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Aridity Induces Nonlinear Effects of Human Disturbance on Precipitation-Use Efficiency of Iberian Woodlands

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ABSTRACT

The effects of ecosystem degradation are pervasive worldwide and increasingly concerning under the present context of global changes in climate and land use. Theoretical studies and empirical evidence increasingly suggest that drylands are particularly prone to develop nonlinear functional changes in response to climate variations and human disturbance. Precipitation-use efficiency (PUE) represents the ratio of vegetation production to precipitation and provides a tool for evaluating human and climate impacts on landscape functionality. Holm oak (*Quercus ilex*) woodlands are one of the most conspicuous dry forest ecosystems in the western Mediterranean basin and present a variety of degraded states, due to their long history of human use. We studied the response of Iberian holm oak woodlands to human disturbance along an aridity gradient (that is, semi-arid, dry-transition and sub-humid conditions) using PUE estimations from enhanced vegetation index (EVI) observations of the Moderate-Resolution Imaging Spectroradiometer (MODIS). Our results indicated that PUE decreased linearly with disturbance intensity in sub-humid holm oak woodlands, but showed accelerated, nonlinear reductions with increased disturbance intensity in semi-arid and dry-transition holm oak sites. The impact of disturbance on PUE was larger for dry years than for wet years, and these differences increased with aridity from sub-humid to dry-transition and semi-arid holm oak woodlands. Therefore, aridity may also interact with ecosystem degradation in holm oak woodlands by reducing the landscape ability to buffer large changes in vegetation production caused by climate variability.

Key words: ecosystem functionality changes; drylands; global change; holm oak woodlands; ecosystem degradation; land use; MODIS EVI.

INTRODUCTION

Ecosystem degradation represents a worldwide pervasive phenomenon that pertains to the loss of ecosystem function and productivity resulting from various factors, including human activities and climatic variations (Bai and others 2013). The present changes in climate and land use are affecting biodiversity and landscape functioning at an unprecedented rate, increasing global concerns about ecosystem degradation (McLean and Willson 2011; Valiente-Baunet and Verdú 2013). Drylands, which extend over 40% of the Earth's surface and support nearly 2.5 billion inhabitants, are significantly impacted by degradation (up to 20% of these lands are affected by some form of severe ecosystem degradation) and face a variety of threats associated with global environmental change (Millennium Ecosystem Assessment 2005). Sustainable dryland management, therefore, demands a sound understanding of the factors and mechanisms that regulate the responses of dryland ecosystems to human pressures and climate change (Maestre and others 2016).

How ecosystems undergo environmental change is recognized as one of the main frontiers in ecology and environmental sciences (Rietkerk and others 2004; Peters and others 2006; Berdugo and others 2017). Ecosystem degradation may take place either linearly, in a gradual way, or more abruptly, in a nonlinear manner, in response to the effects of disturbance and changes in climate (Scheffer and others 2001). Both theoretical studies and empirical evidence increasingly suggest that drylands are particularly prone to develop nonlinear changes in their structure and function in response to external stressors (Noy-Meir 1975; Scheffer and others 2001; Rietkerk and others 2004; Kéfi and others 2007; Bestelmeyer and others 2011). In these dry landscapes, where vegetation cover is typically 'patchy' or spatially heterogeneous, plant–plant positive interactions (that is, facilitation) and efficient spatial redistribution of resources (for example, water, sediments, nutrients, propagules) between bare and vegetated areas by surface runoff provide landscape stability over a range of climate and land-use conditions (Saco and Moreno-de las Heras 2013; Soliveres and others 2015; Bochet 2015; Kéfi and others 2016). However, as climate forcing or disturbance intensity increase, significant deterioration of the stabilizing ecosystem mechanisms may induce rapid, accelerated loss of ecosystem function and the alteration of landscape structure (Moreno-de las Heras and others 2012; Okin and others 2015; Xu and others 2015). The most extreme alterations may take place in the form of largely irreversible landscape changes, thus hindering the natural recovery of ecosystem function (Schlesinger and others 1990; Peters and others 2006; Mayor and others 2013; Moreno-de las Heras and others 2015; Martínez-Valderrama and others 2016).

Precipitation-use efficiency (hereafter termed PUE) represents the ratio of vegetation net primary production (NPP) to precipitation over a given period of time, typically a growing season or hydrological year (Le Houerou 1984). PUE has been widely applied for assessing the degree of degradation or loss of ecosystem function in drylands, where human disturbance of vegetation and soil conditions can induce reductions up to 20–50% on the ecosystem capacity to convert precipitation into vegetation production (Le Houerou 1984; O'Connor and others 2001; Holm and others 2003; Moreno-de las Heras and others 2012). PUE has also shown sensitivity to inter-annual variations of precipitation, reflecting the NPP dependence on climate conditions (Huxman and others 2004; Wessels and others 2007; Ponce-Campos and others 2013; Zhang and others 2014). Therefore, PUE represents an excellent evaluation tool for the assessment of human and climate impacts on landscape functionality (that is, the integrity of landscape functions, such as nutrient cycling, water budgeting and primary production) in drylands (Holm and others 2003; Verón and Paruelo 2010; Moreno-de las Heras and others 2012; Ruppert and others 2012). The availability of decadal series of remote-sensed vegetation indices that strongly correlate with NPP, such as the normalized difference and the enhanced vegetation indices (NDVI and EVI, respectively), facilitates the application of large, regional-scale PUE analysis for monitoring landscape functionality in drylands (Gaitán and others 2014; Zhang and others 2014; Martínez-Valderrama and others 2016).

Dryland ecosystems across the Mediterranean basin exhibit varying degrees of degradation due to their very long history of human use and are reported to be one of the most vulnerable landscapes in relation to future climate scenarios (Grove and Rackham 2001; García-Fayos and Bochet 2009). In the Iberian Peninsula, Martinez-Valderrama and others (2016) estimated that ecosystem degradation affects about 20% of its territory, mainly in agricultural landscapes and woodlands. Holm oak (*Quercus ilex*) woodlands are one of the most conspicuous dry forest ecosystems in the Iberian Peninsula and the western Mediterranean basin, and have been impacted by humans for at least 4
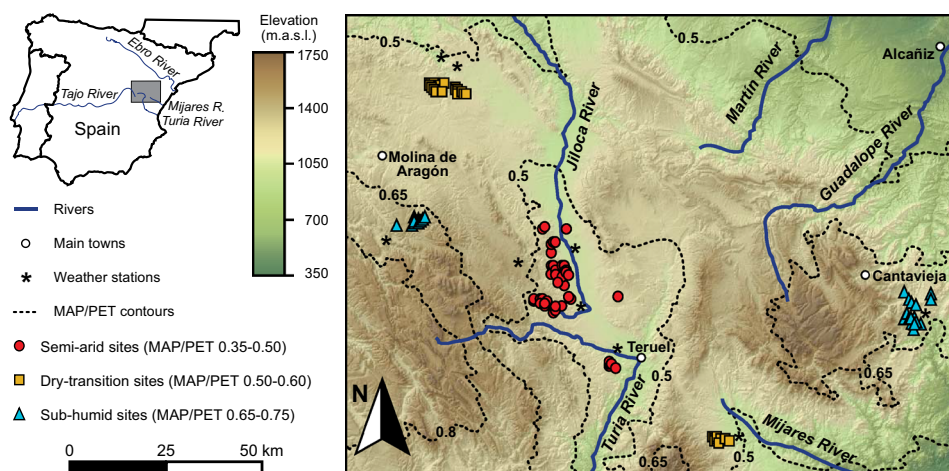
Figure 1. Location map (area is approximately 20,000 km^2). Each study site has a size of 231 × 231 m. Total number of sites is 138 (53, 51 and 34 sites for semi-arid, dry-transition and sub-humid climate conditions, respectively). Coordinates and general characteristics for both the study sites and weather stations are detailed in the electronicsupplementary material of Appendix A: Tables A1 (sites) and A2 (stations).

millennia (Terradas 1999). We studied the response of holm oak woodlands to human disturbance along an aridity gradient (that is, semi-arid, dry-transition and sub-humid conditions) across an approximately 20,000 km^2 region in eastern Spain, using remote-sensing estimations of PUE from decadal (2000–2014) EVI observations from the Moderate-Resolution Imaging Spectroradiometer (MODIS). We hypothesized that aridity largely influences the response of vegetation PUE to human disturbances, with the less arid, sub-humid extreme of the gradient showing linear reductions in landscape functionality and the semi-arid extreme showing accelerated, nonlinear reductions in the amount of vegetation production per rainfall unit. Since climate variability in drylands may interact with the effects of disturbance on ecosystem functions (Pickup 1996; Dube and Pickup 2001; Hein 2006), we also expected human disturbance to cause a stronger impact on PUE values in dry years due to unfavorable conditions for vegetation growth.

MATERIALS AND METHODS

Study Area

Our study sites are located within an extensive 20,000 km^2 region in eastern Spain, comprising areas of the basins of the Tajo, Ebro, Turia and Mijares rivers (Figure 1). The climate is Mediterranean, with two wet periods (April–June and September–November) during which more than 60% total precipitation is concentrated. Mean annual precipitation (MAP) and air temperature are 350–700 mm and 9.0–12.5°C, respectively. Potential evapotranspiration (PET) is 850–950 mm. Aridity, calculated as the ratio of MAP to PET (UNEP 1992), ranges from 0.35 to 0.85. Holm oak woodlands in the region are highly impacted by human activities due to a long history of land use, mainly fuel wood consumption, domestic livestock and agriculture (Stevenson 2000; García-Fayos and Bochet 2009).

We selected 138 study sites for analysis (each 231 × 231 m, corresponding to the pixel size of the UTM-re-projected MODIS MOD13Q1 product that was later applied for the calculation of PUE) distributed within semi-arid, dry-transition and sub-humid climate conditions with a MAP/PET ratio of 0.35–0.50 (53 sites), 0.50–0.60 (51 sites) and 0.65–0.75 (34 sites), respectively (Figure 1). Site selection was decided upon by applying GIS techniques and field validation to identify for each climate aridity level (semi-arid, dry-transition and sub-humid) a large number of representative holm oak sites in a variety of deforestation levels. All the sites were selected in areas with nearby availability of reference meteorological records (that is, daily precipitation series) and homogeneous landscape topography and lithology. Specific site selection methods, site coordinates and their general characteristics are detailed in the electronic supplementary material of Appendix A. Overall, our sites can be described as holm oak woodlands affected by different deforestation intensity levels (but with no signs of agricultural use) on low-gradient terrain (3.8° ± 1.5° hillslope angle). Soils are *Mollic Haploxeralfs* (Soil Survey Staff 1987) over calcare-

Remote-Sensing Estimations of Precipitation-Use Efficiency

The enhanced vegetation index (EVI) is a remote-sensing index that minimizes the influence of soil background and atmospheric conditions for spatial analysis of vegetation dynamics (Huete and others 2002). EVI is strongly sensitive to changes in vegetation canopy and leaf phenology and, therefore, provides a good indicator of the spatiotemporal variations in leaf area and landscape primary production (Pasquato and others 2015). Ponce-Campos and others (2013) showed that the annual integral of EVI (iEVI) is a good remote-sensing estimator ($R^2 = 0.82$) for the annual net primary production (ANPP) across a variety of arid, semiarid and mesic grasslands and woodlands in Australia and the USA. Previous remote-sensing analysis of *Q. ilex* forests in Spain found that iEVI strongly correlates (Pearson's $R = 0.91$) with tree annual diametric increment and provides an excellent proxy for ANPP in Iberian holm oak woodlands (Garbulsky and others 2013). Therefore, we applied iEVI as an ANPP proxy for the estimation of PUE in our study sites.

We compiled decade-scale (2000–2014) series of EVI for the study sites with a 16-day compositing period from the MODIS Terra satellite (MOD13Q1 product, collection 5) by using the NASA's Earth Observing System Reverb tool (http://reverb.echo.nasa.gov/). The data were re-projected to UTM WGS84 (231×231 m pixel size after re-projection). We checked the reliability summary layer of the MODIS products and discarded those EVI values that were affected by snow, ice and cloud anomalies (1% of data). Discarded values were then interpolated using a second-order polynomial. Finally, the EVI time series were filtered by applying a Savitzky–Golay smoothing algorithm to reduce inherent noise (Choler and others 2010; Moreno-de las Heras and others 2015). iEVI was calculated as the sum of the filtered EVI data for each hydrological year (from present September to August of the following year). PUE was estimated for each site and hydrological year as the ratio of iEVI (dimensionless) to annual precipitation (mm), using the rainfall records of the closest reference weather station. We applied rainfall records of 9 meteorological stations facilitated by the Spanish Agency of Meteorology, AEMET (Figure 1, station ID and coordinates in the electronic supplementary material of Appendix A: Table A2). Site mean dis-

tance to the nearest weather station is 6.9 ± 2.9 km. PUE was expressed in 10^{-2} mm^{-1} for analysis to reduce the number of decimal places in the estimation of model coefficients and graphical presentation.

Estimation of Disturbance Intensity Using Local Vegetation Conditions

Tree cover (TC, %) was determined using high-resolution (50 cm per pixel) digital orthophotos of the Spanish National Program for Aerial Orthophotography (PNOA, 2012 campaign). The PNOA orthophotos were downloaded using the IBERPIX web platform (http://www.ign.es/iberpix2/visor/) of the Spanish National Institute of Geography (IGN) and clipped to match the 231×231 m size of the study plots. We used the spectral information of the orthophotos (that is, the red, green and blue bands) to generate binary maps of tree vegetation by applying supervised classification techniques, achieving a mean global accuracy of $95 \pm 4\%$ for the determination of tree cover. Comparison of our remote-sensed estimations of tree vegetation cover with alternative determinations using older (years 2004 or 2006) PNOA orthophotos revealed negligible temporal variations in tree cover ($< 5\%$ in all sites) between 2004/06 and 2012. Consequently, the quantified fractional cover values are representative of the site vegetation conditions for the full (2000–2014) study period.

Vegetation cover patterns in Mediterranean landscapes depend on a variety of factors, including the effects of human disturbance, topographical control of incoming solar radiation, and soil formation and natural erosion processes (Kutiel and Lavee 1998; Grove and Rackham 2001; Bochet and others 2009; Marston 2010). Detailed analysis on the influence of site distance to the nearest settlement (as a proxy of local deforestation by human activities typically concentrated in the proximity of the villages) and landscape geomorphology (that is, hillslope gradient and aspect) on tree cover patterns for our 138 holm oak sites (electronic supplementary material of Appendix B) indicated that tree cover variations within each rural town/hamlet vicinity of the explored region reflect local intensity levels of human disturbance (that is, tree vegetation cover increased with site distance to the nearest human settlement), also discarding any significant topographical effects for these low-gradient terrain landscapes. However, the length of the disturbance (or tree cover reduction) gradients is different for the three climate aridity levels, as

indicated by existing regional differences in maximum tree cover for the climate types. In fact, remote-sensing analysis of tree cover over the complete regional extent of low-gradient ($< 10°$), calcareous holm oak woodlands (920 MODIS pixels, 4900 ha) resulted in maximum values of 87, 75 and 53% cover for sub-humid, dry-transition and semi-arid climate conditions, respectively, suggesting increasing climate limitation for tree cover development along the study aridity gradient. A local deforestation level, Dl, was calculated for each site (as a function of their climate potential for tree cover development) and further applied as a standardized descriptor of disturbance intensity across our aridity gradient:

$$Dl = {(TC_{max} - TC)}/{TC_{max}} \qquad (1)$$

where TC (%) represents tree cover for a particular site, TC_{max} (%) represents the maximum tree cover level for the corresponding climate type of the analyzed site (given by the above-detailed values for sub-humid, dry-transition and semi-arid conditions), and the local deforestation level (Dl) takes values between 0 for undisturbed (TC = TC_{max}) and 1 for entirely deforested (TC = 0% tree cover) site conditions.

Data Analysis

Precipitation-use efficiency of our 138 holm oak sites was modeled as a quadratic function of disturbance intensity (quantified using the local deforestation level), allowing for separate functions for each climate aridity type (semi-arid, dry-transition and sub-humid). We averaged the PUE values over the 14 hydrological years to model the mean trend, yielding a single value for each of the 138 sites. We fitted the following model:

$$\begin{aligned} E(PUE) = &\beta_0 + \beta_1 I_{SA} + \beta_2 I_{DT} + \beta_3 Dl + \beta_4 Dl^2 \\ &+ \beta_5 I_{SA}Dl + \beta_6 I_{DT}Dl + \beta_7 I_{SA}Dl^2 \\ &+ \beta_8 I_{DT}Dl^2 \end{aligned} \qquad (2)$$

where $E(PUE)$ is the mean precipitation-use efficiency (10^{-2} mm^{-1}); I_{SA} is a dummy indicator variable for the semi-arid climate type ($I_{SA} = 1$ if the site is under semi-arid climate and 0 otherwise); I_{DT} is an indicator variable of the dry-transition climate type; Dl is the local deforestation level of the sites; and β_0 through β_8 are parameters to be estimated.

For each climate aridity level, the separate PUE–Dl functions took the form of a second-order polynomial where the intercept, linear, quadratic coefficients and their standard errors were quanti-

fied as linear combinations of the β parameters of equation (2) (electronic supplementary material of Appendix C: equations C2–C4).

We extended the above-described general model to account for the influence of the type of hydrological year (dry *versus* wet years throughout the study period) on the relationship between PUE and disturbance intensity. Dry (wet) years were defined for analysis by using the rainfall records of the reference meteorological stations as those years with precipitation below (above) historical (1998–2014) mean precipitation. We took within-site dry and wet year average PUE values for model computation and extended equation (2) by incorporating a dummy indicator variable for type of year (with values of 1 and 0 for dry and wet year, respectively) as well as all its interactions with climate aridity type and the linear and quadratic terms of the function, totaling 9 additional parameters (electronic supplementary material of Appendix C: equation C5). The model included a random effect for site to account for the lack of independence between dry and wet observations from the same site. We applied a weighed model structure, with weights proportional to the reciprocal of the error variance, to account for differences in the number of observations for dry/wet years among sites. As for the above-described general model, each climate aridity and hydrological year type combination in the extended model was expressed in a separate PUE–Dl function of second-order polynomial structure, where the coefficients and their errors were estimated as linear combinations of the parameters of the extended model (electronic supplementary material of Appendix C: equations C6–C11).

Goodness of fit for the general PUE–Dl model was assessed using the coefficient of determination (R^2). For the extended PUE–Dl model, marginal R^2 (proportion of variance explained by the fixed predictors: local deforestation level, climate aridity level and type of hydrological year) and conditional R^2 (variance explained by both the fixed predictors and the random, site, variable) were calculated following the mathematical approach described by Nakagawa and Schielzeth (2013) for mixed-effect models. Variations in the relationships between PUE and disturbance intensity for the different levels (semi-arid, dry-transition and sub-humid) of climate aridity and (dry/wet) type of hydrological year were assessed by evaluating the size (that is, the absolute values) and statistical significance of the coefficients for the separate PUE–Dl functions.
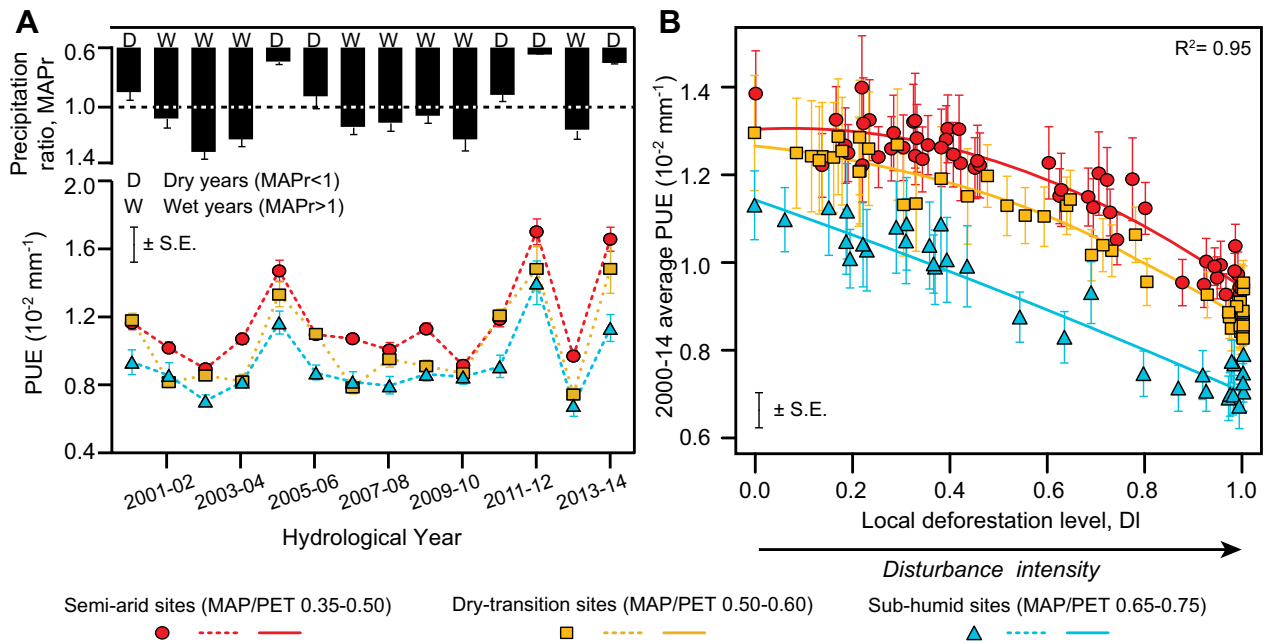
Figure 2. General effects of (**A**) climate conditions (that is, aridity level) and (**B**) disturbance intensity (as described by the local deforestation level, Dl, of the study sites) on precipitation-use efficiency (PUE). Between-year variations of site-averaged PUE values are represented for each climate condition in panel (**A**). 2000–2014 average PUE values for each site and climate condition are detailed in panel (**B**). MAPr in panel (**A**) represents the ratio of present-year precipitation to historical (1998–2014) average precipitation. Reported R^2 and fitted lines in panel (**B**) correspond to the general (14-year average response) model.

RESULTS

PUE for our 138 study holm oak sites varied considerably both between climate aridity levels and among hydrological years (Figure 2A). Vegetation PUE decreased from semi-arid to sub-humid conditions and strongly peaked for the three driest years of the series (hydrological years 2004–2005, 2011–2012 and 2013–2014, with annual precipitation about 60–70% of the historical average precipitation).

Precipitation-use efficiency decreased with increasing local deforestation levels (Dl), overall accounting for an estimated absolute reduction of about $0.4 \ 10^{-2} \ \text{mm}^{-1}$ (30–35%) of 2000–2014 average PUE, irrespective of climate aridity conditions (Figure 2B). However, the shape of the PUE-reduction trend changed along the aridity gradient, as indicated by the differences in size ($F_{2, \ 128} = 3.1$; $P = 0.048$) of the separate quadratic terms in the general PUE–Dl model for semi-arid (SA), dry-transition (DT) and sub-humid (SH) climate conditions (Table 1). The curvature (or abruptness) of the relationship between vegetation PUE and disturbance intensity, measured by the absolute values of the quadratic terms in the general PUE–Dl model, increased from SH (− 0.10) to DT (− 0.29)

and SA (− 0.42) sites. Furthermore, lack of significance of the quadratic term in the general PUE–Dl model for SH holm oak sites ($t_{129} = - 0.98$; $P = 0.33$) indicated that 2000–2014 average PUE values decreased linearly with disturbance intensity under sub-humid conditions (Figure 2B). Differently, for dry-transition and semi-arid holm oak sites there was strong evidence that PUE decreased nonlinearly with increased disturbance intensity (DT and SA quadratic terms in the general PUE–Dl model were significant at $P < 0.001$; Table 1).

Our holm oak sites showed higher vegetation PUE for dry than for wet years (Figure 3). The relationship between PUE and disturbance intensity for separate dry and wet years were consistent with the general patterns described for the SA, DT and SH climate aridity levels by the 2000–2014 average PUE–Dl trends. Indeed, the quadratic coefficients of the extended dry/wet model for both DT and SA sites were statistically significant at $P < 0.05$ (Table 1), pointing out accelerated, nonlinear reductions in vegetation PUE with disturbance intensity under semi-arid and dry-transition conditions (Figure 3A, B). Conversely, the quadratic terms of the extended PUE–Dl functions for SH sites were not statistically different from zero for both dry ($t_{129} = - 1.29$; $P = 0.20$) and wet years

Table 1. Equation Fitting Parameter Estimates and Statistics of the Relationship Between PUE and Disturbance Intensity (as Described by the Local Deforestation Level, Dl, of the Study Sites) for the General (14-Year Average Response) and Extended (Dry/Wet Year) Models.

	Intercept	Linear coefficient	Quadratic coefficient
General model: average PUE–Dl relationship			
SA sites			
Estimate	1.30***	0.06^{ns}	− 0.42***
SE	0.02	0.10	0.08
DT sites			
Estimate	1.27***	− 0.11^{ns}	− 0.29***
SE	0.02	0.09	0.08
SH sites			
Estimate	1.14***	− 0.34**	− 0.10^{ns}
SE	0.03	0.11	0.10
Extended model: dry year PUE–Dl relationship			
SA sites			
Estimate	1.64***	− 0.09^{ns}	− 0.47***
SE	0.03	0.13	0.11
DT sites			
Estimate	1.68***	− 0.42***	− 0.20*
SE	0.03	0.12	0.10
SH sites			
Estimate	1.39***	− 0.37*	− 0.17^{ns}
SE	0.04	0.16	0.13
Extended model: wet year PUE–Dl relationship			
SA sites			
Estimate	1.12***	− 0.01^{ns}	− 0.28**
SE	0.03	0.11	0.09
DT sites			
Estimate	0.96***	0.13^{ns}	− 0.35***
SE	0.02	0.10	0.09
SH sites			
Estimate	0.99***	− 0.39**	0.03^{ns}
SE	0.03	0.12	0.10

SA, semi-arid; DT, dry-transition; SH, sub-humid; SE, standard error.
Significance codes: ***P < 0.001; **P < 0.01; *P < 0.05; ^{ns}non significant at P = 0.05.

($t_{129} = 0.31$; $P = 0.76$), evidencing more gradual, linear effects of disturbance on sub-humid holm oak PUE levels (Figure 3C).

Type of hydrological year, as assessed by the statistical differences in dry/wet year coefficients of the extended PUE–Dl model, significantly affected ($F_{2, 137} = 4.3$; $P = 0.015$) the effect of disturbance on PUE levels. In fact, total reduction in PUE across the analyzed disturbance intensity gradients was in general deeper for dry than for wet years (35–40% and 25–35%, respectively; Figure 3). These effects were, however, influenced by the climate aridity conditions of the studied holm oak sites. Global PUE reductions associated with the loss of tree cover under semi-arid and dry-transition conditions were about 1.5 times stronger for dry than for wet years (Figure 3A, B). In contrast, the drop in PUE along the analyzed (Dl) disturbance intensity

gradient under sub-humid conditions was equivalent for both dry and wet years, accounting for a homogeneous ~35% reduction in PUE levels (Figure 3C).

DISCUSSION

Precipitation-use efficiency provides an integral measure for exploring the response of vegetation primary production to spatiotemporal changes in precipitation and land uses (Le Houerou 1984; Verón and Paruelo 2010; Gaitán and others 2014). Large-scale analysis of remote-sensed precipitation-use efficiency of vegetation in this study facilitated exploration of the interactions between climate aridity, human disturbance and precipitation variability for the emergence of nonlinear changes in the functionality of Iberian holm oak woodlands.
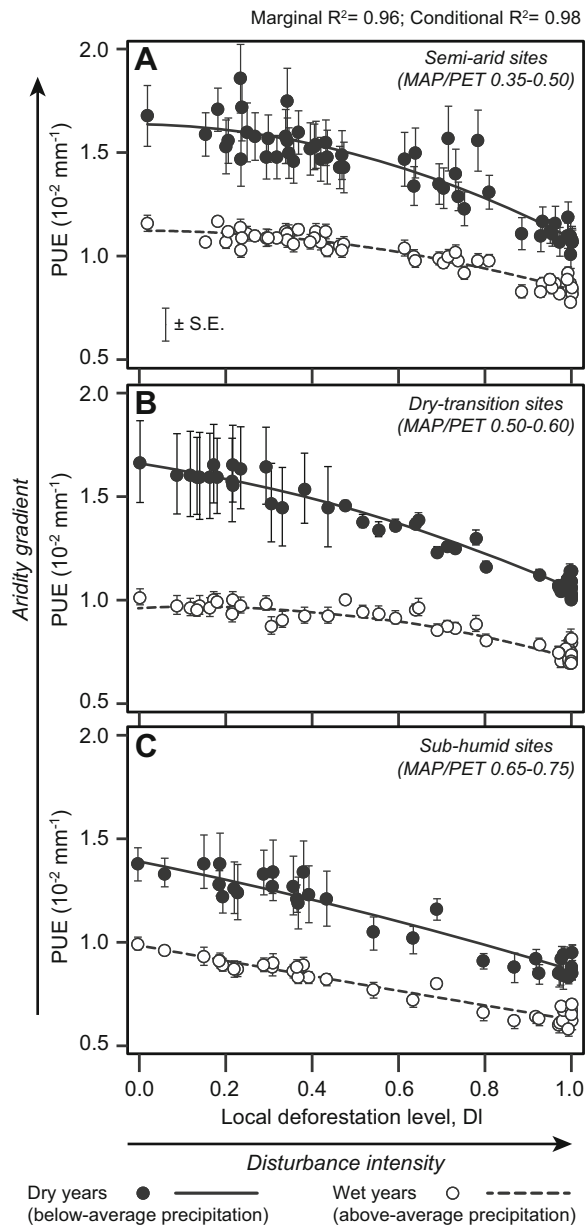
Marginal R^2= 0.96; Conditional R^2= 0.98

Figure 3. Effect of type of hydrological year (dry versus wet years) on the relationship between precipitation-use efficiency (PUE) and disturbance intensity (as described by the local deforestation levels, Dl, of the study sites) for (**A**) semi-arid, (**B**) dry-transition and (**C**) sub-humid sites. Reported marginal and conditional R^2 (on top of the graph) and fitted lines correspond to the extended (dry/wet year response) model.

PUE decreased from semi-arid to dry-transition and sub-humid conditions in our holm oak sites (Figure 2A), which agrees with other studies that pointed out that as water stress decreases from semi-arid to humid conditions with increasing annual average precipitation, primary production is gradually more constrained by other factors, such

as the availability of nutrients and light (Huxman and others 2004; Prince and others 2007; Ruppert and others 2012; Gaitán and others 2014). More importantly, PUE in our study sites also decreased with the intensity of human disturbance (Figure 2B). Accordingly, the precipitation-use efficiency of vegetation has been reported to show a high sensitivity to the alteration of both vegetation and soil conditions (Le Houerou 1984; O'Connor and others 2001; Prince and others 2007). PUE in highly disturbed landscapes generally falls due to enhanced water loss by surface runoff and direct evaporation that, in turn, reduces the proportion of precipitation that is used for transpiration (Ludwig and others 1999; Verón and Paruelo 2010). Our results indicate that the conversion rate of precipitation into vegetation primary production can decrease up to 35% in disturbed Iberian holm oak woodlands. This reduction in PUE values is similar to reported changes for other degraded dryland ecosystems in Australia, Africa and America (Le Houerou 1984; Holm and others 2003; Verón and Paruelo 2010; Moreno-de las Heras and others 2012).

Our findings indicate different precipitation-use efficiency responses to human disturbance of holm oak woodlands as a function of their climate aridity conditions (Figure 2B). Sub-humid conditions showed linear decreases in PUE with increased woodland deforestation. In contrast, semi-arid and dry-transition holm oak sites showed nonlinear decreases in PUE with disturbance intensity; reductions in PUE rapidly accelerated as a quadratic function of local deforestation level. These results provide empirical evidence for the dryland ecosystem stability principles discussed in a variety of theoretical studies, which predict nonlinear behavior for arid and semi-arid ecosystems in response to climate variability and human disturbance (Noy-Meir 1975; Ludwig and others 1999; Scheffer and others 2001; Rietkerk and others 2004; Bestelmeyer and others 2011; Mayor and others 2013). Plant–plant positive interactions (for example, plant facilitation by amelioration of environmental stress), which can effectively provide ecosystem stability to external stressors over a range of vegetation conditions, have been commonly argued to play an important role in the nonlinear behavior of dryland ecosystems (Noy-Meir 1975; Kéfi and others 2007, 2016; Soliveres and others 2015). Similarly, short-range spatial redistribution of water, nutrients, sediments and propagules between bare and vegetated areas is postulated as a fundamental feedback process for structuring and providing stability to dryland

ecosystems with patchy vegetation (Saco and Moreno-de las Heras 2013; Okin and others 2015; Bochet 2015). Both plant–plant interactions and short-range spatial redistribution of surface resources may play a role in the nonlinear behavior of the studied Mediterranean-dry woodlands, where vegetation cover is patchy (that is, tree vegetation for our study sites reached 50–70% maximum cover under semi-arid and dry-transition conditions) and holm oak trees have a key importance in regulating plant–plant interactions and plant–soil feedbacks (Terradas 1999; Cubera and Moreno 2007; Carnicer and others 2013). Significant deterioration of these stabilizing feedbacks (for example, loss of large vegetation patches with high capacity to modify environmental conditions) may induce accelerated, rapid loss of ecosystem function (Kéfi and others 2007; Moreno-de las Heras and others 2012; Berdugo and others 2017).

Precipitation-use efficiency of vegetation was considerably higher for dry than for wet years across 2000–2014 in our study holm oak sites (Figures 2A and 3), which agrees with other studies that perceived similar variations in PUE as an ecosystem resilience mechanism that sustains vegetation production during the driest periods (Huxman 2004; Wessels and others 2007; Ponce-Campos and others 2013; Zhang and others 2014). In general, disturbance induced a stronger decline in PUE values for dry than for wet years resulting, for severely altered landscapes, in a sharp reduction in the ecosystem ability to buffer large changes on primary production caused by drought (Figure 3). In fact, the alteration of landscape conditions in dryland ecosystems typically shows more pronounced effects on primary production and precipitation-use efficiency of vegetation during dry periods, which strongly affects the vulnerability of disturbed landscapes to precipitation variability (Pickup 1996; Dube and Pickup 2001; Hein 2006). For example, the scarcity of deep-rooted trees under the most disturbed conditions of our holm oak study sites very likely constrains vegetation use of deep soil moisture, which has been argued to play an important role in retaining primary production during dry periods in Mediterranean oak woodlands (Baldocchi and Xu 2007; Cubera and Moreno 2007).

The differences between dry and wet years on the response of PUE to disturbance increased with aridity from sub-humid conditions (where PUE reductions with site deforestation were equivalent for both dry and wet years, Figure 3C) to dry-transition and semi-arid conditions (1.5 times

stronger PUE drop along the disturbance gradient for dry than for wet years, Figure 3A, B), suggesting that aridity in the studied Iberian holm oak woodlands may intensify the vulnerability of ecosystems to the combined effects of climate variability and disturbance. The previous analysis of arid to mesic Mediterranean rangelands affected by grazing pointed to a similar reduction in resilience to climate-driven changes in vegetation production that is exacerbated by climate aridity, which may facilitate the collapse of ecosystem functions and services by drought in intensively used dry landscapes (Köchy and others 2008).

In sum, our results indicate that the interaction of climate variability and human disturbance in Iberian holm oak woodlands can result in nonlinear decreases in ecosystem function under semi-arid and dry-transition climate conditions. Changes in climate aridity and drought frequency are currently perceived as chronic contributors to ecosystem degradation in drylands (Suding and others 2004; Moreno-de las Heras and others 2012). Climate change projections for the Iberian Peninsula suggest decreased mean annual rainfall with increased summer temperatures and drought frequency for the next 100 years (de Castro and others 2005), which may exacerbate ecosystem change in Iberian holm oak woodlands. Specifically, sub-humid holm oak woodlands, showing at present gradual, linear reductions in ecosystem function in response to the effects of human disturbance, may also acquire the characteristic nonlinear behavior of the semi-arid and dry-transition sites. There is particular concern that, under certain circumstances, these nonlinear ecosystem changes can be largely irreversible (Noy-Meir 1975; Schlesinger and others 1990; Scheffer and others 2001; Rietkerk and others 2004; Kéfi and others 2016). Historical environmental records indicate that deforestation of Iberian holm oak woodlands at the boundary between arid and semi-arid climate conditions (MAP-to-PET ratio 0.20–0.40) can result in persistent ecosystem changes (Latorre and others 2001). Biodiversity and soil conditions (for example, water retention capacity, soil biological activity, nutrient cycling integrity) play a fundamental role in conferring stability and resilience to dryland ecosystems (Suding and others 2004; García-Fayos and Bochet 2009; Maestre and others 2016). Further exploration of biodiversity patterns and soil functions may assist ascertaining whether observed nonlinear reductions in PUE levels of Iberian holm oak woodlands may hinder natural recovery of disturbed ecosystems.

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