Journal of Environmental Management 370 (2024) 122480

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Research article

Bridging the gap between ecological succession of fleshy-fruited shrubs and restoration frameworks in semiarid oldfields

Martín Amodeo [a,b], Vicente Martínez-López [c,d], Víctor Zapata-Pérez [e], Francisco Robledano-Aymerich [e,*]

[a] Instituto Argentino de Oceanografía, Consejo Nacional de Investigaciones Científicas y Técnicas - CONICET, Argentina
[b] Grupo de Estudios en Conservación y Manejo (GEKKO), Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur, Argentina
[c] Department of Evolution, Ecology and Behaviour. Institute of Infection, Veterinary and Ecological Sciences. University of Liverpool, Liverpool, UK
[d] Department of Zoology and Physical Anthropology, University of Murcia, CEIR Campus Mare Nostrum (CMN), Campus de Espinardo, Murcia, Spain
[e] Department of Ecology and Hydrology. Faculty of Biology. University of Murcia, CEIR Campus Mare Nostrum (CMN), Murcia, Spain

A R T I C L E I N F O

Original content: Amodeo_etal_2024 (Original data)

Keywords:
Oldfields
Ecological succession
Environmental gradients
Fleshy-fruited shrubs
Hierarchical modelling of species communities
Nature-based restoration frameworks

A B S T R A C T

Abandoned agricultural areas (i.e. oldfields) represent an opportunity for natural vegetation recovery, increasing soil carbon sequestration and lessening the impacts of climate change and desertification. Ecological succession in oldfields can be hampered by the harsh conditions of semiarid and arid ecosystems, and hence, restoration actions may be needed in some contexts to reactivate the ecosystem functioning. Fleshy-fruited shrubs are indicators of progression in the ecological succession, which can shift notably across environmental gradients, making difficult to obtain robust conclusions at regional scales. Other poorly studied aspects at such scales (agricultural legacy, structural features and local landscape effects) add to this knowledge gap. Here, we study the species-specific natural colonization patterns of fleshy-fruited shrubs in semiarid oldfields across environmental gradients in the Southeast of the Iberian Peninsula taking into account specific traits of plants. We used Hierarchical Modelling of Species Communities (HMSC) to test the influence of the time since the abandonment and the past land-use history of the oldfields, and the effect of local structural factors, such as the presence of remnant trees and natural patches of vegetation, on the shrub recolonization patterns. We found that altitude and lithology conditioned the structure of shrub communities, allowing the selection of different focal species for making recommendations for restoration. Time since abandonment was not relevant for the colonization process. The persistence of remnant trees in the oldfields showed a positive effect on the occurrence of several shrub species. Close sources of propagules (terrace edges and/or natural vegetation patches) benefited the occurrence of certain species mainly at lower altitudes. Traits of species (growth form, root depth, dispersal mode, fruit length and water content) helped to explain the performance of species along the environmental gradients. We identified the main drivers of natural colonization of fleshy-fruited shrubs in semiarid oldfields across environmental gradients, providing ecological knowledge to guide scientists and practitioners to develop nature-based restoration frameworks. Different management actions are recommended according to the environmental gradient.

1. Introduction

Abandoned agricultural areas (i.e. oldfields) are increasingly targeted by conservationists in restoration policies since they can represent an opportunity for natural vegetation recovery which mitigates erosion and increases soil carbon sequestration (Cramer et al., 2008; Fayet et al., 2022; Lasanta et al., 2019, 2020), but see also Quintas-Soriano et al. (2022) for many other potential positive or negative outcomes of land abandonment. The study of the ecological succession in oldfields can improve our understanding of the drivers that lead to vegetation recovery and can guide restoration initiatives. Vegetation dynamics after land abandonment have been extensively addressed in studies worldwide including tropical, sub-tropical and temperate ecosystems (Bonet, 2004 and references therein; Bowen et al., 2007; Garrote et al., 2019; Hu

* Corresponding author. Department of Ecology and Hydrology. Faculty of Biology. University of Murcia, CEIR Campus Mare Nostrum (CMN). Avda. Teniente Flomesta, nº 5 – 30003, Murcia, Spain.
E-mail address: frobleda@um.es (F. Robledano-Aymerich).

https://doi.org/10.1016/j.jenvman.2024.122480
Received 11 March 2024; Received in revised form 22 August 2024; Accepted 9 September 2024
Available online 19 September 2024

et al., 2021; Moyo and Ravhuhali, 2022). There is less information on this subject in semiarid and arid areas (Basualdo et al., 2019; McLendon et al., 2012; Pausas et al., 2006; Zivec et al., 2021) where high temperatures and low precipitation together with seed predation and seedling herbivory can slow down natural recovery (Pugnaire et al., 2006; Rey-Benayas et al., 2015) and trigger soil erosion increasing the risk of desertification (Romero-Díaz et al., 2017). The restoration of such areas, and other ecosystems located at the extremes of environmental stress gradients (Csákvári et al., 2022), would benefit from studies that evaluate their natural regeneration potential. Furthermore, most studies have assessed the succession in oldfields at small spatial scales which makes difficult to obtain robust conclusions at regional levels in which local succession patterns can shift notably due to environmental gradients, caused, for example, by altitudinal and/or lithological differences. Assessing vegetation recovery through these altitudinal and lithological gradients would increase our understanding of the ecological succession in oldfields. Previous studies in semiarid oldfields of Tenerife Island (Spain) showed that the trajectories of the succession can drastically change at local and regional scales depending on precipitation (Otto et al., 2006). Similarly, investigations in arid ecosystems of California found that local and regional factors can shift from less than 50–800 years the time needed by oldfields to reach full vegetation recovery (McLendon et al., 2012). Other poorly studied aspects in semiarid and arid areas like agricultural legacy, structural features and local landscape effects conform this knowledge gap (Cramer et al., 2008; Scott and Morgan, 2012). Therefore, focusing on semiarid and arid zones, increasing our knowledge on the drivers and mechanisms of vegetation recovery in oldfields along regional environmental gradients would help to develop nature-based restoration frameworks adapted to the environmental heterogeneity of such large territories. This information would be fundamental to increase the success of management and restoration programmes of oldfields, particularly those under physical conditions making them more prone to land degradation (Romero-Díaz et al., 2024).

Land abandonment has increased worldwide since the end of the XIXth century with particular intensity in the northern hemisphere (Cramer et al., 2008; Li and Li, 2017), being the main cause of landscape change in Europe and especially relevant for global change in the Mediterranean Basin (García-Ruiz et al., 2020; Plieninger et al., 2016; Terres et al., 2015; Ustaoglu and Collier, 2018). Furthermore, land abandonment is expected to keep increasing in the upcoming decades (Heinimann et al., 2017). Spontaneous vegetation recovery without human intervention can be an option in abandoned areas where the causes of degradation have ceased and ecological processes have become active again. Managers must in any case be aware that in severely disturbed or naturally stressed habitats (e.g. in arid, Mediterranean, or alpine regions) other factors, such as physical or climatic conditions and/or herbivore pressure, strongly limit the establishment and recruitment of plants and, ultimately, the effectiveness of passive restoration schemes (Prach and Hobbs, 2008). Moreover, Mediterranean areas have suffered intense human management during millennia leaving a strong footprint in the ecosystem processes which are frequently impoverished (Cramer et al., 2008). Afforestation has been found to improve the ecological succession in semiarid oldfields (Zethof et al., 2019) and restoration seems to be more effective than natural vegetation recovery in semiarid oldfields of South Africa (Moyo and Ravhuhali, 2022). The selection of the management strategy to restore oldfields depends on the dynamics of secondary succession which is the result of the interplay among a wide variety of factors such as climate, altitude, lithology, the agricultural legacy, time since abandonment, the availability of seed sources and biotic interactions. The contribution of these elements to oldfields secondary succession has been previously assessed (Bonet, 2004; Cramer et al., 2008; Lasanta et al., 2021). However, few studies have taken into account all these factors together, which limits our understanding of this complex process.

Biotic interactions are pivotal in vegetation recovery of semiarid oldfields where abiotic factors hinder plant recruitment (Bonet, 2004; Gimeno et al., 2012). Plant establishment is also limited by herbivory that can be overcome through facilitation (e.g. by nurse shrubs), a process favored in stressed environments (Bertness and Callaway, 1994). Fleshy-fruited plants, whose fruits are consumed and endozoochorously dispersed by animals, increase recruitment and the diversity of plants in restored lands compared to abiotically dispersed species (Camargo et al., 2020; Viani et al., 2015). These mostly woody plants also confer structure to successional habitats, acting as nurses for other woody and annual plants. Furthermore, plants that bear fleshy fruits attract frugivorous animals which act as vectors mobilizing seeds from natural remnants toward oldfields increasing seed rain and long-distance dispersal in these harsh environments where the lack of seed sources can constrain the secondary succession (Cramer et al., 2008). For instance, seedlings emerging from animal scats are crucial for the vegetation recovery of oldfields in Australia (Zivec et al., 2023) and the Iberian Peninsula (Garrote et al., 2022). Birds perch in remnant trees depositing seeds beneath them (Camargo et al., 2020), which is expected to boost the recolonization generating a nucleation effect in microenvironments where harsh abiotic conditions are ameliorated by reducing insolation and increasing humidity (Verdú and García-Fayos, 1996). In turn, shrubs recruited in these primary nuclei, will act as perches or refuges for birds, or provide shelter to hoarding mammals, all promoting further seed movement (Corbin and Holl, 2012, and references therein). Previous studies have highlighted the importance of the perch effect in endozoochorus shrubs colonization of oldfields in semiarid areas (Pausas et al., 2006). On the other hand, species identity and their functional traits can determine the process of shrub colonization in oldfields (Rolo et al., 2016) and the success of restoration initiatives (Muler et al., 2018; Padilla et al., 2009). However, most studies have investigated shrub colonization of oldfields at the community level while interspecific differences in traits and species-specific responses to abiotic and biotic factors have remained overlooked (e.g. Bonet, 2004; Robledano-Aymerich et al., 2014), limiting our ability to develop effective restoration plans.

Here, we study the species-specific natural colonization patterns of fleshy-fruited shrubs in oldfields along environmental gradients with different lithologies. We assess if the colonization process is conditioned by agricultural legacy effects, the presence of remnant trees within the oldfields due to potential perch and facilitation effects, and by the proximity of areas with natural vegetation which can act as sources of propagules. Our main goal is to identify the main drivers of vegetation recovery at a regional scale to develop nature-based restoration frameworks of abandoned lands taking into account specific traits of woody plants. We attempt to provide guidance for a regional restoration framework based on natural recolonization in line with expectations from previous research. With this aim, we surveyed a large sample of rainfed oldfields with different time since abandonment along an environmental gradient at a regional scale in the Southeast of the Iberian Peninsula, and analyzed shrub recolonization using Hierarchical Modelling of Species Communities (HMSC; Ovaskainen and Abrego, 2020) which allows to disentangle the relative contribution of each predictor variable to the species distribution and interpret them in relation to the species traits. Our hypothesis is that there are species-specific differences in the recolonization pattern of fleshy-fruited shrubs at regional scale mediated by environmental conditions and functional traits, and influenced by local factors such as the presence of remnant trees and adjacent areas with natural vegetation.

To summarize, the study of the ecological succession in oldfields is seen as a guide for restoration frameworks, particularly when spontaneous vegetation recovery is assessed along large-scale gradients. The selection of the restoration strategy depends, however, on ecological dynamics resulting from the interplay among factors such as climate, altitude, lithology, the agricultural legacy, time since abandonment or the availability of propagule sources, modulated by ecological traits of plants and biotic interactions. The contribution of these ecological factors to secondary succession in oldfields has been already assessed but rarely taking into account all of them together regionally, which is precisely the approach of this study.

2. Materials and methods

2.1. Study area

We surveyed 116 rainfed oldfields widely distributed throughout 11,313 km^2 in the Southeast of the Iberian Peninsula (Murcia Region, Spain) which were abandoned between 1945 and 2013. The survey ranged over a regional altitudinal gradient (54–1566 m a.s.l.) and sought an even representation of the bioclimatic domains and different lithologies (Fig. 1). This area has a semiarid Mediterranean climate where habitats and species are exposed to limited water supply and unpredictable rainfall, conditions intensified by climate change (Underwood et al., 2009) under which woody vegetation acquires great importance for ecosystem structure and functionality. Climate in the study area is strongly conditioned by altitude which varies from sea level to 1600 m a.s.l., defining three bioclimate domains (i.e. areas with similar climatic conditions) in a gradient of decreasing temperatures and increasing precipitations as altitude increases: Thermomediterranean (50–540 m a.s.l.), Mesomediterranean (220–850 m a.s.l.), Supramediterranean (700–1600 m a.s.l.; see Figures in Supporting Information 1; Rivas-Martínez, 1983). Thermomediterranean areas are characterized by frosts already present (especially in January–February), but being scarce and not very intense, and totally absent in the lowest altitudes. The average annual temperature is usually >17 °C. Mesomediterranean areas have more frequent frosts in winter and can be intense in higher altitudes. Average annual temperature is between 12 and 17 °C. Finally, the Supramediterranean domain has intense and frequent frosts in winter and average annual temperatures between 8 and 12 °C (Alcaraz et al., 1991, updated by the authors). This classification is based exclusively on thermal characteristics, which do not coincide with rainfall zoning, which classifies most of the Thermo-Mediterranean domain and part of the Mesomediterranean as semi-arid (200–350 mm annually), the rest of the Mesomediterranean as dry (350–650 mm) and most of the Supramediterranean as subhumid (>650 mm).

2.2. Description of the oldfields

The oldfields consisted in continuous units of abandoned rainfed agricultural fields (surface ranging from 3621 m^2 to 116,146 m^2) where arboreal (mostly almond, occasionally walnut and olive trees) or herbaceous (cereal) crops had been cultivated. Time since abandonment ranged between two and seventy years, 54 % of the oldfields had been abandoned between 1981 and 1997 (17–36 years of abandonment). Past land-use history is an important predictor of natural regeneration in abandoned agricultural sites (Bonet, 2004; Cramer et al., 2008; Lasanta et al., 2021). It is expected that sites previously cultivated with cereals present different past land-use legacies than sites previously cultivated with trees, not only related to the presence of remnant trees, but also to the different management practices applied to each crop type. From a total of 116 fields, 46 corresponded to arboreal crops where lines of remnant trees were still present, 78 contained hand-built stone terraces, approximately half (60) had adjacent patches of natural vegetation (less than 200 m apart). These natural patches were mainly mosaics of pines and oaks where shrubs could be found growing spontaneously, with similar species compositions as in the oldfield (more details and images in Supporting Information 1).

2.3. Survey description

Each field was sampled once during the autumn season between 2014 and 2017. Sampling was carried out along 200 m transects, recording every individual fleshy-fruited shrub within 2 m on both sides. All fields had a transect in the open space located 10 m apart from remnant trees in order to avoid potential perch effects. In fields which had contained tree crops, another transect was set along the line of remnant trees, and where terraces existed, another along its edge. Where there was an adjacent natural vegetation patch, an additional transect was performed there. Our data comprise the abundances of fleshy-fruited shrub species surveyed in 299 transects distributed over 116 oldfields, each field hosting one to four transects depending on their structure (Table 1, Supporting Information 1 Figure S1.1).

2.4. Statistical analysis

Data were analyzed using Hierarchical Modelling of Species

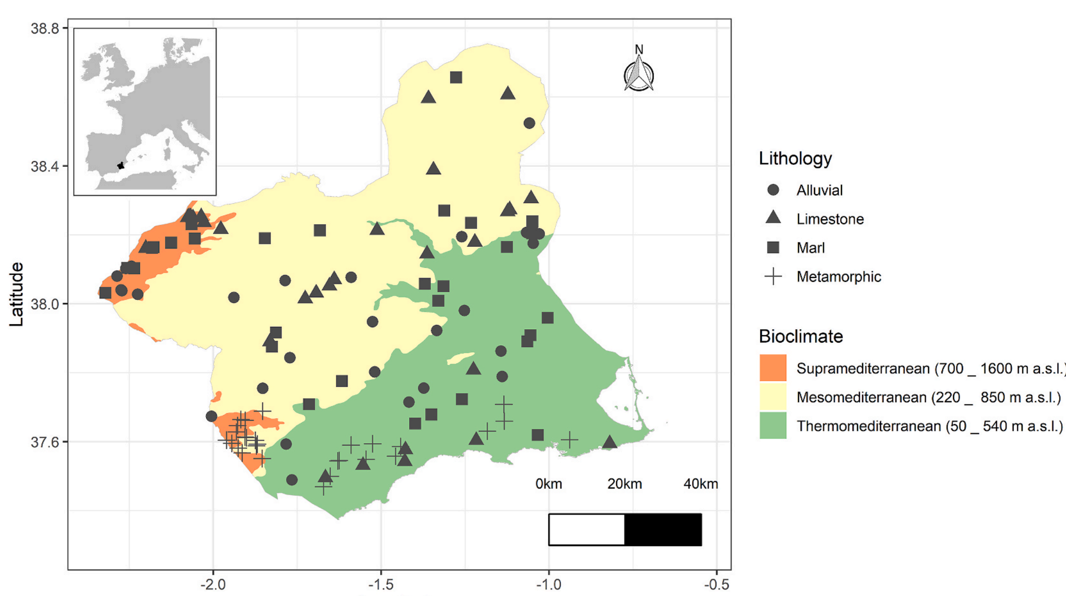

Fig. 1. Study area and distribution of the oldfields surveyed in the Southeast of Iberian Peninsula. Colours indicate bioclimate domains related to altitude and symbols indicate the lithology of the oldfield.

Table 1
Number of transects (number of oldfields) under each combination of bioclimate and lithology, of the total of 299 transects located in the 116 oldfields surveyed.

	Limestone	Alluvial	Marl	Metamorphic
Supramediterranean (700–1600 m a.s.l.)	17 (8)	15 (7)	21 (8)	19 (8)
Mesomediterranean (220–850 m a.s.l.)	38 (14)	31 (11)	25 (9)	21 (9)
Termomediterranean (50–540 m a.s.l.)	25 (8)	21 (10)	35 (13)	31 (11)

Communities (HMSC; Ovaskainen and Abrego, 2020), a multivariate hierarchical generalized linear mixed model fitted with Bayesian inference. Firstly, a species selection procedure was performed based on their prevalence (proportion of the total number of samples containing the species). Species with less than 10 occurrences (prevalence $< 3.34\%$) were excluded to remove rare species, narrowly distributed species or species at the extreme of their distribution range, all considered bad candidates to be included in restoration frameworks at regional scales.

The count of each of the species was used as the response variable and, because of the zero-inflation nature of the data, we applied a Hurdle model approach: one model (probit regression approach) for the occurrence data (presence-absence) and another (normal linear regression approach) for the abundance conditional on presence (henceforth abundance-COP model), declaring zeros as missing data, log-transforming and scaling to zero mean and unit variance within each species (Ovaskainen and Abrego, 2020).

We included seven predictor variables as fixed effects following an additive structure (more details in Supporting Information 2).

- **Altitude**, numerical (meters above sea level);
- **Lithology**, categorical with levels Alluvial, Limestone, Marl, Metamorphic;
- **Time since abandonment**, numerical. Years since last cultivation obtained from sequences of aerial orthophotographs (Agricultural Plots Geographic Information System of Spain; Martínez Hernández and Cánovas-García, 2016), considering the oldest image without activity;
- **Transect type**, categorical with levels open space, tree line, terrace edge, adjacent natural vegetation;
- **External TE**, binary, presence/absence of a terrace edge in the oldfield;
- **External NV**, binary, presence/absence of a natural vegetation patch adjacent to the field;
- **Legacy**, binary, indicating if the field had contained a tree crop or not.

Binary indicators (External TE, External NV, Legacy) test the effect of the predictor variable on the species occurrence/abundance in the Open Space within the field (reference transect type). Additionally, the information of the transects performed in those zones identified as potential sources of propagules (terrace edge, natural vegetation patch) was used to calculate the proportion of fields where each species co-occurred within the field and in those zones.

We used the geographical coordinates of the field as a spatial random effect to control for the spatial autocorrelation and dependency structure in the hierarchical study design, which also takes into account the species distributions.

Climatic numerical variables obtained for each field from the EuMedClim database were also explored as predictor variables (Fréjaville and Benito Garzón, 2018). We considered a total of 21 variables regarding temperature, precipitation and water balance, for the period 2010–2014. A selection procedure was conducted based on correlation analyses, leading to three selected variables: Annual Mean Temperature (°C), Annual Precipitation (mm) and Annual Water Balance (precipitation minus potential evapotranspiration). We calculated a Variance Inflation Factor on a Generalized Linear Model using total abundance as a response variable and the selected climatic variables and altitude as predictors. Based on solid evidence of redundancy (VIF values > 17, Fox and Weisberg, 2011), altitude was used in the model as an indicator of climatic variables, in order to avoid collinearity. According to Pearson correlation coefficients, altitude showed a strong negative correlation with Annual Mean Temperature (Pearson $r = -0.99$, $p < 0.001$) and positive with Annual Precipitation ($r = 0.98$, $p < 0.001$) and Annual Water Balance ($r = 0.97$, $p < 0.001$).

We included information about functional and life-history traits in a joint species modeling approach to analyze how species traits affect the natural recolonization of shrubs in oldfields (Ovaskainen and Abrego, 2020). Of 27 traits initially analyzed several were redundant, hence a selection procedure was conducted based on correlation analyses (Supporting Information 2). Selected traits were Growth Form, Leaf Phenology, Root Depth, Specific Leaf Area, Sexual System, Dispersal Category, Fruit Length, Seed Dry Mass and Fruit Water Content, obtained from databases BROT2 (Tavşanoğlu and Pausas, 2018) and FRUBASE (Jordano, 2013).

We examined the model fit by measuring the explanatory power and the predictive power, using species-specific Tjur's R^2 and the usual R^2, for the presence-absence probit models and the abundance-COP models, respectively. We partitioned the explained variation among the fixed and random effects included in the models to identify the main drivers of the ecological succession. We examined species-specific responses to the explanatory variables (beta parameters) and the relationship with species traits (gamma parameters) considering responses that were positive or negative with at least 95% posterior probability (Ovaskainen and Abrego, 2020).

We fitted the HMSC model using the R-package *Hmsc* (Tikhonov et al., 2020). Custom plots were constructed using the package *ggplot2* (Wickham, 2009) in R (R Core Team, 2020).

3. Results

3.1. Descriptive statistics

The averaged species richness of fleshy-fruited shrubs in transects was 1.86 species (range = 0–9, 3rd quartile = 3) and the averaged abundance was 10.81 individuals per transect (range = 0–115, 3rd quartile = 13). Species richness and total abundance did not vary with time since abandonment (>15 % overlapping credible intervals between two and 70 years of abandonment, Figure S3.1). Limestones showed a species richness at least 1.8 times higher than other lithologies. The tree line and the natural vegetation areas showed an average species richness in the range of one to three species, while this index was lower than 0.9 in the open space and terrace edges (based on 95% credible intervals). A similar tendency was observed in the total abundance although without strong support (mean values and credible intervals in Supporting Information 3, Table S3.1).

A total of 26 species of fleshy-fruited shrubs were observed in the studied oldfields. Our main results refer to 12 species included in the models, which comprised a 93.5% of the total abundance: *Asparagus acutifolius* (*AspAcu*), *Asparagus albus* (*AspAlb*), *Asparagus horridus* (*AspHor*), *Daphne gnidium* (*DapGni*), *Ephedra fragilis* (*EphFra*), *Juniperus oxycedrus* (*JunOxy*), *Juniperus phoenicea* (*JunPho*), *Olea europaea* var. *sylvestris* (*OleEur*), *Pistacia lentiscus* (*PisLen*), *Rhamnus lycioides* (*RhaLyc*), *Rubia peregrina* (*RubPer*), *Rosa* sp. (*RosSp*). Information on disregarded species (those with <10 occurrences) can be found in Supporting Information 3 Table S3.2.

3.2. Model fit and performance

The MCMC convergence of the HMSC models was satisfactory (potential scale reduction factors below 1.1, Supporting Information 2) and they showed a good fit to the data in terms of explanatory power: the mean Tjur R^2 in the presence-absence model was 0.41 and the mean R^2 in the abundance-COP model was 0.44 (species-specific model fits in Fig. 2). Regarding their predictive power, the Tjur R^2 was on average 0.24 for the presence-absence model and the mean R^2 was 0.04 for the abundance-COP model. Altitude was the main predictor modulating the occurrence of the species (32% of explained variation on average across the species) followed by lithology (15%). Local factors such as the presence of remnant trees and the existence of natural vegetation explained some of the remaining variation (Fig. 2a). Time since abandonment and legacy effects showed a low relevance. Considering the explanatory power of abundance-COP model, the main factors modulating the abundance of the species were altitude (21%), lithology (21%) and transect type (20%, Fig. 2b). The legacy effects, the existence of a terrace edge and the existence of natural vegetation explained some of the remaining variation (12%, 8%, 6%, respectively).

3.3. Species responses to influencing factors

We can define groups of species with different responses to altitude according to the beta (Fig. 3) and the gamma parameters (Fig. 4 and Figure S3.3) of the presence-absence model. Tall shrubs with mixed dispersal systems involving birds and mammals (*JunOxy, JunPho* and *RosSp*) were positively associated with altitude. Similarly, species with larger fruits and greater rooting depth showed a higher probability of occurrence as altitude increases. On the other hand, species with liana-like habits (*AspAlb*, *AspHor*) and higher fruit water content (*AspAlb*, *AspHor*, *OleEur* and *RhaLyc*) prevailed at low altitudes.

Most species showed the highest prevalence on limestones (Table S3.1). Marls showed a negative effect on the occurrence of seven species. *AspAcu* showed a positive association to metamorphic lithology (Fig. 3). Similar trends were observed in the species-specific responses of the abundance-COP model (Figure S3.2).

The presence of remnant trees in the field favored the occurrence of eight species growing beneath them: *AspAcu, AspHor, DapGni, EphFra, JunPho, OleEur, PisLen, RhaLyc* (Fig. 3 and Fig. 5).

The presence of a terrace edge promoted the occurrence of seven species within the oldfield: *AspAlb, AspHor, JunOxy, JunPho, OleEur, PisLen, RubPer* (Fig. 5). Three of them (*AspAlb, AspHor, RubPer)* showed a high coincidence rate between the species occurrences within the field

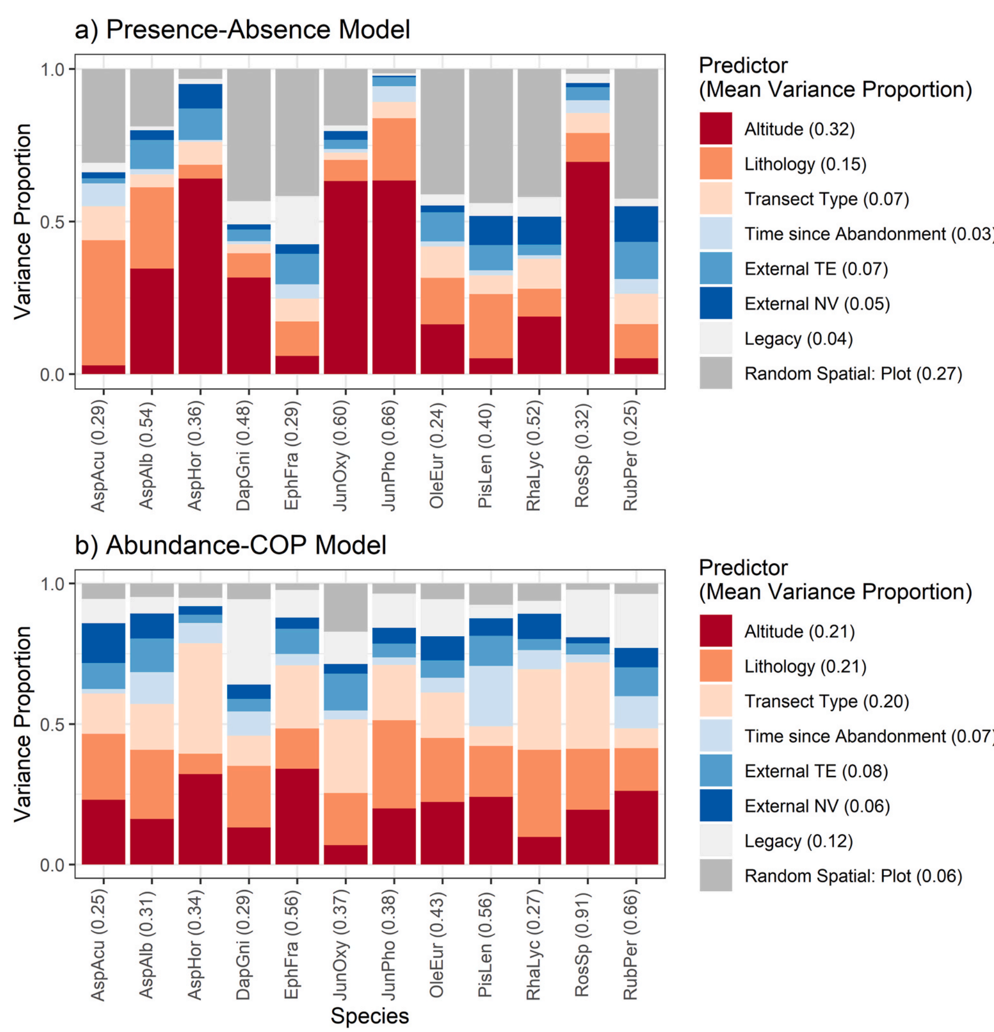

Fig. 2. Variance partitioning among the explanatory variables included in the Presence-Absence models (a) and the Abundance-COP models (b) for the analyzed species. The explanatory power for each species is indicated beside the species name (Tjur R^2 for Presence-Absence model and R^2 for Abundance-COP model). Bars represent the total explanatory power for each species set to 1. The legends give the mean variance proportion for each explanatory variable averaged across the species.

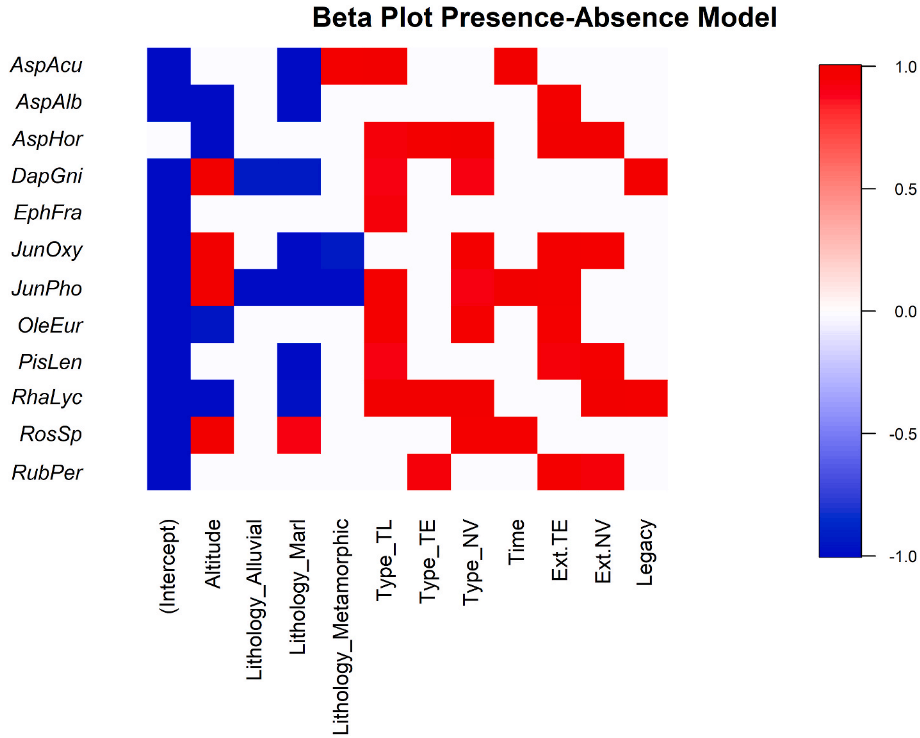

Fig. 3. Species-specific responses to predictor variables in the HMSC presence-absence model (beta parameters). The intercept represents the reference level for the factors (limestone for the lithology and open space for the transect type). The categories TL, TE, NV are Tree Line, Terrace Edge and Natural Vegetation for the factor Transect Type. Time (time since abandonment) is a numerical variable. External sources of propagules (Ext.TE, Ext.NV) and Legacy are binary indicators. Positive responses with at least 95% posterior probability are shown in red, negative responses with at least 95% posterior probability are shown in blue, and responses that did not gain strong statistical support are shown in white. The species are ordered alphabetically.

and in the terrace edge (>50% of coincidences, Table 2).

The presence of a patch of natural vegetation adjacent to the oldfield favored the occurrence of five species within the oldfield: *AspHor, JunOxy, PisLen, RhaLyc and RubPer* (Fig. 5). Two of them (*PisLen, RhaLyc*) showed a high coincidence rate between the species occurrences within the field and in the natural vegetation patch (>50% of coincidences, Table 2).

4. Discussion

In this study, we identified the main drivers of natural colonization of fleshy-fruited shrubs in semiarid oldfields across environmental gradients. Altitude and lithology conditioned the composition and structure of the shrub communities at a regional scale, allowing us to identify focal species. Local factors such as the presence of remnant trees and natural patches of vegetation favored the occurrence of several species, showing different functionalities across the environmental gradient. Interestingly, some species traits such as fruit length, root depth and shrub growth form showed a positive relationship with altitude, in contrast with fruit water content and liana-like habits which were associated with lower altitudes. This information can be used to guide practitioners in designing regional restoration frameworks across environmental gradients, prioritizing restoration efforts and species choices at such scale (García-Ruiz et al., 2020; Huebner et al., 2022; Muler et al., 2018).

4.1. Main drivers of natural vegetation recolonization in oldfields

Altitude is expected to be a key element driving the ecological succession in oldfields since it determines the climatic gradient in mountainous areas (Pueyo and Beguería, 2007 and references therein). In our study area, the altitudinal gradient conditioned the composition of the communities of fleshy-fruited shrubs (accounting on average for a third of the explained variation, across the species, in the presence/absence model; see section 3.2), thus giving a general framework for designing restoration actions. Our results are in line with other studies which also identify elevation as a critical factor shaping vegetation composition in oldfields (Bonet, 2004; Martínez-Duro et al., 2010; Pueyo and Beguería, 2007 and references therein).

Lithology is one of the main factors which determines erosion risk in abandoned fields and it also affects plant species richness (Robledano-Aymerich et al., 2014, 2016). Indeed, we found that lithology is one of the main factors conditioning the structure of shrub communities in semiarid oldfields (average 15% of explained variation across species in the presence/absence model; see section 3.2). This is attributable to the fact that lithology conditions the soil properties which seem paramount in the vegetation recovery of oldfields in several parts of the world such as North America (Fridley and Wright, 2012) and China (Zheng et al., 2023). Species richness and abundance of fleshy-fruited shrubs were low in all substrates probably due to the limiting semiarid climate and the herbivore pressure, which together can strongly limit plant establishment and recruitment (Prach and Hobbs, 2008). Although most species were able to grow in the four lithologies, most of them showed the highest prevalence in limestones, which together with alluvial lithologies, showed higher shrub abundances than marls and metamorphic substrates. Marls showed to be unsuitable for most fleshy-fruited shrubs (negative effect on the occurrence of 7 out of 12 species; section 3.2) given they are more sensitive to erosion and soil degradation (Robledano-Aymerich et al., 2014). In concordance with our results, these authors found that *Asparagus horridus* was the most abundant species in marls (Figure S3.4). Likewise, the bird-dispersed liana *Asparagus acutifolius* was associated with metamorphic lithologies (Figure S3.2). This could be because root depth is negatively associated with metamorphic lithologies (Figure S3.3) and *Asparagus* species show smaller root length than other fleshy-fruited shrubs (see Supporting Information 3).

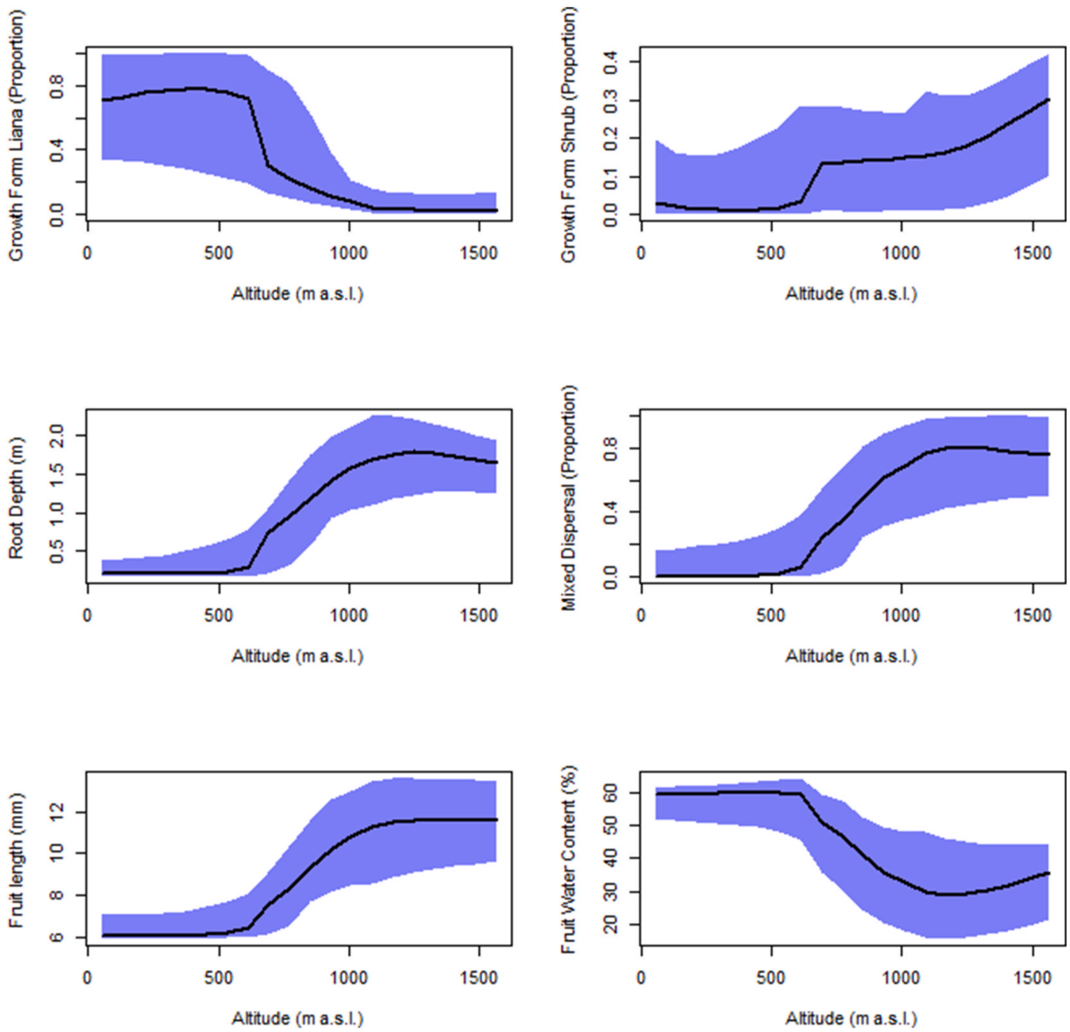

Fig. 4. Relationships between biological traits and altitudinal gradient in the HMSC presence-absence model. The traits shown are those for which the probability of the values at the end of the gradient differed significantly from the initial values of the gradient (less than 5 % overlap between the credible intervals). The black line and shaded area indicate model predictions and 95% credible interval, respectively.

4.2. Effect of time since abandonment on vegetation recovery

Our results showed that time since abandonment by itself is not relevant for recolonization of fleshy-fruited shrubs (0,03 of variation explained, on average, in the presence/absence model, Fig. 2a). These results are congruent with other studies from the Iberian Peninsula (Martínez-Duro et al., 2010; Robledano-Aymerich et al., 2014). However, investigations performed in semiarid oldfields of China (Hu et al., 2021), California (McLendon et al., 2012) and Australia (Zivec et al., 2021) reported that time since abandonment is critical in determining the ecological succession of semiarid oldfields. This contrast could be explained by differences in the temporal scale and the taxonomic groups considered in the studies. Firstly, our study focuses on fleshy-fruited shrubs which need more time than herbs and forbs to colonize oldfields (Bonet, 2004). On the other hand, oldfields in our study were abandoned no longer than 70 years ago while oldfields under semiarid and arid conditions can require centuries to reach full vegetation recovery (McLendon et al., 2012; Scott and Morgan, 2012). In any case, pilot sites similar to those studied previously by us showed high stability in terms of soil conservation and even arrested succession, which suggests that full recovery is out of reach without human intervention (Robledano-Aymerich et al., 2014 and references therein). The relevance of the time since abandonment could become higher at longer temporal scales and for other plant taxa.

4.3. Effect of remnant trees on fleshy-fruited shrubs occurrence and abundance

Our results refer mainly to the species occurrence and not to their abundance. The low predictive power in our abundance-COP model does not allow us to make robust conclusions about species-specific responses. Fleshy-fruited shrub abundance is probably affected by additional factors not analyzed in this study such as the herbivory pressure (Bertness and Callaway, 1994). Remnant trees (8 out of 12 species) and to a lesser extent nearby sources of propagules (5 out of 12 species) promoted the occurrence of fleshy-fruited shrubs (section 3.3; Fig. 5) but did not strongly affect their abundance once these were present. The positive effect of remnant trees on the occurrence of several shrub species can be attributed to the perch effect caused by birds that deposit seeds beneath the tree canopy (Pausas et al., 2006) and to the facilitation effect of the canopy creating suitable conditions for recruitment under harsh environmental conditions (Rühl and Schnittler, 2011; Verdú and García-Fayos, 1996). However, there were interspecific differences as not all shrubs were benefited by the presence of remnant trees in the field in spite of being effectively dispersed by birds (Acosta-Rojas et al., 2019). This could be due to differences in bird preferences. Some species prefer to feed on shrubs or areas with dense vegetation (e.g. *Curruca melanocephala* and *Sylvia atricapilla*), while others usually occur in open areas such as oldfields and are more likely to perch in remnant trees (e.g.

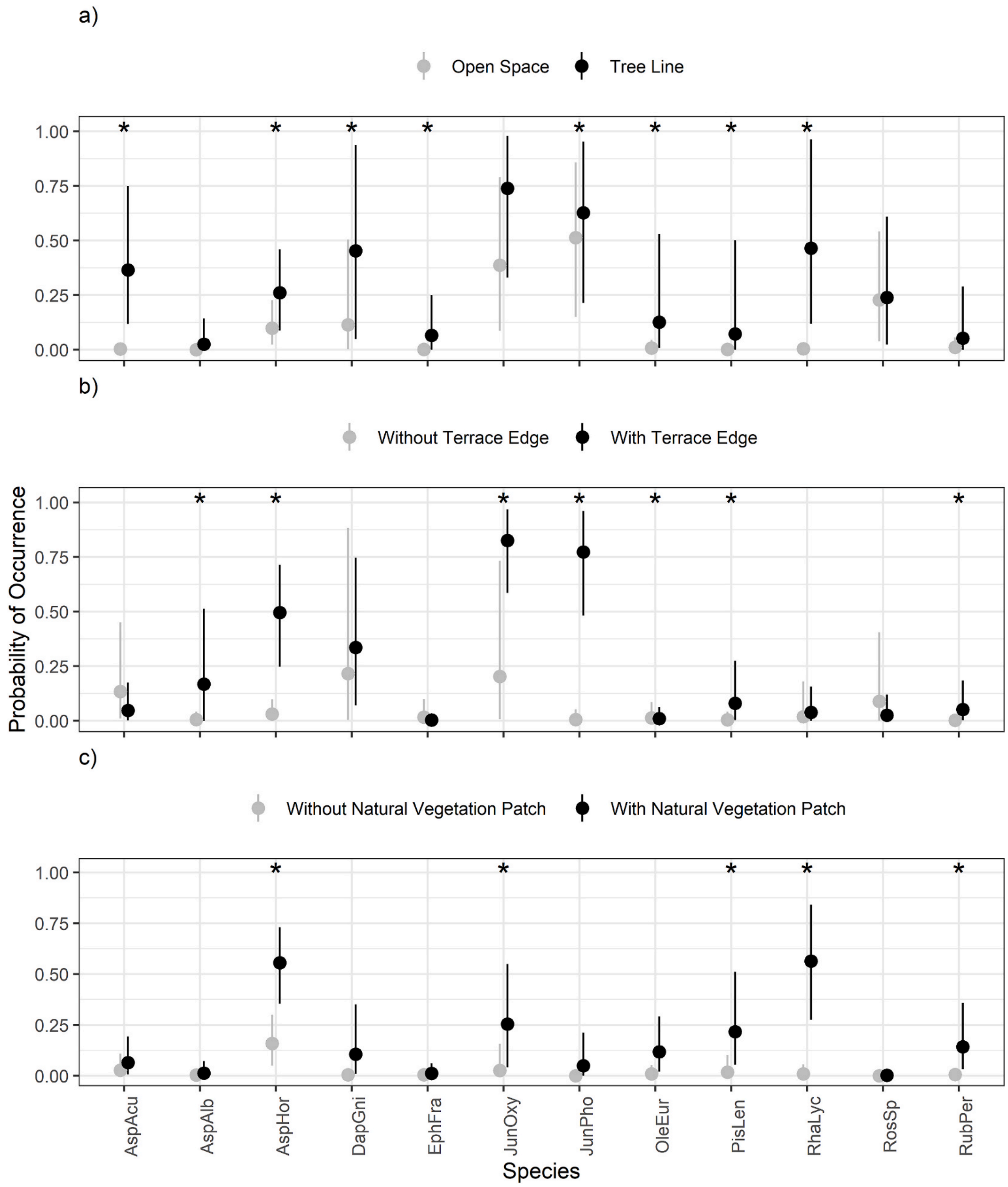

Fig. 5. Probability of occurrence of the species in: open space and tree line transects (a), open space transects in oldfields with and without terrace edges (b), open space transects in oldfields with and without an adjacent natural vegetation patch (c). The average (point) and 95% confidence interval (error bars) are shown for the expected probability based on model predictions. Asterisks indicate positive responses in the presence-absence model (difference with at least 95% posterior probability) to transect type tree line (a), to the indicator External TE (b), to the indicator External NV (c).

Turdus viscivorus and *Phoenicurus ochruros*) (see Martínez-López et al., 2019 and references therein). In our study, since most remnant trees were dead or had very sparse canopies, the facilitation effect might not be relevant. We postulate that the positive effect would be based mainly on their role as perching sites where birds deposit seeds (Pausas et al., 2006), an effect that could vary depending on the type of tree crop interacting with bird preferences (Martínez-López et al., 2019). However, it cannot be ruled out that the shrubs that manage to establish themselves beneath remnant trees may act as nurse plants facilitating the establishment of other plant species in successive cohorts. On the other hand, the fruits of some species are also consumed by mammals, which may also play a role in the seed arrival regardless of the presence of remnant trees.

4.4. The role of surrounding natural areas in oldfields vegetation recolonization

We found that the presence of natural areas that can act as natural repositories of shrublands are important to promote the colonization of some fleshy-fruited shrub species in oldfields. The role of surrounding natural vegetation enhancing the regeneration process is well supported (Csákvári et al., 2022; Muñiz-Castro et al., 2006; Zivec et al., 2021). According to Zapata-Pérez et al. (2016), at mid elevations, the species richness in oldfields with adjacent natural vegetation areas was expected to be higher than in those without them, while in lowland sites with harsher conditions this pattern would not occur. This possibly relates to difficulty in the establishment and recruitment due to climatic or biological limitations experienced in the oldfield, even when the arrival of seeds from these natural repositories is occurring (Martínez-López et al.,

Table 2
Proportion of coincidences on the species occurrences within the field and a zone identified as potential source of propagules (terrace edge, natural vegetation patch), expressed as a proportion of the total fields where the species was present.

Species	Coexistence Field - Terrace Edge	Coexistence Field - Natural Vegetation Patch
AspAcu	18,8%	25,0%
AspAlb	90,0%	30,0%
AspHor	65,6%	43,8%
DapGni	36,8%	42,1%
EphFra	42,9%	42,9%
JunOxy	38,5%	42,3%
JunPho	26,3%	47,4%
OleEur	30,0%	10,0%
PisLen	41,7%	50,0%
RhaLyc	40,7%	74,1%
RosSp	25,0%	50,0%
RubPer	50,0%	12,5%

2019). Here, we found that five species showed a positive response to the adjacency of a natural vegetation patch. Moreover, we found evidence that small natural patches of vegetation within the cultivated areas such as terrace edges, showed beneficial effects on the occurrence of 7 out of 12 species (section 3.3; Fig. 5), which can be classified into two groups: species that had historical uses (e.g. wood, fruits, etc) and could have been intentionally kept within the fields (*JunOxy*, *JunPho*, *OleaEur, PisLen* and to some extent *Asp Alb and AspHor*) and small plants which can quickly grow associated with structural elements such as rocks or other shrubs (the two *Asparagus* species and *RubPer*). Our results support mixed restoration strategies (combining active and passive approaches), like those based on creating or enhancing patches of natural vegetation inside agricultural areas (Pueyo and Alados, 2007; Rey-Benayas et al., 2008; Rühl and Schnittler, 2011). Active interventions to prevent or break shrub encroachment may also be necessary, although more as a local strategy to reactivate an eventual arrested succession, than a general recommendation to face other types of risks (fire, loss of habitat heterogeneity) that do not occur in our study area but can show up in other contexts (see Quintas-Soriano et al., 2022, and references therein). The need for active interventions stems also from the difficulty for seedling establishment once seed arrival has been enhanced through the attraction of dispersers (Martínez-López et al., 2019 and references therein). Under such situations, restoration actions must be focused not only on improving recruitment (e.g. using nurse shrubs or favorable microsites) but also on its maintenance (e.g. by watering seedlings in summer).

4.5. The need to assess biotic interactions and functional traits

In any case, before the degree of active intervention required can be specified, it is essential that ecological processes such as seed dispersal must be evaluated taking into account all the terms involved in the mutualism and their performance. The species composition and structure of vertebrate disperser assemblages and their activity may vary depending on context, requiring a comprehensive study equivalent to that devoted here to woody flora. Unfortunately, in the investigated oldfields these assemblages have been little studied. However, the assemblage of dispersers seems not qualitatively different along the gradient (see Supporting Information 1, Figure S1.1), although further research is needed on the specific performance of birds and mammals in oldfield colonization.

Regarding traits, the observed relationships (Fig. 4) can be explained in terms of improved environmental conditions along altitudinal gradients (when these are associated with decreasing aridity). Larger fruits would generally predominate at higher elevations (Herrera, 1995). In Mediterranean-type regions of California (but not in those of Chile), average size of fruits increases from dry to wet conditions (Hoffmann et al., 1989). Plant communities growing in moist soils showed higher values of specific root length (as occurs in this study at higher altitudes) as a rapid resource-uptake strategy, in contrast to a more conservative one in species living in drier places (de la Riva et al., 2016). The decrease of fruit water content observed at higher altitudes is also consistent with the findings of Herrera (1982), that species ripening fruits under drier conditions would have the most watery fruits as a strategy to attract dispersers when the water demand is high. This is in concordance with our findings about the negative effect of altitude on the occurrence of species producing small fruits with high water content (e.g. *AspAlb, AspHor* and *RhaLyc*). Fruits eaten by mammals tend to be larger (Herrera, 1989), as it occurs at higher altitudes in our study where mixed dispersal seems also more probable. Unfortunately, we do not have enough knowledge about the variation in bird and mammal density with altitude to explain this association. The observed trait-altitude relationships are in any case promising in the selection of strategies for the restoration of abandoned fields in semiarid areas. The application of restoration techniques based on plant-animal interactions (Genes and Dirzo, 2022) will be better guided by the integration of these relationships in decision-making. For this, it will be essential to know the composition and quantitative importance of the animal component along the gradient, with a depth similar to that dedicated here to the study of the plant component.

5. Conclusion and restoration framework proposal

Our results provide some ecological knowledge to guide scientists and practitioners to develop nature-based restoration frameworks of oldfields at regional scales. The approach could also be replicated to develop restoration frameworks across environmental gradients in other types of disturbed landscapes (burnt areas, mining sites), and in general those located along gradients of environmental stress (Csákvári et al., 2022; Romero-Díaz et al., 2024), where there is a need to graduate the application of passive restoration schemes (Prach and Hobbs, 2008). We identified which shrub species are more likely to colonize oldfields according to the local factors (e.g. the presence of remnant trees and natural vegetation patches) and that can be used to design restoration frameworks based on ecological evidence. Some management actions can be indicated for the different altitudinal ranges based on our results.

- Oldfields at high altitudes (700–1600 m a.s.l.): shrubs with large fruits and mixed dispersal systems (*Juniperus* species) should be the key components of restoration programs given their high prevalence in these oldfields, and their known ecological role as facilitators for other shrub species, acting as nurses or even promoting nucleation, both attracting seed dispersers and easing recruitment (Pugnaire et al., 2011). Remnant cultivated trees should be left in the oldfields in order to promote colonization and, in their absence, these structures should be artificially recreated, for instance, by providing artificial perches (Martínez-López et al., 2019) or other structures such as branch piles (Castillo-Escrivà et al., 2019). Terrace edges can be beneficial for the colonization by these key species, alleviating physical or biotic restrictions (heath or water stress, herbivory) either by directly providing safe microsites (Rühl and Schnittler, 2011) or by hosting potential nurse shrubs.
- Oldfields at intermediate altitudes (200–850 m a.s.l.): The presence of remnant trees in the oldfield can make an important difference and should be the focus of restoration designs, since they can promote the colonization of several species increasing species richness. The presence of natural vegetation repositories, either small areas such as terrace edges or large nearby patches are also beneficial. The set of shrubs involved in restoration would cover a greater number of species, excluding those with higher water requirements and those preferable for drier environments. The active introduction of these species, taking advantage of existing nurse plants whenever possible to improve survival, would be punctual and dependant on the

available local pool, although structural interventions should be the priority.

- Oldfields at low altitudes (0–550 m a.s.l.): Restoration efforts should focus on small-fruited bird-dispersed lianas such as some *Asparagus* species which can act as pioneer species under harsh environmental conditions. Furthermore, the high water content of their fruits will attract dispersers increasing seed dispersal in oldfields. The internal spread of these species would be reinforced through structural interventions that favor dispersal or buffer environmental stress, such as the maintenance of the edges of terraces as natural repositories of propagules for benefiting short-distance dispersal by birds. Active plantations should also give priority to these species, again recurring to existing nurse plants whenever possible.

CRediT authorship contribution statement

Martín Amodeo: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Vicente Martínez-López:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Víctor Zapata-Pérez:** Methodology, Investigation, Conceptualization. **Francisco Robledano-Aymerich:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

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

Datasets and codes available at Zenodo (https://doi.org/10.5281/zenodo.13127370).

Acknowledgements

We thank all the students and collaborators that supported us in fieldwork. The study was funded by Fundación Séneca (15233/PI/10). MA was funded by a postdoctoral grant from the European Commission (Erasmus Mundus Cruz del Sur 2014-0869/001-001). VML was funded by a postdoctoral fellowship (21260/PD/19), Fundación Séneca, Región de Murcia (Spain).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2024.122480.

References

Acosta-Rojas, D.C., Jiménez-Franco, M.V., Zapata-Pérez, V.M., De la Rúa, P., Martínez-López, V., 2019. An integrative approach to discern the seed dispersal role of frugivorous guilds in a Mediterranean semiarid priority habitat. PeerJ 7, e7609. https://doi.org/10.7717/peerj.7609.

Alcaraz, F., Sánchez-Gómez, P., de la Torre, A., Ríos, S., Álvarez Rogel, J., 1991. Datos sobre la vegetación de Murcia (España). Guía geobotánica de la Excursión de las XI Jornadas de Fitosociología. DM & PPU, Lérida.

Basualdo, M., Huykman, N., Volante, J.N., Paruelo, J.M., Piñeiro, G., 2019. Lost forever? Ecosystem functional changes occurring after agricultural abandonment and forest recovery in the semiarid Chaco forests. Sci. Total Environ. 650, 1537–1546. https://doi.org/10.1016/j.scitotenv.2018.09.001.

Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. Trends Ecol. Evol. 9, 191–193. https://doi.org/10.1016/0169-5347(94)90088-4.

Bonet, A., 2004. Secondary succession of semi-arid Mediterranean old-fields in south-eastern Spain: insights for conservation and restoration of degraded lands. J. Arid Environ. 56, 213–233. https://doi.org/10.1016/S0140-1963(03)00048-X.

Bowen, M.E., McAlpine, C.A., House, A.P.N., Smith, G.C., 2007. Regrowth forests on abandoned agricultural land: a review of their habitat values for recovering forest fauna. Biol. Conserv. 140, 273–296. https://doi.org/10.1016/j.biocon.2007.08.012.

Camargo, P.H.S.A., Pizo, M.A., Brancalion, P.H.S., Carlo, T.A., 2020. Fruit traits of pioneer trees structure seed dispersal across distances on tropical deforested landscapes: implications for restoration. J. Appl. Ecol. 57, 2329–2339. https://doi.org/10.1111/1365-2664.13697.

Castillo-Escrivà, A., López-Iborra, G.M., Cortina, J., Tormo, J., 2019. The use of branch piles to assist in the restoration of degraded semiarid steppes. Restor. Ecol. 27, 102–108. https://doi.org/10.1111/rec.12704.

Corbin, J.D., Holl, K.D., 2012. Applied nucleation as a forest restoration strategy. For. Ecol. Manag. 265, 37–46. https://doi.org/10.1016/j.foreco.2011.10.013.

Cramer, V.A., Hobbs, R.J., Standish, R.J., 2008. What's new about old fields? Land abandonment and ecosystem assembly. Trends Ecol. Evol. 23, 104–112. https://doi.org/10.1016/j.tree.2007.10.005.

Csákvári, E., Molnár, Z., Halassy, M., 2022. Estimates of regeneration potential in the Pannonian sand region help prioritize ecological restoration interventions. Commun. Biol. 5, 1136. https://doi.org/10.1038/s42003-022-04047-8.

de la Riva, E.G., Pérez-Ramos, I.M., Tosto, A., Navarro-Fernández, C.M., Olmo, M., Marañón, T., Villar, R., 2016. Disentangling the relative importance of species occurrence, abundance and intraspecific variability in community assembly: a trait-based approach at the whole-plant level in Mediterranean forests. Oikos 125, 354–363. https://doi.org/10.1111/oik.01875.

Fayet, C.M.J., Reilly, K.H., Van Ham, C., Verburg, P.H., 2022. What is the future of abandoned agricultural lands? A systematic review of alternative trajectories in Europe. Land Use Pol. 112, 105833 https://doi.org/10.1016/j.landusepol.2021.105833.

Fox, J., Weisberg, S., 2011. An R Companion to Applied Regression, Second Edition. Sage, Thousand Oaks CA. https://www.john-fox.ca/Companion/.

Fréjaville, T., Benito Garzón, M., 2018. The EuMedClim database: yearly climate data (1901–2014) of 1 km resolution grids for Europe and the Mediterranean Basin. Front. Ecol. Evol. 6, 31. https://doi.org/10.3389/fevo.2018.00031.

Fridley, J.D., Wright, J.P., 2012. Drivers of secondary succession rates across temperate latitudes of the Eastern USA: climate, soils, and species pools. Oecologia 168, 1069–1077. https://doi.org/10.1007/s00442-011-2152-4.

García-Ruiz, J.M., Lasanta, T., Nadal-Romero, E., Lana-Renault, N., Álvarez-Farizo, B., 2020. Rewilding and restoring cultural landscapes in Mediterranean mountains: opportunities and challenges. Land Use Pol. 99, 104850 https://doi.org/10.1016/j.landusepol.2020.104850.

Garrote, P.J., Castilla, A.R., Fedriani, J.M., 2022. The Eurasian badger-generated seed rain drives the natural (re)colonization of vacant human-altered areas by a keystone pioneer palm. Perspect. Plant Ecol. Evol. Systemat. 56, 125685 https://doi.org/10.1016/j.ppees.2022.125685.

Garrote, P.J., Castilla, A.R., Fedriani, J.M., 2019. The endemic Mediterranean dwarf palm boosts the recolonization of old-fields: implications for restoration. J. Environ. Manag. 250, 109478 https://doi.org/10.1016/j.jenvman.2019.109478.

Genes, L., Dirzo, R., 2022. Restoration of plant-animal interactions in terrestrial ecosystems. Biol. Conserv. 265, 109393 https://doi.org/10.1016/j.biocon.2021.109393.

Gimeno, T.E., Escudero, A., Delgado, A., Valladares, F., 2012. Previous land use alters the effect of climate change and facilitation on expanding woodlands of Spanish juniper. Ecosystems 15, 564–579. https://doi.org/10.1007/s10021-012-9529-z.

Heinimann, A., Mertz, O., Frolking, S., Egelund Christensen, A., Hurni, K., Sedano, F., Parsons Chini, L., Sahajpal, R., Hansen, M., Hurtt, G., 2017. A global view of shifting cultivation: recent, current, and future extent. PLoS One 12, e0184479. https://doi.org/10.1371/journal.pone.0184479.

Herrera, C.M., 1995. Plant-vertebrate seed dispersal systems in the mediterranean: ecological, evolutionary, and historical determinants. Annu. Rev. Ecol. Systemat. 26, 705–727. https://doi.org/10.1146/annurev.es.26.110195.003421.

Herrera, C.M., 1989. Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed mediterranean habitats. Oikos 55, 250. https://doi.org/10.2307/3565429.

Herrera, C.M., 1982. Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. Ecology 63, 773–785. https://doi.org/10.2307/1936798.

Hoffmann, A.J., Teillier, S., Fuentes, E.R., 1989. Fruit and seed characteristics of woody species in mediterranean-type regions of Chile and California. Rev. Chil. Hist. Nat. 62, 43–60. http://rchn.biologiachile.cl/pdfs/1989/1/Hoffmann_et_al_1989.pdf.

Hu, A., Chang, S., Chen, X., Hou, F., Nan, Z., 2021. Temporal heterogeneity has no effect on the direction of succession in abandoned croplands in a semiarid area of northwest China. Land Degrad. Dev. 32, 91–100. https://doi.org/10.1002/ldr.3780.

Huebner, L., Fadhil Al-Quraishi, A.M., Branch, O., Gaznayee, H.A.A., 2022. New approaches: use of assisted natural succession in revegetation of inhabited arid drylands as alternative to large-scale afforestation. SN Appl. Sci. 4, 80. https://doi.org/10.1007/s42452-022-04951-y.

Jordano, P., 2013. Data from: angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant-animal interactions. https://doi.org/10.5061/DRYAD.9TB73.

Lasanta, T., Arnáez, J., Nadal-Romero, E., 2019. Chapter Three - soil degradation, restoration and management in abandoned and afforested lands. In: C, P. (Ed.), Pereira Environmental Management and Protection, P.B.T.-A. Soil Degradation, Restoration and Management in a Global Change Context. Elsevier, pp. 71–117. https://doi.org/10.1016/bs.apmp.2019.07.002.

Lasanta, T., Nadal-Romero, E., Khorchani, M., Romero-Díaz, A., 2021. Una revisión sobre las tierras abandonadas en España: de los paisajes locales a als estrategias globales de gestión. Cuadernos de Investigación Geográfica. Geographical Research Letters 47. https://doi.org/10.18172/cig.4755.

Lasanta, T., Sánchez-Navarrete, P., Medrano-Moreno, L.M., Khorchani, M., Nadal-Romero, E., 2020. Soil quality and soil organic carbon storage in abandoned agricultural lands: effects of revegetation processes in a Mediterranean mid-mountain area. Land Degrad. Dev. 2830–2845. https://doi.org/10.1002/ldr.3655.

Li, S., Li, X., 2017. Global understanding of farmland abandonment: a review and prospects. J. Geogr. Sci. 27, 1123–1150. https://doi.org/10.1007/s11442-017-1426-0.

Martínez Hernández, C., Cánovas-García, F., 2016. In: . Identificación de áreas abandonadas en la Región de Murcia. In: Abandono de Cultivos en la Región de Murcia Consecuencias Ecogeomorfológicas, Editum, Murcia, pp. 139–159. https://dialnet.unirioja.es/servlet/libro?codigo=662206.

Martínez-Duro, E., Ferrandis, P., Escudero, A., Luzuriaga, A.L., Herranz, J.M., 2010. Secondary old-field succession in an ecosystem with restrictive soils: does time from abandonment matter? Appl. Veg. Sci. 13, 234–248. https://doi.org/10.1111/j.1654-109X.2009.01064.x.

Martínez-López, V., Zapata-Pérez, V.M., De la Rúa, P., Robledano-Aymerich, Francisco, F., 2019. Uncovering mechanisms of bird seed dispersal in semiarid environments to help to restore them. Ecosphere 10. https://doi.org/10.1002/ecs2.2673.

McLendon, T., Naumburg, E., Martin, D.W., 2012. Secondary succession following cultivation in an arid ecosystem: the Owens Valley, California. J. Arid Environ. 82, 136–146. https://doi.org/10.1016/j.jaridenv.2012.02.011.

Moyo, B., Ravhuhali, K.E., 2022. Abandoned croplands: drivers and secondary succession trajectories under livestock grazing in communal areas of South Africa. Sustainability 14, 6168. https://doi.org/10.3390/su14106168.

Muler, A.L., Canham, C.A., van Etten, E.J.B., Stock, W.D., Froend, R.H., 2018. Using a functional ecology approach to assist plant selection for restoration of Mediterranean woodlands. For. Ecol. Manag. 424, 1–10. https://doi.org/10.1016/j.foreco.2018.04.032.

Muñiz-Castro, M.A., Williams-Linera, G., Benayas, J.M.R., 2006. Distance effect from cloud forest fragments on plant community structure in abandoned pastures in Veracruz, Mexico. J. Trop. Ecol. 22, 431–440. https://doi.org/10.1017/S0266467406003221.

Otto, R., Krüsi, B.O., Burga, C.A., Fernández-Palacios, J.M., 2006. Old-field succession along a precipitation gradient in the semi-arid coastal region of Tenerife. J. Arid Environ. 65, 156–178. https://doi.org/10.1016/j.jaridenv.2005.07.005.

Ovaskainen, O., Abrego, N., 2020. Joint species distribution modelling: with applications in R, ecology. Biodiversity and Conservation. Cambridge University Press, Cambridge. https://doi.org/10.1017/9781108591720.

Padilla, F.M., Ortega, R., Sánchez, J., Pugnaire, F.I., 2009. Rethinking species selection for restoration of arid shrublands. Basic Appl. Ecol. 10, 640–647. https://doi.org/10.1016/j.baae.2009.03.003.

Pausas, J.G., Bonet, A., Maestre, F.T., Climent, A., 2006. The role of the perch effect on the nucleation process in Mediterranean semi-arid oldfields. Acta Oecol. 29, 346–352. https://doi.org/10.1016/j.actao.2005.12.004.

Plieninger, T., Draux, H., Fagerholm, N., Bieling, C., Bürgi, M., Kizos, T., Kuemmerle, T., Primdahl, J., Verburg, P.H., 2016. The driving forces of landscape change in Europe: a systematic review of the evidence. Land Use Pol. 57, 204–214. https://doi.org/10.1016/j.landusepol.2016.04.040.

Prach, K., Hobbs, R.J., 2008. Spontaneous succession versus technical reclamation in the restoration of disturbed sites. Restor. Ecol. 16, 363–366. https://doi.org/10.1111/j.1526-100X.2008.00412.x.

Pueyo, Y., Alados, C.L., 2007. Effects of fragmentation, abiotic factors and land use on vegetation recovery in a semi-arid Mediterranean area. Basic Appl. Ecol. 8, 158–170. https://doi.org/10.1016/j.baae.2006.03.009.

Pueyo, Y., Beguería, S., 2007. Modelling the rate of secondary succession after farmland abandonment in a Mediterranean mountain area. Landsc. Urban Plann. 83, 245–254. https://doi.org/10.1016/j.landurbplan.2007.04.008.

Pugnaire, F.I., Armas, C., Maestre, F.T., 2011. Positive plant interactions in the Iberian Southeast: mechanisms, environmental gradients, and ecosystem function. J. Arid Environ. 75, 1310–1320. https://doi.org/10.1016/j.jaridenv.2011.01.016.

Pugnaire, F.I., Luque, M.T., Armas, C., Gutiérrez, L., 2006. Colonization processes in semi-arid Mediterranean old-fields. J. Arid Environ. 65, 591–603. https://doi.org/10.1016/j.jaridenv.2005.10.002.

Quintas-Soriano, C., Buerkert, A., Plieninger, T., 2022. Effects of land abandonment on nature contributions to people and good quality of life components in the Mediterranean region: a review. Land Use Pol. 116, 106053 https://doi.org/10.1016/j.landusepol.2022.106053.

R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/.

Rey-Benayas, J.M., Bullock, J.M., Newton, A.C., 2008. Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. Front. Ecol. Environ. 6, 329–336. https://doi.org/10.1890/070057.

Rey-Benayas, J.M., Martínez-Baroja, L., Pérez-Camacho, L., Villar-Salvador, P., Holl, K. D., 2015. Predation and aridity slow down the spread of 21-year-old planted woodland islets in restored Mediterranean farmland. N. For. 46, 841–853. https://doi.org/10.1007/s11056-015-9490-8.

Rivas-Martínez, S., 1983. Pisos bioclimáticos de España. Lazaroa 5, 33–44. https://dialnet.unirioja.es/servlet/articulo?codigo=906098.

Robledano-Aymerich, F., Romero-Díaz, A., Belmonte-Serrato, F., Zapata-Pérez, V.M., Martínez-Hernández, C., Martínez-López, V., 2014. Ecogeomorphological consequences of land abandonment in semiarid Mediterranean areas: integrated assessment of physical evolution and biodiversity. Agric. Ecosyst. Environ. 197, 222–242. https://doi.org/10.1016/j.agee.2014.08.006.

Robledano-Aymerich, F., Zapata-Pérez, V.M., Martínez-López, V., García-Meseguer, A., García-Castellanos, F., Zamora, A., Pérez-Navarro, M.A., 2016. Indicadores de biodiversidad en campos abandonados de la Región de Murcia: flora y fauna. In: Abandono de Cultivos En La Región de Murcia. Consecuencias Ecogeomorfológicas. Editum, Murcia, pp. 111–137. https://dialnet.unirioja.es/servlet/libro?codigo=662206.

Rolo, V., Amat, B., Cortina, J., 2016. Water availability and species identity control shrub colonization in abandoned semiarid steppes. Agric. Ecosyst. Environ. 228, 62–69. https://doi.org/10.1016/j.agee.2016.05.014.

Romero-Díaz, A., Pérez-Morales, A., Marín-Sanleandro, P., 2024. Prevalence, causes, and consequences of agricultural land abandonment: a case study in the Region of Murcia, Spain. Catena 241, 108071. https://doi.org/10.1016/j.catena.2024.108071.

Romero-Díaz, A., Ruiz-Sinoga, J.D., Robledano-Aymerich, F., Brevik, E.C., Cerdà, A., 2017. Ecosystem responses to land abandonment in western mediterranean mountains. Catena 149, 824–835. https://doi.org/10.1016/j.catena.2016.08.013.

Rühl, J., Schnittler, M., 2011. An empirical test of neighbourhood effect and safe-site effect in abandoned Mediterranean vineyards. Acta Oecol. 37, 71–78. https://doi.org/10.1016/j.actao.2010.11.009.

Scott, A.J., Morgan, J.W., 2012. Recovery of soil and vegetation in semi-arid Australian old fields. J. Arid Environ. 76, 61–71. https://doi.org/10.1016/j.jaridenv.2011.08.014.

Tavşanoğlu, Ç., Pausas, J.G., 2018. A functional trait database for Mediterranean Basin plants. Sci. Data 5, 180135. https://doi.org/10.1038/sdata.2018.135.

Terres, J.-M., Scacchiafichi, L.N., Wania, A., Ambar, M., Anguiano, E., Buckwell, A., Coppola, A., Gocht, A., Källström, H.N., Pointereau, P., Strijker, D., Visek, L., Vranken, L., Zobena, A., 2015. Farmland abandonment in Europe: identification of drivers and indicators, and development of a composite indicator of risk. Land Use Pol. 49, 20–34. https://doi.org/10.1016/j.landusepol.2015.06.009.

Tikhonov, G., Opedal, Ø.H., Abrego, N., Lehikoinen, A., Jonge, M.M.J., Oksanen, J., Ovaskainen, O., 2020. Joint species distribution modelling with the r -package H msc. Methods Ecol. Evol. 11, 442–447. https://doi.org/10.1111/2041-210X.13345.

Underwood, E.C., Viers, J.H., Klausmeyer, K.R., Cox, R.L., Shaw, M.R., 2009. Threats and biodiversity in the mediterranean biome. Divers. Distrib. 15, 188–197. https://doi.org/10.1111/j.1472-4642.2008.00518.x.

Ustaoglu, E., Collier, M.J., 2018. Farmland abandonment in Europe: an overview of drivers, consequences, and assessment of the sustainability implications. Environ. Rev. 26, 396–416. https://doi.org/10.1139/er-2018-0001.

Verdú, M., García-Fayos, P., 1996. Nucleation processes in a mediterranean bird-dispersed plant. Funct. Ecol. 10, 275–280. https://doi.org/10.2307/2389853.

Viani, R.A.G., Vidas, N.B., Pardi, M.M., Castro, D.C.V., Gusson, E., Brancalion, P.H.S., 2015. Animal-dispersed pioneer trees enhance the early regeneration in Atlantic Forest restoration plantations. Natureza & Conservação 13, 41–46. https://doi.org/10.1016/j.ncon.2015.03.005.

Wickham, H., 2009. ggplot2: Elegant Graphics for Data Analysis. Springer, New York, New York, NY. https://doi.org/10.1007/978-0-387-98141-3.

Zapata-Pérez, V.M., Robledano-Aymerich, F., Martínez-López, V., 2016. Dinámica recolonizadora de la vegetación en campos abandonados de la Región de Murcia. In: Abandono de Cultivos En La Región de Murcia. Consecuencias Ecogeomorfológicas. Editum, Murcia, pp. 139–159.

Zethof, J.H.T., Cammeraat, E.L.H., Nadal-Romero, E., 2019. The enhancing effect of afforestation over secondary succession on soil quality under semiarid climate conditions. Sci. Total Environ. 652, 1090–1101. https://doi.org/10.1016/j.scitotenv.2018.10.235.

Zheng, J., Zhang, F., Zhang, B., Chen, D., Li, S., Zhao, T., Wang, Q., Han, G., Zhao, M., 2023. Biodiversity and soil pH regulate the recovery of ecosystem multifunctionality during secondary succession of abandoned croplands in northern China. J. Environ. Manag. 327, 116882 https://doi.org/10.1016/j.jenvman.2022.116882.

Zivec, P., Balcombe, S., McBroom, J., Sheldon, F., Capon, S.J., 2021. Patterns and drivers of natural regeneration on old-fields in semi-arid floodplain ecosystems. Agric. Ecosyst. Environ. 316, 107466 https://doi.org/10.1016/j.agee.2021.107466.

Zivec, P., Sheldon, F., Capon, S., 2023. Regenerative capacity of old-fields on semi-arid floodplains in the northern Murray–Darling basin. Restor. Ecol. 31, e13781 https://doi.org/10.1111/rec.13781.