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Ecosystem productivity drives the breeding success of an endangered top avian scavenger in a changing grazing pressure context

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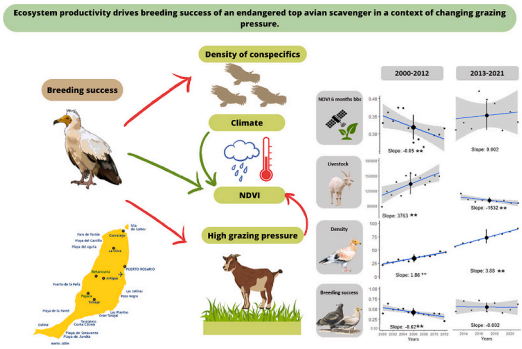
HIGHIGHTS

- Grazing pressure disrupts the breeding success of a top avian scavenger.
- Breeding success was related to ecosystem productivity.
- High grazing pressure is a major driver of arid environments.
- Long-term monitoring programmes are required to fully disentangle ecosystem shifts.
- Agricultural policies cause cascade effects on trophic interactions.

GRAPHICAL ABSTRACT



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ABSTRACT

Environmental conditions and resource availability shape population dynamics through direct and indirect effects of climate, biological interactions and the human modification of landscape. Even when a species seems dependent on predictable anthropogenic food resources or subsidies, ecosystem-level factors can still determine population dynamics across taxa. However, there is still a knowledge gap about the cascade effects driven by climate, vegetation functioning, resource availability and governmental policies on key aspects of species reproduction for top scavengers. Here we put to good use 22 years (2000–2021) of extensive population monitoring from the endemic Canary Egyptian vulture (*Neophron percnopterus majorensis*) on the Fuerteventura Island (Canary Islands, Spain) to study the relative importance of demographic factors, ecosystem conditions and availability of anthropogenic food sources on breeding success. Our results suggest that ecosystem-level primary productivity, the number of livestock animals present on the island and Density-dependent processes determine the temporal changes in the breeding success of this species. We firstly accounted for a top-down effect of livestock on island vegetation, where overgrazing directly reduces landscape-level vegetation biomass. We, consequently, found a bottom-up effect between vegetation and the Egyptian vulture's breeding success. In this context, minimal changes in ecological conditions can impact the species inhabiting these ecosystems, with direct consequences on a key population stage, such as breeding season, when energy requirements are higher. These

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results are especially relevant because cascading and indirect effects of ecosystem processes and governmental policies are often overlooked when pursuing conservation goals of endangered species.

1. Introduction

Natural- or human-driven ecosystem changes have a key influence on species survival and reproduction at different trophic levels, and from plants to vertebrates. Some cascading effects of ecosystem changes on species become extremely important in arid environments because the biota is driven by variable and ephemeral ecosystem conditions (Beever et al., 2017). Therefore, subtle changes in environmental and ecological conditions may have direct consequences for the species inhabiting harsh ecosystems, especially during critical periods like breeding season, when energy requirements are higher (Salamolard and Weimerskirch, 1993). Additionally, perturbations, such as droughts or overgrazing, can catastrophically disturb ecosystem functioning (Van De Koppel and Rietkerk, 2004), which results in potential shifts in species demographic tendencies.

Population dynamics are shaped by both environmental conditions and resource availability through direct and indirect effects of climate, biological interactions and the human modification of landscapes (Coulson et al., 2001; SÆther et al., 2004; Simard et al., 2010). Even when species seem largely dependent on predictable anthropogenic food resources or subsidies (Oro et al., 2013), ecosystem-level primary productivity can still determine changes in the life parameters of vertebrates (Donázar et al., 2020), in addition to habitat selection and movement ecology (general review, (Pettorelli et al., 2011). Recent studies have demonstrated the key role that ecosystem productivity plays in species demographical parameters through trophic cascading effects on primary, and even on secondary, consumers (Barbosa et al., 2020; Donázar et al., 2020). The relation between primary productivity and breeding success, however, remains largely unknown (but see (Marcelino et al., 2020)). Breeding success is conditioned by numerous factors, e.g. favourable weather conditions, habitat availability and condition, individual-level fitness and life-stage and resource availability. Intraregulatory mechanisms, such as Density-dependence effects, can also interfere negatively with raptors' breeding success (Chambert et al., 2020), with direct competence for resources (i.e. lack of feeding resources or mating partners). In fact there is compelling evidence that during the breeding season, the diet of many species changes to either exploit transient food resources or overcome the stress of raising offspring (Dhondt and Hochachka, 2001; Jiguet, 2002; Montague et al., 1986). Indeed we expect these natural ecosystem processes to interact with anthropic factors to determine breeding success.

Livestock farming has been identified as one of the main feeding resources for scavengers (O'Neal, 2016). However, it is also highlighted as a major ecosystem disruptor that affects ecosystem structure, functioning and stability (Li et al., 2018). Several studies have suggested that man-introduced herbivores can perturb the whole ecosystem through processes, such as overgrazing, nitrification, or even the alteration of moisture retention and soil fertility (Campbell and Donlan, 2005; Coblentz, 1978). These processes may aggravate insular ecosystems, where the evolutionary context of plant-herbivore interactions differ from the mainland, and are characterised by the presence of a high rate of endemism. Insular vegetation is usually well-adapted to local climatic conditions, and has evolved without vertebrate herbivores being present (Bowen and Vuren, 1997), which allow them to allocate resources and energy that would otherwise be used to defend other destinations (Moreira et al., 2021). This, in turn, favours greater palatability, which triggers a higher rate of predation from herbivores (Cubas et al., 2019).

The Egyptian vulture (*Neophron percnopterus*) is a medium-sized (2–3 kg), globally endangered obligate scavenger that lives in a variety of habitats, mainly open landscapes in arid ecosystems (BirdLife International, 2022). It is widely distributed across South Europe and North Africa, the Middle East, Central Asia and India, but there are numerous island populations (Donázar et al., 2005). Egyptian vultures have the peculiarity of exploiting a wide prey range, from livestock carcasses on which they very much depend (Cabrera-García et al., 2020; Milchev et al., 2012) to animal faeces (Negro et al., 2002), to carcasses of wild prey, such as small mammals, birds and reptiles, which has been positively related to breeding success (Margalida et al., 2012).

In the present work, we put to good use the 22 years (2000–2021) of extensive population monitoring of the Canary Egyptian vulture (*Neophron percnopterus majorensis*) on the Fuerteventura Island (Canary Islands, Spain) to study the relative importance of climate, primary productivity, livestock and intraspecific competition on breeding success. On Fuerteventura, goats were introduced by pre-European colonisers in 500 BCE. Indigenous people maintained a farming subsistence system on the island, which implied that the goat population was limited by environmental conditions and extreme events, such as droughts. According to (Cabrera, 1996), Europeans kept the Density of the goats on the island stable (approximately 30,000) in the 18th century, until 1970 when the number of domestic cattle started to sharply rise. Past and future livestock farming changes may, therefore, produce cascading effects on different trophic levels, even on top obligate scavengers. One important question to be addressed is whether these human-induced changes on ecosystem processes are persistent or reversible over time. Our main hypothesis is that breeding success depends on food availability (both livestock and wild prey carcasses). Livestock carcasses largely depend on agricultural policies and external sources of feed inputs (Schillhorn Van Veen, 1999). Therefore, contrasting changes in agricultural policies may lead to disruptive patterns in Canary Egyptian vulture reproductive traits. Wild prey carcasses might be related mostly to ecosystem primary productivity (Grande et al., 2009). Consequently, we expect higher ecosystem-level primary productivity to enhance the breeding success of the Egyptian vulture population through trophic cascading effects between primary productivity and primary consumers. Finally, in a scenario of increasing vulture population growth favoured by EU LIFE funds, we expect intraspecific competition might also negatively influence breeding success.

2. Methods

2.1. Study area and target population

The Canary Islands are situated in the north-east Atlantic Ocean, 97 km from Morocco and 1400 km from the Iberian Peninsula. This study was located on Fuerteventura (1660 km^2), the south-eastern island of the Canary archipelago, which is located at 28°25′57″N 14°00′11″O. It is an arid landscape, composed mainly of grasslands and shrublands, where woodland is almost completely absent. The annual rainfall on this island is 105 mm, with a mean temperature of 19 °C, reached in summer, and autumn daily temperatures of over 40 °C (Rodríguez Delgado et al., 2000; Zazo et al., 2002).

The endemic subspecies of Egyptian vulture *Neophron percnopterus majorensis*. Inhabits the Canary Islands. This subspecies was once abundant across the entire archipelago early the 20th century, but in the last few decades its populations has steeply declined due to heavy unnatural mortality linked with power lines and illegal poisoning, as well as shootings and lead intoxication through bullet ingestion (Donázar et al., 2002; Gangoso et al., 2009; Gangoso and Palacios, 2002). Nowadays, it is only present on the Lanzarote and Fuerteventura Islands, with the bulk (> 90 % of the total population) on the latter (Donázar et al., 2002; Gangoso et al., 2009). Since 2006, its population has grown owing to conservation measures funded by EU LIFE projects (Badia-

Table 1
Environmental variables fitted in the MARSS models. For analytical purposes, we split the natural year into two 6-month periods: (1) from January to June, which comprises most of this species' breeding season (copulation, nest building, common roost, chicks' firsts months of life, when they rely more on parental care); (2) from July to December, which corresponds to non-breeding season. The response variable was the breeding success (number of chicks per number of occupied territories) per year for our study period (2000–2021). For all the variables, we calculated the mean and standard deviation. For visual support and guidance, please check Fig. 1.

Family	Variable	Nomenclature	Description
NDVI	NDVI current breeding season	*NDVI breeding season*	Corresponding to the first 6 months of the year (January to June, first period of the year) of the current breeding season.
	NDVI 6 months before the breeding season	*NDVI 6 months bbs*	Corresponding to the 6 months before the start of the breeding season (previous year).
	NDVI 12 months	*NDVI 12 months*	Corresponding to the 6 months before the breeding season and the current breeding season, i.e. the second period from the previous year and the first period of the corresponding year.
	NDVI 1 year before the breeding season	*NDVI 1-year bbs*	Corresponding to the 6 months before the breeding season and the breeding season from the previous year, i.e. is period 1 and period 2 from the previous year.
	NDVI previous breeding season	*NDVI previous breeding season*	Corresponding to the previous breeding season, i.e. period 1 from the previous year.
Precipitation	Precipitation current breeding season	*Precipitation breeding season*	Corresponding to the first period of the year.
	Precipitation 6 months before the breeding season	*Precipitation 6 months bbs*	Corresponding to the second period of the previous year, i.e. 6 months before the start of the breeding season.
	Precipitation 12 months	*Precipitation 12 months*	Corresponding to the 6 months before the breeding season and the current breeding season, i.e. the second period from the previous year and the first period of the corresponding year.
	Precipitation 1 year before the breeding season	*Precipitation 1-year bbs*	Corresponding to period 2 of the previous year (6 months before the breeding season) and the breeding season from the previous year, i.e. period 1 and period 2 from the previous year.
	Precipitation previous breeding season	*Precipitation previous breeding season*	Corresponding to the previous breeding season, i.e. period 1 from the previous year.
Temperature	Temperature current breeding season	*Temperature breeding season*	Corresponding to the first period of the year.
	Temperature 6 months before the breeding season	*Temperature 6 months bbs*	Corresponding to the second period of the previous year, i.e. 6 months before the start of the breeding season.
	Temperature 12 months	*Temperature 12 months*	Corresponding to the 6 months before the breeding season and the current breeding season, i.e. the second period from the previous year and the first period of the corresponding year.
	Temperature 1 year before the breeding season	*Temperature 1-year bbs*	Corresponding to period 2 of the previous year (6 months before the breeding season) and the breeding season from the previous year, i.e. period 1 and period 2 from the previous year.
	Temperature previous breeding season	*Temperature previous breeding season*	Corresponding to the previous breeding season, i.e. period 1 from the previous year.

Boher et al., 2019).

2.2. Field procedures: vultures' breeding success and density

Breeding success was calculated for the whole study area as the number of chicks per number of territories occupied every year for our study period (2000–2021). All the known territories were monitored and other areas were surveyed for new territories from February to the end of April. Then those territories with a pair displaying breeding behavior, i.e. copulation, nest building, common roost etc., were monitored at least 3 times a week for egg laying. Then if laying behavior was detected, the nest was monitored twice a week until the egg hatched, and the nest was closely monitored thereafter. When chicks were 50–60 days old, they are ringed with both metal and PVC rings. This good capture effort allowed over 90 % of the population to be individually identified in 2022 (Badia-Boher et al., 2019). The average breeding success was 0.49 for our study period, with a maximum of 0.63 in 2002 and of 0.2 in 2012. After reaching this minimum in 2012, breeding success presented a highly fluctuating pattern (Supplementary Material, Fig. S1 - A).

The *Density* of breeding territories was measured as the number of breeding territories occupied every year. This parameter showed a steady increase throughout the study period. The maximum number of occupied territories was reached in 2021 with 81 territories (Supplementary Material, Fig. S1 - D).

2.3. Environmental variables

The NDVI (Normalised Difference Vegetation Index) has been pointed out as a good proxy for monitoring vegetation response to climate and to estimate ecosystem-level productivity (Pettorelli et al., 2005; Schloss et al., 1999). For this study, we calculated the NDVI by combining the satellite data from LANDSAT 5, 7, 8 and MODIS. We filtered satellite images and discarded those with clouds or shadows by means of the per-pixel Quality Assessment metadata. Then we used the CORINE Land Cover 2018 map (https://land.copernicus.eu/pan-european/corine-land-cover) to identify and mask the satellite pixels with natural vegetation (i.e., natural grasslands, mixed forest, sparsely vegetated areas and sclerophyllous vegetation). We then fitted a Multivariate Autoregression State-Space model (MARSS) to fill any missing data in the satellite temporal series (see Barbosa et al., 2020 for details on this procedure). We averaged a single NDVI value per month for our entire study area, i.e. the Fuerteventura Island. By proceeding in this way, we avoided any discrepancy in the spatial resolution that could result from combining different satellites.

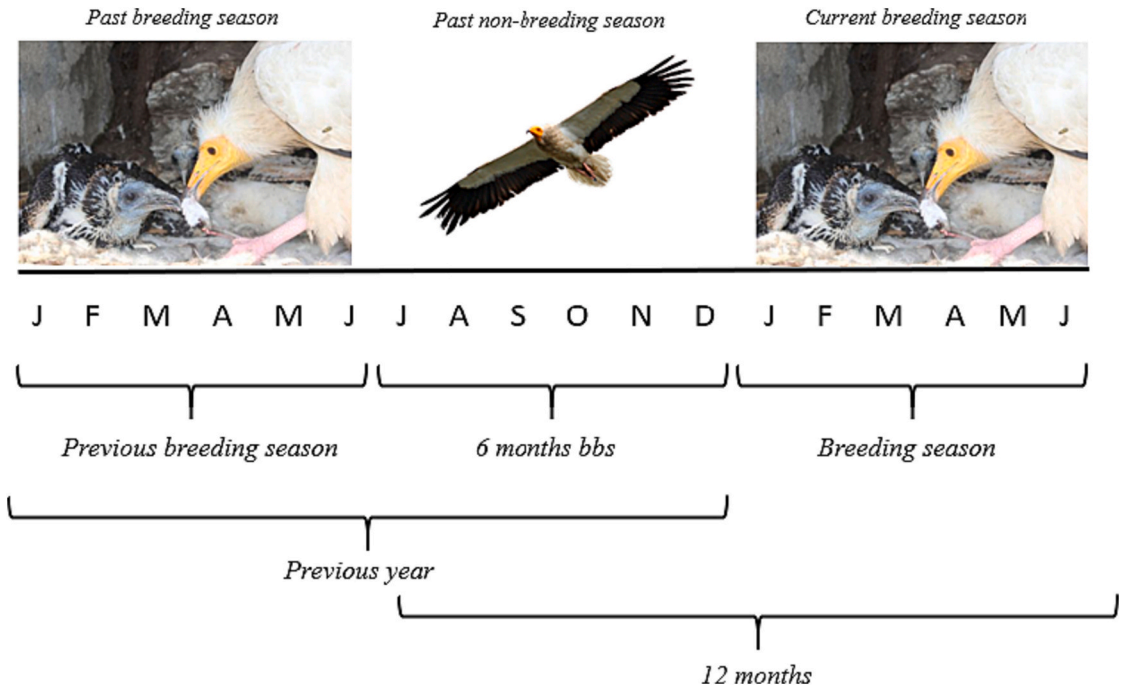

Fig. 1. Time periods used in the explanatory variables fitted in each MARSS model (see Table 1 for details). Bbs stands for before the breeding season. Photography: Manuel de la Riva.

All the environmental variables are detailed in Table 1. We took the precipitation data from the CHIRPS dataset (https://www.chc.ucsb.edu/data/chirps) by first summing accumulated precipitation per month. The temperature data were extracted from the NOAA (https://www.ncei.noaa.gov/) by averaging the monthly values.

2.4. Livestock

The annual numbers of goats (the main livestock species on the island) and sheep were extracted from the annual livestock censuses from the Canarian Institute of Statistics (ISTAC, http://www.gobiernodecanarias.org/istac/estadisticas/sectorprimario/agricultura/ganaderia/C00013A_1.html.) We observed that the numbers of livestock fluctuated during the study period, with the minimum in 2020 with 80,228 goats and sheep (48.2 animals per km^2), and a maximum of 155,311 in 2006 (93.56 animals per km^2). Interestingly, we identified a drastic drop in the number of livestock from 149, 161 livestock animals in 2012 to 99,126 in 2013, which entails a decrease of 50,035 individuals in a single year (33.5 % reduction). This livestock heard reduction period matches the year when financial subsidies from the European Common Agricultural Policy were drastically cut (https://www.fega.gob.es/es/datos-abiertos/informes/ayudas-directas), which heavily funded sheep and goat farming on the island. From 2010 to 2011, there was a 78.63 % decrease in financial aid (Supplementary Material Fig. S2).

2.5. Model fitting

We ran several MARSS models (Multivariate Autoregressive State-Space models) to test whether the environmental conditions, anthropogenic resources and population size shaped the breeding success of our target population of Egyptian vultures on the Fuerteventura island. We selected MARSS models because they are designed for considering the linear stochastic dynamical system within a time-series framework, which perfectly fits long-term climatic data (Holmes et al., 2012; Hsieh et al., 2022; Walsh et al., 2016). The model was fitted with the MARSS package in R (Holmes, 2013) and it is formulated as follows:

$$\boldsymbol{x}_t = \boldsymbol{B}\boldsymbol{x}_{t-1} + \boldsymbol{u}_t + \boldsymbol{C}_{ct_t} + \boldsymbol{w}_t; \text{where } \boldsymbol{w}_t \sim \text{MVN}(\boldsymbol{0}, \boldsymbol{Q}_t) \quad (1)$$

$$\boldsymbol{y}_t = \boldsymbol{x}_t + \boldsymbol{v}_t; \text{where } \boldsymbol{v}_t \sim \text{MVN}(\boldsymbol{0}, \boldsymbol{R}_t) \quad (2)$$

The MARSS models are composed of two models: a process model (Eq. (1)) and an observation model (Eq. (2)). The process model comprises a state process, whose parameters are **B**, **u** and **Q**. In the first equation (process model), x_t refers to the data observed at time t. In our scenario, it refers to the observed breeding success (x) per year (t). This model is the sum of the mathematical parameters of the state process (**B**, u, **Q** and **C**), plus the biologically-related variables (x_t, c_t). Matrix **B** allows the interaction between state processes. In our scenario, this parameter (**B**) accounted for a Density-dependent effect between the current breeding season and the previous one ($\mathbf{Bx_{t-1}}$). Vector u describes the mean trend of the state process. In our scenario, we did not fit any biological variable attached to this parameter because it is often used for auto-regressive trend processes (stochastic level models) and was, hence, set to the default setting (see below). **C** is the matrix whose elements describe the effect of each covariate (ct, environmental variables, such as the NDVI, precipitation or temperature, for each fitted time period, plus Density and Livestock) on breeding success, and w is a matrix of the process error per year (t), with process errors (those intrinsic errors associated with the observation process) at time t being distributed as a multivariate normal with mean **0** and covariance matrix **Q**.

The observation model (y_t) aims for "true" values for breeding success with the sum of the observed values (xt) and the error associated with those observations (v_t). This error has a multivariate normal distribution, with mean **0** and covariance matrix **R**. The particular settings for all the parameters are detailed in Supplementary Material – Appendix 1. We set 10,000 iterations using the *kem* method, which is based on the EM algorithm (expectation-maximisation) with a Kalman filter. This approach is both faster and robuster for reaching the vicinity of maximum likelihood (Holmes, 2013).

We ran a MARSS model for each fitted time period (as defined in Table 1 and Fig. 1) to test the effect of the different environmental variables (NDVI, precipitation and temperature), Density and Livestock

Table 2
All the possible combinations of variables per considered time period. MARSS models are ranked by AICc. The response variable was breeding success (number of chicks per number of occupied territories) per year for our study period (2000–2021). We fitted only one time period per model due to correlation issues among the environmental variables across time periods.

Order	Variables	LogLike	AICc	ΔAICc
1	Mean NDVI 6 months bbs + Livestock + Density	−25.568	68.736	0
2	Mean NDVI 12 months + Livestock + Density	−25.992	69.584	0.848
3	Mean NDVI 12 months + Mean Precipitation 12 months + Mean Temperature 12 months	−26.236	70.071	1.335
4	Mean NDVI 6 months bbs + Mean Precipitation 6 months bbs + Mean Temperature 6 months bbs	−26.287	70.175	1.439
5	Mean NDVI previous year + Livestock + Density	−26.658	70.917	2.181
8	Mean NDVI previous year + Mean Precipitation previous year + Mean Temperature previous year	−27.34	72.28	3.544
10	SD NDVI 12 months + Livestock + Density	−27.723	73.046	4.31
11	Mean NDVI previous bs + Livestock + Density	−27.761	73.123	4.387
12	Mean NDVI breeding season + Livestock + Density	−27.778	73.156	4.42
13	SD NDVI previous year + Livestock + Density	−27.827	73.254	4.518
15	Mean NDVI breeding season + Mean Precipitation breeding season + Mean Temperature breeding season	−29.079	75.757	7.021
6	Mean NDVI 6 months bbs + Livestock + Density + Mean Precipitation 6 months bbs + Mean Temperature 6 months bbs	−24.691	76.459	7.723
18	Mean NDVI previous bs + Mean Precipitation previous bs + Mean Temperature previous bs	−29.597	76.794	8.058
7	Mean NDVI 12 months + Livestock + Density + Mean Precipitation 12 months + Mean Temperature 12 months	−25.053	77.183	8.447
20	SD NDVI 12 months + SD Precipitation 12 months + SD Temperature 12 months	−30.137	77.874	9.138
9	Mean NDVI previous year + Livestock + Density + Mean Precipitation previous year + Mean Temperature previous year	−25.549	78.175	9.439
21	SD NDVI previous year + SD Precipitation previous year + SD Temperature previous year	−30.404	78.408	9.672
14	SD NDVI 12 months + Livestock + Density + SD Precipitation 12 months + SD Temperature 12 months	−26.992	81.061	12.325
16	SD NDVI previous year + Livestock + Density + SD Precipitation previous year + SD Temperature previous year	−27.297	81.67	12.934
17	Mean NDVI previous bs + Livestock + Density + Mean Precipitation previous bs + Mean Temperature previous bs	−27.33	81.737	13.001
19	Mean NDVI breeding season + Livestock + Density + Mean Precipitation breeding season + Mean Temperature breeding season	−27.617	82.311	13.575

variables on breeding success. We subsequently used the same time period per environmental variable (i.e. NDVI, precipitation and temperature) so that all the environmental variables that were inputted in each MARSS model occurred during the same time period. We did not fit two different time periods in the same model because environmental variables across periods had a Spearman's correlation of over |0.5| ((Graham, 2003), see Fig. 1 for further details). Model selection was done by relying on the model with the lowest AICc (Akaike Information Criterion corrected for small samples, Sugiura, 1978).

Table 3
Output for the best model selected by AICc. The response variable was breeding success (number of chicks per number of occupied territories) per year for our study period (2000–2021). ML estimate is "Maximum Likelihood algorithm", Std Error is Standard Error, CI is for Credibility Interval (95 %). For further details about the mathematical parameters (B, u and Q), please see the Methods section, subsection "Model fitting".

Type of parameter	Parameters	ML estimate	Std Error	Low CI	Up CI
State process	B	−0.191	0.177	−0.538	0.157
	U	−0.007	0.165	−0.331	0.316
	Q	0.598	0.180	0.245	0.952
Covariates	NDVI 6 months bbs	0.443	0.189	0.072	0.952
	Livestock	−0.331	0.223	−0.767	0.105
	Density	−0.247	0.211	−0.661	0.165

3. Results

All the MARSS models reached convergence in <15 iterations (Table 2). The model with the lowest AICc value indicates that the mean NDVI for the 6 months before breeding season (*NDVI 6 months bbs*) positively affected breeding success (Table 3). Besides, both *Livestock* and *Density* showed negative effects on reproductive success because the credibility intervals remained above zero in 88 % of the cases for *Livestock* and 77 % for *Density* (Table 3). These results indicate that ecosystem-level primary productivity, the amount of livestock and density-dependence processes collectively determine this species' breeding success (Fig. 2). Interestingly, primary productivity played a key role within the 6 months prior to the start of the breeding season. The output from the MARSS models within ΔAICc<2 is detailed in Table S1 (Supplementary Material). Although precipitation and temperature were not included in the best model (Table 2), mean precipitation and temperature prior to the breeding season were included in two models with ΔAICc <2. Both climatic variables are widely pointed out as being closely related to primary productivity.

We found differences in the temporal tendencies of breeding success before and after 2012 when comparing the averages and slopes from the raw data (Fig. 3). During the first period (2000−2012), when the island presented high livestock density, primary productivity and breeding success drastically declined. During the second period (2013−2021), when livestock density dropped, primary productivity and breeding success stabilised. For both period, *Density* significantly increased and had doubled for the second period.

4. Discussion

Using a two-decade long dataset, we found that the top-down and bottom-up processes modulated the breeding success of a top obligated scavenger. We firstly accounted indirectly for a top-down effect of livestock on island vegetation, i.e. overgrazing directly affects the ecosystem-level primary productivity. Secondly, we also accounted for a bottom-up effect between the vegetation and breeding success of the Egyptian vulture. This is especially relevant because bottom-up and top-down processes usually relate two consecutive trophic levels (e.g. plant-herbivores, primary consumers-secondary consumers, e.g. (Hunter and Price, 2008), but very few studies have linked these types of ecosystem processes with the population dynamics of top scavengers (Coulson et al., 2011; Donázar et al., 2020).

Previous studies have highlighted that long-term monitoring is needed to fully understand population dynamics because it particularly underlines the fact that extrapolation from short-term surveys may indeed mislead subjacent population trends (Collins, 2001; Gagnon et al., 2011; Gosz, 1999). This is especially true for ecosystem-level processes, where longer study periods are required to obtain robust results. Within the time range of our study, we also observed a coincident

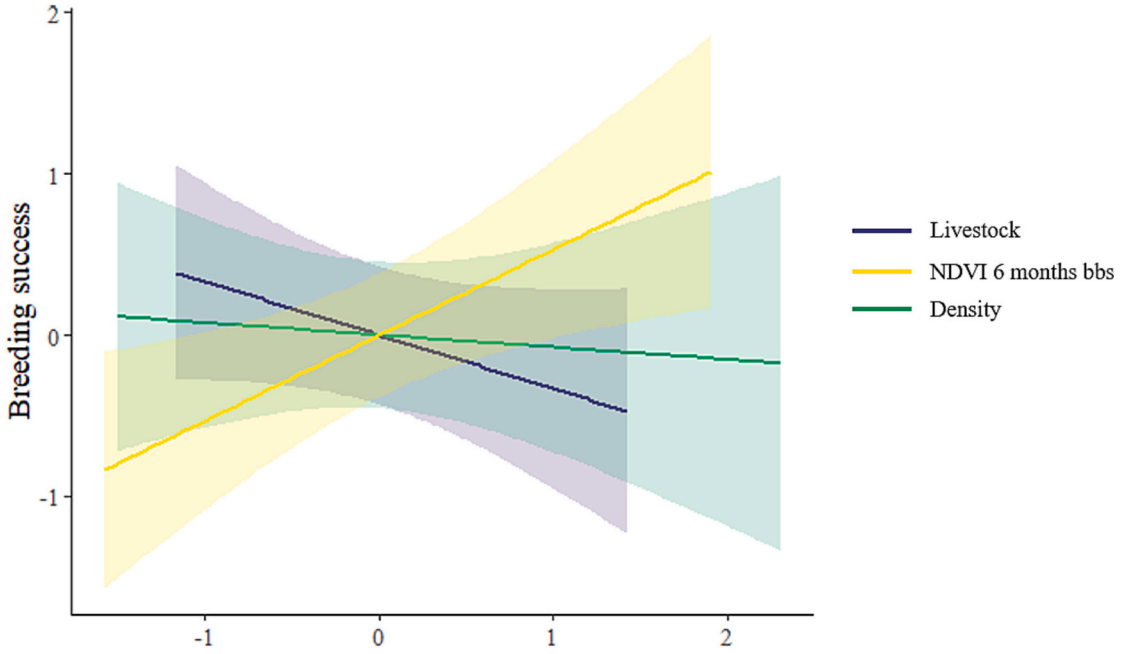

Fig. 2. Linear relation among the three fitted variables from the best model selected by AICc and the response variable "breeding success". Together, these variables drive the breeding success of the Egyptian vulture. The effect of *Livestock* on breeding success is represented on the black line; the NDVI from the 6 months before the breeding season (*NDVI 6 months bbs*) on the yellow line; and *Density* of conspecifics (number of territories occupied every year on the island) on the green line.

shift in temporal tendencies of ecosystem-level primary productivity, the Egyptian vulture's breeding success, the number of breeding territories occupied every year (*Density*), livestock production and governmental subsides for agricultural production. Together, these results support the potential occurrence of a regime shift between 2012 and 2013, which was triggered by declining livestock production.

The most striking finding was a significant declining trend in primary productivity and breeding success during the period of high livestock abundance. These tendencies shifted in 2013 (after a drastic reduction in goat numbers) to wide interannual variability with a constant trend of ecosystem productivity and vulture breeding success. In addition, the increase in the rate of the number of breeding territories occupied every year (*Density*) after 2013 was twice rate that during the period before that year. This might be related to the fact that population dynamics of long-lived birds, such as vultures, are more sensitive to survival than to breeding success (Sæther and Bakke, 2000). Overall, our results suggest that long-term overgrazing may have shifted island ecosystem functioning, which merits further research to understand how reversible these shifts are and whether the relative importance of both top-down and bottom-up play a role in these processes. Ecological regime shifts are marked changes in ecological processes that are profound enough to reconfigure the ecosystem, which affects several trophic levels (Lees et al., 2006). Although identifying regime shifts and thresholds is challenging, it is a subject of recent interest shown in ecology, which might be particularly relevant to address science-based conservation strategies for long-lived species (Andersen et al., 2009).

Unexpectedly, livestock negatively affected the breeding success of the studied population. Livestock presence has been acknowledged as being key for sustaining vulture populations (Dobrev et al., 2016; Olea and Mateo-Tomás, 2009). Some studies have highlighted the close relation between Egyptian vulture and livestock carcasses (Cabrera-García et al., 2020; Mateo-Tomás and Olea, 2010). Hence we expected the relation between the livestock and breeding success of the Egyptian vulture to be positive. However, other studies have noted the overlooked importance of wild prey in this species' diet (Donázar et al., 2020; Margalida et al., 2012). Interestingly, our results suggest that the high grazing pressure (overgrazing) as a consequence of greater governmental subsidies and livestock production may have triggered unexpected cascading effects on ecosystem functioning, which impact several trophic levels. In our study area, Fuerteventura, there have been wide fluctuations in livestock abundance before and after 2012, which temporally overlap with CAP subsidies. Changes in CAP subsidies are known to have a profound impact on the ecosystem, by ranging from determining or changing livestock composition or stocking rates (Ramos et al., 2021), to impacting the ecosystem through land-use changes (Chiron et al., 2013).

Livestock overgrazing may disrupt the presence and abundance of small herbivores (Filazzola et al., 2020) and, consequently, provoke a shortness in the availability of the wild preys of Egyptian vultures, which would comprise several taxa (e.g. reptiles, small mammals like rodents, rabbits, birds (Milchev et al., 2012; Oro, 1992)). This entails a disruption in the bottom-up processes that regulate the vegetation-primary consumers interaction and would, therefore, affect the next trophic levels, i.e., the primary consumers-scavenger relation. As we found positive effects of primary productivity and negative effects of livestock on breeding success, our results suggest that this scavenger species very much relies on natural ecosystem dynamics and is not as dependent on livestock carrion as suggested for other populations (Cabrera-García et al., 2020; Tauler-Ametller et al., 2018). Interestingly, we also found that the mean precipitation and temperature prior to breeding season affected breeding success. Although these climatic variables were not included in the best selected model, they were present in two of the four models (Table S1, Supplementary Material). Both precipitation and temperature are closely related to primary productivity (Schloss et al., 1999).

Lastly, it is important to note that we found a negative relation between the breeding success and density of conspecifics, measured as the number of occupied territories per year. Following (Krüger et al., 2012), a reduction in fecundity, coupled with an increase in population, is usually caused by a decline in the quality of available resources due to increasing intraspecific competition for mates, nesting sites or food. With fewer resources, and given an increase in energy expenditure due to increased antagonistic encounters, vital rates might also be negatively affected (Fernández-Bellon et al., 2016).

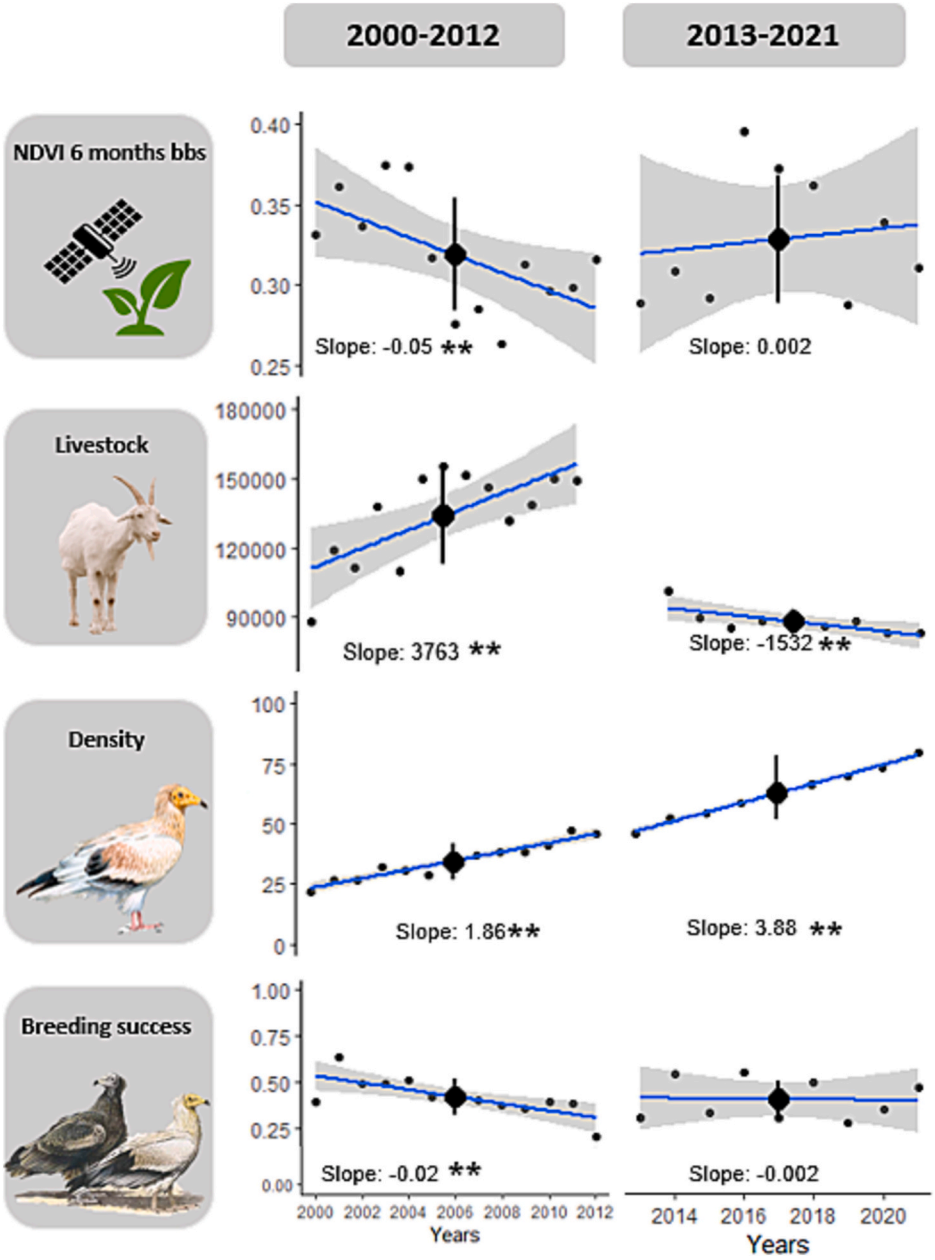

Fig. 3. Temporal tendencies before and after 2012 for NDVI 6 months before the breeding season (*NDVI 6 months bbs*), *Livestock*, *Density* and *Breeding success*. Black dots represent the raw data. The blue line denotes the long-term trend for each period (A, C, E and G for 2000–2012; B, D, F, H for 2013–2021). The grey-shaded area depicts the associated 95 % confidence interval of each linear trend. The central black dots represent the average of each variable per period. The vertical black lines refer to the associated standard deviation. Asterisks represent statistical significance of the corresponding slope (** for *p*-values <0.03).
Credit images: Juan Varela.

4.1. Management implications

Long-term overgrazing has been identified as one of the greatest threats to biodiversity and ecosystem functioning in grasslands worldwide, especially for arid and semi-arid ecosystems (Filazzola et al., 2020; Li et al., 2018). This process tends to aggravate insular ecosystems, where goats are one of the most widely-spread species of all introduced vertebrates on islands. In addition, goat is the second species in number of eradication attempts on Mediterranean islands (Capizzi, 2020). The negative pressures and effects they have on soil and vegetation properties have also been widely described (Capó et al., 2022). However, livestock carcasses that derive from human activities are also the main feeding resource for avian scavengers, and some of these species are endangered (Cortés-Avizanda et al., 2016). This entails a contradiction in conservation programmes for scavengers because, on the one hand, livestock carcasses provide feeding resources and determine the assemblages between the scavenger's guild (Cortés-Avizanda et al., 2010) but, on the other hand, it deeply disturbs the ecosystem through changes in primary productivity (Milchunas et al., 1988) by threatening the survival of highly endangered endemic plant species (Gangoso et al., 2006). This study provides scientific evidence for the cascading effects of these perturbances at several trophic levels, which interfere with top-down and bottom-up processes. These indirect effects are often overlooked in pursuit of direct straightforward effects and are not, therefore, considered in conservation strategies and guidelines. Here we have disentangled how political changes in European funding can impact an ecosystem at several trophic levels by contributing to unforeseen impacts on an endangered species. Our results may help to inform

European policies that account for ecosystem functioning and biodiversity conservation.

CRediT authorship contribution statement

LF-G: Methodology, Data curation, Writing- Original draft preparation. **JMB**: Methodology, Conceptualization, Writing, Data Validation, Supervision. **JAS-Z**: Conceptualization, Writing, Supervision. **XB:** Statistic Validation, Data Validation. **JAD:** Data Provision, Writing, and Supervision. All authors give final approval for this manuscript.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.168553.

References

Andersen, T., Carstensen, J., Hernández-García, E., Duarte, C.M., 2009. Ecological thresholds and regime shifts: approaches to identification. Trends Ecol. Evol. 24, 49–57. https://doi.org/10.1016/j.tree.2008.07.014.

Badia-Boher, J.A., Sanz-Aguilar, A., de la Riva, M., Gangoso, L., van Overveld, T., García-Alfonso, M., Luzardo, O.P., Suarez-Pérez, A., Donázar, J.A., 2019. Evaluating European LIFE conservation projects: improvements in survival of an endangered vulture. J. Appl. Ecol. 56, 1210–1219. https://doi.org/10.1111/1365-2664.13350.

Barbosa, J.M., Pascual-Rico, R., Eguia Martínez, S., Sánchez-Zapata, J.A., 2020. Ungulates attenuate the response of Mediterranean mountain vegetation to climate oscillations. Ecosystems 23, 957–972. https://doi.org/10.1007/s10021-019-00449-8.

Beever, E.A., Hall, L.E., Varner, J., Loosen, A.E., Dunham, J.B., Gahl, M.K., Smith, F.A., Lawler, J.J., 2017. Behavioral flexibility as a mechanism for coping with climate change. Front. Ecol. Environ. 15, 299–308. https://doi.org/10.1002/fee.1502.

BirdLife International, 2022. Species Factsheet: *Neophron percnopterus*.

Bowen, L., Vuren, D. Van, 1997. Insular endemic plants lack defenses against herbivores. Conserv. Biol. 11, 1249–1254.

Cabrera, J.C., 1996. La Prehistoria de Fuerteventura: Un modelo insular de adaptación. Servicio de Publicaciones de Cabildo Insular de Fuerteventura, Puerto del Rosario, Spain.

Cabrera-García, M.E., Olea, P.P., Mateo-Tomás, P., 2020. Livestock prevalence in the Egyptian vulture diet during European sanitary restrictions on carcass disposal. Food Webs 25, e00169. https://doi.org/10.1016/j.fooweb.2020.e00169.

Campbell, K., Donlan, C.J., 2005. Feral goat eradications on islands. Conserv. Biol. 19, 1362–1374. https://doi.org/10.1111/j.1523-1739.2005.00228.x.

Capizzi, D., 2020. A review of mammal eradications on Mediterranean islands. Mammal Rev. 50, 124–135. https://doi.org/10.1111/mam.12190.

Capó, M., Cursach, J., Picorelli, V., Baraza, E., Rita, J., 2022. Eradication of feral goats, not population control, as a strategy to conserve plant communities on Mediterranean islets. J. Nat. Conserv. 65, 126108 https://doi.org/10.1016/j.jnc.2021.126108.

Chambert, T., Imberdis, L., Couloumy, C., Bonet, R., Besnard, A., 2020. Density dependence in Golden Eagle *Aquila chrysaetos* fecundity better explained by individual adjustment than territory heterogeneity. Ibis 162, 1312–1323. https://doi.org/10.1111/ibi.12826.

Chiron, F., Princé, K., Paracchini, M.L., Bulgheroni, C., Jiguet, F., 2013. Forecasting the potential impacts of CAP-associated land use changes on farmland birds at the national level. Agric. Ecosyst. Environ. 176, 17–23. https://doi.org/10.1016/j.agee.2013.05.018.

Coblentz, B.E., 1978. The effects of feral goats (*Capra hircus*) on island ecosystems. Biol. Conserv. 13, 279–286. https://doi.org/10.1016/0006-3207(78)90038-1.

Collins, S.L., 2001. Long-term research and the dynamics of bird populations and communities. Auk 118, 583–588. https://doi.org/10.2307/4089922.

Cortés-Avizanda, A., Carrete, M., Donázar, J.A., 2010. Managing supplementary feeding for avian scavengers: guidelines for optimal design using ecological criteria. Biol. Conserv. 143, 1707–1715. https://doi.org/10.1016/j.biocon.2010.04.016.

Cortés-Avizanda, A., Blanco, G., Devault, T.L., Markandya, A., Virani, M.Z., Brandt, J., Donázar, J.A., 2016. Supplementary feeding and endangered avian scavengers: Benefits, caveats, and controversies. Front. Ecol. Environ. 14, 191–199. https://doi.org/10.1002/fee.1257.

Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H., Crawley, M.J., Grenfell, B.T., 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science 1979 (292), 1528–1531. https://doi.org/10.1126/science. 292.5521.1528.

Coulson, T., Macnulty, D.R., Stahler, D.R., VonHoldt, B., Wayne, R.K., Smith, D.W., 2011. Modeling effects of environmental change on wolf population dynamics, trait evolution, and life history. Science 1979 (334), 1275–1278.

Cubas, J., Irl, S.D.H., Villafuerte, R., Bello-Rodríguez, V., Rodríguez-Luengo, J.L., Del Arco, M., Martín-Esquivel, J.L., González-Mancebo, J.M., 2019. Endemic plant species are more palatable to introduced herbivores than non-endemics. Proc. R. Soc. B Biol. Sci. 286 https://doi.org/10.1098/rspb.2019.0136.

Dhondt, A.A., Hochachka, W.M., 2001. Variations in calcium use by birds during the breeding season. Condor 103, 592–598.

Dobrev, V., Boev, Z., Arkumarev, V., Dobrev, D., Kret, E., Saravia, V., Bounas, A., Vavylis, D., Nikolov, S.C., Oppel, S., 2016. Diet is not related to productivity but to territory occupancy in a declining population of Egyptian Vultures *Neophron percnopterus*. Bird Conserv. Int. 26, 273–285. https://doi.org/10.1017/S0959270915000155.

Donázar, J.A., Palacios, C.J., Gangoso, L., Ceballos, O., González, M.J., Hiraldo, F., 2002. Conservation status and limiting factors in the endangered population of Egyptian vulture (*Neophron percnopterus*) in the Canary Islands. Biol. Conserv. 107, 89–97. https://doi.org/10.1016/S0006-3207(02)00049-6.

Donázar, J.A., Gangoso, L., Forero, M.G., Juste, J., 2005. Presence, richness and extinction of birds of prey in the Mediterranean and Macaronesian islands. J. Biogeogr. 32, 1701–1713. https://doi.org/10.1111/j.1365-2699.2005.01294.x.

Donázar, J.A., Barbosa, J.M., García-Alfonso, M., van Overveld, T., Gangoso, L., de la Riva, M., 2020. Too much is bad: increasing numbers of livestock and conspecifics reduce body mass in an avian scavenger. Ecol. Appl. 30, e02125 https://doi.org/10.1002/eap. 2125.

Fernández-Bellon, D., Cortés-Avizanda, A., Arenas, R., Donázar, J.A., 2016. Density-dependent productivity in a colonial vulture at two spatial scales. Ecology 97, 406–416. https://doi.org/10.1890/15-0357.1.

Filazzola, A., Brown, C., Dettlaff, M.A., Batbaatar, A., Grenke, J., Bao, T., Peetoom Heida, I., Cahill, J.F., 2020. The effects of livestock grazing on biodiversity are multi-trophic: a meta-analysis. Ecol. Lett. 23, 1298–1309. https://doi.org/10.1111/ele.13527.

Gagnon, J.W., Dodd, N.L., Ogren, K.S., Schweinsburg, R.E., 2011. Factors associated with use of wildlife underpasses and importance of long-term monitoring. J. Wildl. Manag. 75, 1477–1487. https://doi.org/10.1002/jwmg.160.

Gangoso, L., Palacios, C.J., 2002. Endangered Egyptian Vulture (*Neophron percnopterus*) entangled in a power line ground-wire stabilizer. J. Raptor Res. 36, 238–239.

Gangoso, L., Donázar, J.A., Scholz, S., Palacios, C.J., Hiraldo, F., 2006. Contradiction in conservation of island ecosystems: plants, introduced herbivores and avian scavengers in the Canary Islands. Biodivers. Conserv. 15, 2231–2248. https://doi.org/10.1007/s10531-004-7181-4.

Gangoso, L., Álvarez-Lloret, P., Rodríguez-Navarro, A.A.B., Mateo, R., Hiraldo, F., Donázar, J.A., 2009. Long-term effects of lead poisoning on bone mineralization in

vultures exposed to ammunition sources. Environ. Pollut. 157, 569–574. https://doi.org/10.1016/j.envpol.2008.09.015.
Gosz, J.R., 1999. Ecology challenged? who? why? where is this headed? Ecology 475–481.
Graham, M.H., 2003. Confronting multicollinearity in ecological multiple regression. Ecology 84, 2809–2815. https://doi.org/10.1890/02-3114.
Grande, J.M., Serrano, D., Tavecchia, G., Carrete, M., Ceballos, O., Díaz-Delgado, R., Tella, J.L., Donázar, J.A., 2009. Survival in a long-lived territorial migrant: effects of life-history traits and ecological conditions in wintering and breeding areas. Oikos 118, 580–590. https://doi.org/10.1111/j.1600-0706.2009.17218.x.
Holmes, E.E., 2013. Derivation of an EM Algorithm for Constrained and Unconstrained Multivariate Autoregressive State-Space (MARSS) Models 1–58.
Holmes, E.E., Ward, E.J., Wills, K., 2012. MARSS: multivariate autoregressive state-space models for analyzing time-series data. R. J. 4, 11–19. https://doi.org/10.32614/rj-2012-002.
Hsieh, T.T., Chiu, M.C., Resh, V.H., Kuo, M.H., 2022. Biological traits can mediate species-specific, quasi-extinction risks of macroinvertebrates in streams experiencing frequent extreme floods. Sci. Total Environ. 806 https://doi.org/10.1016/j.scitotenv.2021. 150313.
Hunter, M.D., Price, P.W., 2008. Playing Chutes and Ladders: Heterogeneity and the Relative Roles of Bottom-up and Top-down Forces in Natural Communities Published by: Ecological Society of America Stable URL: http://www.jstor.org/stable/1940152. America (NY), 73, pp. 724–732.
Jiguet, F., 2002. Arthropods in diet of little bustards *tetrax tetrax* during the breeding season in western France: Seasonal, age- and sex-related variations in the diet were studied during march to october. Bird Study 49, 105–109. https://doi.org/10.1080/00063650209461253.
Krüger, O., Chakarov, N., Nielsen, J.T., Looft, V., Grünkorn, T., Struwe-Juhl, B., Møller, A.P., 2012. Population regulation by habitat heterogeneity or individual adjustment? J. Anim. Ecol. 81, 330–340. https://doi.org/10.1111/j.1365-2656.2011.01904.x.
Lees, K., Pitois, S., Scott, C., Frid, C., MacKinson, S., 2006. Characterizing regime shifts in the marine environment. Fish Fish. 7, 104–127. https://doi.org/10.1111/j.1467-2979.2006. 00215.x.
Li, W., Li, X., Zhao, Y., Zheng, S., Bai, Y., 2018. Ecosystem structure, functioning and stability under climate change and grazing in grasslands: current status and future prospects. Curr. Opin. Environ. Sustain. 33, 124–135. https://doi.org/10.1016/j.cosust.2018.05.008.
Marcelino, J., Silva, J.P., Gameiro, J., Silva, A., Rego, F.C., Moreira, F., Catry, I., 2020. Extreme events are more likely to affect the breeding success of lesser kestrels than average climate change. Sci. Rep. 10, 1–11. https://doi.org/10.1038/s41598-020-64087-0.
Margalida, A., Benítez, J.R., Sánchez-Zapata, J.A., Ávila, E., Arenas, R., Donázar, J.A., 2012. Long-term relationship between diet breadth and breeding success in a declining population of Egyptian Vultures *Neophron percnopterus*. Ibis 154, 184–188. https://doi.org/10.1111/j.1474-919X.2011.01189.x.
Mateo-Tomás, P., Olea, P.P., 2010. Diagnosing the causes of territory abandonment by the Endangered Egyptian vulture *Neophron percnopterus*: the importance of traditional pastoralism and regional conservation. Oryx 44, 424–433. https://doi.org/10.1017/S0030605310 000189.
Milchev, B., Spassov, N., Popov, V., 2012. Diet of the Egyptian vulture (*Neophron percnopterus*) after livestock reduction in Eastern Bulgaria. North West J. Zool. 8, 315–323.
Milchunas, D.G., Sala, O.E., Lauenroth, W.K., 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. Am. Nat. 132, 87–106. https://doi.org/10.1086/284839.
Montague, T.L., Cullen, J.M., Fitzherbert, K., 1986. The diet of the short-tailed shearwater *puffinus tenuirostris* during its breeding season. Emu 86, 207–213. https://doi.org/10.1071/MU98 60207.
Moreira, X., Castagneyrol, B., García-Verdugo, C., Abdala-Roberts, L., 2021. A meta-analysis of insularity effects on herbivory and plant defences. J. Biogeogr. 48, 386–393. https://doi.org/10.1111/jbi.14003.
Negro, J.J., Grande, J.M., Tella, J.L., Garrido, J., Hornero, D., Donázar, J.A., Sánchez-Zapata, J.A., Benítez, J.R., Barcell, M., 2002. An unusual source of essential carotenoids. Nature 416, 807.
Olea, P.P., Mateo-Tomás, P., 2009. The role of traditional farming practices in ecosystem conservation: the case of transhumance and vultures. Biol. Conserv. 142, 1844–1853. https://doi.org/10.1016/j.biocon.2009.03.024.
O'Neal, M., 2016. Vultures: Their Evolution, Ecology and Conservation. CRC Press, Choice Reviews Online. https://doi.org/10.5860/choice.194195.
Oro, D., 1992. A preliminary study of the diet of the Egyptian vulture *Neophron percnopterus* on Minorca (Balearic Islands). Butll. GCA 9, 25–27.
Oro, D., Genovart, M., Tavecchia, G., Fowler, M.S., Martínez-Abraín, A., 2013. Ecological and evolutionary implications of food subsidies from humans. Ecol. Lett. 16, 1501–1514. https://doi.org/10.1111/ele.12187.
Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.M., Tucker, C.J., Stenseth, N.C., 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends Ecol. Evol. 20, 503–510. https://doi.org/10.1016/j.tree.2005.05.011.
Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M., Kausrud, K., 2011. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. Clim. Res. 46, 15–27. https://doi.org/10.3354/cr00936.
Ramos, R.F., Diogo, J.A., Santana, J., Silva, J.P., Reino, L., Schindler, S., Beja, P., Lomba, A., Moreira, F., 2021. Impacts of sheep versus cattle livestock systems on birds of Mediterranean grasslands. Sci. Rep. 11, 1–10. https://doi.org/10.1038/s41598-021-89975-x.
Rodríguez Delgado, O., García Gallo, A., Reyes Betancort, J.A., 2000. Estudio fitosociológico de la vegetación actual de Fuerteventura (Islas Canarias). Vieraea 28, 61–98.
Sæther, B.E., Bakke, Ø., 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81, 642–653. https://doi.org/10.1890/0012-9658 (2000)081[0642:alhvac]2.0.co;2.
SÆther, B.E., Sutherland, W.J., Engen, S., 2004. Climate influences on avian population dynamics. Adv. Ecol. Res. 35, 185–209. https://doi.org/10.1016/S0065-2504(04)35009-9.
Salamolard, M., Weimerskirch, H., 1993. Relationship between foraging effort and energy requirement throughout the breeding season in the wandering albatross. Funct. Ecol. 7, 643. https://doi.org/10.2307/2390184.
Schillhorn Van Veen, T.W., 1999. Agricultural policy and sustainable livestock development. Int. J. Parasitol. 29, 7–15. https://doi.org/10.1016/S0020-7519(98)00174-X.
Schloss, A.L., Kicklighter, D.W., Kaduk, J., Wittenberg, U., 1999. Comparing global models of terrestrial net primary productivity (NPP): comparison of NPP to climate and the Normalized Difference Vegetation Index (NDVI). Glob. Chang. Biol. 5, 25–34. https://doi.org/10.1046/j.1365-2486.1999.00004.x.
Simard, M.A., Coulson, T., Gingras, A., Côté, S.D., 2010. Influence of density and climate on population dynamics of a large herbivore under harsh environmental conditions. J. Wildl. Manag. 74, 1671–1685. https://doi.org/10.2193/2009-258.
Sugiura, N., 1978. Further analysis of the data by Anaike's information criterion and the finite corrections. Commun. Stat. Theory Methods 7, 13–26. https://doi.org/10.1080/0361092780 8827599.
Tauler-Ametller, H., Hernández-Matías, A., Parés, F., Pretus, J.L., Real, J., 2018. Assessing the applicability of stable isotope analysis to determine the contribution of landfills to vultures' diet. PLoS One 13, 1–18. https://doi.org/10.1371/journal.pone.0196044.
Van De Koppel, J., Rietkerk, M., 2004. Spatial interactions and resilience in arid ecosystems. Am. Nat. 163, 113–121. https://doi.org/10.1086/380571.
Walsh, J.R., Carpenter, S.R., Van Der Zanden, M.J., 2016. Invasive species triggers a massive loss of ecosystem services through a trophic cascade. Proc. Natl. Acad. Sci. U. S. A. 113, 4081–4085. https://doi.org/10.1073/pnas.1600366113.
Zazo, C., Goy, J.L., Hillaire-Marcel, C., Gillot, P.Y., Soler, V., González, J.Á., Dabrio, C.J., Ghaleb, B., 2002. Raised marine sequences of Lanzarote and Fuerteventura revisited - a reappraisal of relative sea-level changes and vertical movements in the eastern Canary Islands during the Quaternary. Quat. Sci. Rev. 21, 2019–2046. https://doi.org/10.1016/S0277-3791 (02)00009-4.