



Alternative vegetation trajectories through passive habitat rewilding: opposite effects for animal conservation

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Received: 27 June 2023 / Accepted: 25 February 2024 / Published online: 20 March 2024
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Abstract

Context Passive habitat rewilding after rural abandonment can affect wildlife differently depending on the type of habitats that it generates.

Objective Evaluate and compare the effects of two alternative vegetation trajectories that occur through passive habitat rewilding in Mediterranean ecotone areas (crop-scrub and crop-pine forest transitions) on the long-term population dynamics of animal species.

Methods We used the spur-thighed tortoise (*Testudo graeca*), a characteristic long-lived species of cultural landscapes, as study species. We applied a spatially explicit and individual-based model (STEPLAND) to simulate the movement and demographic processes

in a long-term period, by comparing an “impact scenario” (i.e., historical land-use changes) to a “control scenario” (no land-use changes).

Results The two landscape scenarios resulted in different population trends. In the crop-scrub scenarios (control and impact), population densities increased similarly over time. However, the crop-pine forest scenario negatively affected population density throughout the simulation period, and showed a time-lag response of three decades. The extinction risk was 55% with a time-lag response of approximately 110 years.

Conclusions Our study highlights the need to analyse the legacy effects on long-lived ectotherms, using them as a proxy to understand the future effects of dynamic landscapes created by “passive habitat rewilding”. Our results showed how traditional

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10980-024-01880-6>.

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agriculture in Mediterranean ecotone areas may generate “ecotone effects” (i.e. increase in demographical parameters), but also population extinction on long-lived ectotherms. Therefore, we consider it relevant to maintain traditional agricultural areas in Mediterranean landscapes, especially in ecotone areas associated with pine forests (generating mosaics with open habitats).

Keywords Crop-scrub transition · Crop-pine forest transition · Cultural landscapes · Extinction probability · Individual-based model · Long-lived species · *Testudo graeca*

Introduction

Rural abandonment is one of the main processes of land-use change that has occurred worldwide in recent decades. By 1992, 2.35 million km² of croplands had been abandoned (Ramankutty and Foley 1999). This process has occurred since the 20th century in Europe, and was caused by migration to cities, novel agricultural techniques, and low productivity in some areas (García-Ruiz and Lana-Renault 2011). Rural abandonment has enormous socio-economic and environmental consequences in Europe, where land can evolve towards either land degradation or natural revegetation (van Leeuwen et al. 2019). On the one hand, land degradation generally involves soil erosion and desertification, loss of cultural and/or aesthetic values, and the reduction in landscape diversity and water provision (Subedi et al. 2022). On the other hand, natural revegetation, due to secondary succession or by reforestation (Alcamo et al. 2005; Rey Benayas et al. 2007), may show heterogeneous landscape developments (Daskalova et al. 2020), which may range from natural or seminatural landscapes (Moreira and Russo 2007; Queiroz et al. 2014; Ameztegui et al. 2016; Vadell et al. 2016; Whytock et al. 2018) to other renaturalised areas that include opportunistic species (especially near periurban areas). Natural revegetation has consequences on landscape ecological processes, such as hydrological processes, carbon dynamics or fire disturbances, which impact society via ecosystem services (García-Ruiz and Lana-Renault 2011). Although natural revegetation may restore ecological functions (Moreira and Russo 2007; Navarro and Pereira 2012;

Queiroz et al. 2014), it also may lower the landscape diversity and biodiversity levels associated with traditional agroecosystems (Suárez-Seoane et al. 2002; Gaüzère et al. 2020). Thus, to develop successful conservation measures, it is a priority to address the consequences of passive habitat rewilding due to agricultural abandonment on specific ecosystems (Navarro and Pereira 2012).

In Mediterranean ecosystems located in transition areas between biomes (Kark and van Rensburg 2006), climatic gradients often lead to ecotones between Mediterranean scrublands (hereafter, “scrub”) and Mediterranean conifer-sclerophyllous-broadleaf forests (hereafter, “pine forest”) (Walter 1981; Esteve et al. 2013). In these Mediterranean ecotone areas (Kark 2013), the rural abandonment of cultural landscapes, characterized by heterogeneous fine-mosaic of natural areas and agricultural lands, can result in passive habitat rewilding through natural revegetation following two alternative transition pathways: the crop-scrub or the crop-pine forest transition. The resulting transition depends on local drivers like topography (relief effects) and precipitations. When these local drivers lead to more humid conditions (e.g. shaded side of a mountain), woody or shrubby plants increase in density, cover and biomass, and induce vegetation maturation towards conifer or sclerophyll forest, i.e. “the crop-pine forest transition” (Vadell et al. 2016). However, in ecotone areas with more arid conditions (e.g. the sunny side of the mountains) the natural revegetation caused by agricultural abandonment leads to “the crop-scrub transition”, generating natural open habitats, such as grasslands and low scrublands.

Therefore, the passive habitat rewilding of these ecotone areas may reconfigure biodiversity and pose new challenges for the adaptation and conservation of the animal species inhabiting them (Queiroz et al. 2014; Robledano-Aymerich et al. 2014). For instance, newly revegetated landscapes may lead to closed forest areas with increased vegetation density (Ribeiro et al. 2009). These areas may be favourable for more forest-dependent species, but detrimental to species like ectotherms because they prefer open habitats and use sun-exposed shelters for diurnal thermoregulation (Jäggi and Baur 1999; Webb et al. 2005). The expansion of these natural areas is altering the structure and connectivity of the landscape; however, the threats that they pose to biodiversity remain poorly

understood (Sirami et al. 2008; Lasanta et al. 2021). In particular, there is a lack of comparative long-term studies that consider time lags or adaptation processes in species relevant to conservation (Sirami et al. 2017), as well as analyses of land-use legacies (Lira et al. 2012; Jiménez-Franco et al. 2022).

The general objective of this study is to evaluate the effects of passive habitat rewilding due to abandonment of Mediterranean agroecosystems located in ecotone areas on the population dynamics of long-lived animals associated with these cultural landscapes. Specifically we aim to: (1) evaluate how agroecosystems, composed of different proportions of scrub vs. pine forest, influence long-term population viability; (2) compare the effects of these two alternative vegetation trajectories through passive habitat rewilding (i.e. dynamic landscapes with crop-scrub and crop-pine forest transitions) on long-term population viability. We studied the spur-thighed tortoise (*Testudo graeca*), a long-lived ectotherm species characteristic of Mediterranean cultural landscapes (Anadón et al. 2006a; Graciá et al. 2017), since this species has proven to be sensitive to land use change caused by agricultural abandonment (De Aranzabal et al. 2008; Martínez-Fernández et al. 2015).

To address the population effects of crop-pine forest and crop-scrub transition on *T. graeca*, we analyse how changes in movement patterns, driven by land-use changes, affect mate-finding in low-density populations, and different aspects of population dynamics and viability. We focus on changes in movement behaviour because empirical studies have found that the estimated reproductive output of tortoises is sensitive to environmental variation, but not survival estimates (Rodríguez-Caro et al. 2021). To do so, we use the spatially explicit individual-based model STEPLAND (Graciá et al. 2020b), parameterized with data from almost two decades of intense field studies on the movement, habitat use and demography of *T. graeca*. This model integrates an individual-based and spatially explicit movement subprocess that considers habitat composition and structure (Anadón et al. 2012). We conduct new analyses for the crop-pine forest transition and compare them to the results of our previous study focused on crop-scrub transition effects (Jiménez-Franco et al. 2022) by applying a Control-Impact (CI) study design (Roedenbeck et al. 2007). Our framework allowed us to compare the effect of different management actions on

biodiversity. In this context, we raise the question of whether the conservation of ecotonal species may be improved -or worsened- by passive habitat rewilding in ecotones (i.e. impact scenarios or landscapes with rural abandonment by generating alternative dynamic landscapes) or through the maintenance of different Mediterranean ecotones types with natural and traditional agricultural areas (i.e. control scenarios).

In the present study, we hypothesise that the passive habitat rewilding in Mediterranean ecotones of the type crop-pine forest transition may have different effects on population dynamics of animal species than the crop-scrub transition (Fig. 1). While the effects of the crop-scrub transition on *T. graeca* were evaluated in a previous study (Jiménez-Franco et al. 2022) showing an “ecotone effect” (i.e. the increasing of abundance and richness patterns of animal species in ecotones) (Kark 2013), we expect that measures of population viability of *T. graeca* to decline in response to the crop-pine forest transition with a certain time lag, as this landscape scenario leads to the homogenisation of the landscape with habitats that are less preferred by ectotherm species (Subedi et al. 2022).

Materials and methods

Study system: the spur-thighed tortoise in SE Spain

T. graeca is a medium-sized long-lived tortoise that lives at a slow pace with steady population growth rates (Rodríguez-Caro et al. 2017, 2019), delayed maturation (9–12 years) (Rodríguez-Caro et al. 2013) and a clutch size of 1–7 eggs. In southeastern Spain, *T. graeca* inhabits heterogeneous cultural landscapes in the coastal mountains of the most arid region of SW Europe, formed by a shrubland/pine forest matrix that includes other uses, mainly non-irrigated crops (Anadón et al. 2006a, b). It is endangered (Vulnerable) (Escoriza et al. 2022), with the main threats in southeastern Spain being habitat loss and fragmentation caused by anthropogenic activities (e.g. irrigated lands, greenhouses, tourist/urban development) (Anadón et al. 2007; Graciá et al. 2020a). Since the 1950s, this area has undergone an intense rural depopulation (De Aranzabal et al. 2008), and since the 1980s it has also been subject to agricultural intensification, the development of urban and tourist

Passive habitat rewilding in Mediterranean ecotone areas

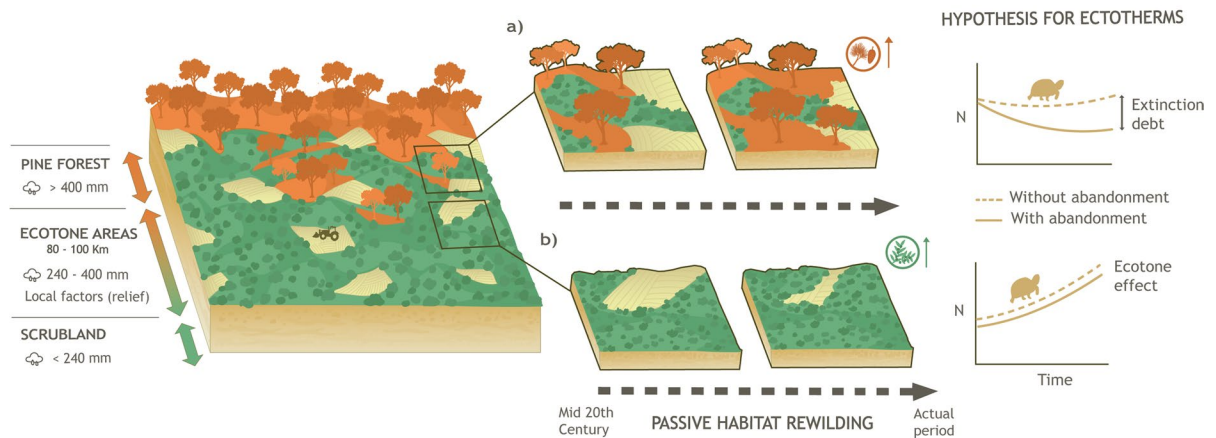


Fig. 1 Diagram representing the temporal dynamics of passive habitat rewilding in Mediterranean areas with ecotones between scrubland and pine forest on a regional scale. **a** represents the crop-pine forest transition of the study area

“Chuecos”; **b** represents the crop-scrub transition of the study area “Los Mayorales”. The small graphs show the initial hypothesis about the population trends of ectotherm species such as *Testudo graeca* in the corresponding study areas

areas, and infrastructure development (Martínez-Fernández et al. 2015). In the last 60 years, these processes have created a complex landscape in which both natural and anthropised areas co-occur (Jiménez-Franco et al. 2022).

Modelling framework by applying STEPLAND

We applied the modelling framework of Jiménez-Franco et al. (2022) by using the spatially explicit individual-based model STEPLAND, which was developed to integrate demographic processes, i.e., reproduction, mortality and ageing (Graciá et al. 2020b; Jiménez-Franco et al. 2020a), with an individual-based model of tortoise movement (Anadón et al. 2012). For the model description, we followed the Overview, Design concepts and Details protocol (ODD) proposed by Grimm et al. (2010). Regarding model calibration, we summarised the model and the simulation conditions in Appendix S1, including a full ODD version. The model was implemented in Python 2.7, and its code, parameterisation and the main result files are available in the Figshare repository (Jiménez-Franco et al. 2024). The model validation and its parameterization were conducted in a previous study where a population expansion process was simulated, replicating real-world

conditions. The resulting genetic patterns were compared with empirical data, showing agreement (Graciá et al. 2023).

In short, STEPLAND contains two types of entities: landscape and tortoises. Landscapes are composed of a grid of 10 m × 10 m cells. Each grid cell is assigned to one of the five habitat quality parameters in STEPLAND that influence movement by reclassifying land-use cover (see more details of landscape reclassification in Appendix S2). Tortoises have the attributes sex, age and their location over time, and the model is composed of specific submodels for movement, reproduction and mortality (Fig. S1, Appendix S1). The model’s overall time step is 1 year. Reproduction results from the interaction of movement with landscape structure and is strongly conditioned by landscape connectivity. Annual mortality occurs at the end of the year before the age of surviving tortoises is updated, and newborn tortoises are added at the beginning of the next year. However, the movement submodel operates on a finer intraday scale with sex-specific movement probabilities depending on the month (see Appendix S1 for details of the submodels of movement, reproduction and mortality; and Appendix S3 for the data to implement STEPLAND).

Landscape scenarios: agricultural abandonment in Mediterranean ecotones

The two selected study areas are located in the Almeria mountain range at the core of the *T. graeca* species' range in SE Spain (Anadón et al. 2007; Anadón et al. 2006a, b) (Fig. 2a). These areas are cultural landscapes located in Mediterranean ecotones between scrubland and pine forests, and represent the history of land-use changes in the past century and, to a certain extent, also the history of many rural landscapes from developed countries based on agricultural abandonment processes. These study areas were originally similar in terms of the percentage of natural land-use areas vs. traditional agricultural areas covering 5×5 km (Fig. 2b, c). The historical land-use dynamics were characterised by mapping land-use cover in 1956, 1987 and 2010. Rural abandonment includes the abandonment of traditional agricultural uses (involving crops, pastures and woody species, e.g. olives, almond trees, grapevines, etc.). Rural abandonment results in the replacement of traditional agricultural lands (crops) by natural areas and, depending on climate conditions and local topography, these crop areas can be transformed towards scrublands or pine forests of Aleppo pine (*Pinus halepensis*) (Esteve et al. 2018) (Fig. 1). Particularly, crop-pine forest transitions may arise due to either an expansion of nearby forest lands or the transformation of cover and biomass by woody or shrubby plants, which induce vegetation maturation towards conifer or sclerophyll forests in humid microclimates. Therefore, the two alternative landscape evolutions are a crop-scrub transition and a crop-pine forest transition, being here represented by the “*Los Mayorales*” and “*Chuecos*” study areas, respectively (Figs. 1, 2b, c).

We built three landscape maps (3 periods) with eight land-use cover categories for the *Chuecos* study area, and we used the landscape scenarios of the *Los Mayorales* study area from Jiménez-Franco et al. (2022) (Fig. 2b, c). The original land-use categories were then transformed into five habitat types (see more details of the mapping process in Appendix S2). We selected these habitat types because they differently influence *T. graeca* movement patterns (Anadón et al. 2012) (see the ODD for details). Each habitat type is associated with one parameter (i.e., H1W, H2W, ...H5W) that gives the weight in the

habitat-biased random walk. Habitat types include: (i) null habitat quality (H5W): urban areas and highways (which are never used); (ii) with very low habitat quality (H1W): intensive agriculture (irrigated crops, citric crops and greenhouses), pine forest areas (Mediterranean pine forest of *P. halepensis*) and roads (paved roads, except motorways); (iii) with good habitat quality (H4W, H3W and H2W): natural areas on slope (Mediterranean scrub on slope), flat natural areas (flat Mediterranean scrub) and traditional agricultural lands, respectively (see more details in Appendix S2). The inclusion of broad habitat categories, comprising Mediterranean scrub on slopes and flat land, traditional agriculture and pine forest, represent broad vegetation types, rather than species-specific compositions (Anadón et al. 2012; Rodríguez-Caro et al. 2017).

In natural landscapes, males and females show similar movement profiles with a strong home behaviour component, and little individual variability. However, in altered landscapes, movement greatly varies among individuals, particularly in females that show from strong home behaviour to an unbounded movements (Anadón et al. 2012). Then, at the landscape level, our landscapes were classified as “natural” or “altered”, what influenced individual movement parameterisations. As in our previous work (Jiménez-Franco et al. 2022), landscapes with more than 23.8% of the cover types (i) and (ii) defined above (i.e. with null or very low habitat quality composition) were classified as “altered” landscape, and “natural” otherwise. Therefore, the 2010 landscape in the *Chuecos* study area was classified as “altered”, whereas all the other five landscapes were classified as “natural” (Appendix S1).

Design of simulation experiments

We simulated the *T. graeca* population dynamics from the 1950s to the present-day based on the time-series data of real landscapes that represent historical land-use changes in *Chuecos*, and made a comparison with the simulations developed in *Los Mayorales*. We also projected the population dynamics into the future (using the present-day landscape) and tracked changes in several emerging demographic characteristics. We followed the modelling framework of Jiménez-Franco et al. (2022) by using initial population sizes of 250 individuals in a 5×5 km area that represented low *T.*

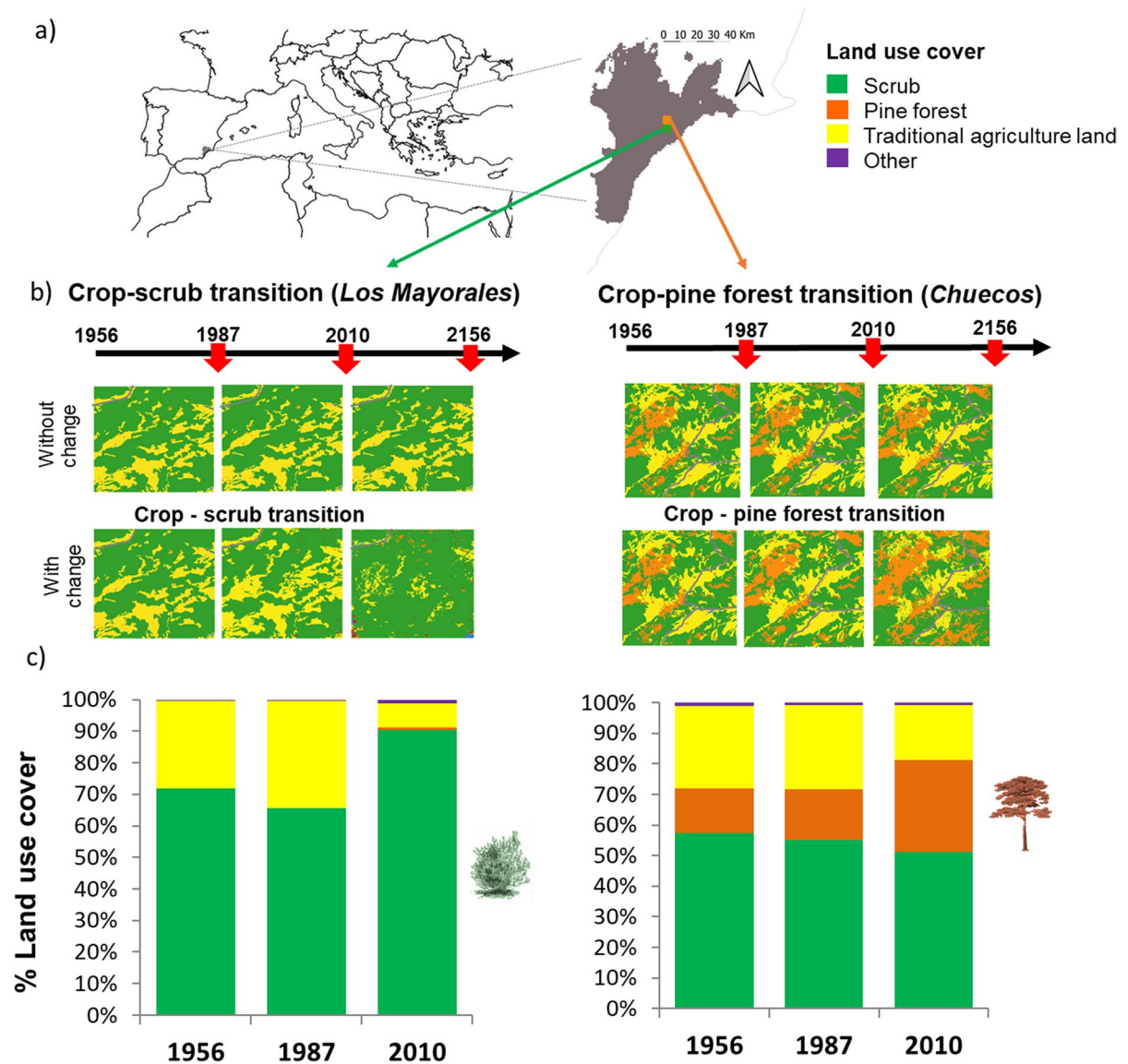


Fig. 2 General framework to study the effects of passive habitat rewilding after agricultural abandonment on the *T. graeca* population dynamics using the individual-based model STEP-LAND. **a** Distributional species range in the study area (SE Spain, in grey) and location of the two study areas of 5×5 km. **b** The spatio-temporal land-use scenarios. Black arrows indicate the 200-year simulation period from 1956 to 2156; red arrows denote the time period. A given land-use map was used in simulations with two landscape changes that occurred in 1987 and 2010, and the final simulation year was 2156. The “without change” land-use scenarios assume that no changes occurred throughout the simulation period (control scenarios).

In the mid-20th century, the two areas comprised a mosaic of natural vegetation and traditional rainfall agriculture. The “with change” land-use scenarios follows the real changes of each landscape area that underwent agricultural abandonment (impact scenarios): the *Los Mayoraes* study area (left) underwent crop-scrub transition. The *Chuecos* (right) study area underwent crop- pine forest transition. **c**) Percentage of land-use cover of the landscape scenarios at three historic times for the two study areas of 5×5 km. Note that the crop-scrub transition (study area *Los Mayoraes*) is taken from the previous study by Jiménez-Franco et al. (2022)

graeca population densities in natural Spanish populations (0.1 tortoises/ha (Anadón et al. 2009)).

As in previous parameterisations (Graciá et al. 2020b; Jiménez-Franco et al. 2020a, 2022), the initial age structure was the same for all simulations. It was based on a stable age distribution predicted by an age-stage structured deterministic matrix population model using the same parameterisation of the survival and reproduction parameters as the simulation model. For this purpose, we employed the *popbio* package (Stubben and Milligan 2007) in the statistical R programme, version 3.5.1 (R Core Team 2019) (R scripts are shown in Appendix S4). To avoid an unrealistic initial distributions (e.g., too many individuals placed in low suitability areas), we allowed the initial population to adjust to habitat types. We accomplished this by initially distributing tortoises randomly across all the good habitat quality areas (i.e., habitat types H2, H3 and H4) and simulating movement without demography (i.e., reproduction, mortality or ageing) over 50 years to allow individuals to adjust to the initial landscape map. We then took these individual locations as the starting position in the simulations of the two selected landscapes with the “without”/“with” change land-use scenarios since 1956 (Fig. 2b).

We assessed the effect of the different landscape scenarios on the reproductive rate (*RR*), population density (ind/ha), population growth rate (λ) and extinction probability (P_{ext}) of *T. graeca* over a period of 200 years. To this end, we conducted “impact” scenarios where we simulated population dynamics with agricultural abandonment in the two study areas: *Los Mayorales* (represents crop-scrub transitions) and *Chuecos* (represents crop-pine forest transitions). We also conducted “control” simulations by assuming that the landscape had not changed since 1956 (Fig. 2b). To account for stochastic processes, especially for estimating extinction probabilities, we repeated each scenario 256 times. Therefore, the total number of independent model simulations came to 1024 (2 study areas \times 2 land-use scenarios \times 256 replicates).

Data analysis

The outputs of the model simulations in each landscape scenario were used to calculate three demographic variables, obtained by averaging every 10

years across the 256 simulation replicates. The first demographic variable was the reproductive rate *RR* in time step t , defined as the mean number of offspring of reproductive females, and calculated by dividing the number of individuals born in time step t by the number of reproductive females (those aged 10 years or older) that were present at time step t . Only the non-extinct trajectories in each time step were used to calculate the *RR*. The *RR* is a short-term measure of the demographic condition. As a second demographic variable to capture demographic trends on an intermediate time scale, we used the population growth rate λ_t at interval $(t - T, t)$, calculated as $\lambda_t = (N_t/N_{t-T})^{1/T}$, where N_t is the population density in time step t , being T 10 years. Finally, we calculated the extinction rate P_{ext} for each year t as the proportion of extinct replicates (i.e., having a population size of $N_t \leq 1$).

We also quantified the total legacy effects of the historical land-use changes at the end of the simulation period. To this end, we calculated the differences in population densities and the P_{ext} values between the corresponding control vs. the impact scenarios. The extinction debt for a given scenario was the difference between the population viability after habitat change and at the end of the simulation period (Kuussaari et al. 2009). The time lag for the *RR* and population density was quantified by considering the initial period of the land-use change (in 1987) until the first year when the confidence intervals of the control/impact scenarios no longer overlapped. We considered that there was a time-lag response for population viability when there was a difference in the control/impact scenarios values equalling or higher than 0.05 throughout the simulation period (Jiménez-Franco et al. 2022).

Results

Initially (1956), both study areas showed similar characteristics (they represent a typical mosaic structure of cultural landscapes located in Mediterranean ecotones), which are composed mainly of natural areas (i.e. scrub and/or pine forest areas) and anthropogenic areas (i.e. traditional agricultural areas and others). We estimated a proportion of 72:28 natural/crop habitats for both study areas (Fig. 2c). Although natural areas were mostly scrub in *Los Mayorales* (approx.

72%), the natural areas in *Chuecos* were 57% scrub and 15% pine forest areas. Moreover, the anthropogenic areas were mainly traditional agricultural areas, and the “other” land use contributed very little (i.e. urban areas, intensive agriculture and roads; 0.4% and 0.9% for the *Los Mayorales* and *Chuecos* study areas, respectively; Fig. 2c).

The results of the “control” scenario simulations, which used the land-use cover of 1956, gave different mean reproductive rates at the end of the simulation period for both study areas of 1.61 (1.52–1.70 CI) and 1.32 (1.21–1.44 CI; Table 1) for *Los Mayorales* and *Chuecos*, respectively (Fig. 3a, b). Population density increased over time in *Los Mayorales*, but was stable in *Chuecos* (Fig. 3c, d; see the “without change” scenarios, the lines with triangle symbols), and the mean was 0.34 ind/ha (*Los Mayorales*) and 0.09 ind/ha (*Chuecos*) at the end of the simulation period in 2156 (Table 1). The growth rates in 2156 showed values above and below the critical growth rate of 1 in

Los Mayorales and *Chuecos* (1.005 and 0.99, respectively; Table 1). Consequently, the extinction probabilities in 2156 were much lower in *Los Mayorales* than in *Chuecos* (0.07 and 0.3, respectively, Table 1).

Rural abandonment caused natural revegetation in both study areas (1956 to 2010). The *Los Mayorales* study area represents agricultural abandonment with loss of traditional agricultural land (20%) and increased scrub (18%; Fig. 2c; see Appendix S2 for details). Therefore, its main land-use change is the crop-scrub transition (Fig. S1a; see more details in the transition matrices from Appendix S2). The *Chuecos* study area represents agricultural abandonment with loss of traditional agricultural areas (9%), loss of scrub areas (6%) and increased Aleppo pine forest areas (15.42%; Fig. 2c; see Appendix S2 for details), which results in the crop-pine forest transition. These landscape transformations were more complex because agricultural areas changed to different habitats during the two analysed periods, they

Table 1 Demographic variables (reproductive rate, population density, growth rate—mean of simulations and confidence intervals—and extinction probability) for the two 5 × 5 km study areas (*Los Mayorales* and *Chuecos*) consid-

ering the effects of land-use change over time (see Fig. 2 for details of the simulation scenarios) and between the “without change”/“with change” land-use scenarios for each study area

Land-use scenario	t_0 (year 1956) ^a	t_{200} (year 2156) ^b		Temporal effect ^c		Land-use change effect (year 2156) ^d
	Without/with change	Without change	With change	Without change	With change	
Reproductive rate (<i>RR</i>)						
<i>Los Mayorales</i>	1.7	1.61 (1.52–1.70)	1.46 (1.36–1.56)	– 0.09	– 0.24	– 0.15
<i>Chuecos</i>	1.7	1.32 (1.21–1.44)	0.51 (0.37–0.65)	– 0.38	– 1.19	– 0.81
Population density (ind/ha)						
<i>Los Mayorales</i>	0.1	0.34 (0.30–0.37)	0.31 (0.27–0.35)	0.24	0.21	– 0.03
<i>Chuecos</i>	0.1	0.09 (0.07–0.11)	0.008 (0.004–0.01)	– 0.01	– 0.09	– 0.08
Growth rate (λ)						
<i>Los Mayorales</i>	1.008	1.005 (1.003–1.008)	1.005 (1.002–1.007)	– 0.003	– 0.003	0
<i>Chuecos</i>	1.008	0.99 (0.99–0.10)	0.97 (0.97–0.98)	– 0.018	– 0.038	– 0.02
Extinction probability (P_{ext})						
<i>Los Mayorales</i>	0	0.07	0.09	0.07	0.09	0.02
<i>Chuecos</i>	0	0.30	0.55	0.30	0.55	0.25

Symbols (+/–) indicate an increase or decrease in the demographic variables, respectively. The results of the crop-scrub transition (*Los Mayorales* study area) are taken from Jiménez-Franco et al. (2022)

^aInitial demographic variables for each land-use scenario (year 1956)

^bDemographic variables at the end of the simulation period (year 2156)

^cDifference in demographic variables for each land-use scenario from the end to the initial simulation period ($t_{200} - t_0$)

^dDifference in demographic variables for each study area from the land-use scenarios at the end of the simulation period (year 2156; i.e. “with change”–“without change”)

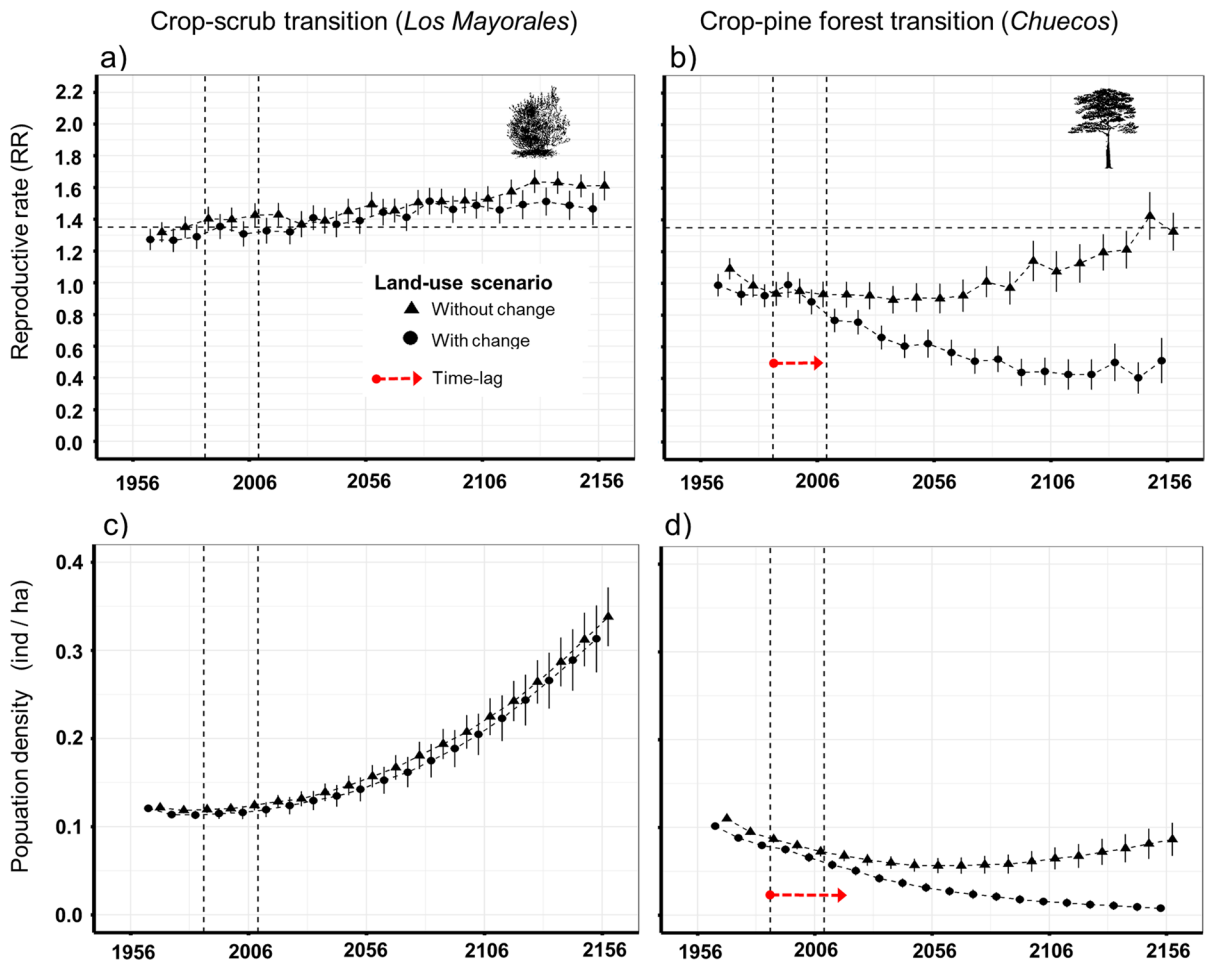


Fig. 3 Time series showing the different *T. graeca* demographic variables during the model simulations for both study areas (*Los Mayoriales* and *Chuecos*) and for both land-use scenarios over 200 years (see Fig. 2). **a, b** Reproductive rate (RR, mean number of offspring per reproductive female \pm confidence intervals). Horizontal lines represent the critical RR of *T. graeca* (1.35) that would result from a critical growth rate of 1. **c, d** Mean population density (individuals per hectare, mean \pm confidence intervals) for all four scenarios. Each simulation was repeated 256 times. Triangles (\blacktriangle) denote the “with-

out change” land-use scenarios (i.e., control scenarios with no change in land-use cover during the simulation period); circles (\bullet) depict the “with change” land-use scenarios, i.e. the impact scenarios with a change in land-use cover during the simulation period (crop-scrub transition and crop-pine forest transition for each study area, respectively). The vertical dashed black lines represent the two land-use changes of the “with change” scenarios in 1987 and 2010. The results of the crop-scrub transition (*Los Mayoriales* study area) are taken from Jiménez-Franco et al. (2022).

were replaced with scrub areas during the first period, and some percentage of these areas were further transformed into pine forest during the second period (Fig. S1a).

The results of the simulations performed in the “impact” scenarios showed opposite temporal trends for the demographic variables in the two study areas (Fig. 3) for both, reproductive rates (Fig. 3a, b) and population densities (Fig. 3c, d; see the lines with

triangle/circle symbols for control/impact, respectively). In the *Los Mayoriales* study area, which underwent the crop-scrub transition, tortoise density increased over time (Fig. 3c) with a mean density of 0.31 ind/ha at the end of the simulation period (Table 1). On the contrary in *Chuecos*, which underwent the crop-pine forest transition, tortoise density decreased over time (Fig. 3d) and reached near population extinction at the end of the simulation period

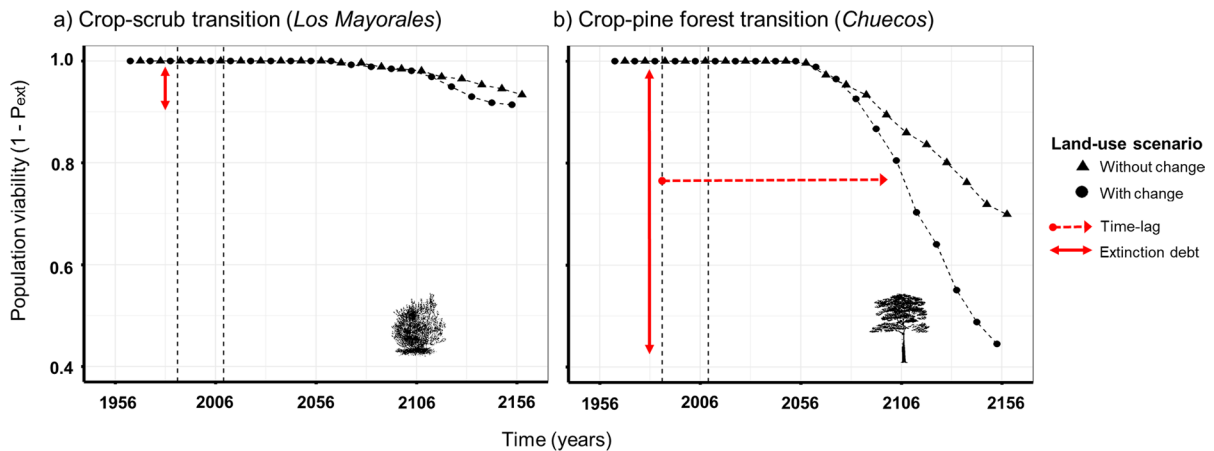


Fig. 4 Population viability ($1 - P_{ext}$) for both study areas: **a** *Los Mayoraes* (crop-scrub transition) and **b** *Chuecos* (crop-pine forest transition) over 200 years. The red solid arrows in panels (**a**) and **b** depict the extinction debt (calculated as the difference between the population viability after habitat change and the end of the simulation period in the “with change” scenario). Each simulation was repeated 256 times. Triangles (\blacktriangle) denote the “without change” land-use scenarios (i.e., control scenarios with no

change in land-use cover during the simulation period); circles (\bullet) depict the “with change” land-use scenarios, i.e. impact scenarios with a change in land-use cover during the simulation period **a** crop-scrub transition and **b** crop-pine forest transition for each study area, respectively). The vertical dashed black lines represent the two land-use changes of the “with change” scenarios in 1987 and 2010. The results of the crop-scrub transition (*Los Mayoraes* study area) are taken from Jiménez-Franco et al. (2022).

(mean density of 0.008 ind/ha; Table 1). Therefore, the land-use legacy effects from the beginning of the habitat changes until the end of the simulation period (i.e., 169 years) resulted in a 55% extinction debt in *Chuecos* (Fig. 4b, solid red arrow), but a small extinction debt in *Los Mayoraes* (0.09; Fig. 4a, solid red arrow).

The comparison between the control and impact scenarios in *Los Mayoraes* (crop-scrub transition) showed similar trends in reproductive rates (Fig. 3a) and tortoise densities (Fig. 3c; Table 1). Conversely, in the *Chuecos* study area (crop-pine forest transition), the demographic variables markedly differed between the control/impact scenarios, and for both reproductive rates (Fig. 3b) and population densities (Fig. 3d), which considerably lowered for the impact scenarios. This resulted in a difference of population density between the control/impact scenarios of -0.08 ind/ha, and the extinction probability increased by 183% at the end of the simulation period (Table 1). The time lags in response to historical land-use changes for *Chuecos* differed among the demographic metrics (Figs. 3b, d and 4b; see the red arrows). Although changes in reproductive rates were immediately visible with a 20-year time lags,

even before the second land-use change occurred (Fig. 3b), stronger effects on population density were not expected before 2016 and resulted in a 30-year time-lag response (Fig. 3d). Finally, the effects on the extinction risk appeared in approximately 2096, 110 years after the land-use change began (Fig. 4b).

Discussion

Our study shows how passive habitat rewilding due to the rural abandonment of Mediterranean cultural landscapes can give rise to animal species population trends in opposite direction according to the generation of alternative transition pathways; that is, increased land-use pine forests compared to increased land-use scrubland (this last was previously evaluated in Jiménez-Franco et al. 2022). Our results firstly revealed that the maintenance of the initial agroecosystems (mosaics with natural and crop habitats; i.e. the “control” scenarios) resulted in a temporally stable response of the *T. graeca* demographic variables in the *Chuecos* study area and a positive response in *Los Mayoraes*. Secondly, as the agricultural abandonment that led to the crop-pine forest transition

caused decreasing *T. graeca* population trends over time, the crop-scrub transition increased the *T. graeca* population trends. Consequently, we observed an extinction rate of 55% at the end of the simulation period for the *Chuecos* study area (crop-pine forest transition) compared to 9% in *Los Mayoriales* (crop-scrub transition).

These results are highly relevant for species conservation because they show that a more nuanced view is required to assess the effects of habitat rewilding due to rural abandonment on the animal populations that inhabit these dynamic landscapes. Previous studies have suggested that natural ecotones can harbour high abundances or species richness due to the shared influence of adjacent transition areas (Kark and van Rensburg 2006) (i.e., the “ecotone effect”; Kark 2013). However, some species may have a preference only for certain habitats that appear during habitat rewilding, but not for others, which is the case of several reptile species that prefer scrubland to pine forests (Ribeiro et al. 2009; Ali et al. 2018), including *T. graeca* (Rodríguez-Caro et al. 2017). Such habitat preferences have important management implications and may suggest, for example, maintenance of agroecosystems for ectotherm conservation. In line with this, our analysis of the “control” scenarios showed that *T. graeca* could persist well in these cultural landscapes, especially when the natural habitat composition was mainly scrub. However, our simulated framework revealed that passive habitat rewilding in cultural landscapes (i.e. analysing “impact” scenarios) would not necessarily lead to an improvement in *T. graeca* populations, or could even become worse in the case of pine forest revegetation. The results of our study reinforce the need to establish modelling approaches to evaluate the long-term legacy effects of dynamic landscapes (Jiménez-Franco et al. 2022), and to evaluate the effects of potential management actions on the cultural landscapes in these Mediterranean ecotones between biomes in relation to long-term conservation of low-movement species.

Population dynamics in cultural landscapes

Although the two study areas initially comprised similar proportions of natural vs. cultivated areas (control scenarios), the resulting population dynamics of our study species differed. This effect was caused by differences in the habitat composition of the

natural areas (i.e. with a higher proportion of scrub and pine forest for the *Los Mayoriales* and *Chuecos* study areas, respectively), which favoured the species in *Los Mayoriales*, but led only to stable population density in *Chuecos*. These results agree with previous studies that have found low reptile abundances in pine forest areas (Ribeiro et al. 2009; Rodríguez-Caro et al. 2017; Ali et al. 2018). This pattern, noted for ectotherm species like *T. graeca*, arises due to difficulties in thermoregulation and movement through extensive pine forest masses (Anadón et al. 2006a, b; Rodríguez-Caro et al. 2017) that impede mate-finding between individuals (Jiménez-Franco et al. 2020a) and provide little food for individuals (based especially on pastures and compound vegetation) (Hichami and Znari 2023). Therefore, our results demonstrate that, depending on landscape composition, the ecotone areas between scrublands and pine forest areas may support different population densities depending on the type of habitat preferences of the animal species (Lasanta et al. 2021).

Legacy effects of rural abandonment of the cultural landscapes located in Mediterranean ecotones

Rural abandonment in the ecotones of the SE Iberian Peninsula has led to an increase in scrubland or pine forest depending on precipitation that ranges between 280 and 400 mm and local compensation factors such as orientation (Esteve et al. 2013). In the *Los Mayoriales* study area, increased scrubland had very little effect on the *T. graeca* demographic variables and implied only a low extinction risk. However, the impact scenario of the “crop-pine forest transition” that occurred at *Chuecos* led to a 55% extinction rate (extinction debt), compared to the 30% risk of the “control” scenario (Table 1). These high extinction rates for *Chuecos* are consistent with the decreasing reproductive rates, which declined by a mean of 0.38 and 1.19 offspring by female at the end of the study period for the control and impact scenarios, respectively. This suggests that the viability of *T. graeca* in pine forests is strongly decremented as a consequence of population fragmentation that increase mate-finding failures (Anadón et al. 2012; Jiménez-Franco et al. 2020a, 2022). In addition, our study design with control/impact scenarios allowed us to identify possible time-lag effects of the *T. graeca* demographic variables (Morris et al. 2008; Metzger et al. 2009).

The effects of the crop-pine forest transition were propagated with a time-lag response across various demographic parameters of *T. graeca*. Initially, the transition altered habitat conditions and influenced movement parameters, subsequently affecting the reproductive rate (*RR*), population densities, and finally, population viability with time-lag effects of 20, 30, and 110 years, respectively. These time lags were similar to those obtained with landscape anthropisation (i.e. urban areas, agricultural intensification and lineal infrastructures), with a time-lag effect on *T. graeca* population viability of orders of about 4 or 5 generations (Jiménez-Franco et al. 2022). Time-lagged responses across population variables have been barely explored (Benton et al. 2006), yet their implications for species conservation seems compelling.

In the study area, agricultural intensification stands out as the primary driver of landscape change. The process of passive habitat rewilding into pine forest habitat, however, is slower and lacks defined environmental reforestation policies. As an example of a tool for guiding habitat management policies considering their effects on biodiversity, the STEPLAND model considers broad habitat categories, comprising Mediterranean scrub on slopes and flat land, traditional agriculture, pine forest and unsuitable habitats. Further refinements of the model could incorporate other habitat categories or even species-specific compositions of these habitats, if they demonstrate any influence on movement patterns.

Management and conservation implications:
maintenance of agroecosystems vs. passive habitat
rewilding to promote biodiversity

Simulating the effects of biodiversity in different landscape scenarios provides an experimental laboratory to better understand population dynamics in areas that undergo rural abandonment (Stillman et al. 2015). Mediterranean ecotones generally allow for three main landscape scenarios that can be associated with different landscape management options. Firstly, natural ecotones are transition zones between scrublands and pine forests that, according to previous studies, can generate increased richness or abundance (ecotone effect) (Kark 2013). Such effects have been evaluated in different biomes worldwide (e.g. Mediterranean ecosystems, deserts, among Amazonia,

Cerrado and Pantanal biomes, etc.) and with different taxa, such as birds (Van Rensburg et al. 2004; Jiménez-Franco et al. 2019), mammals (dos Santos-Filho et al. 2017) or insects (Neves et al. 2013). Secondly, traditional agriculture in natural ecotones leads to cultural landscapes (i.e. our control scenarios) that show, according to Jiménez-Franco et al. (2022) (for the *Los Mayorales* study area) and this study (for the *Chuecos* study area), a very high potential for species associated with traditional agricultural practices (Moreira and Russo 2007). Finally, rural abandonment (also called “passive habitat rewilding”) leads to natural revegetation in Mediterranean ecotones, where the landscape is homogenised towards one of the two alternative transitional biomes (e.g. toward scrublands or pine forests) (Lasanta-Martínez et al. 2005).

Our study analyses landscape scenarios that correspond to both the maintenance and abandonment of cultural landscapes. Firstly, management practices that favour the maintenance of traditional agriculture (i.e. generating agroecosystems) may be considered beneficial in European cultural landscapes. Indeed the European Common Agricultural Policy aims to prevent abandonment of traditional agricultural management, which is stated to be one of the main drivers of biodiversity loss in European ecosystems (Queiroz et al. 2014). Thus one important way to preserve vertebrate diversity in the Mediterranean region is by means of policies that are specifically designed to prevent abandonment and to maintain traditional farmland (Moreira and Russo 2007), but by always considering the quality of the landscape matrix (Souza et al. 2022) and the connectivity of the natural areas in these agricultural Mediterranean environments (Hidalgo et al. 2021). Based on our simulated results, we propose that the traditional mosaic landscapes from historical periods with high proportions of scrublands and crops (like the landscape scenario “control” with scrubland) are appropriate for policies to restore natural landscapes for ectotherm species like *T. graeca* (Pulsford et al. 2017), where these individuals can access different open areas for both food in herbaceous areas in traditional crops and refuge in open-forested areas.

Secondly, the passive habitat rewilding of cultural landscapes involves secondary succession following agricultural land abandonment in areas formerly used for crop or livestock farming (Barral et al. 2015).

Our results show that the cultural landscapes undergoing passive habitat rewilding do not generate any benefit to our study species compared to the landscapes without such land abandonment. Abandoned landscapes can even have negative impacts because rewilding often simplifies the landscape, species associated with agroecosystems are lost (Queiroz et al. 2014; Vadell et al. 2016), and the risk of wildfires increases (Benton et al. 2006). However, passive habitat rewilding, accompanied by increasing homogeneous landscapes with scrub or pine forests, may favour the specialist species of these habitats (Ribeiro et al. 2009; Jiménez-Franco et al. 2018) at the expense of those adapted to cultural landscapes (i.e. *T. graeca*). An example of less generalist species includes forest birds (Gil-Tena et al. 2007; Jiménez-Franco et al. 2019) and raptor, which prefer pine forests for territorial occupancy (Jiménez-Franco et al. 2014, 2020b), as well as some owl species that prefer scrublands (Michel et al. 2016; León-Ortega et al. 2017). Therefore, the consequences of habitat rewilding on biodiversity depends on the geographical context and the species involved. Certain species may be deemed “winners” or “losers”, while others may remain unaffected (Navarro and Pereira 2012). On the one hand, winner species benefit from habitat regeneration and greater connectivity of fragmented natural landscapes at different spatial scales (Perino et al. 2019). An example of a small spatial scale would be local features such as hedgerows, which support the occupancy of birds or insects. An example of large scale would be ecological corridors that allow recolonization by large mammals over long distances (e.g., the case of the European carnivores such as Iberian lynx, the brown bear or the wolf) (Enserink and Vogel 2006; Stoate et al. 2009). On the other hand, the looser species, such as farmland birds, are often associated with the high nature value of agricultural landscapes characterized by habitat heterogeneity. Habitat rewilding that results in habitat homogenization may have negative impact on these species (Anderle et al. 2023). Given the varied responses of species to habitat alteration in Mediterranean cultural landscapes, there is an urgent need for a comprehensive evaluation of the effects of rewilding processes on biodiversity and the implementation of associated policies. This evaluation should specifically consider the impacts of different landscape compositions and structures (Phalan et al. 2011).

Conclusion

Our study evaluates the long-term effects of the cultural landscapes located in Mediterranean ecotones between scrubland and pine forest biomes and the different rural abandonment processes that has occurred since the 20th century on low-movement species population dynamics (i.e. *T. graeca*). The strongest effect on our study species appears in the crop-pine forest transition, where an extinction debt is generated with a time-lag response. This result suggests that the maintenance of those cultural landscapes comprising scrub areas will favour the ecotone effect, whereas passive habitat rewilding, which is associated with increased pine forests, will diminish ectotherm species like *T. graeca*. Moreover, different habitat managements may result in very important landscape transformations with distinct effects on biodiversity. Thus, to protect biodiversity in agroecosystems, a specific and strategic policy should be considered for each specific area by considering not only particular landscape characteristics, but also the demographic characteristics of priority species for conservation. For instance, our study species, *T. graeca*, is a long-lived species with a low movement capacity, so its population effects are observed only with a time lag. It is therefore necessary to promote landscape connectivity to facilitate mate finding by maintaining open forests for species associated with agroecosystems, which are also beneficial habitats for steppe birds.

Our general modelling framework relates the movement patterns of *T. graeca* to land-use changes and allows to predict its long-term demography and dynamics. We expect our framework to be applied to different dynamic landscapes to predict the influence of land-use changes on animal population demography, and to evaluate different management actions, such as the maintenance of agroecosystems vs. habitat regeneration policies. For instance, future studies could assess critical thresholds in landscape composition (e.g., proportions of high or low-quality habitat) and landscape configuration (e.g., fragmentation metrics) (Wiegand et al. 2005), which result from passive habitat rewilding. Such assessments could improve our understanding of potential population extinctions, such as the effects of pine forest cover on the species studied in our research. Therefore, spatially explicit modelling approaches, such as the IBMs used in this

study, can be very useful in addressing conservation issues for long-lived species (Stillman et al. 2015).

Acknowledgements We thank Ángel Luis García for his help in developing STEPLAND. We also thank José Antonio Palazón for helping with the simulation process and the Scientific Calculation Service of the Murcia University (ATICA), where simulations were carried out, as well as Paqui Carreño and Jesus Miñano for their work on preparing historical habitat mapping. We are grateful to the two anonymous reviewers who made valuable comments on the manuscript. Figure 1 is by Carmen Cañizares (@canitailustradora).

Author contributions AG, EG and TW conceived ideas. JDA, EG, TW, and AG developed the IBM. MVJF, RCRC, and EG analysed data. MVJF led the writing of the manuscript. All the authors contributed critically to the draft and gave their approval for its publication.

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. M.V.J.F. was supported by a postdoctoral grant cofunded by the Regional Valencian Government and the European Social Fund (APOSTD/2018/043) and a “Juan de la Cierva-Incorporación” research contract (reference IJC2019-039145-I) financed by the Spanish Ministry of Science, Innovation and Universities (MCIN/AEI/10.13039/501100011033). R.C.R.C. was supported by the Regional Valencian Government and the European Social Fund with a postdoctoral grant (APOST/2020/090) and the European Union-Next Generation EU in the Maria Zambrano Programme (ZAMBRANO 21-26). JDA was supported by a Ramón y Cajal contract (RYC-2017-22783) cofunded by the Spanish Ministry of Science, the Agencia Estatal de Investigación and the European Social Fund. This work was supported by Projects PID2019-105682RA-I00, funded by the Spanish Ministry of Science, Innovation and Universities (MCIN/AEI/10.13039/501100011033), Grupos Investigación Emergentes CIGE/2021/157 and AICO/2021/145 (funded by Regional Valencian Government).

Data availability Model name: STEPLAND. Availability: The full code of STEPLAND, its parameterization and the main results files are available in the Figshare repository at https://figshare.com/articles/software/_/25232630. Licence: Apache 2.0

Declarations

Conflict of interest The authors declare no competing interests.

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