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ECOSYSTEMS

Ungulates Attenuate the Response of Mediterranean Mountain Vegetation to Climate Oscillations

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ABSTRACT

In regions with a long-standing history of grazing pressure, vegetation has co-evolved with herbivores by developing intrinsic functional dynamics. Although this type of trophic interaction has been recognised as being important for shaping how vegetation responds to climate, better knowledge about how this process occurs on the landscape scale and over a long time range is necessary. Here, we evaluated the potential roles of herbivores in modulating the response of mountainous Mediterranean vegetation to seasonal and long-term climate oscillations. To understand the relations among climate, plants and animal population, we fitted a Bayesian model to a combination of long-term (1995–2014) climate datasets, satellite greenness maps (NASA Landsat NDVI) and exotic Barbary sheep census data (breeding success and abundance of *Ammotragus lervia*). We also used the intrinsic mode function and Hilbert spectrum transformations to decompose NDVI time series and to evaluate their periodic oscillations. We found remarkable dissimilarities as to how climate affects the temporal oscillation of vegetation greenness between landscapes both with and without ungulates, albeit their similarities under environmental conditions. Vegetation responses to climate are particularly attenuated in landscapes with ungulates, an effect that depends on ungulate population abundance. In a world where extreme climate events are becoming frequent and intense, our results indicate that ungulates can strongly modulate how grasslands and scrublands respond to climate change. Increasing our knowledge as to how this type of trophic interaction affects vegetation responses to climate variability is of much importance for managing ungulate rewilding strategies.

Key words: herbivore; ungulates; exotic animals; Normalised Difference Vegetation Index; primary productivity; plant biomass; climate change; climate adaptability.

HIGHLIGHTS

- We evaluate vegetation–herbivores interactions under variable climate conditions.
- Ungulates modulate how ecosystem-level primary production responds to climate.

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Authors Contributions JMB and JASZ designed the study. JMB, RPR, SEM and JASZ performed research and coordinated the fieldwork. JMB analysed the data. JMB, RPR and JASZ wrote the paper.

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- Exotic ungulates may partially replace native ecosystem functions.

INTRODUCTION

In a global climate change context, much emphasis has been placed on the question about how vegetation functioning is subject to oscillations in climate-based limiting factors (Huxman and others 2004; Yi and others 2010; Li and others 2017). Such studies highlight the importance of changes in climate to ecosystem-level primary productivity and vegetation biomass. However, biotic factors are also crucial for shaping vegetation functioning. For example, primary productivity in more diverse plant communities can be more resilient to extreme climatic events (Tilman and Downing 1994; Isbell and others 2015). Moreover, herbivores determine individual to community-level vegetation functioning because herbivorism can affect water-use efficiency, the photosynthetic rate of the remaining biomass, competitive release and plant–plant facilitation (McNaughton 1985). Consequently, primary consumers might affect how vegetation productivity responds to climate on local and landscape scales. Although some studies have already highlighted the importance of trophic interactions in modulating vegetation responses to climate (Post and Pedersen 2008; Kaarlejärvi and others 2015; Olofsson and Post 2018), better knowledge on how this process occurs on the landscape scale and over a long time period is necessary.

In regions with a long-standing history of grazing pressure, vegetation has co-evolved with large herbivores by developing intrinsic functional dynamics (Milchunas and Lauenroth 1993). However, these important trophic interactions and their functional dynamics have been disrupted following severe declines in animal populations due to a long history of humans overexploiting large- and medium-sized herbivores (Doughty and others 2010, 2016). Missing trophic interactions over large areas may enhance uncertainties as to whether vegetation under climate change will persist in its original regime (that is, the same plant community) or shift to an alternative regime (that is, new community composition and functioning) (Kaarlejärvi and others 2015).

If we can measure and map the effects of herbivory on vegetation–climate feedbacks over time, it may help land managers to implement trophic rewilding, that is, reintroduction of primary consumers and their missing trophic interactions, as a mitigation tool to climate change (Cromsigt and others 2018). The distribution of wild medium-sized ungulates in particular largely depends on human intervention on the landscape scale, from animal exploitation and reintroduction to land use (Navarro and Pereira 2012; Anadón and others 2018). Therefore, management decisions about where to eliminate or reintroduce ungulates may impact vegetation–animal interactions on the landscape scale and might consequently affect ecosystem functioning.

Trophic interactions between vertebrate herbivores and plant community depend on the interplay between top-down and bottom-up controls (for example, Hunter and Price 1992; Augustine and others 2003; Letnic and Ripple 2017). The relative importance of these controls may be affected by climate conditions. In wetter regions with less variable rainfall, biotic factors (for example, carrying capacity, grazing pressure, density dependence) are the most important drivers of vegetation–herbivores dynamics (Vetter 2005; Derry and Boone 2010). Conversely in arid and semi-arid regions where rainfall seasonality is high, stochastic abiotic factors (that is, droughts) are important drivers of primary productivity, while grazing intensity may have a negligible impact (Sullivan and Rohde 2002; Vetter 2005). Indeed, wet years in arid and semi-arid regions also result in herbivores having a stronger impact on vegetation productivity and biomass (top-down control), whereas resource-limited conditions diminish plant productivity in dry years, which leads to stronger bottom-up controls (Meserve and others 2003). Therefore, top-down and bottom-up controls are likely to occur simultaneously and their relative importance would oscillate over time. The occurrence, absence or changes in the strength of these interaction-based controls may mediate plant responses to temporal climate variability because medium-sized herbivores (that is, ungulates) usually influence the plant biomass, soil nutrient dynamics and species composition of plant communities (Frank and Groffman 1998; Pascual-Rico and others 2018).

Remote sensing data offer a unique opportunity to understand relations among climate, vegetation and herbivores in large regions (Pettorelli and others 2011). Thousands of satellite images provide long-term information on climate (for example, precipitation and temperature) and vegetation greenness (that is, Normalised Difference Vegetation Index (NDVI), which is a metric for photosynthetic activity and biomass). Overlapping such information with ungulate census data facilitates the assessment of the direct and indirect interactions among climate, animals and vegetation (Nielsen and others 2012), for example, by following Bayesian approaches to evaluate feedback on these relations and to bridge information gaps.

Here, we combine multi-temporal remote sensing data and ungulate census data to evaluate the potential roles of herbivores in modulating the response of mountainous grasslands and scrublands to climate variability in a Mediterranean region. Our study focuses on the long-term dynamics of climate, ungulates and vegetation greenness (primary productivity and biomass) to answer the following specific questions: do top-down and bottom-up controls occur simultaneously in a long-term plant–herbivore interaction; and do exotic ungulates modulate the responses of vegetation to seasonal and long-term climate variability in Mediterranean mountain habitats? To answer these questions, we fitted an explicit Bayesian model to a combination of long-term (1995–2014) climate datasets, satellite greenness maps (NASA Landsat NDVI) and exotic Barbary sheep census data (breeding success and abundance of *Ammotragus lervia*), by specifying the relations among environmental, plant and animal variables. We also evaluated how seasonal fluctuations in NDVI are affected by ungulates. We discuss our findings in the trophic rewilding context with exotic species and their potential to mitigate ecosystem responses to climate change. We benefit from a natural landscape-scale experiment, in which we compared a region undergoing dynamic temporal changes in grazing intensity with two other regions that have been virtually ungrazed over time (the control treatment), but all with very similar climate and vegetation conditions.

STUDY AREA

The study was conducted in three mountainous areas of southeast Spain, that is, Sierras de Espuña, Pila and Ricote (17,804; 8836; and 4219 ha, respectively, Figure 1). These three mountainous areas are public lands, where environmental protection laws restrict animal and vegetation management. They are very close in geographical terms (~ 40 km) and present very a similar vegetation structure and composition. These areas are covered by Mediterranean vegetation, mainly pine forest (*Pinus* halepensis, *P. nigra* and *P. pinaster*), shrubs (*Rosmarinus* officinalis L., *Lithodora fruticosa* (L.) Griseb, *Thymus vulgaris* L.), small patches of oak forest (*Quercus ilex* and *Q. faginea*) and grassland (mostly dominated by native species such as *Macrochloa tenacissima* (L.) Kunth or *Helictotrichon filifolium* (Lag.) Henrard) (Rivas-Martínez 1986; Buhk and others 2006; Fernández-Olalla and others 2016). Elevation ranges from 200 to 1583 m a.s.l. Sierra Espuña, from 200 to 1150 m a.s.l. at Sierra de Pila and from 200 to 1000 m a.s.l. at Sierra de Ricote. Mean annual precipitation ranges from 277 mm in lower mountain areas to 510 mm in upper Sierra Espuña parts. At Pila and Ricote, mean annual precipitation ranges from 250 mm to 400 mm. Most of the annual precipitation in the three above-mentioned study zones occurs in autumn and spring, where summers are particularly dry. Average annual temperatures range from 13 to 18°C in Sierra Espuña and from 14 to 16°C in Sierras de Pila and Ricote (Figure 1).

We focused our study on the trophic interactions between vegetation and the exotic ungulate Barbary sheep (*Ammotragus lervia* Pallas; 40–132 kg) in these three study zones. This species was introduced into southeast Spain in the 1970s due to hunting interests. Barbary sheep abundance increased at Sierra Espuña in the 1980s followed by a near extinction at the start of 1990s because of an outbreak of sarcoptic mange (González-Candela and others 2004). After this disease outbreak, Barbary sheep populations have continuously recovered at Sierra Espuña (1995–2010). This species has been abundant at Sierra Espuña (reaching up to 12 ind/km^2), but is very scarce at Sierra de Ricote ($<$ 0.1 ind/km^2) and absent at Sierra de La Pila. The last native ungulate herbivore, the Spanish Ibex (*Capra pyrenaica*), was extinct in the study area by the early twentieth century, but it has been recolonising the study area in very recent years (Anadón and others 2018). Domestic ungulates, mainly sheep and goat, had also disappeared by the late 1970s as a result of human rural abandonment.

METHODS

In our analysis, we intentionally merged data from both Sierras Pila and Ricote given their close spatial proximity and marked climate and vegetation similarities, and the absence of ungulates. We performed our analysis by separating the three study zones into two groups (zones), that is, ‘‘Sierra Espuña’’ and ‘‘Sierras Pila–Ricote’’. We opted for this approach because we were interested in comparing areas where the overall vegetation and environmental conditions are similar, but ungulate occurrence varies. (Ungulates are quasi absent at Sierras Pila–Ricote.) Therefore, we describe the following methodology and results after considering two separate study zones (Sierra Espuña and

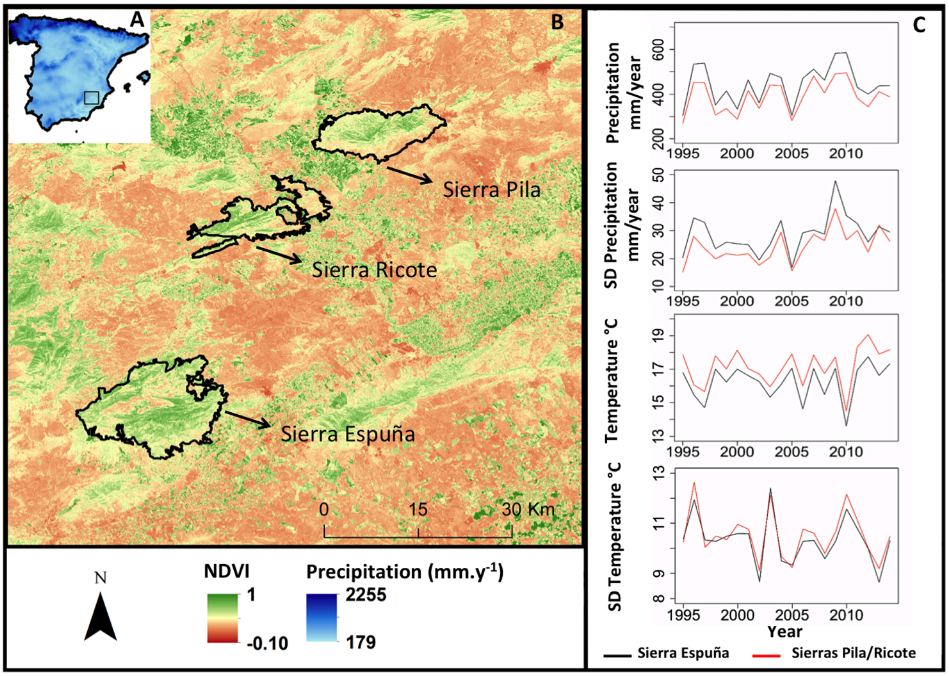

Figure 1. (A) Mean annual precipitation map (mm year^{-1}) for Spain, which highlights the location of the study zones (black square). (B) The average NDVI between 1995 and 2014 showing the spatial delimitations of Sierra Espuña, Sierra de Ricote and Sierra de Pila. (C) Temporal changes in precipitation (mm year^{-1}, mean and standard deviation—SD) and temperature (degree Celsius, mean and standard deviation—SD). The red lines in all the graphics represent the average values for Sierras de Pila and Ricote. The black lines in all the graphs represent Sierra Espuña.

Sierras Pila–Ricote). Both study zones sum together approximately 30,000 ha, which cover a wide variety of vegetation type, soil, topography and microclimatic conditions.

In Figure 2, we provide an overview of the datasets and the methodological framework used herein. We firstly performed Bayesian models to bridge any data gaps about NDVI time series and to evaluate the effects of temporal climate dynamics on the vegetation greenness of both study zones (''Statistical Analyses'' section). We then used a second set of Bayesian models to understand the relative importance of the top-down and bottom-up controls in the climate–plant–herbivore interactions (''Statistical Analyses'' section). We finally evaluated whether exotic ungulates did or did not modulate the responses of vegetation to seasonal and long-term climate variability by analysing the relation between the amplitude in seasonal fluctuation of NDVI (standard deviation and amplitude) and ungulate abundance (''Statistical Analyses'' section).

Datasets

Ungulate Abundance and Breeding Success

The Barbary sheep census consisted in performing the same linear transects (n = 17; total distance covered 144 km) each year (1995–2014) at Sierra Espuña during the rutting season (September–October). All Barbary sheep individuals were counted, and their sex and age were identified to provide a relative abundance index. By estimating the number of females and offspring born the previous spring (March to May), we established the population's breeding success (number of births per female). Censuses started in the morning immediately after sunrise and ended some 2–3 h later. During this time, Barbary sheep individuals were easily detected in the study area because of them performing more foraging activity early in the morning (Pascual-Rico and others 2018). The linear transects were the same each year and were surveyed simultaneously every year to avoid double counting, which allowed us to compare population change over time (González-Candela and others 2004). The staff who participated in the census were familiar with the study species and the study area. They included public gamekeepers, rangers, environmental consultants and scientific researchers.

Climate Data

We obtained precipitation data between 1995 and 2014 from the Climate Hazards Group InfraRed

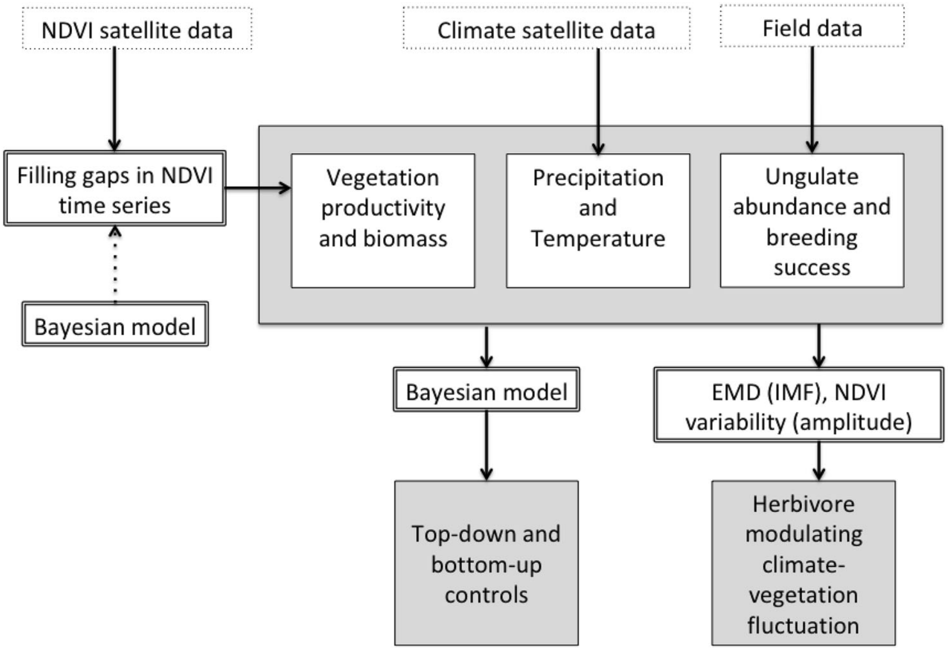

Figure 2. Study's methodological framework. Our datasets include satellite images to obtain climate and plant productivity/biomass information on the landscape scale, along with field data of ungulate abundance and breeding success. We used a Bayesian model to bridge the NDVI data gaps in the time series and to evaluate the relative importance of climate factors on plant productivity/biomass. We then used a second Bayesian modelling approach to understand the relative importance of the top-down and bottom-up controls in the climate–plant–herbivore interactions. We finally evaluated the influence of exotic ungulates on climate–vegetation temporal oscillation.

Precipitation with Station data [CHIRPS; (Funk and others 2015)], which is a gridded rainfall map with 0.05° × 0.05° spatial resolution and 6 days of temporal resolution. For the two study zones (Sierra Espuña and Sierras Pila–Ricote), we then calculated cumulative precipitation each month (mm/month), and for the last 3, 6 and 12 months (mm/year, for example, Figure 1), as well as total precipitation (mm/season) in spring (March to May), summer (June to August), autumn (September to November) and winter (December to February) from 1995 to 2014. We also calculated the standard deviation (SD) of precipitation for all these time intervals.

We used the NOAA Climate Data Record of Reflectance and Brightness Temperatures from AVHRR Pathfinder Atmospheres-Extended (PATMOS-x) (Heidinger and others 2014) to obtain the means and standard deviations (SD) of temperature (°C) between 1995 and 2014 with a spatial resolution of 0.1° × 0.1° and 6 h of temporal resolution. We then calculated the average and SD temperature within each study zone per month, year, and the previous 3, 6 and 12 months, as well as seasonal periods (spring, summer, autumn and winter from the current and past years according to each ungulate census).

NDVI Data

Normalised Difference Vegetation Index (NDVI) has been mostly used in studies about vegetation functioning in grasslands and scrublands to evaluate relations between ungulates and vegetation (Pettorelli and others 2011). Here, we used the NDVI to infer the vegetation function and the greenness of grasslands and scrublands (that is, temporal dynamics in both photosynthetic activity and vegetation biomass). We obtained NDVI data from the Landsat 5 ETM (L5) and Landsat 7 ETM + (L7) sensors of the NASA Land Processes Distributed Active Archive Center (https://lpdaac.usgs.gov/). We detected a good agreement in the temporal NDVI pattern from sensors with a different spatial resolution (Figure S1 in Supplementary Material). In the following methodological steps, we only used Landsat data given their smaller spatial resolution, helping to minimise the fusion among the different land cover types (that is, grassland and forest) within a unique NDVI value. The Landsat NDVI products are computed from the atmospherically corrected bidirectional surface reflectance that have been masked for water, clouds, heavy aerosols and cloud shadows. Per-pixel Quality Assessment metadata were used to check the product performance for measuring the NDVI among study sites and over the years (Foga and others 2017). We obtained NDVI-L5 images for 41 dates and NDVI-L7 images for 179 dates between 1995 and 2014. We filtered the images for the pixels of grassland and scrublands using the CORINE 2012 Land Cover map obtained from the European Environment Agency (https://www.eea.europa.eu/publications/COR0-landcover). Using these pre-processed NDVI time series from both L5 and L7 independently, we then calculated the average monthly NDVI for each study zone (Sierra de Espuña and Sierras de Pila–Ricote) using only the pixels from grassland and scrubland.

Statistical Analyses

Retrieving the Monthly NDVI and Effect Size of Environmental Factors

To obtain a continuous time series of NDVI data, we applied a gap-filling approach to the NDVI time series of each study zone using Bayesian statistics. We also evaluated the consistency between the L5 and L7 NDVI time series to integrate them into a unique NDVI temporal dataset. With this methodological approach, we fitted a mechanistically explicit Multivariate Auto-Regressive State-Space (MARSS) model between NDVI (from L5 and L7) and the environmental covariates (monthly precipitation, cumulative precipitation in the previous 3, 6 and 12 months, monthly average temperature and average temperature in the previous 3, 6 and 12 months) for each study zone separately. We built MARSS models using the "MARSS" R-package (Holmes and others 2018) that provides support for fitting MARSS models to multivariate data via maximum likelihood. MARSS models allow the inclusion of observation errors from different data sources in the model inferences, which is advantageous because the NDVI data from L5 and L7 may present different sources of errors. An MARSS model includes a process model (equation 1) and an observation model (equation 2):

$$x_t = B_t x_{t-1} + C c_{t-1} + w_t;\ w_t \sim \text{MVN}(0, Q) \quad (1)$$

$$y_t = Z_t x_t + v_t;\ v_t \sim \text{MVN}(0, R) \quad (2)$$

Data were included in the model in y (with y_t being the monthly NDVI at time t and values standardised to the same scale, that is, z-scored) and in c (with c being the time lagged covariate data at sampling site s, z-scored for continuous covariates, particularly temperature and precipitation). The y_t data are a linear function of the ''hidden'' or true NDVI in x_t. Each element in y_t is the observed NDVI with ''n'' replicates, when monthly NDVI coincides in both L5 and L7. Each element in x_t is the true NDVI. As the NDVI time series (L5 and L7) in our study zones presented data values with very proximate dates, it allowed the model to separate the two sources of error variance (observation vs. process error).

In the state process equation (1), B is the matrix whose elements are parameters that estimate the effect of the data sources on one another and on themselves, C is the matrix whose elements describe the effect of each covariate on NDVI (climate data), and w is a matrix of the process error, which represents the effects of environmental stochasticity, with process errors at time t being multivariate normal with mean 0 and covariance matrix Q. Z_t are the additional regression parameters. In the observation process equation (2), v is a vector of non-process errors, with observation errors at time t being multivariate normal with mean 0 and covariance matrix R.

We evaluated the consistency in the greenness temporal trends of L5 and L7 using Akaike information criterion with correction for finite sample sizes (AICc). We compared the AICc values from the models that assumed both the L5 and L7 NDVI temporal dynamics to be similar and different. From the Bayesian models, we used the Q matrix (equation 1) to compare the models that assumed sensor-specific process errors and the models that considered a single process error across sensors (that is, L5 and L7). In the B matrix (equation 1), we only selected the models with no sensor measurement interactions. In the R matrix (equation 2), we compared models by considering sensor-specific observation errors with models that contemplated constant observation errors (that is, equal across both sensor types). We searched for the models with ΔAICc below 2 as the most plausible models. Using the model with the lowest AICc, we finally generated the state–state predictions from 3000 permutations to generate estimates and gap-fill missing NDVI data and to create credibility intervals (95% confidence intervals). We produced the confidence intervals of the retrieved NDVI outputs to evaluate precision in the estimates and to access any potential changes in errors with time. We also calculated the root-mean-square error (RMSE) in the NDVI estimates from the best Bayesian model. To do so, we first randomly selected 80% of the Landsat data to build the model and 20% of the Landsat data to test the accuracy of the MARSS model to estimate NDVI. We repeated these steps 100 times and finally obtained a mean and SD of RMSE (%) from this loop procedure.

We based our parameter estimates for the predicted state–state process on 3000 permutations using the best above-mentioned model structure. Climatic effects on NDVI were assessed via the 95% confidence intervals of the parameters (3000 permutations). We assumed that if the 95% credibility intervals did not overlap zero, they would indicate statistically significant effects.

Annual Trends in the Vegetation–Ungulate Interaction

We built a second MARSS model to evaluate the interactions among annual ungulate abundance, annual ungulate breeding success and annual average NDVI by including the relative importance of environmental drivers as covariates (temperature and precipitation in spring, summer, autumn and winter from the same and previous years). We used the same model structure presented in equations 1 and 2.

In equation 1, y_t refers to a data matrix with all the response variables, and in this case z-scored annual ungulate abundance, breeding success and annual NDVI at time t. The NDVI data were obtained from the retrieving methodological approach (see previous section). In addition, c refers to the time lagged and z-scored environmental covariates. B is an interaction matrix and models the effect of the data source (NDVI, ungulate abundance and breeding success) on one another and on themselves, C is the matrix whose elements describe the effect of each covariate in $\mathrm{y_t}$ (temperature and precipitation in spring, summer, autumn and winter from the same and previous years), and w is a matrix of the process error that represents the effects of environmental stochasticity, with process errors at time t being multivariate normal with mean 0 and covariance matrix Q. In the observation process of equation (2), v is a vector of non-process errors, with observation errors at time t being multivariate normal with mean 0 and covariance matrix R. As the climate data from the present and previous years are important drivers of vegetation productivity (Sala and others 2012; Reichmann and others 2013) and animal fitness, we created models that included covariates which represent current and past climate conditions, that is, cumulative and average precipitation and temperature (see previous section).

We selected the best model structure using AICc. The best model structure (that is, that which yielded the lowest AIC) was that which assumed that each y_t observed different hidden state trajectories, with independent process errors and different observation variances, and assumed an interaction among all the y_t (NDVI, ungulate abundance and breeding success). To evaluate eventual background temporal autocorrelation, we checked for temporal trends in the residuals between the estimated state predictions and the original data. We based our parameter estimates for the predicted state process on 3000 permutations using the best model structure (bootstrapping approach, for example, Stoffer and Wall 1991; Holmes and others 2018). The covariate effects on ungulates and ungulate–vegetation interactions were assessed via the 95% confidence intervals (3000 permutations).

Herbivores Modulate NDVI Oscillation

Using these retrieved NDVI values, we evaluated the temporal differences in NDVI between Sierra Espuña and Sierras Pila–Ricote over the years. We calculated the monthly and annual NDVI ratios as a measure of similarity in vegetation greenness, that is, the NDVI ratio is the ratio between NDVI from Sierra Espuña and Pila/Ricote, as follows:

$$\text{NDVI ratio}\,(t) = \frac{\text{NDVI Espuña}\,(t)}{\text{NDVI Pila/Ricote}\ \ (t)} \qquad (3)$$

where (t) is the mean NDVI in 1 month or 1 year when obtaining monthly or yearly NDVI ratios, respectively. To calculate the 95% confidence interval of the NDVI ratio, we applied equation 3 to the lower and upper confidence intervals of the NDVI estimates (previous section) of each study zone. Using these data, we then evaluated the potential relationship between the annual NDVI ratio and ungulate abundance.

We also compared the mean and standard deviation of annual NDVI from both study zones to search for allometric relations. We then evaluated the relative effects of total plant productivity/biomass and ungulate abundance on the annual NDVI temporal oscillation of Sierra Espuña with a generalised linear model. In this analysis, we first calculated the variance inflation factor (VIF) for the predictor variables using the car package (O'brien 2007) to assess collinearity. We then calculated the relative importance of the mean NDVI and ungulate abundance on the standard deviation of NDVI. We compared model performance using the Akaike information criterion (AIC) and explained variance.

Finally, we used the intrinsic mode function (IMF) to decompose the time series (monthly NDVI, precipitation and temperature) and to evaluate its periodic oscillation by extracting their seasonal component (specifically frequency and amplitude of NDVI at time t). We used this analysis to compare the temporal changes in the ''NDVI instantaneous amplitude'' between study zones (Espuña and Pila/Ricote). The IMF is based on the concept of empirical mode decomposition (EMD), a self-adaptive signal-processing method applied to non-stationary processing (Huang and others 1998; Junsheng and others 2006). We explicitly maintained time ''*t*'' on the *x*-axis (monthly basis), which allowed us to compare both study zones (Espuña and Pila/Ricote) in NDVI temporal oscillation terms. We calculated the IMF as follows. Given an NDVI signal at time ''*t*'', $y(t)$, we first determined the location of all the NDVI maxima and minima, that is, $y\max(t)$ and minima $y\min(t)$, respectively. Usually NDVI *y*max and *y*min are located in spring and summer in Mediterranean regions. We fitted a cubic spline through $y\max(t)$ and another through $y\min(t)$. Then, we calculated the mean of the spline curves at each point $m(t) = (y\max(t) + y\min(t))/2$. We then removed the trend, $m(t)$, by calculating $d(t) = y(t) - m(t)$. This procedure removes the trend, but maintains information about frequency and amplitude on a monthly basis. We repeated the above-mentioned IMF calculations until the trend had been completely removed (Figures S2 and S3 in Supplementary Material). For each IMF (Figures S2 and S3), we calculated a Hilbert spectrum transformation to extract the temporal change in amplitude (see a detailed description of the Hilbert transformation of IMF in (Huang and others 1998)). We employed the EMD R-package (Kim and Oh 2009) to extract the IMF from a given signal and to calculate amplitude. We averaged all the amplitudes from each study zone to obtain the final NDVI amplitude.

RESULTS

Temporal Changes in NDVI and Climatic Drivers

The best model structure (that is, that delivering the lowest AICc) used to retrieve the monthly NDVI was that which assumed L5 and L7 have the same hidden state trajectory, with independent process errors, similar observation variance and no interactions. NDVI was affected by climate covariates. This result corroborates with other studies that have shown a large consistency in the temporal greenness dynamics between satellite sensors (for example, Teillet and others 2001). Using the Bayesian model with the lower AICc, we predicted NDVI with a mean RMSE of 9.24% (SD = 1.9%) for Sierra Espuña and an RMSE of 10.69% (SD = 2.01%) for Sierras Pila/Ricote. The NDVI at both Sierra Espuña and Sierras Pila–Ricote increased from 1995 to 2010, followed by a drop between 2010 and 2014 (Figure 3). The grey lines in Figure 3 denote the 95% confidence interval of the estimated NDVI values from satellite sensors L5 and L7 and indicate narrow and quasi-homogeneous errors in the estimates with time.

As expected, both study zones (Sierra Espuña and Sierras de Pila–Ricote) showed concomitant seasonal oscillation in NDVI (Figure 3), which suggests synchronic vegetation responses to a similar climate seasonality (Figure 1). However, marked dissimilarities in vegetation functioning also occurred between these two study zones. For example, the differences in NDVI (that is, the NDVI ratio) between study zones decreased continuously from 2000 to 2010 (Figures S4 and S5). The relative effect size of the climate variables on the NDVI

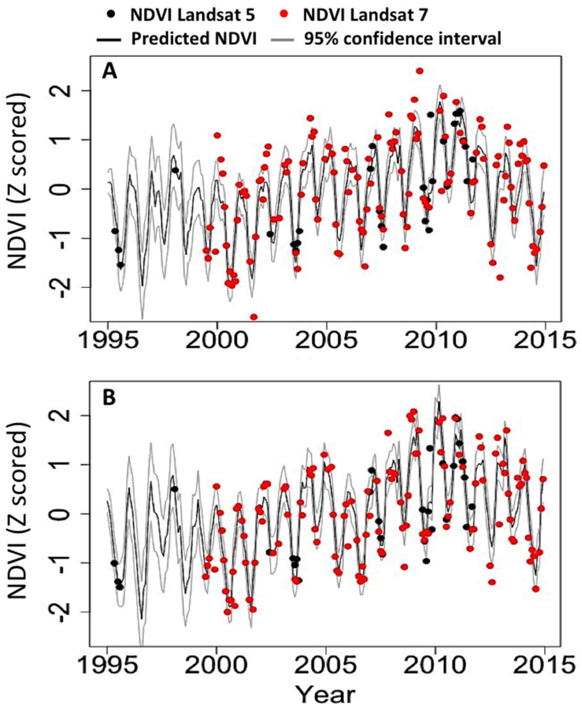

Figure 3. Monthly NDVI between 1995 and 2014 for (A) Sierra Espuña and (B) Sierras Pila–Ricote. The NDVI values are standardised to the same scale and range (that is, *z*-scored). Dots indicate the average NDVI of grasslands and scrublands, obtained from Landsat 5 (black) and Landsat 7 (red). The solid black lines indicate the posterior estimates for the predicted states from a Bayesian model that uses both satellites (Landsat 5 and 7) and climate data as covariates. The grey lines indicate the 95% confidence interval of the estimate (Color figure online).

dynamics also diverged between study zones (Table 1), despite similarity in the temporal oscillation of both temperature and precipitation (Figures S6 and S7). Temperature was the most important covariate to drive NDVI. However, temperature was found to have a stronger negative influence on the NDVI at Sierra Espuña than at Pila–Ricote. Precipitation had positive effects on NDVI, but precipitation at Sierra Espuña presented a very weak effect size and wide credibility intervals. Cumulative precipitation (the summed precipitation from the previous 3 and 6 months) did not affect the NDVI in both study zones over the study period. An average temperature within the previous 6 months showed a positive effect on NDVI (Table 1). These results suggest a potential influence of herbivores on the response differences of vegetation to climate between both study zones.

Top-Down and Bottom-Up Controls in the Plant–Herbivore Interaction

The best model to describe ungulate–vegetation interactions and environmental covariate effects (ΔAICc < 2) indicates bidirectional effects between ungulates and vegetation at Sierra Espuña (Table 2 and Figure 4). This model presented very small or no background temporal autocorrelation (Figure S8, Supplementary Material). Ungulate abundance and breeding success had a negative relative effect on the NDVI at Sierra Espuña (Table 2). NDVI had more positive effects on breeding success than ungulate abundance, but the effect size of NDVI on breeding success was bigger. The ungulate population at Sierra Espuña presented apparent density dependency (Table 2). Precipitation had a positive effect on ungulate abundance (particularly precipitation in autumn and precipitation from the previous year) and a negative effect on breeding success (precipitation in the previous year) (Table 3). The average temperature in the same year had a negative effect on the annual NDVI (Table 3).

Herbivore Modulates NDVI Responses to Climate

The temporal increase in similarity in the annual NDVI between Espuña and Pila/Ricote was highly correlated with an increased ungulate population at Sierra Espuña (Figure 5; $R^2 = 0.5$ and $p < 0.001$). NDVI ratio values close to 1 indicate a greater similarity between Espuña and Pila/Ricote (Figure 5). Ungulates had a negative effect on NDVI (Table 2), which lowered the rate at which the NDVI at Sierra Espuña increased when climate conditions were favourable (for example, Figures S4 and S5).

We found that the maximum and minimum NDVI values in both study zones partially overlapped (for example, Figure 6) and the NDVI oscillation in these areas was apparently driven by similar ecosystem processes (Figures 1 and S4–S7). Indeed, we found a reduction in the NDVI standard deviation as the mean NDVI from both mountainous systems increased (Figure 6), which demonstrates that the annual oscillation in NDVI could be partially explained by the mean annual NDVI. However, and particularly at Sierra Espuña, both the mean NDVI and ungulates affected the standard deviation (SD) of NDVI, that is, the mean NDVI and ungulate abundance had a negative and positive influence on SD NDVI, respectively (Table 4). At the Pila/Ricote Sierras, the instantaneous NDVI amplitude showed a negative trend over time (Figure 7), as expected from the data in Figure 6. However, at Sierra Espuña, the NDVI amplitude

Table 1. Mean effect size and 95% credibility intervals (CI) of the different covariates on the monthly Normalised Difference Vegetation Index (NDVI) for the 1995–2014 Period

Covariates	NDVI Pila/Ricote			NDVI Espuña		
	Mean	Low CI	Up CI	Mean	Low CI	Up CI
Rainfall	0.17**	0.015	0.33	0.04	−0.18	0.25
Temperature	−0.32*	−0.54	−0.09	−0.48*	−0.76	−0.20
Cumulative precipitation (3 months)	−0.08	−0.24	0.07	−0.02	−0.27	0.21
Cumulative precipitation (6 months)	0.049	−0.03	0.12	0.05	−0.06	0.17
Average temperature (3 months)	0.08	−0.21	0.38	0.23	−0.14	0.59
Average temperature (6 months)	0.22**	0.08	0.37	0.13**	0.05	0.30

**A statistically significant negative effect*
***A statistically significant positive effect*

Table 2. Mean effect size (interaction strengths) and 95% credibility intervals (CI) of the different variables (annual data set) for the 1995–2014 Study Period

Covariates	Abundance			Breeding			NDVI		
	Mean	Low CI	up CI	Mean	Low CI	up CI	Mean	Low CI	up CI
Abundance	– 0.35*	– 0.36	– 0.34	– 0.28*	– 0.30	– 0.26	– 0.13*	– 0.16	– 0.10
Breeding	– 0.08	– 0.09	– 0.07				– 0.16*	– 0.19	– 0.13
NDVI	0.12**	0.11	0.13	0.29**	0.27	0.32			

Abundance and breeding refer to ungulate abundance and breeding success, respectively. NDVI refers to the normalised difference vegetation index
**A statistically significant negative effect*
***A statistically significant positive effect*

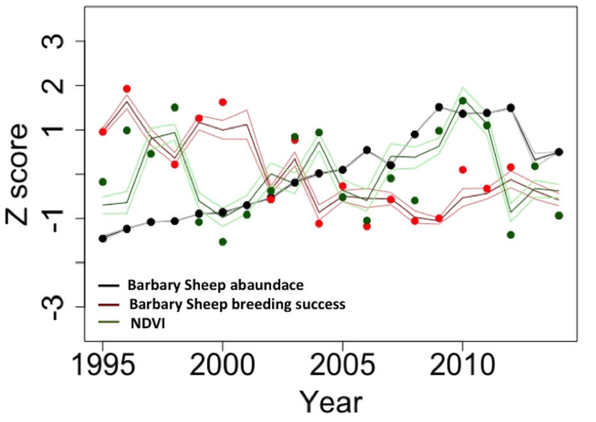

Figure 4. Annual time series of the interactions among Barbary sheep abundance, breeding success and NDVI (vegetation productivity and biomass) between 1995 and 2014. The black line indicates Barbary sheep abundance. (The grey line indicates the 95% confidence interval of the estimate.) The red line represents Barbary sheep breeding success. (The light red line indicates the 95% confidence interval of the estimate.) The green line indicates the NDVI values. (The light green line indicates the 95% confidence interval of the estimate.) All the values are standardised to the same scale and range (that is, *z*-scored) (Color figure online).

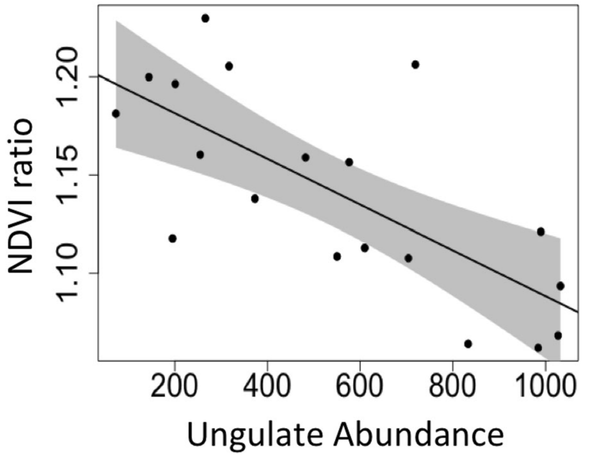

Figure 5. Relation between ungulate abundance at Sierra Espuña and the annual NDVI ratio (R^2 = 0.5 and $p < 0.001$).

showed a continuous trend with time (Figure 7), which suggests that increases in ungulate abundance attenuated changes in the intra- and inter-annual oscillations of vegetation productivity/biomass, as also indicated in Table 4.

Table 3. Mean effect size and 95% credibility intervals (CI) of the different environmental covariates on annual ungulate abundance, breeding success and the Normalised Difference Vegetation Index (NDVI) for the 1995–2014 Period

Covariates	Abundance			Breeding			NDVI		
	Mean	Low.CI	Up.CI	Mean	Low.CI	Up.CI	Mean	Low.CI	Up.CI
Precipitation autumn	0.37**	0.36	0.37						
Precipitation last year	0.21**	0.20	0.21	– 0.41*	– 0.43	– 0.39			
Temperature same year	– 0.07*	– 0.08	– 0.07	0.06**	0.05	0.06			
Temperature same year							– 0.43*	– 0.75	– 0.10

**A statistically significant negative effect*
***A statistically significant positive effect*

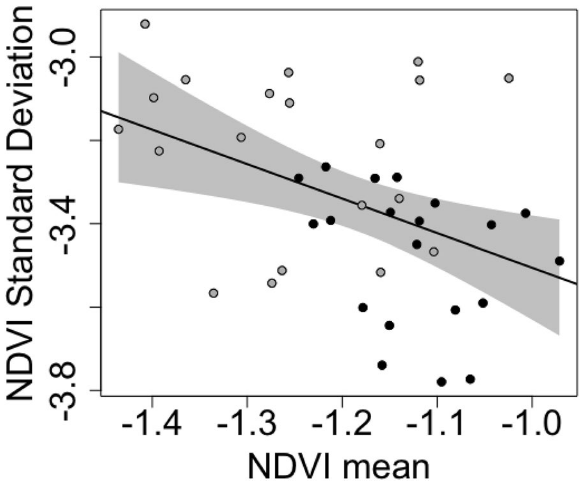

Figure 6. Relation between the mean annual NDVI and standard deviation ($R^2 = 0.16$ and $p = 0.005$). Each point indicates the mean and standard deviation of NDVI in a given year. The black points are from Sierra Espuña, and the grey points are from Sierras de Pila/Ricote. Values are in logarithms. The black line shows linear regression, and the grey-shaded areas indicate the 95% confidence intervals.

DISCUSSION

Here, we evaluated a long-term vegetation–climate dynamics against a background of changing herbivore pressure in mountainous grasslands and scrublands by applying Bayesian models to a large spatial-scale dataset. By this methodological approach, we found that vegetation greenness favoured ungulate abundance and further Barbary sheep breeding success. Interestingly, ungulates attenuate the influence of climate on both the intra- and inter-annual temporal dynamics of NDVI in mountainous Mediterranean grassland and scrubland areas. Taken together, these results highlight that both top-down and bottom-up controls occur simultaneously in a long-term plant–herbivore interaction by reiterating the bidirectional feedback between them with equivalent forces (Meserve and others 2003; Nielsen and others 2012). Undoubtedly, large herbivores influence worldwide plant populations and communities by affecting species reproduction, survival and standing biomass, as demonstrated in numer-

Table 4. Models showing the effect of the mean annual Normalised Difference Vegetation Index (NDVI) and ungulate abundance on the annual standard deviation of NDVI (SD NDVI) at Sierra Espuña

SD NDVI Espuña	Variables	Coefficient	*p*	ΔAIC	Explained variance
Model 1	Ungulate abundance	(+) 0.12	0.042	0	30%
	Mean NDVI	(−) 0.14	0.020		
Model 2	Mean NDVI	–	–	5	–
Null model	~ 1	–	–	6	–

Signals indicate positive or negative relations. The variance inflation factor (VIF) between the mean NDVI and ungulate abundance is 3.09, which indicates no collinearity between the explanatory variables in Model 1 (for example, ungulate abundance and mean NDVI).

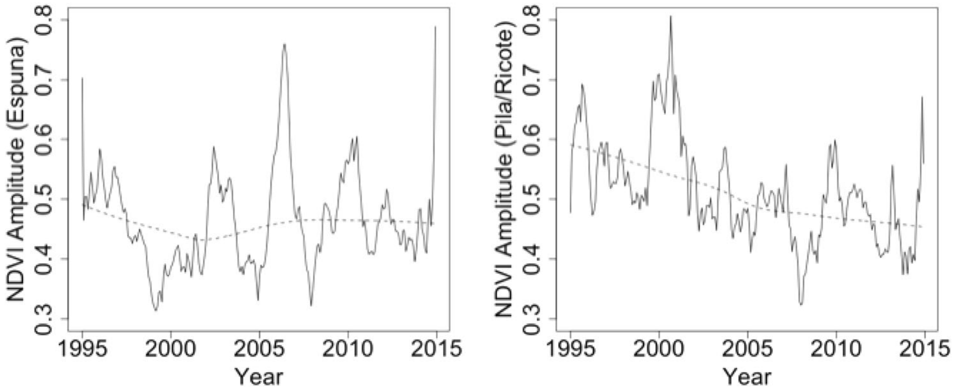

Figure 7. NDVI amplitude indicating instantaneous temporal oscillation and variability. Values were obtained from the Hilbert transformation of the intrinsic mode functions (IMF) for Sierra Espuña and Sierras de Pila–Ricote between 1995 and 2014. The black-dotted line shows a smoothed temporal trend for each study zone.

ous studies (Milchunas and Lauenroth 1993; Wittemyer and others 2007; Moyes and others 2011; Jia and others 2018). However, very few studies have evaluated the importance of herbivores on the adaptability of Mediterranean vegetation to climate oscillation, neglecting increases in searing heat and dryness expected in the future for this region (Deutsche Akademie der Naturforscher Leopoldina 2013). As far as we know, we herein show for the first time that ungulates mediate both the seasonal and long-term responses of vegetation to climate on the landscape scale in Mediterranean mountains. Our results suggest that herbivory is important for shaping vegetation responses to climate in both conserved and disturbed environments.

Vegetation–Herbivore Interactions: Buffering Climate Effects

In our study region, ungulates mitigated changes in the long-term patterns of the seasonal variability of plant productivity/biomass, even though environmental conditions changed. These results suggest that vegetation–herbivore trophic interactions can minimise the climate dependence of vegetation at the ecosystem level. Previous studies have reported similar processes (for example, MacNaughton 1985), but on a plant-level scale. Such information indicates that trophic interactions can help grasslands and scrublands to better support transient extreme climatic events. For example, in arctic plant communities, Post and Pedersen (2008) showed that environmental warming increased total community biomass by promoting the growth of deciduous shrubs and, consequently, shifts in the system's function only when herbivory was absent (also see Olofsson and Post 2018). Interestingly, herbivores also contribute to the resilience of these arctic systems by allowing them to return to the original low-biomass regime after warming events stop (Kaarlejärvi and others 2015). Our study suggests that Mediterranean plant communities, where the biota has undergone a longer history of human intervention (Blondel 2006; Ellis and others 2013) and vegetation is under regeneration (MacDonald and others 2000; Bowen and others 2007; Plieninger and others 2014), might follow a similar pattern, whereas herbivores may contribute to the resilience of Mediterranean mountain ecosystems.

We particularly found a long-term negative trend in the NDVI amplitude (oscillation) with the absence of herbivores following an increase in the annual NDVI. However, the long-term trend in NDVI amplitude was quasi-constant in the presence of herbivores, which supports the contribution of ungulates to ecosystem stability (for example, Tilman and others 2014). Overall, the increase in the mean NDVI with better climate conditions brought about reductions in intra-annual NDVI variability. However, ungulates limited the increase in NDVI and enhanced intra-annual NDVI variability by compensating potential changes in long-term NDVI variability and by also explaining why we did not find a negative long-term reduction in NDVI amplitude as better climatic conditions occurred. Therefore, together our results suggest that ungulates play an important rule in NDVI temporal dynamics in Mediterranean mountains. Although the vegetation composition and structure between the study zones seemed similar, our results highlight major differences in the NDVI temporal trends between them.

The effect size of climate variables on NDVI can change from arid to wet regions; for example, vegetation greenness in drier environments can be affected more by rainfall than wetter environments (Schultz and Halpert 1993; Zhao and Running 2010; Liu and others 2015). Biotic factors, such as herbivory, can add complexity to these climate–vegetation relations. Indeed, the relative importance of biotic feedbacks (for example, between herbivores and their resources) and stochastic abiotic factors for determining vegetation productivity can also change with precipitation patterns (Sullivan and Rohde 2002; Vetter 2005). Even in places where abiotic factors are the main drivers of vegetation productivity, as in arid and semi-arid environments, herbivores still determine composition, diversity (Manier and Thompson Hobbs 2006) and long-term patterns of plant demography (Sankaran and others 2013). Therefore, the effect of climate change on vegetation dynamics should also consider feedback with biotic factors.

Management Implications: Insights of Trophic Rewilding

Native ungulates have been extirpated or have sharply declined in population size terms in regions where, historically, vegetation is well adapted to the presence of these animals (Di Marco and others 2014). However, in some regions like the southeast Iberian Peninsula, exotic and native ungulates have recolonised mountainous areas, driven by reintroduction programmes and natural recolonisation (Anadón and others 2018). These processes are the basis of trophic rewilding and may be an important component of mitigating the ecosystem response to future climate changes (Bakker and Svenning 2018; Cromsigt and others 2018). Trophic rewilding has been presented as an ecological restoration strategy that uses species introductions to restore top-down trophic interactions and associated trophic cascades to promote self-regulating biodiverse ecosystems (Svenning and others 2016). Our results suggest that exotic Barbary sheep help regulate vegetation and might improve the resilience of semi-arid Mediterranean habitats to climate change. Barbary sheep, whose populations in their African native range are threatened, was released for conservation and hunting purposes in southeast Spain in the 1970s. This could be considered a pioneering assisted colonisation programme (Seddon 2010) and, consequently, a controversial management tool because it is usually hard to predict the consequences of such species introduction (Hoegh-Guldberg and others 2008; Ricciardi and Simberloff 2009). Our results show that the contribution of exotic invasive Barbary sheep to vegetation regulation might be considered an unintended positive goal of this assisted colonisation.

Conversely, the potential competition of Barbary sheep with the native Spanish ibex might be considered a detrimental side effect of this introduction. Both species show a marked similarity in their trophic and environmental niches at Sierra Espuña (Pascual-Rico and others unpublished data). The δ^{15}N and δ^{13}C values of both species (performed on hair samples) are similar (Pascual-Rico and others, unpublished data), which means that both species might play an equivalent functional role in Mediterranean ecosystems by attenuating vegetation responses to climate oscillations. Similar δ^{13}C values indicate that both ungulate species feed on the same kind of vegetation, namely C3 plants in our case, that is, they are mainly browsers.

In this context, land managers should identify control strategies in reintroduction and game hunting programmes that incorporate cascade effects of vertebrate herbivores on vegetation adaptability to climate. Long-term monitoring of populations of both ungulate species and more detailed information about their interactions with vegetation processes and community structure might be very useful for decision-making within the trophic rewilding framework in a climate change scenario. Fortunately, the native Spanish ibex is recolonising most of the original mountain ranges in southeast Spain and might play a similar ecological role to that described herein for Barbary sheep.

Exotic ungulates (wild or domesticated) may partially replace some missing trophic interactions via the intake of excess plant tissue or by affecting nutrient cycling in grazed areas (Milchunas and others 1989; Veblen and others 2016). Even though exotic species are welcome for maintaining missing ecosystem processes, their use to replace native species is not void of controversy. For example, livestock activities may often decline depending on economic cycles and political decisions (Bernués and others 2011) and could leave entire grassland regions ungrazed. These controversies undermine the potential use exotic animals to re-establish any missing trophic interactions in ecosystems as a mitigation tool to climate change (for example, Cromsigt and others 2018). These scenarios also highlight the need for more studies to be conducted on this topic, in which the rate of climate change is expected to be high.

Caveats and Further Directions

We recognise some limitations in our methodological framework because vegetation greenness measurements like those used herein may present confounding aspects as to whether vegetation biomass or productivity is being measured. NDVI has been mostly used in the literature as a successful proxy to assess general landscape-scale patterns in wildlife–vegetation interactions using both productivity and biomass (see a literature review in Pettorelli and others 2011). Fortunately, productivity and biomass usually show congruent temporal fluctuations in dryland environments (for example, Boelman and others 2003). We also understand that the spatial resolution of our climate dataset is coarse and may restrict comparisons being made between small nearby areas. An increasing number of ecological studies employ a variety of satellite data to obtain vegetation and climate data, each of which contains their own sources of uncertainty and spatio-temporal resolution (Pettorelli and others 2007; Yi and others 2010; Nielsen and others 2012). Scale-dependent biases can determine the accuracy and precision of the inferences made with the results (Murthy and Bagchi 2018). However, there is a usual trade-off between spatial and temporal resolutions in remote sensing analyses (Zhang and others 2016). We suggest more studies to be conducted in order to evaluate the effect of using datasets with different spatio-temporal resolutions on knowledge about the temporal dynamics of climate–vegetation–herbivores. Yet, we believe that the spatial resolution of our climate data was appropriate for the biology of the species in question and the distance between our study zones.

In short, our analytical approach enabled us to estimate the relative effect size and credibility intervals among ungulate population structure, vegetation greenness and environmental variables. We provide critical information for understanding reciprocal influences between vegetation and vertebrate herbivores under variable climate conditions. Increasing our knowledge as to how different trophic levels affect vegetation responses to climate variability is of vital importance in today's climate change context. Although our study shows a bidirectional influence between ungulates and vegetation, we still need to evaluate whether these influences occur independently or their relative importance is interchanged with time. Indeed, future studies could extend the number of landscapes used to evaluate the patterns found herein (for example, Nielsen and others 2012) and to also evaluate the importance of other herbivore taxa in modulating the responses of vegetation to climate variability on the landscape scale in a rewilding and climate change context.

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DATA AVAILABILITY

Data used in the paper are freely available in the web pages cited in the ''Methods'' section of the manuscript.

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