).

DI values were balanced among climate aridity levels and ranged from 0 to nearly 1 along a gradient from lightly to highly disturbed plots, respectively (DI = 0 when TC = TCmax and DI = 1 when TC = 0).

Without evident signs of fire and cultivation, agents of disturbance in the selected plots were mainly wood consumption (for fuel, timber and charcoal production) and domestic livestock (Aranbarri et al., 2014). Previous studies based on historical land use data point out that these main agents of disturbance were extensive and homogeneous across aridity levels in the entire study area (Aranbarri et al., 2014 for wood consumption; Pascua Echegaray, 2012 and García-Fayos et al., 2020 for type of livestock and stocking rates).

2.4. Soil variables

Soil was sampled in autumn 2015 in ten 10 × 2-m sub-plots, 50 m apart from each other and regularly distributed within each plot. A composite topsoil sample was collected from five sub-samples of constant volume (1155 cm^3) taken up to a depth of 10 cm at 2-m intervals along the 10-m-long side of each sub-plot. The uppermost litter layer and large rock fragments were removed before sampling. The composite sample was further divided into two portions. One portion was kept cold in an ice chest and taken to the laboratory where it was sieved through a 2-mm mesh and stored at 4 °C until soil respiration was measured within one month of sampling. The other portion was transported to the laboratory, air-dried at room temperature for one month, and sieved through a 2-mm mesh before performing all other soil analyses.

We measured soil variables that are considered good proxies of soil functioning in drylands and have been used as part of multifunctionality indices in recent research (Hector and Bagchi, 2007; Maestre et al., 2012): soil organic matter (SOM), total nitrogen (Nt) and mineral nitrogen (mineral N) contents, potential soil respiration rate (PSRR) and the activity of three extracellular enzymes (β-glucosidase, urease and phosphatase). A synthetic enzymatic index (SEI) was calculated as the sum of the three enzyme activities (Appendix A) and used as a proxy of enzyme activity (Martínez et al., 2016). The synthetic index was robust, since climate and disturbance intensity influenced all three individual enzymatic activities in the same direction. Whereas PSRR and SEI are functions that represent fast time-scale processes measured as a rate, the other three variables (SOM, Nt and mineral N) are nutrient pools or stocks of matter that represent effects of biological processes that take place on slower time-scales (Garland et al., 2020).

Moreover, SOM and Nt provide relevant information about soil fertility and quality because they make up the primary sources of energy for soil microorganisms (Bardgett, 2005). Mineral N, which results from N mineralization and nitrification processes, represents the primary available N source for plants and microorganisms. Soil microbial activity, i.e. microbial respiration and enzyme activity, provide an integrated measure of soil health and respond quickly to natural or human-induced soil changes and stress (Pankhurst et al., 1995). Enzyme activity, which plays a fundamental role in nutrient mineralization, is considered a good indicator of plant and soil microorganism nutrient demand (Bell et al., 2014). Specifically, β-glucosidase, urease and phosphatase are extracellular enzymes produced by soil microorganisms involved in organic matter degradation and subsequent carbon, nitrogen and phosphorus cycling. A detailed description of soil chemical and biological analyses is provided in Appendix A.

2.5. Vegetation variables

Vegetation was surveyed in spring 2016 in all plots. Vegetation variables were determined in the same ten 10 × 2 m sub-plots where the soil was sampled. We recorded all perennial species in each sub-plot and calculated perennial species richness as the average total number of species per plot from the ten sub-plots. Although the way plant diversity influences ecosystem functioning is still controversial (Loreau et al., 2002), species richness is positively correlated with the functional state of a wide range of ecosystem conditions and with the ecosystem ability to maintain multiple functions (Hector and Bagchi 2007; Maestre et al., 2012; Quero et al., 2013). At the time of vegetation survey, we also determined the perennial herbaceous (H) and all woody (W) species covers using the line-intercept method along the 10-m-long side of each sub-plot (opposite side to soil sampling) and calculated the ratio of perennial herbaceous species to woody species cover (H/W). As the proportion of functional groups, structural properties of the vegetation play an indirect important role in key ecosystem functions such as net primary productivity, litter decomposition and nutrient cycling (Garnier et al., 2016). The study was restricted to perennial plants due to their role in maintaining ecosystem functioning and preventing desertification in drylands (Maestre and Escudero 2009), to the very low cover (<0,1%) of annual species in the ecosystem under study (García-Fayos and Bochet 2009) and to the high inter-annual variability in the abundance of annual plants caused by variations in the amount and temporal distribution of annual precipitation (Sher et al., 2004).

2.6. Statistical data analyses

We modelled the soil and vegetation variables (response variables) from the 36 holm oak sites as a quadratic function of disturbance intensity, including indicator variables for the climatic conditions and their interactions with the disturbance intensity linear and quadratic terms (detailed description in Appendix B). The full model (Appendix B: Eq. B1) allowed for separate quadratic functions for each climate aridity level (semi-arid, dry-transition and sub-humid). Thus, for each climate aridity level, the separate response variable-DI functions were a second-order polynomial where the intercept, linear, quadratic coefficients were linear combinations of the parameters of the full model (Appendix B: Eq. B2-B4). Testing those parameters allows to determine whether the response variable-DI functions are the same for each aridity level, whether they are quadratic or linear, and to estimate the most parsimonious function for each aridity level. Goodness of fit for the general response variable-DI model was assessed using residual plots and the coefficient of determination (R^2). Variations in the explored degradation trends were assessed by evaluating the size (absolute values) and statistical significance of the coefficients for the separate response variable-DI functions. We averaged the values of the soil and vegetation variables from the 10 sub-plots per plot to yield a single value for each of the 36 sites.

The data were analyzed using the lm function from the stats package in R, version 3.6.1.

3. Results

Overall, all the functional soil properties followed a similar pattern (Fig. 2 and Appendix C for model descriptions and detailed statistical results). The relationship between each soil variable and DI was non-linear in sub-humid conditions, but linear in dry-transition and semi-arid conditions (Fig. 2a–e).

More specifically, in sub-humid conditions there was a sharp downward followed by a gentler upward trend as DI increased. Minimum values of the quadratic functions were reached at disturbance intensities ranging from 0.61 to 0.82 depending on the soil variable. Conversely, in semi-arid and dry-transition conditions, the soil variable-DI functions showed no evidence of curvature. In all cases, they were linear, either declining as DI increased (SOM, SEI, PSRR, and Nt) or remaining constant throughout the DI gradient (mineral N). The slopes of the linear functions were in all cases identical in semi-arid and dry-transition sites, showing a similar rate of soil degradation throughout the gradient in both climatic conditions (0.53% (SE: 0.06) unit decrease in SOM, 0.24 μmol g-soil^{-1}h^{-1} (SE: 0.05) in SEI, 1.24 mg C-CO_2 kg-soil^{-1} day^{-1} (SE: 0.35) in PSRR, 0.15 g kg-soil^{-1} (SE: 0.05) in Nt, and 0 mg kg-soil^{-1} in mineral N, for each 0.1 unit increase in DI). Functions describing the relationships between SEI, Nt, mineral N and DI were identical in dry-transition and semi-arid conditions, with a same slope and intercept value. However, SOM and PSRR mean values were 1.12% (SE of the difference, 0.35%) and 5.54 mg C-CO_2 kg^{-1} day^{-1} (SE of the difference, 2.57 mg C-CO_2 kg^{-1} day^{-1}) higher, respectively, in dry-transition than in semi-arid conditions (Appendix C).

Besides the observed differences in the shape of the soil variable-DI functions, mean values of the soil variables were in all cases higher or in few situations equal to, in sub-humid than in dry-transition and semi-arid conditions at equivalent levels of past human disturbance (Fig. 2). However, the observed reductions in the values of these soil variables

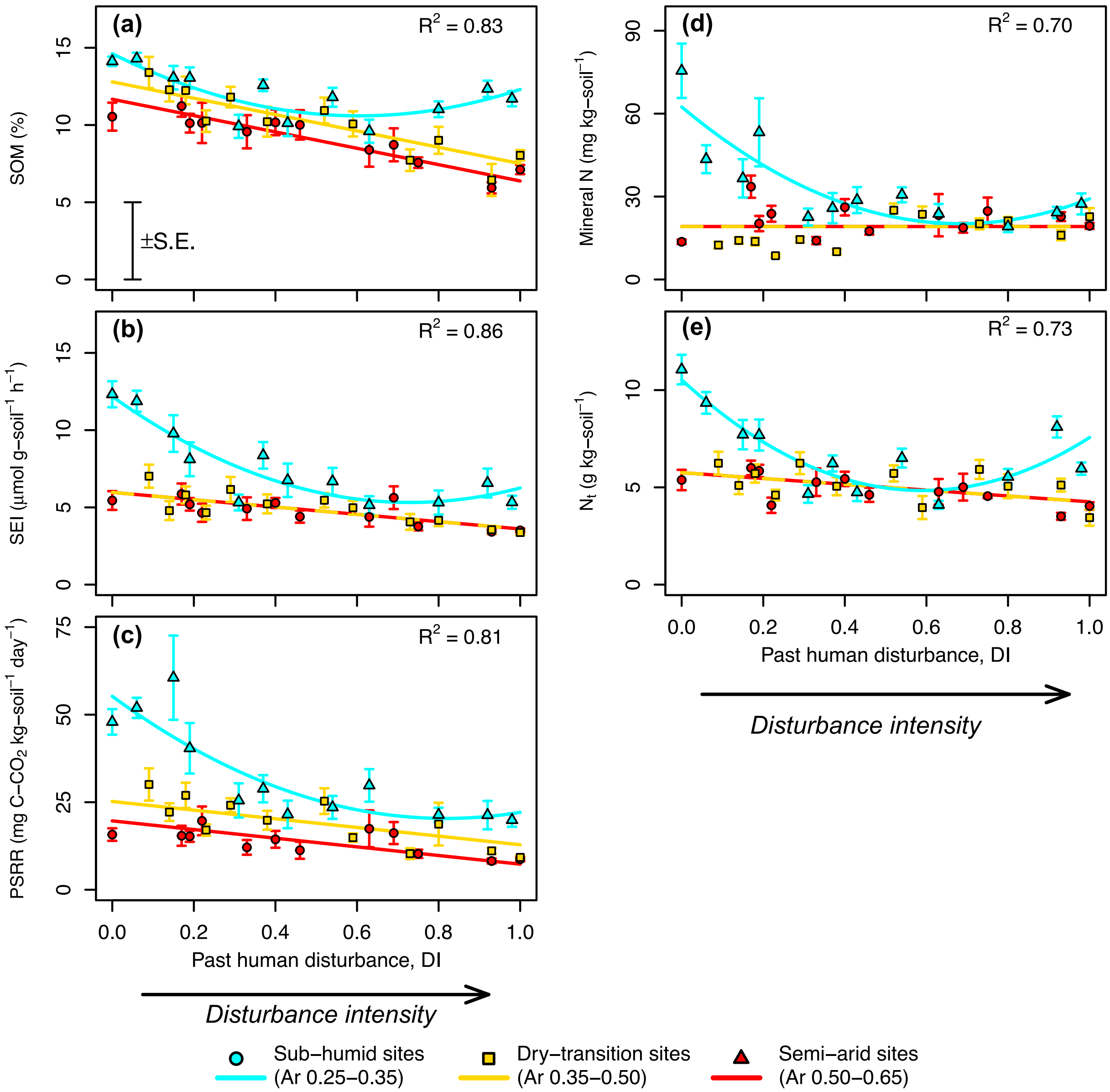

Fig. 2. Variation of soil variables. Variation of soil properties along the past human disturbance gradient (DI) in three climatic aridity levels (semi-arid, dry-transition and sub-humid): (a) soil organic matter content (SOM), (b) synthetic enzymatic index (SEI), (c) potential soil respiration rate (PSRR), (d) mineral N content, (e) total nitrogen content (Nt). Aridity, Ar = 1- MAP/PET (where MAP is mean annual precipitation and PET is potential evapotranspiration). R^2: proportion of the variance explained by the model.

throughout the disturbance gradient were higher in sub-humid than in dry-transition and semi-arid conditions. Thus, in sub-humid conditions, reduction rates in the low-to-moderately disturbed plots (from the optimal values of the soil variables that are reached at DI = 0 down to the minimum value of the non-linear soil variable-DI functions) were 28, 56, 63, 54 and 68% for SOM, SEI, PSRR, Nt and mineral N, respectively. For the same soil properties and range of disturbance intensities, they were 25, 29, 40, 15 and 0% and 27, 29, 51, 15 and 0%, respectively in dry-transition and semi-arid conditions. Nevertheless, in the most disturbed sites (approaching DI = 1), the values of all soil variables slightly increased or at least stabilized in sub-humid conditions, whereas they continued to decrease in dry-transition and semi-arid sites.

Unlike soil properties, linear functions best described the relationship between vegetation variables and DI functions for all three climatic aridity levels, without evidence of curvature (Fig. 3, Appendix C). However, the association between vegetation variables and DI depended on the vegetation property and climatic aridity level considered. No effect of past human disturbance was found on perennial species richness, as the number of perennial species remained constant throughout the DI gradient in all three climatic aridity levels (Fig. 3c). Mean number of perennial species per 20 m^2 was identical in sub-humid and dry-transition conditions (28.41, SE: 0.52) but it was significantly lower in semi-arid conditions (22.58, SE: 0.74). The effect of disturbance on herb cover and H/W ratio strongly depended on climatic aridity level (Fig. 3a, b and Appendix C), with a significantly higher increase of both variables with disturbance in sub-humid than in dry-transition and semi-arid conditions. More specifically, herb cover increased fast, at a rate of 2.98% per 0.1 unit increase in DI (SE: 0.70%), in sub-humid conditions, whereas it remained unchanged throughout the disturbance intensity gradient in dry-transition and semi-arid conditions (constant mean value of 15.76%, SE: 1.58%). Moreover, herb cover was always higher in the sub-humid than in the dry-transition and semi-arid climatic conditions, regardless of the degree of disturbance, with values ranging between 27 and 57%. The rate of H/W increase was significantly higher in

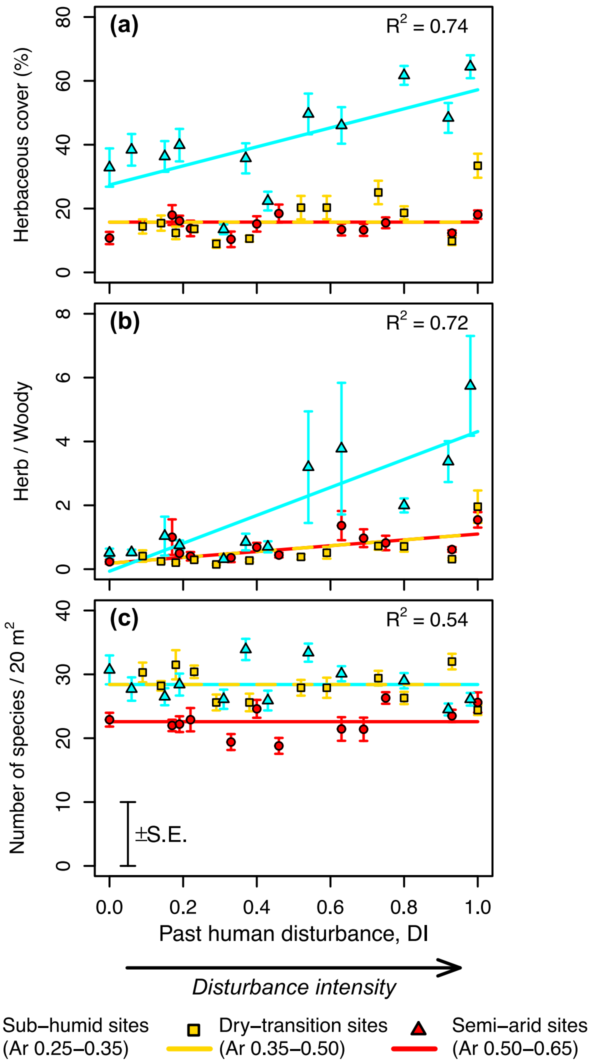

Fig. 3. Variation of vegetation variables. Variation of vegetation variables along the past human disturbance gradient (DI) in three climatic aridity levels (semi-arid, dry-transition and sub-humid): (a) herbaceous perennial cover, (b) herbaceous perennial cover to woody cover ratio, (c) number of perennial species. Aridity, Ar = 1- MAP/PET (where MAP is mean annual precipitation and PET is potential evapotranspiration). R^2: proportion of the variance explained by the model.

sub-humid than in dry-transition and semi-arid conditions (p-value < 0.0001), with 0.44 (SE: 0.058) and 0.092 (SE: 0.043) unit increases in mean H/W per 0.1 unit increase in DI, respectively. Unlike sub-humid conditions, in dry-transition and semi-arid conditions, H/W mean values remained below 1 throughout the disturbance intensity gradient, indicating an overall dominance of woody over herbaceous cover.

4. Discussion

4.1. Non-linear vs linear responses and interaction of drivers

Our study evidences a strong interaction of past human disturbance and aridity on the functional state of Mediterranean holm oak woodlands, but differently as expected. According to our hypothesis, we expected (i) non-linear patterns in the soil function of holm oak woodlands along the past human disturbance gradient, with abrupt changes at critical thresholds of disturbance intensities in the most severe climatic conditions (semi-arid and dry-transition), and (ii) linear trends in the gentlest climatic conditions (sub-humid). However, our results show the opposite trend: as disturbance increased, there was a linear decrease in soil function in semi-arid and dry-transition conditions and a non-linear trend in sub-humid conditions. Thus, while woodlands in semi-arid and dry-transition conditions underwent a continuous gradual loss of soil function along the past human disturbance gradient, in sub-humid conditions they went through a sharp decline at low-to-moderate levels of disturbance but partially recovered or plateaued at moderate-to-high levels of disturbance.

It is noteworthy that the same general pattern (linear vs non-linear) was found for all soil variables considered. This common pattern highlights the high consistency of the results. However, it also emphasizes the tight relationships between soil variables through processes that involve the decomposition and mineralization of organic matter by microorganisms and the contribution of specific enzymatic activities of microorganisms to soil respiration and nutrient cycling (Rodríguez et al., 2017).

4.2. Abrupt shift, underlying mechanisms and conceptual model

Our results indicate that the interaction of both drivers influences the state of the ecosystem through convergent changes in the functional structure of the vegetation (unlike species richness) and key functional soil properties and triggers abrupt shifts in the ecosystem state (from a non-linear to a linear pattern) at critical values of past human disturbance and aridity, as explained hereafter.

4.2.1. Savannization process in sub-humid conditions along the DI gradient

In sub-humid conditions, a sharp increase in the perennial herbaceous cover along the past human disturbance gradient, and the resulting replacement of a woody-dominated vegetation (H/W < 1) in the less disturbed areas by a perennial herbaceous-dominated vegetation (H/W >1) in the moderately-to-highly disturbed areas, shifts the dense woodland into a grassland with scattered trees (savanna-like vegetation). Similar changes in the dominance between woody and herbaceous species mediated by resource gradients (e.g. water, soil fertility) and disturbance regimes (e.g. drought, tree cutting) have been reported in other Mediterranean woodland ecosystems in the central part of the Iberian Peninsula (Lloret et al., 2014; Rodríguez et al., 2017). In these studies, climate-induced holm oak (Rodríguez et al., 2017) and *Juniperus* (Lloret et al., 2014) die-off triggered a savannization process at the ecotype scale with important consequences for microbial activity and nutrient cycling. These authors attributed the higher soil respiration rates recorded in the grasslands (as compared to woodlands) mainly to the lower proportions of lignin and C:N or C:P ratios of herbaceous tissue, more degradable for microbial consumption than the tissue of woody species, but also to changes in the rhizosphere and related exudates. Changes in the amount and type of litter accompanying the shift in the functional structure of the vegetation along the human disturbance gradient could partly explain the decline in soil function in the woodland at low-to-moderate disturbance intensities and the partial recovery, or at least maintenance, of the overall soil function in the grassland despite increasing disturbance ("half-pipe" shape in Fig. 4). The sharp downward trend in carbon and nitrogen contents observed as tree biomass declines in the lightly to moderately disturbed sites dominated by a woody vegetation could result from the decline in litter inputs into the soil and their consequent effect on soil microbial activity (i.e. SEI and PSRR). The change of a dominant slow degradable oak litter in the woodland by a rapidly degradable herbaceous litter in the grassland should enhance litter decomposition and could explain the gentle upward trend of microbial activity and mineral N release in the grassland. Although higher decomposition rates in the grassland should reduce SOM contents as compared to the woodland, SOM values slowly increased in the grassland at moderate to high disturbance intensities. This result could be attributed to the sharp increase in the density of perennial herbaceous species, characterized by high fine root production and turnover (Kooch et al., 2016), in the grassland despite

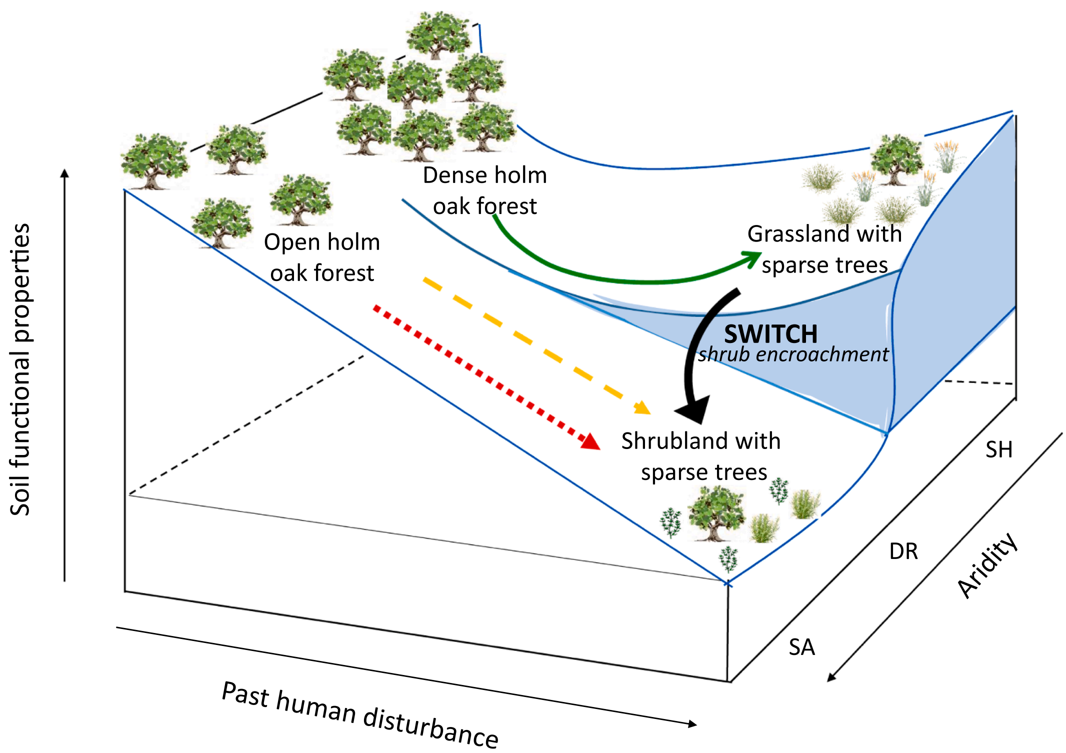

Fig. 4. Conceptual model. Model illustrating the onset of abrupt shifts in the soil functional response of holm oak woodlands to the joint effect of increasing aridity and past human disturbance and the underlying mechanisms in relation to changes in vegetation composition and structure discussed in Section 4.2. Woodlands show a linear decline in their soil function in semi-arid (SA) and dry-transition (DR) conditions at the same time as they are being transformed into shrublands (red dotted and yellow dashed arrows). However, they show a non-linear trend in sub-humid (SH) conditions along the past human disturbance gradient, where they undergo a sharp decline at low-to-moderate disturbance levels but tend to gently recover at moderate-to-high levels of disturbance. This downward-upward trend is accompanied by a shift from a dense woodland to an herbaceous perennial grassland ("savannization" process, green solid arrow). The different responses to the interaction of both drivers between climate aridity levels imply the existence of a critical climatic threshold in the boundary between sub-humid and dry-transition conditions where the effects of disturbance on soil function shift from a curvilinear (half-pipe) to a linear (straight-toboggan) pattern with increasing aridity. Accordingly, once climatic conditions exceed a critical aridity threshold in the boundary between sub-humid and dry-transition conditions at high levels of disturbance, the system switches from a fertile grassland into a degraded shrubland ("shrub encroachment", black dark arrow) and loses its ability to buffer the effects of increasing disturbance. SH: sub-humid, DR: dry-transition, and SA: semi-arid conditions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

increasing disturbance. Assumptions concerning changes in litter quality should be further investigated in future research.

4.2.2. Changes from woodlands to shrublands in semi-arid and dry-transition conditions along the DI gradient

In contrast, in dry-transition and semi-arid areas, conditions are more limiting for the establishment of herbaceous species (Austin and Sala 2002) and the vegetation is dominated by woody species (H/W < 1). This woody-dominated vegetation seems to be unable to buffer the impact of disturbance and avoid the continuous decline of soil function towards high levels of degradation ("straight-toboggan" shape in Fig. 4). Whereas trees tend to be substituted by shrubs along the disturbance gradient within the functional group of woody species, the cover of perennial herbaceous species remains constant and very low throughout the gradient (mean cover < 20%). In the most degraded sites, holm oak cover was almost completely substituted by low bushes, as the H/W ratio increased only slightly along the gradient despite the removal of holm oaks. The progressive replacement of holm oak trees by low bushes has been largely documented to describe the degradation of Mediterranean evergreen forests caused by different types of disturbance such as deforestation, overgrazing or fire (e.g. Grove and Rackham 2001). Concerning soil properties, our results are consistent with other studies in semi-arid ecosystems that also described a negative influence of tree decline or vegetation removal on biogeochemical cycles and microbial activity (Martínez-Mena et al., 2002; García et al., 2002). These authors attributed declines in C and N contents to reduced plant C and N inputs into the soil, mainly caused by the direct removal of plant biomass, but also by the indirect decline in microbial activity and enhanced losses of stored nutrients in the soil through water erosion (although runoff rates might be low in our nearly flat plots).

4.2.3. Abrupt shift and climatic threshold

The contrasting responses of holm oak woodlands in sub-humid vs dry-transition/semi-arid conditions to the interaction of both (past human disturbance and aridity) drivers imply the existence of a critical climatic threshold in the boundary between sub-humid and dry-transition conditions where the effects of disturbance on soil functioning shift from a curvilinear (half-pipe) to a linear (straight-toboggan) pattern with increasing aridity (Fig. 4). Accordingly, abrupt changes in the soil function occur at critical levels of aridity and disturbance. As shown in the model proposed in Fig. 4, once climatic conditions exceed a critical aridity threshold in the boundary between sub-humid and dry-transition conditions, the system switches from a fertile grassland to a degraded shrubland at high levels of disturbance. This switch has critical consequences for ecosystem functioning as it involves the loss of the grassland's ability to buffer the effects of increasing disturbance and a shift towards highly degraded soil conditions. Many studies reported a similar negative impact of shrub encroachment on key soil properties in other worldwide arid and semiarid regions (Schlesinger et al., 1990; Soliveres et al., 2014; but see Eldridge et al., 2011 for a review on the universality of this relationship). Limiting plant-available soil moisture at a critical value of our aridity gradient, between sub-humid and dry-transition conditions, could be mainly responsible for the colonization of perennial grasslands by woody species as available soil water controls perennial grass dynamics and collapse in drylands (Lohmann et al., 2012; Moreno-de las Heras et al., 2016). Shrub species living in Mediterranean shrublands are usually adapted to low soil-resource availability and display traits that allow them to withstand limiting water conditions and erratic rainfall patterns (Chapin, 1991).

4.3. Consequences for holm oak management

4.3.1. Associated shifts in holm oak ecosystem services

According to Garnier et al., 2016, for a review), functional trade-offs at the level of plant traits (lifeforms) control trade-offs at the level of processes (e.g. amount and quality of litter and root production, rate of biogeochemical cycles) and these, in turn, determine ecosystem services. Thus, the observed shifts in vegetation structure may have major consequences for ecosystem services. Ecosystem services oriented towards carbon storage, fertility, water and air quality in the woodlands (Marañón et al., 2012) may shift into services mainly oriented towards high forage, livestock production and, to a lower extent, fertility in the palatable grasslands and these latter may lose their capacity to provide services when they switch into a highly degraded state with increasing aridity.

4.3.2. Vulnerability of holm oak woodlands to projected increased aridity

In the context of climate change, we could also infer from our space-for-time substitution approach that holm oak woodlands in sub-humid regions will be especially vulnerable to projected increased aridity (Giorgi and Lionello 2008; IPCC 2013), because they could lose their capacity to buffer the impacts of past human disturbance and suffer abrupt shifts in their functionality. Other studies also reported a greater impact of drivers (e.g. erosion or drought) on ecosystem function in resource-rich habitats than in resource-poor habitats due to the already limiting intrinsic constraints of the latter that negatively affect ecosystem function (García-Fayos and Bochet 2009; Pérez-Ramos et al., 2017). In this sense, the very similar soil function patterns with increasing disturbance in dry-transition and semi-arid conditions suggest that projected increased aridity will not affect much ecosystem functionality in the former conditions, which are already climatically constrained. However, in a study based on a large dataset from global drylands along a worldwide aridity gradient, Berdugo et al. (2020) identified a series of non-linear thresholds in multiple vegetation and soil attributes in even drier conditions in the transition between semi-arid and arid ecosystems (Ar: 0.54, 0.70 and 0.80 for plant productivity, soil fertility and plant cover and richness, respectively). The gentler critical climatic conditions found in our study at which holm oak woodlands suffer abrupt changes in their soil function (between sub-humid and dry-transition, Ar around 0.35) suggest that threshold values of abrupt changes driven by aridity may take place at even wetter conditions when aridity interacts with another driver (i.e. past human disturbance).

5. Conclusions

Our study evidences a strong interaction of past human disturbance and aridity on the functional state of Mediterranean holm oak woodlands. The contrasting responses of holm oak woodlands in sub-humid vs dry-transition and semi-arid conditions to the interaction of both drivers imply the existence of a critical climatic threshold in the boundary between sub-humid and dry-transition conditions where the effects of disturbance on soil functioning shift from a curvilinear (half-pipe) to a linear (straight-toboggan) pattern with increasing aridity. At the same time, the system switches from a fertile grassland to a degraded shrubland at high levels of disturbance, loosing its ability to buffer the effects of increasing disturbance.

Our study provides one of the few empirical evidences of the onset of abrupt changes in the functional response of drylands to the interaction of drivers, i.e. past human disturbance and aridity. It contributes to a better understanding of the ecological mechanisms underpinning abrupt shifts in the functionality of holm oak woodlands, which requires considering structural changes in the dominant plant lifeforms associated to key soil functions, along environmental and human disturbance gradients. It also warns about the possibility that threshold values of abrupt changes in these ecosystems driven by aridity may take place at even wetter conditions when aridity interacts with another driver (i.e. past human disturbance), geopardizing in this way the functionality of sub-humid holm oak woodlands.

However, the use of categorical aridity levels in accordance with the hypothesis tested, does not allow a precise determination of the critical aridity value between sub-humid and dry-transition conditions where the system shifts abruptly. A continuous climatic gradient could help identify this critical threshold value in future work. Next to that, additional empirical studies analyzing the simultaneous effect of multiple global change drivers on the functionality of drylands are needed to further validate theoretical models that predict the onset of abrupt shifts in such environments. Moreover, the analysis of temporal series or inclusion of dynamical features (e.g. plant regeneration, see Garcia-Fayos et al. (2020) are also needed to determine the resilience of holm oak woodlands to disturbance with increasing aridity, analyze the reversible or irreversible nature of the abrupt shift and, in this latter case, identify the factors limiting ecosystem structural and functional recovery.

Our conclusions may help to improve ecologically-based management of Mediterranean holm oak woodlands and identify critical climatic conditions that make these ecosystems particularly vulnerable to suffer abrupt changes in a scenario of global change.

Declaration of Competing Interest

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

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2021.105514.

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