



Ecogeomorphological consequences of land abandonment in semiarid Mediterranean areas: Integrated assessment of physical evolution and biodiversity



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ABSTRACT

This paper is based on an integrated assessment of abandoned farmland in the Iberian Southeast, a representative area of rich-biodiversity landscapes subject to strong physical stress and highly sensitive to environmental change. It is framed within the concept of natural reforestation and seeks an integration of physical and biodiversity features relevant for management. In pilot areas of different lithology (marly, limestone, and metamorphic) and abandonment age (< or >20 years), several physical (soil characteristics, evidences of erosion) and biodiversity (flora and birds) indicators have been assessed. It is concluded that these two sets of indicators often follow divergent or contrasting trajectories, particularly in the less coherent substrates where soil degradation and erosion concur with steppic physiognomy and high ornithological value. Lithology conditions the compositional and structural development of woody vegetation, but local landscape degradation can also reduce the pool of potential colonizers. Ecosystem development can be described as the interplay of positive and negative forces acting on physical evolution and biodiversity change. Abandonment *per se* is not a widely applicable management option but in many instances it can naturally improve soil and vegetation conditions. In more resistant lithologies, succession could lead to landscape homogenization, although recovery is usually slow and can eventually be arrested in stages dominated by a few woody species. Although our results are not generalizable to all semiarid land abandonment, they provide a framework for selecting management measures and for setting the scale and intensity of their application.

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1. Introduction

1.1. Farmland abandonment in the Iberian Peninsula: consequences and management options

Agricultural land abandonment is a common phenomenon in the Mediterranean Basin (Rey-Benayas et al., 2007), taking place over different types of lithological substrates and in varied environmental and socio-economic contexts. In the Iberian Peninsula, it has occurred since the end of the XIXth Century, but with maximum intensity during the decades of 1960 and 1970 (García-Ruiz and Lana-Renault, 2011). Its main causes have been

socio-economic changes and the corresponding economic and demographic synergies, as well as, more recently, the subsidies for land set-aside from the European Union's Common Agricultural Policy (CAP). It has taken place mainly in mountain areas (Lasanta, 1989; García-Ruiz, 2010), although large extensions of lower altitude semiarid lands have also been affected (Romero-Díaz et al., 2007; Lesschen et al., 2008a). In Spain there are many published studies on the hydro-geomorphological consequences of farmland abandonment, most made on the eastern part of the Iberian Peninsula (Cerdà, 1997a; Cammeraat et al., 2010; García-Ruiz and Lana-Renault, 2011).

The effects of abandonment can be positive or negative (Kosmas et al., 2000; Zaragoza et al., 2012), depending on soil and climate. Deeper soils under wet climates may ameliorate with time since abandonment, gaining organic matter inputs, enhancing microbial and faunal activity, improving their structure, increasing their infiltration capacity and reducing the erosion

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potential (Trimble, 1990). On the contrary, under dryer climates, abandoned crops on degraded soils are a favorable scenario for erosion (Navarro and Pereira, 2012). If plant colonization is not enough to generate a progressive vegetation dynamics, as it is usual in arid and semi-arid areas (Navarro et al., 1993), land degradation can become very important (Romero-Díaz, 2003). Vegetation, however, cannot be evaluated solely by its soil protection effect (De Baets et al., 2009). The biological value of plant communities and their associated fauna need also be taken into consideration (Navarro et al., 2003; Plieninger et al., 2013).

Oldfield management must consider a range of options, from the active maintenance and restoration of the abandoned spaces, to the stewardship of natural reforestation or rewilding processes (Navarro and Pereira, 2012). The choice is conditioned by the successional dynamics, resulting from the interaction between biophysical characteristics, natural ecological processes, and the agricultural legacy (Rey-Benayas et al., 2007). This restricts in practice the eligible options for each specific field or territory.

As a general feature, the traditional Mediterranean agriculture contributes greatly to the biological and cultural richness of landscapes, either compositionally, structurally or functionally (Reidsma et al., 2006; Blondel et al., 2010; Peco et al., 2012). In an abandonment scenario, biodiversity is also expected to play a critical role in the dynamics of the secondary habitats that develop since the end of farming (Bonet and Pausas, 2007). The particular role of key structural and functional components of the biota, like woody vegetation (Cortina et al., 2011) and vertebrate fauna (Jordano, 2000), can vary considerably depending on the lithological and geomorphological framework, even in similar climatic contexts. Different responses are also predicted for different plant and animal taxa, with some thriving in early or intermediate successional stages and others in late ones (Russo, 2007; Sirami et al., 2008; Blondel et al., 2010).

Thus, a compromise has to be achieved between the mitigation of physical impacts (erosion, soil loss and degradation, disruption of the hydrological cycle) and the conservation of the biodiversity associated to the different successional stages (Debussche et al., 1996; Bonet and Pausas, 2007; Vallecillo et al., 2008). Despite the importance of these issues (Detsis, 2010), few studies have addressed them from an integrated perspective, coupling the underlying physical and ecological factors involved in land degradation and biodiversity loss. Similarly, approaches are missing which, in the same socio-environmental context, seek an integration of the measures addressed to the physical environment and those focused on biodiversity (Robles et al., 2009; Cañadas et al., 2010; Martínez-Duro et al., 2010).

In the Spanish Mediterranean, a great deal of scientific work has been focused at the restoration of oldfields and other spaces in risk of physical degradation (Bonet, 2004; Bocio et al., 2004; Valdecantos et al., 2006; Bonet and Pausas, 2007). However, studies on forest restoration techniques seem much more developed than those dealing with the management or stewardship of the self-recovery of abandoned farmland (Bocio et al., 2004; Vallejo et al., 2005). Although techniques assayed for vegetation implantation are diverse and adapted to different situations (Vallejo et al., 2012), active reforestation has historically been the preferred solution and the only available to owners of marginal farmland (Maestre and Cortina, 2004; Nainggolan et al., 2012; Sánchez-Oliver et al., 2014).

Although the topic of land abandonment and its management has been addressed here mainly through representative studies from Spain, concern about its importance is much more widespread. This has boosted a great deal of research around the world, especially in the Mediterranean countries (see e.g., MacDonald et al., 2000; Abu Hammad and Tumeizi, 2012; Debolini et al., 2013; Jones et al., 2014).

1.2. Biodiversity and fragility of Mediterranean semiarid landscapes: the case of the Iberian Southeast

In Mediterranean semiarid regions, the greater physical fragility and consequent risk of degradation, is often associated with the presence of unique biodiversity features, related to the transition towards desert biomes (Blondel et al., 2010). Thus, they represent an ideal scenario for studies that integrate these two features. Among these regions, the Iberian Southeast (ISE, thereafter) is a territory of rich biodiversity (Armas et al., 2011), and a representative scenario of research on actions to combat erosion and desertification (García Ruiz and López Bermúdez, 2009; Romero-Díaz, 2010), being recognized as one of the areas of Spain with higher risk regarding these processes (PAND, 2008; Romero-Díaz et al., 2011a).

Our case studies are located in the Region of Murcia, a core area of the ISE. It is a true biogeographical ecotone between the Mediterranean Basin and the southern sub-tropical deserts (Esteve-Selma et al., 2010), hosting a rich biological diversity determined by two nested sets of causes (Calvo et al., 2000): (i) at a biogeographical scale, by its position regarding the center of the Mediterranean domain and the consequent frontier character and (ii) at a local one, by a high intrinsic physical heterogeneity (geological, topographic, geomorphological, edaphic, etc.), resulting from a long sedimentary evolution and an intense tectonic activity.

Many semiarid abandoned lands are included in steppe-like landscapes with scarce forest potential, but prone to strong physical risks if not properly used (Le Houérou, 2002). Their management requires a simultaneous focus on the conservation of natural resources like soil and water, the protection of livelihoods and man-made infrastructures, and on the preservation of their most representative biodiversity. Steppization of abandoned fields can be considered an undesirable state (Martínez-Fernández and Esteve, 2010), although it can result in ecologically valuable landscapes (Suárez et al., 1991; Cañadas, 2008). In the ISE, as a result of marginal land overexploitation and subsequent rural depopulation (Puigdefábregas and Mendizábal, 1998), large extensions of land have been converted into subdesertic xerosteppes, one of the land cover types experiencing a greater expansion in recent decades (Martínez-Fernández and Esteve, 2010).

Despite all, there is a lack of integrated studies about the contribution of different physical and biotic components to the ecogeomorphological dynamics of semi-arid abandoned areas, which can help to set specific guidelines for action against desertification and in favor of biodiversity. Precedent research in the ISE has focused on a specific type of substrate (Romero-Díaz, 2003), on a single biological component, usually the plant community (Cañadas, 2008), or taking a limited approach to biodiversity (floristic studies, e.g., Navarro et al., 2003). Since different responses are expected for each type of substrate, depending on the component evaluated (Table 1), an integrated assessment is essential to guide any management policy addressed at the whole biophysical system.

1.3. Research framework and objectives

This work is based on a first characterization of succession dynamics in oldfields of Murcia Region in course of spontaneous naturalization. It is framed within the concept of natural reforestation (Sitzi et al., 2010) supported by the proximity to patches of natural vegetation and by the existence of active dispersal processes from these sources (Fuentes-Castillo et al., 2012). For this, the study covers pilot areas of different substrate type and age since abandonment, in which different trajectories are expected as a result of the interaction of their physical and biological characteristics (Table 1). Previous knowledge predicts

Table 1
Expected negative and positive (–/+) environmental responses to farmland abandonment, with special reference to semiarid Mediterranean areas (selected references).

Component	Consequences of abandonment	Expected responses in semiarid Mediterranean areas
Landscape	(–) Homogenization and loss of open habitats (+) Mosaic heterogeneity	Expansion of sub-desert xerosteppes (Martínez-Fernández and Esteve, 2010) Shrub encroachment (Maestre et al., 2009; Nainggolan et al., 2012) Increase of dense forest patches and connectivity (Nainggolan et al., 2012)
Soils	(–) Erosion and desertification (+) Edaphic recovery and improvement	Important in less coherent soils (i.e., marls), intense sub-surface erosion phenomena (piping) (López-Bermúdez and Romero-Díaz, 1989; López-Bermúdez et al., 1998) More stable and even progressive situations in other substrate types (Faulkner et al., 2003; Bonet, 2004)
Soil water	(–) Availability and holding capacity (+) Quality and regulation	Increased consumption by vegetation, reduced infiltration (García-Ruiz and Lana-Renault, 2011; Otero et al. 2011) Increase of holding capacity, improved quality (Navarro and Pereira, 2012; Zaragoza et al., 2012)
Biodiversity	(–) Decrease of non-forest components (+) Increase of forest components	Degradation of grasslands and loss of steppic animal components (Moreira, 1999; Moreira and Russo, 2007) Increase of carnivores and forest birds, especially euro-siberian elements (Sirami et al., 2010; Pita et al. 2009)
Aesthetic, cultural and socioeconomic aspects	(–) Loss of cultural value (+) Increase of economic income	Loss of scenic and cultural value associated to traditional management (Sitzia et al., 2010; Navarro and Pereira, 2012) Increased attraction for ecotourism and hunting (Sitzia et al., 2010; Navarro and Pereira, 2012)

important erosion processes in the less coherent soils and increasingly stable or even progressive situations in other soil types. Then, stronger physical risks and higher difficulties for forest colonization are predicted for the less favorable lithologies. The responses of plant and animal biodiversity will vary depending on the degree of structural and functional recovery of the system. While for plants, diversity usually responds to the physical heterogeneity (climatic, geological) of the habitat (Pausas et al., 2003), for animal communities it depends more on the structure and productivity of the ecosystem (Huston, 1979; Wiens, 1989).

In any case, a synthetic approach to the expectedly divergent trajectories of these two biodiversity components, as regards semi-arid oldfields, is currently lacking. We have attempted that synthesis, through the concurrent and interrelated analysis of physical and biodiversity features. On the basis of floristic and structural vegetation descriptors and bird indices we have quantified, for each type of lithological substrate, the occurrence of positive (dispersal and germination) and negative (ecological filtering) forces (Luzuriaga et al., 2012). We have also assessed the conservation value of flora and birds, as a measure of the change of biodiversity along the post-abandonment trajectory. Birds have been also assessed as indicators of ecosystem services (i.e., dispersal) that can help in the natural recovery of forest ecosystems (Vallejo et al., 2005). Then, we have discussed the ecogeomorphological and biological syndromes identified and their potential application to land management and ecological restoration.

Focusing on semiarid post-agricultural habitats of the Iberian Southeast (Murcia Region), the study addresses the following specific objectives:

- (1) To characterize type-areas of agricultural abandonment on representative lithologies, through the examination and interpretation of physical and biodiversity indicators.
- (2) To analyze the differences in the selected indicators within and between type-areas, on the basis of their intrinsic features, and other biological or anthropogenic constraints.
- (3) To make an integrated assessment of the post-abandonment trajectories and their consequences with reference to the expected trends of physical and biological change

- (4) To propose a framework for the management of such areas taking into account the risks of physical degradation and the conservation of biodiversity values and services.

2. Materials and methods

2.1. Pilot areas and general study design

Three pilot areas of the Region of Murcia (SE Spain) were selected, with different lithological substrate (Fig. 1, Table 2): (1) La Fuensanta, metamorphic (MET); (2) La Murta, limestone (LIM); and (3) Corvera, marly (MAR), and age since abandonment: ancient (AA, >20 years) and recent (AR, < 20 years) (Fig. 1). The selected areas are old dryland almond fields which were abandoned most probably due to their low economic returns, during one of these two main temporal windows of abandonment (established only for operational purposes). The class of abandonment age was assigned through the examination of temporal sequences of aerial orthophotographs and satellite images (1981–2011), the oldest fields studied having remained at least 30 years uncultivated. Rural exodus from the areas where the studied fields are located makes it difficult to check the precise abandonment date through direct interviews with previous farmers/owners or current land users (i.e., shepherds, hunters) which were rarely encountered during field work. This is in part because there has not been an intense grazing activity in the pilot areas since their abandonment, nor fire or any other type of disturbance-based management. Evidences of livestock activity (trampling, browsing, faeces) were rare or absent, suggesting a sporadic presence, insufficient to have a measurable effect on plant colonization. Each pilot area included at least three abandoned fields per age class, although after a detailed inspection, all those selected in area (3) had to be assigned to the AA class, except a very small area where only soil and physical characteristics were sampled. Pilot areas can be ascribed to the same ecogeographical context (inland hillslopes under semiarid Mediterranean climate), but there was a smooth but recognizable W–E gradient, slightly colder and wetter in MET and somewhat hotter and drier in LIM and MAR (Table 2), which was unavoidable given the coarse spatial correlation between substrate distribution and climate. Since worse conditions for cultivation could have led to earlier agricultural cessation, in order to isolate the effect

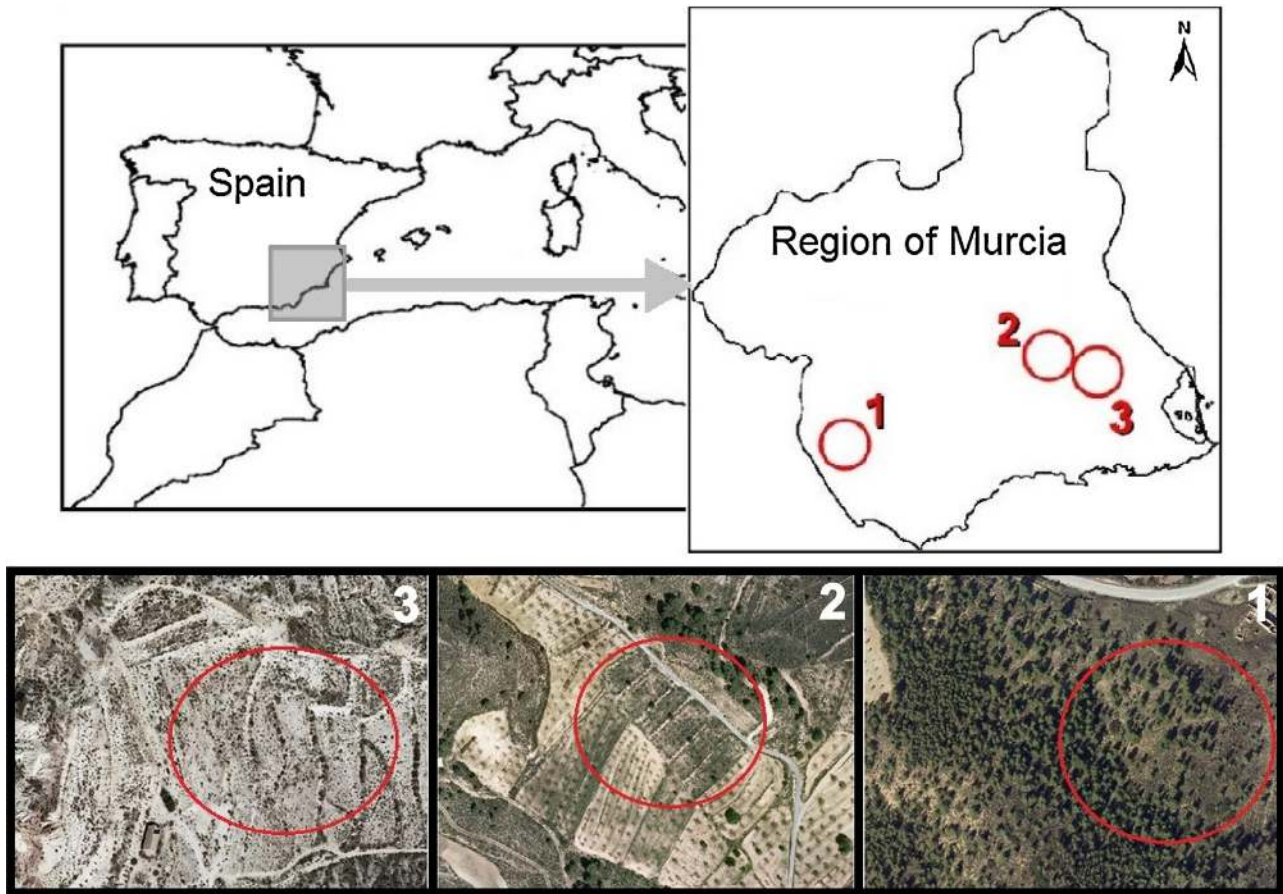


Fig. 1. Location of the three pilot areas included in the study: 1 = La Fuensanta (MET); 2 = La Murta (LIM); 3 = Corvera (MAR), and satellite orthoimages with indication of the areas of ancient abandonment (AA). From left to right: Marly oldfields of Corvera (MAR), limestone oldfields of La Murta (LIM), and metamorphic oldfields of La Fuensanta (MET). In the last two, recently abandoned oldfields are those found Southwards (in La Murta) and Westwards (in La Fuensanta). All the area of Corvera was confirmed to be of ancient abandonment except small fields located towards the East (not represented).

of age since abandonment from other potentially confounding effects (i.e., topography, edaphic quality, plot size), fields were chosen so as to represent comparable initial conditions within each lithological class. The surface of each discrete sampling area (lithology \times age), varied between 0.47 ha (LIM_AA) and 3.77 ha (MAR_AA).

Geomorphological and edaphic changes, as indicators of physical degradation (or improvement) were assessed with regard to the active agricultural areas of the same locations. Vegetation recovery was assessed with respect to surrounding forest patches, interpreted both as theoretical endpoints of successional trajectories, and as source areas for plant colonization. Previous cultivation techniques suggest that very scarce (if any) natural woody vegetation was retained in field margins inside ploughed areas. Woody plant richness and relative abundance are expected to

indicate both biodiversity change and mitigation of physical risks. Forest bird populations were used to assess animal biodiversity changes from a double perspective: contributors to biological richness and providers of ecosystem services (dispersal of fleshy-fruited shrubs towards oldfields). In general, biotic assemblages (plants and birds) were regarded under this double approach to biodiversity assessment: compositional (biological conservation value) and structural/functional (resilience and service provision regarding ecosystem recovery).

2.2. Recording of physical characteristics and erosion phenomena

2.2.1. Edaphic properties

Soil samples were collected with a random distribution. In the laboratory, the following physical determinations were made:

Table 2
General characteristics of the study areas.

	La Fuensanta (MET)	La Murta (LIM)	Corvera (MAR)
UTM coordinates (ETRS89) of the area's centroid	x = 596995 y = 4172386	x = 655723 y = 4188563	x = 663270 y = 4193992
Lithology	Metamorphic rocks	Limestones	Marls
Altitude (m a.s.l.)	650–700	400–430	330–370
Average annual rainfall (mm)	355	286	286
Average yearly temperature ($^{\circ}$ C)	16	18	18
PET (mm)	800	950	950
Bioclimatic classification ^a	(Lower = warm) Mesomediterranean	(Upper) Termomediterranean	(Upper) Termomediterranean

^a Rivas-Martínez (1983).

color, consistency, texture, aggregate stability, and bulk density. Chemical determinations were: organic matter content (OM), pH, electrical conductivity, calcium carbonate (total or equivalent), total organic carbon, total nitrogen, cation exchange capacity, and assimilable sodium, potassium, magnesium, manganese, iron, zinc, and copper.

2.2.2. Evidences of erosion

Erosion was assessed qualitatively through visual inspection, recognizing different erosive forms in each lithological type-area, and recording their presence and magnitude within each of the studied fields (usually a reduced set of agricultural plots in comparable topographical position within a small basin or hillslope). This was made along transects of 30 m long, with a separation of 1 m, covering all the topographic gradient of each studied field. Evidences recorded were: weak sheet erosion (WSE), strong sheet erosion (SSE), and rill and gully erosion (R&G). Transects were conducted both in abandoned and in active agricultural fields.

2.2.3. Infiltration capacity of soils

Infiltration trials were made with minidisk infiltrometers, using a simple cylinder of 12 cm of diameter, and with dry soil (5–10%). The accumulated infiltration (during a given time) allows to estimate the non-saturated hydraulic conductivity of the soil (Knosat), applying the equation of Zhang (1997) as described in Ruiz-Sinoga et al. (2003). The minidisk infiltrometer consists of a graduated glass tube with an approximate length of 20 cm and a diameter of 2 cm, the lower part of which lies on a porous ceramic disc. There is a small capillary tube inserted on the glass wall just above the ceramic basis, while the upper end of the glass tube remains open to allow filling it with water. This type of infiltrometer allows infiltrations to be made at different suction tensions (from 0.5 to 6 cm of water column). The saturated hydraulic conductivity is obtained when all the pores, including the macropores (cracks or holes made by microfauna) are filled with water. Abandonment entails important changes in these macropores; through the use of the minidisk infiltrometer it is possible to prevent water to enter them, by exerting a negative pressure or suction, thus allowing to analyze its magnitude in each case. A total of 108 trials were conducted ($4 \times 3 \times 3 \times 3$), corresponding to four trials per tension (0.5, 2, and 6), lithology (marls, limestones and metamorphic), and land use class (cultivation, recent and ancient abandonment).

2.3. Sampling of biological components

We focused on two groups easy to sample and with proven indicator value (Kati et al., 2004; Zapata and Robledano, 2014): woody plants and forest avifauna.

2.3.1. Flora and vegetation

Pilot areas were sampled four times (one per station) in two consecutive years, between September 2011 and May 2013, with circular units of 100 m² (6–10 per discrete area, i.e., lithology x age). The central points of samples were distributed at random, but displaced when necessary to make half of them coincide with the nearest arboreal structure (an almond tree wholly or partially withered) and the remainder with open spaces. In each unit, the presence of any woody species was recorded, differentiating four morphological types, or life forms (nanophanerophytes, small shrubs, climbers, and chamaephytes), four modes of dispersal depending on the prevailing agent or force transporting the seeds (anemochorous, barochorous –including autochorous–, ectozoochorous, endozoochorous), and three interaction modes, on the basis of the main effect on other plants (positive, i.e.,

facilitation or nurse effects; neutral or indifferent; and negative, i.e., competitive or inhibitory). Although the typology primarily used, especially for modes of dispersal, was that of Bonet (2004), in other aspects it was adapted to achieve a better fit to the stages analyzed (the earlier periods of colonization, with predominantly herbaceous species, were not evaluated), and for a greater discrimination between species according to their structural and functional role in the ecosystem (Annex 1). Besides, the coverage of different physical (bare soil, rocks, litter) and vegetation strata was measured along four orthogonal 10 m transects centered on the sampling point. The variables included in Annex 3 were used as indicators of compositional (taxonomic), structural (cover, life forms), and functional (dispersal and interaction modes) diversity (Coote et al., 2013). The reference peripheral forest patches were sampled only once (winter 2013), using a comparable number of identical sampling units (six per pilot area).

2.3.2. Birds

To characterize the bird community, in the winter and spring of 2012 and 2013, three 10' point counts were carried out in each discrete area (lithology x age), during which all individuals seen or heard were recorded in a previously mapped area recognizable in the field. The 'forest' character of avifauna was interpreted loosely (i.e., both specialist and generalist forest bird species were included). Consequently many species favoring open habitats were taken into account (Gil-Tena et al., 2009; Coote et al., 2013) with the exception of large birds of prey (species with much wider home ranges).

2.3.3. Conservation value and functional indexes

The ornithological and floristic interest was assessed by calculating an index of conservation value obtained as the summatory of the abundance of each species recorded in a sample multiplied by a numerical value corresponding to its category of protection. These indices, adapted from Pons et al. (2003), have been used in previous research in fragmented forest areas (Zapata and Robledano, 2014). Indexes were averaged for each discrete area (lithology x age class). Bird species were ranked according to three conservation assessments (Table 3): (i) SPEC categories (Species of European Concern) as reported in the 'Birds in Europe' assessment (Birdlife International, 2004); (ii) European Birds Directive 2009/147/EC; and (iii) IUCN threat status from the Red Data Book of the Birds of Spain (Madroño et al., 2004). On the basis of these ranks (Table 3), three indexes were constructed (SPEC, BDIR, and RBBS). For flora, the ranks considered were the categories of threat of the Red Data Book of Protected Wild Plants of Murcia Region (Sánchez-Gómez et al., 2002) and the rarity of the species according to Sánchez Gómez and Guerra, 2007, to generate three indexes (Table 3): RBWP (based on the threat status), RBWP+USE (value of RBWP index plus one point, for species whose exploitation may be subject to administrative control), and RARE (based on the degree of regional rarity). The functional index (DISP), calculated only for birds, ranked species according to their contribution to dispersal after Herrera (1984), who differentiates legitimate frugivores (those that do not damage the seeds that are deposited in faeces or regurgitations), and illegitimate frugivores (those that eat the fruit consuming all its parts and thus interfere with dispersal, a condition that is penalized). An intermediate category includes occasional frugivores that can eventually behave as dispersers (e.g., *Phylloscopus collybita*; Cramp, 1998). Breeding bird species do not depend as closely as wintering ones on fruiting shrubs, but since at the end of the summer these fruits still provide breeding species (and their offspring) with a significant food resource, the DISP index was calculated both for winter and breeding bird assemblages.

Table 3

Score assigned to each category in the ranks of conservation importance for birds and flora, used in the calculation of conservation value indexes. NT: near threatened, LC: least concern; DD: deficient data; VU: vulnerable; END: endangered; SMS: species whose exploitation may be subject to special management measures; SI: special interest; VR: very rare; R: rare; X: Uncommon; C: common; and VC: very common.

Value	Birds				Flora	
	SPEC	BDIR	RBBS	DISP	RBWP	RARE
–1	–	–	–	Illegitimate	–	–
0	–	Non-Annex I	Not evaluated	Non-frugivore	–	VC
1	Non-SPEC	–	NT, LC, DD	Occasional frugivore	SMS	C
2	–	–	VU	–	SI	X
4	SPEC-3	Annex I	EN	Legitimate frugivore	–	R
6	SPEC-2	–	–	–	–	VR

2.4. Statistical analysis and integration of results

The biodiversity indicators described in the previous sections, were used as dependent variables in generalized linear mixed models (GLMMs), performed with the nlme package (Pinheiro et al., 2013) of the freely distributed “R” statistical software (R Development Core Team, 2009). Since vegetation samples were repeated in different dates in the same locations, there is a risk of temporal autocorrelation which is minimized with this modeling approach. Consequently, the date of sampling (four seasonal surveys in two consecutive years) was included as a random factor in the models and the remaining variables whose influence was sought (substrate type, age since abandonment and substrate x age) as fixed factors. Two groups of analyses were performed. First, we searched for effects of lithological substrate type and age of abandonment separately. Variables with significant responses were analyzed taking into account lithology and age of abandonment together (five categories). All the vegetation and floristic indexes (Annex 3) were tested as dependent variables. For representative woody species (fleshy-fruited nanophanerophytes, mainly endozoochorous, vertebrate-dispersed), the lists of species found in oldfields and reference areas were qualitatively compared with the pool of potential colonizers predicted by distribution models created by the research team of M.A. Esteve (López, 1999; and personal communication).

Non-parametric tests were used to look for differences among lithology and age classes for five ornithological variables (derived from the bird dataset): the three conservation value indexes, an index of diversity (species richness), and the functional index of dispersal (based on frugivory type). We pooled together counts from each season in order to integrate interannual variability (Shochat et al., 2001).

In a final step, the mutual influence of physical evolution and biodiversity change along the abandonment trajectory was discussed for each pilot area in the framework of the expected responses and considering the management options. For this, a general scheme summarizing the directions of change of each set of variables was built as a basis for the discussion and setting of management guidelines, and for the reformulation of hypothesis and the consequent establishment of future research directions.

Table 4

Results of the determinations of granulometry, organic matter (OM) content and structural stability (SS) of the soils in the oldfields of each pilot area.

Pilot areas	Use	Clay	Silt	Sand	Gravel	OM	SS
Corvera (Marls)	Cultivated fields (C)	23.0	51.7	8.0	17.3	0.87	8.5
(MAR)	Recent abandonment (RA)	24.0	52.4	7.5	17.1	0.80	18.4
	Ancient abandonment (AA)	24.4	61.9	6.4	7.3	0.71	27.3
La Murta (Limestones)	Cultivated fields (C)	11.0	30.9	39.6	18.5	1.46	48.4
(LIM)	Recent abandonment (RA)	6.5	40.8	41.0	11.6	1.34	43.6
	Ancient abandonment (AA)	11.8	39.8	33.7	14.7	1.63	51.4
La Fuensanta (Metamorphic)	Cultivated fields (C)	10.5	27.9	26.6	35.0	1.66	38.7
(MET)	Recent abandonment (RA)	11.2	25.7	25.8	37.3	3.50	47.3
	Ancient abandonment (AA)	12.5	23.2	28.0	36.3	1.98	42.3

3. Results

3.1. Physical evolution of abandoned areas

3.1.1. Edaphic characteristics

The soils of pilot areas presented few granulometric changes in relation to their use (cultivation, recent or ancient abandonment), keeping a similar texture through their post-abandonment evolution, that in the case of marls is silt loam, in limestones loam or slightly sandy loam, while metamorphic areas have a loam texture.

In MAR, %OM is within the range of mean values reported by Romanya et al. (2007) for agricultural soils under Mediterranean climate (0.71–1.03%), and decreases with age since abandonment. In LIM and MET %OM is somewhat higher than these mean values, and increases with abandonment time. This trend is consequent with the degree of regeneration of natural vegetation, although it does not attain the mean values (2.41–5.67%) of Mediterranean forest soils (Romanya et al., 2007; Table 4).

Structural stability is rather low (Table 4), with less than 50% of stable aggregates, typical of human-influenced soils of other areas of the region (Marín-Sanleandro et al., 2007). However, stability shows a marked trend to increase with abandonment age in marly soils, and somewhat less in limestone and metamorphic ones, without reaching in any case the mean values characteristic of natural soils (75%).

3.1.2. Evidences of erosion

In all the lithologies, the weak sheet erosion (WSE) is dominant, but it loses importance after the abandonment. By contrast, the strong sheet erosion (SSE) increases with time since abandonment. In the MET area there were clear signs of sheet erosion, but no evidences of rill and gully (R&G) erosion. In LIM, breakings occur in the slopes between terraces protected by stone walls, and furrows in those without such protection. In MAR, terraced soils have facilitated the occurrence of piping processes, in some cases highly evolved and giving rise to deep gullies (Fig. 2).

Certainly, the degree of erosion is directly related to the vegetation cover that is installed after the abandonment. Therefore, evidences of erosion are lower in areas over

metamorphic rocks where plant cover develops relatively easily after abandonment. By contrast, in marly areas – those more prone to the development of gullies –, protection from vegetation is sparse and evidences of erosion – of all types – become much higher.

3.1.3. Infiltration capacity

The results display a great variability depending on the lithological characteristics of soils and time since abandonment (Fig. 3). In general, infiltration rates are higher in cultivated areas than in oldfields. Specifically, in the marly soils (MAR), infiltration is made difficult, whatever the suction potential applied. In LIM, when suction is increased to -2 cm (i.e., only the pores with a suction capacity greater than this value can be filled with water), the recently abandoned oldfields behave in a similar way than active cultures, but in the older ones infiltration is slowed. However, when the suction tension is increased up to -6 cm, then the more recently abandoned ones behave better in relation to infiltration. In MET, whatever the suction tension, cultures and recently abandoned areas behave in a similar way. The areas of oldest abandonment, however, display a different functioning, since at tensions of -0.5 and -2 cm, infiltration is much slower, i.e., with water entering only into the macropores, infiltration is much faster.

3.2. Changes in biological indicators

3.2.1. Flora and vegetation

Values of vegetation and floristic indicators (mean \pm SE) are presented in Annex 2 (the classification of species according to typification criteria appears in Annex 1). When comparing perennial plant species richness between type-areas (Annex 2), total richness was higher in MET oldfields, whether or not perennial and tussock-forming grasses were included (Fig. 4). The species richness of MET areas (37), whatever their abandonment age, doubled that of MAR and LIM_AR (18). The lack of differences related to age in the richest pilot area is due to an early presence of most species and a low replacement rate along succession (only three species in each age class are not shared with the other). In LIM, 10 species were added with increasing age but none of the previously established was lost.

Not all the potential colonizers of pilot areas were present in oldfields (Annex 2), especially in LIM_AR where only one out of six potential species were found (rising to five in ancient ones). This was not the case in MET areas where all except two endozoochorous species were already present in recently abandoned fields. Moreover, if we look only at the species recorded in sampling plots, metamorphic oldfields experienced an important temporary enrichment during the succession towards forest areas (where only four species, out of a maximum of ten, were present in a density that allowed their detection in the samples).

Table 5 describes a rather poor scrubland assemblage, especially in MAR where none of the species concerned was sampled either in the oldfields or in the nearby reference forest patches. In LIM only one out of six potential species was found locally (in ancient oldfields and reference patches). Only two species of the potential vegetation pool (*Chamaerops humilis* and *Juniperus phoenicea*) were not sampled in MET, where the same four remaining species appeared both in ancient oldfields and forest patches.

The expected progression towards more 'natural' woody formations, as expressed by the richness of endozoochorous shrubs, was only evident in MET (Table 5, Annex 2), while in MAR and LIM very few species of this life form were present even in ancient abandonment stages. The contribution of endozoochorous species to shrub cover estimated from basal area measurements (unpublished data, *Quercus coccifera* not included), was in any case very low. In ancient oldfields these shrubs covered 0.27% of the soil surface in MAR, 0.04% in LIM and 0.22% in MET, a very small fraction of the 4.14%, 16.13%, and 28.89% total shrub cover, respectively. It is noticeable that in MAR a single endozoochorous chamaephyte (*Asparagus horridus*) achieves a higher cover than all fleshy-fruited species pooled together in MET areas. Although cover does not directly translate into size (i.e., biovolume) or fruit crop, the structural and functional role of *Asparagus* in the physically stressed MAR areas cannot be denied.

The full results of GLMMs are presented in Annexes 4 and 5, the most relevant effects being illustrated in Figs. 5 and 6. MET substrates had a positive effect on total species richness compared with other lithologies, and LIM over MAR (whether perennial grasses – as defined here – are included within woody species or not). Focusing on life forms, differences appeared also for



Fig. 2. Examples of piping processes in oldfields of the pilot area of Corvera (MAR).

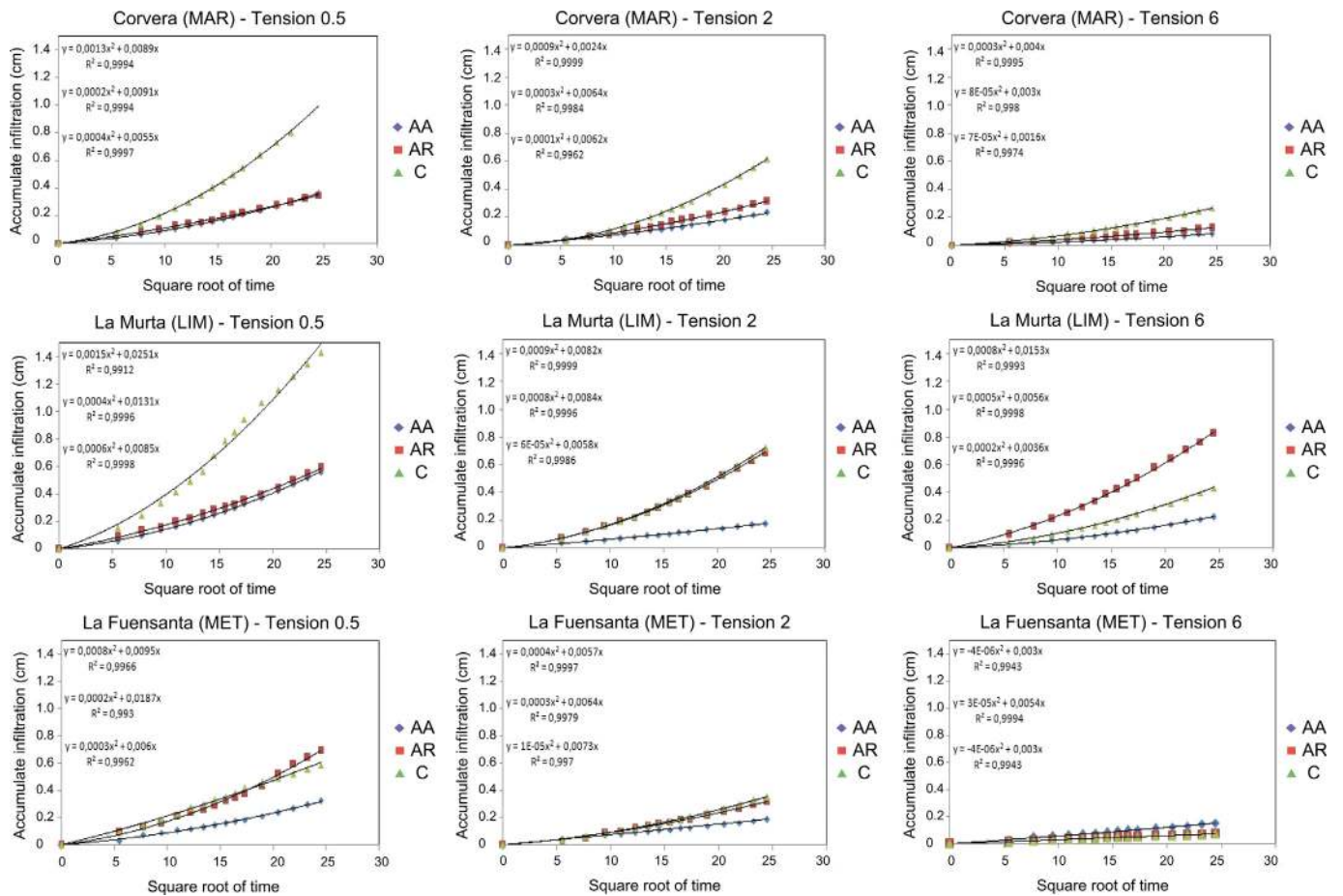


Fig. 3. Accumulated infiltration curves in relation to time. AA = ancient abandonment; AR = recent abandonment; and C = cultivated.

nanophanerophytes in favor of MET areas compared with LIM ones. The richness of small (non-endozoochorous) shrubs showed a totally opposite response (MAR > LIM > MET), and chamaephytes responded in the same way. The importance of this last life form within the Mediterranean flora is reflected in the conservation value of its component species, delivering significantly higher values of the RBWP index. This responded also to the relative abundance of *Genista cinerea* (Sánchez-Gómez et al., 2002), rare in LIM and absent from MET. The floristic index incorporating species subject of management regulations (RBWP + use) is also enhanced in MAR compared with the two other types, and in MET over LIM. Climbers, absent from marls, were more diverse in metamorphic areas than in limestones. The richness of perennial grasses was positively affected by metamorphic and marly substrates. Differences among substrates did not hold when the mean frequency of occurrence of life forms (a measure of their relative abundance) was tested instead of species richness, except in the case of perennial grasses (Annex 4). Marly substrates had a positive effect on the mean frequency of that life form, which in general also increased with time since abandonment.

With regard to dispersal modes (Annex 4), the richness of anemochorous, barochorous, and ectozoochorous species was usually higher in MET than in other substrates, and in recently abandoned oldfields than in ancient ones. The frequency of endozoochorous species was favored on MAR compared with other substrates, as a result of a single species (*A. horridus*) occurring in most samples (mean frequency = 0.75 ± 0.03). In general, ancient abandonment was also associated with a higher frequency of this dispersal mode. Among the three models of plant-plant interaction, the richness of potential facilitator or nurse species was

significantly higher in MAR than in other substrates. In accordance, the richness of inhibitory or competitor species was lower (Annex 4). There was a marginal positive effect of MAR on the mean frequency of facilitator species compared with LIM, but not with MET, and also a significant effect of the latter with respect to LIM.

Regarding cover, marked differences appeared in several strata (Fig. 5). Although compositionally important in marly oldfields, chamaephytes contributed less to vegetation structure there than in other substrates. Chamaephyte cover was maximum in MET, where the cover of larger shrubs was also higher than in MAR, but lower than in LIM. Percent bare soil was significantly higher in MAR, where lower values of plant litter and rock cover were also recorded. The analysis of overlap between different strata revealed a significant positive effect of MET over other substrate types on this variable, and of LIM over MAR when arboreal cover (tree canopy) was taken into account (Fig. 5). When tree cover was excluded, the differences between MET and LIM were no longer displayed, and only the negative effect of MAR persisted due to the minimal overlap recorded on this substrate.

Combined effects of substrate type and age since abandonment were found only for three variables (Annex 5). Richness of facilitator (or nurse) species was always favored on marly substrates, and with marginal significance in ancient with regard to recently abandoned limestone areas. Cover of tree canopy displayed higher values in LIM_AR compared to LIM_AA, an apparently unexpected result explainable by the persistence of live almond trees. On the other hand, MET areas of both ages had higher values than LIM ones, but there was no effect of age within this substrate, in this case due to pine tree cover in older areas replacing almond tree cover in younger ones. Finally, the cover of annuals

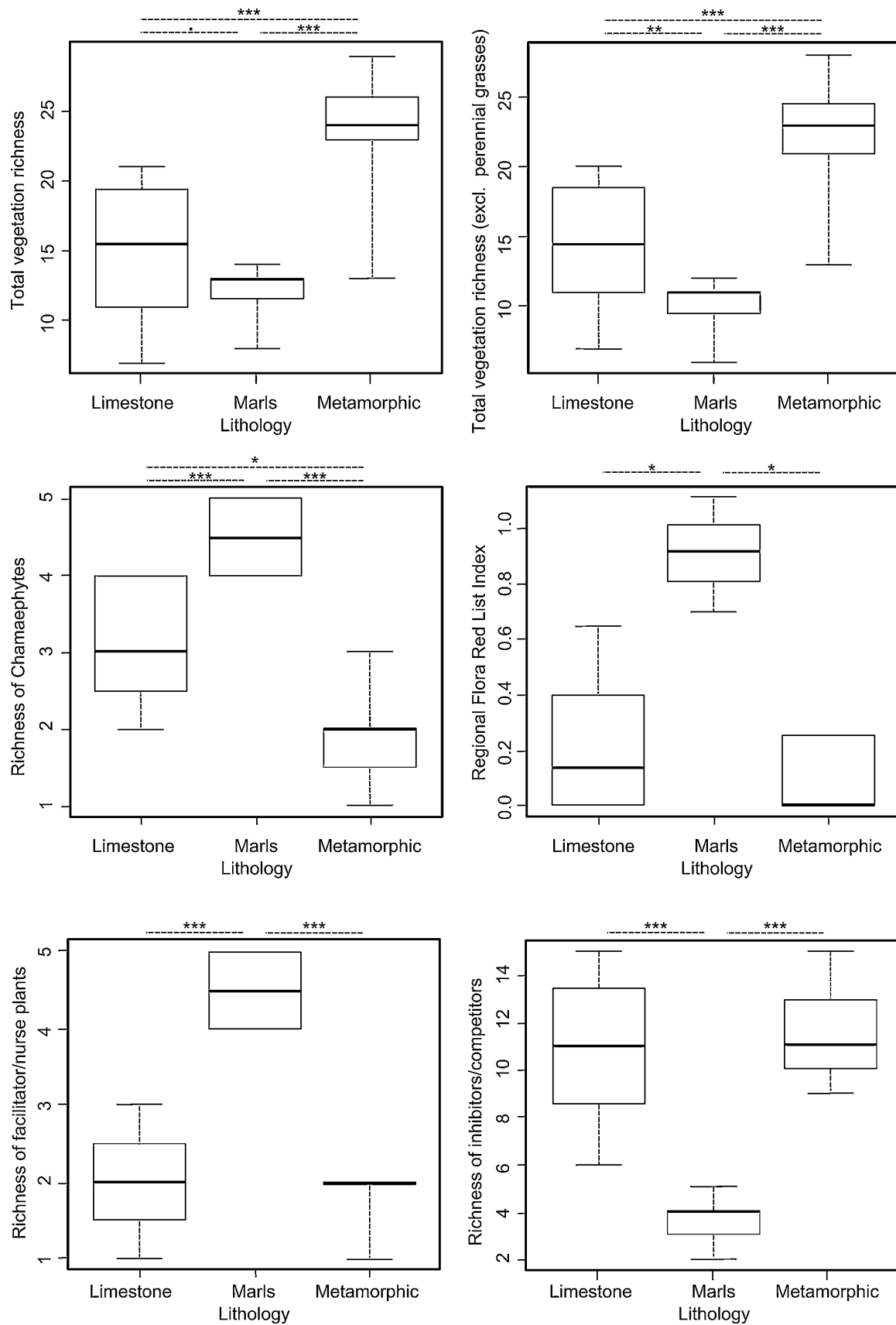


Fig. 4. Box-plots representing differences among lithology classes in perennial plant indicators. Significant change between classes (joined by the dashed lines over the top of the graphs) indicated when p -values of GLMMs < 0.001 (***), 0.01 (**), 0.05 (*), and 0.1 (.). Upper left, total perennial plant richness; upper right, total richness (excluding perennial grasses); middle left, richness of chamaephytes; middle right, Regional Flora Red Data Book (RBWP) index; lower left, richness of facilitator/nurse plants; lower right, richness of inhibitor/competitor plants.

Table 5

Endozoochorous shrub species represented in oldfields and in the corresponding forest reference areas sampled within pilot areas, as well as the species of potential presence according to regional models developed by López (1999) and M.A. Esteve (personal communication), which predict the expected frequency in 1 × 1 UTM squares.

Species:	CORVERA (marls)			LA MURTA (limestone)				LA FUENSANTA (metamorphic)			
	Forest (model)	Forest (local)	Ancient oldfields	Forest (model)	Forest (local)	Ancient oldfields	Recent oldfields	Forest (model)	Forest (local)	Ancient oldfields	Recent oldfields
<i>Rhamnus lycioides</i>	+	–	–	+	+	+	–	+	+	+	+
<i>Chamaerops humilis</i>	+	–	–	+	–	–	–	+	–	–	–
<i>Pistacia lentiscus</i>	+	–	–	+	+	+	–	+	+	+	+
<i>Quercus coccifera</i>	+	–	–	+	–	–	–	+	+	+	–
<i>Juniperus oxycedrus</i>	+	–	–	+	–	–	–	+	+	+	–
<i>Juniperus phoenicea</i>	+	–	–	+	–	–	–	+	–	–	–

was always significantly higher in recent than in ancient oldfields, with minimum values in MET_AA.

3.2.2. Birds

Annex 6 includes a full list of the species recorded in each sampling period (spring and winter), their scores in the conservation assessments, and their functional classification (regarding frugivory and hence contribution to dispersal of late-successional species). The mean abundances of species are shown in Annex 7 and Annex 8, and the results of statistical comparisons in Annex 9. In breeding communities the main differences detected were higher values of total bird density and species richness in MET compared to other lithologies (Annex 9, Fig. 6). The density of legitimate frugivores was also higher in MET (irrespective of age), and intermediate in LIM_AR, although differences were marginally significant except in the comparison between MET and MAR ($p < 0.05$). Expectedly, the index of dispersal potential (DISP) varied significantly in the sequence MET > LIM > MAR (Fig. 7). The two conservation indexes displaying significant differences (SPEC and RBBS), however, gave greater value to marly oldfields over metamorphic and limestone ones (in that order). When comparisons were made on the classes combining lithology and abandonment areas, in the SPEC index LIM_AR scored higher than LIM_AA. Although not significantly, recently abandoned oldfields attained also higher values of the RBBS index than their respective ancient counterparts.

In winter, total bird density was significantly higher in MAR, followed by MET and LIM_AR, while species richness peaked in MET followed by MAR (Annex 9; Fig. 8). Density of legitimate frugivores was higher in MAR and MET, and globally (although with marginal significance) in ancient than in recently abandoned areas. When considering lithology × age classes, in some cases recently abandoned oldfields were locally favored over ancient ones, while LIM areas scored always worse in this indicator. This was reflected in the value of DISP index, higher in MET and LIM. Regarding conservation value, in this case the SPEC index peaked in MET, followed by MAR and LIM, while the Bird Directive Index (BDIR) reached a marginally significant higher value in MAR (Fig. 9).

The species contributing to bird conservation value varied depending on the index concerned. Peak SPEC values were related to the presence of *Oenanthe hispanica*, *Lanius senator*, *Acanthis cannabina*, *Sylvia undata* and *Parus cristatus*. In breeding assemblages this index tends to reach maximum values in MAR (mainly due to *L. senator* and *O. hispanica*), while in winter it peaks in MET, with *P. cristatus* as the most abundant species, particularly in MET_AA. In both seasons the minimum values occur in LIM. For

RBBS, the maximum values of MAR are attributed to *L. senator* and *O. hispanica*, and the intermediate values of LIM_AR and MET_AR to *L. senator* and *Streptopelia turtur*. All these species (except *P. cristatus*) are typical of agroforestry Mediterranean mosaics of low shrub and/or sparse tree cover, with *O. hispanica* displaying a more steppic character and *S. turtur* higher forest affinity. BDIR did not vary significantly, except marginally (in winter) in favor of MAR, due to the presence of *S. undata*, *Anthus pratensis* and *Galerida* sp. The two latter, with a more marked steppic character, are also found in LIM_AR and MET_AR, although in lower density.

Finally, DISP, which gave greater value to species of the families *Sylviidae* and *Turdidae*, reached higher values in MET but, counterintuitively, increased in recently abandoned fields (although not globally, due to the weight of the ancient MAR oldfields). This is related, among other things, to the abundance of *Phoenicurus ochruros*, a legitimate frugivore favoring open habitats (Madroño et al., 2004), added to a non-negligible presence of other frugivores (*Sylvia* spp., *Erithacus rubecula*).

3.3. Integrated assessment

Table 6 shows the scheme aimed at summarizing the main drivers and directions of change of the different sets of indicators used to assess physical and biological evolution of oldfields on different lithologies. Although the differentiation is often not totally precise, we have tried to distribute biodiversity indicators among three categories (compositional, structural and functional) on the basis of their relevance for the assessment, particularly in the context of management.

Eight indicators of soil and geomorphological evolution characterized MAR areas as those with higher physical risks, while five ornithological and three floristic indicators gave them the highest biodiversity scores. On the opposite, MET oldfields performed better in eight biodiversity indicators (different from those peaking in MAR), but also in nine physical ones. LIM areas displayed only a somewhat worse physical performance than MET ones, but had intermediate or lower scores in most biodiversity indicators.

4. Discussion

The drivers of farmland abandonment in the Iberian Southeast are reasonably well established (Nainggolan et al., 2012), and the effects of this process on soils and plant communities are being studied since the late 1980's (Francis, 1990; Padilla, 1997). But their consequences for biodiversity have usually been inferred on the basis of literature from other Mediterranean areas (Nainggolan

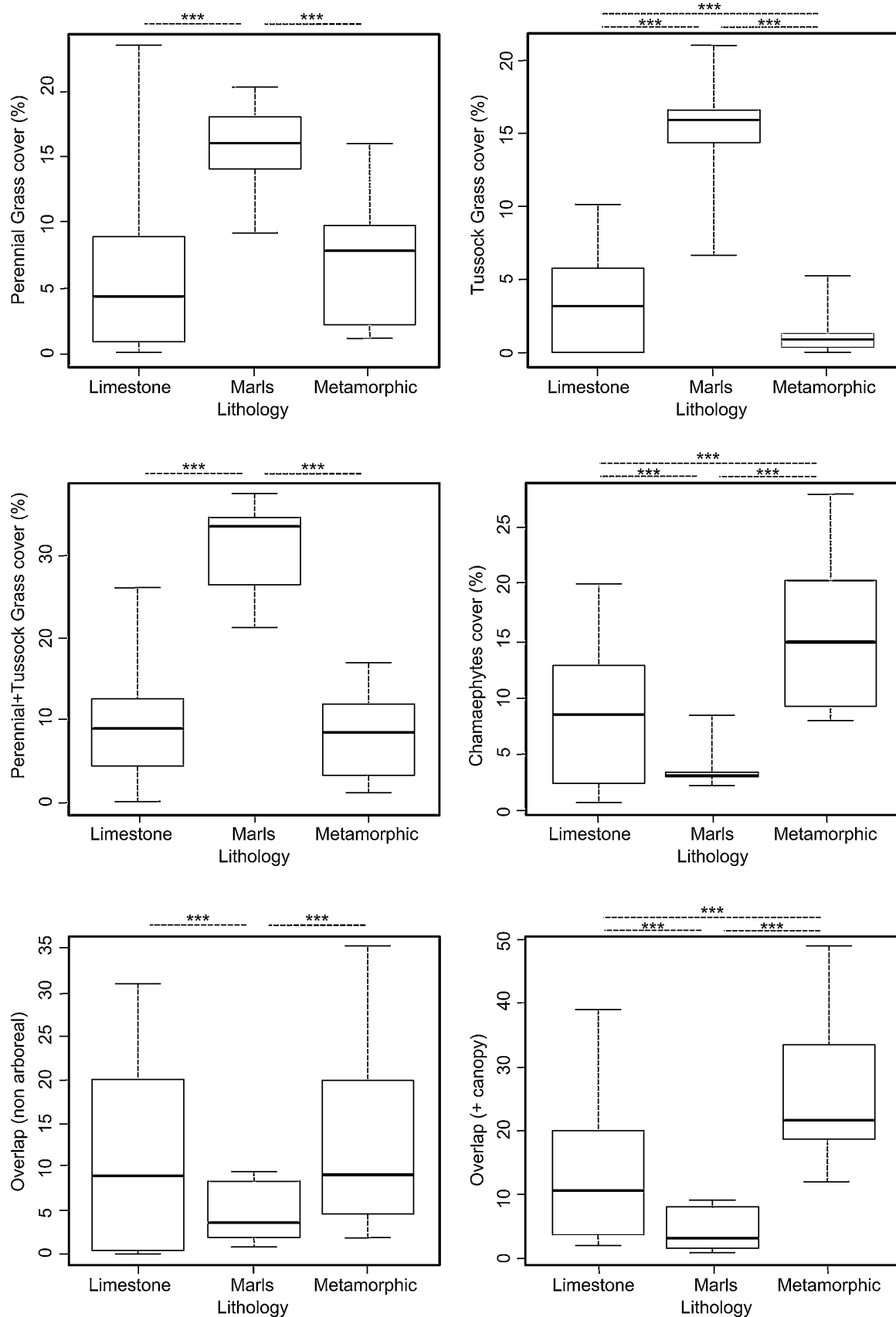


Fig. 5. Box-plots representing differences among lithology classes in cover of different vegetation strata. Significant change between classes (joined by the dashed lines over the top of the graphs) indicated when p -values of GLMMs were lower than 0.001 (***), 0.01 (**), 0.05 (*), and 0.1 (.). Upper left, cover of perennial grasses; upper right, cover of tussock-forming gramineae (*Stipa*, *Lygeum*); middle left, cover of all perennial herbaceous plants (grasses + tussock); middle right, cover of chamaephytes; lower left, overlap of strata (cover >100%) excluding tree canopy; lower right, overlap considering tree canopy cover.

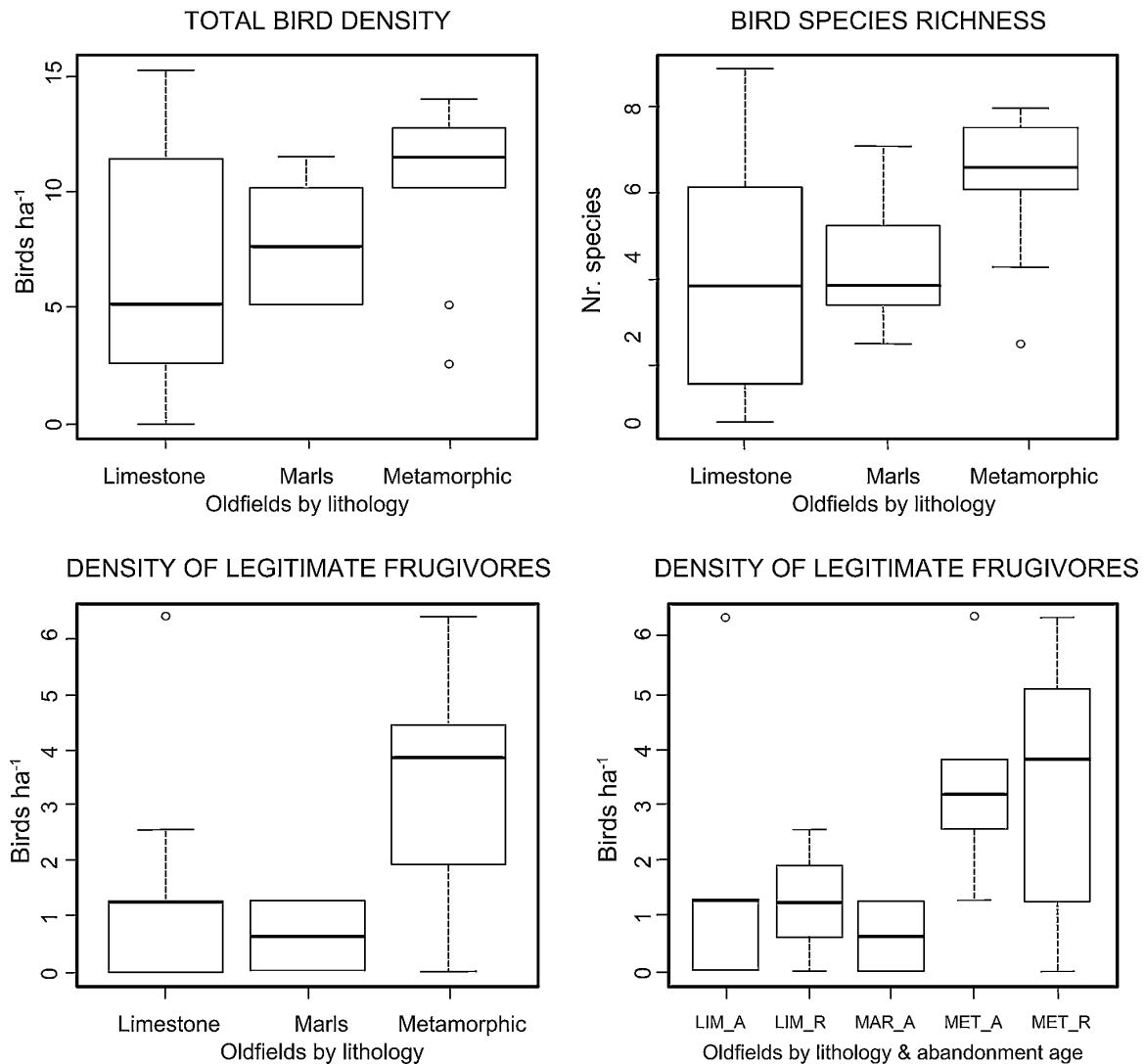


Fig. 6. Box-plots representing breeding bird community indexes displaying significant differences (Kruskal–Wallis non parametric analysis of variance) among lithology and lithology x abandonment age classes.

et al., 2012). Despite the key role that abandoned agricultural areas can play in protected areas (Ostermann, 1998), there is a scarce knowledge for taking advantage of their spontaneous naturalization in management and restoration, at least in the ISE. This is in part due to the lack of an integrated assessment of physical and biodiversity issues.

Under our study aims, the assessment of abandoned agricultural fields should follow two main steps. First, it is necessary to analyze and interpret the basic indicators (both physical and biological) used to characterize each type-area, which allow them to be ordered along biophysical gradients (i.e. substrate erodibility, edaphic quality, habitat structural complexity, strength of biotic interactions), and to be classified under a characteristic ecogeomorphological syndrome (e.g., steppe-like marly areas with high erosion risk). After such integration, it is possible to focus on management decisions for each situation, taking full advantage of the processes and services related to biodiversity. Rather than searching for unique patterns of oldfield succession, we have attempted to assess the interaction of physical and biological variables in each substrate type-area. We have quantified the different progressive, stabilizing and regressive forces, stressing the role of biodiversity both as an intrinsic feature and as a driver of ecosystem development (Van der Putten et al., 2000). In the future, our approach will allow exploring the degree of

generalization of these syndromes under comparable ecogeomorphological conditions.

4.1. Evolution of physical indicators

4.1.1. Edaphic characteristics

This section sought to verify whether the main properties of soils improved after abandonment, or if instead these worsened as a result of it. The main findings were:

- Apparent density became worse in MAR, and by contrast, improved in LIM and MET.
- Regarding texture, in MAR soils the silt fraction increased and the sandy one was diminished, while in LIM the trends were opposite; in MET, clays increased and sands decreased, the granulometric fractions being more compensated and thus improving the characteristics of soil as regards this feature. Stands out the high presence of gravels in MET soils, which contributes to their surface protection.
- The aggregate stability improved with abandonment in the three lithologies, which is related to the increase of plant cover as a result of a relatively intense spontaneous colonization, especially in LIM and MET oldfields.

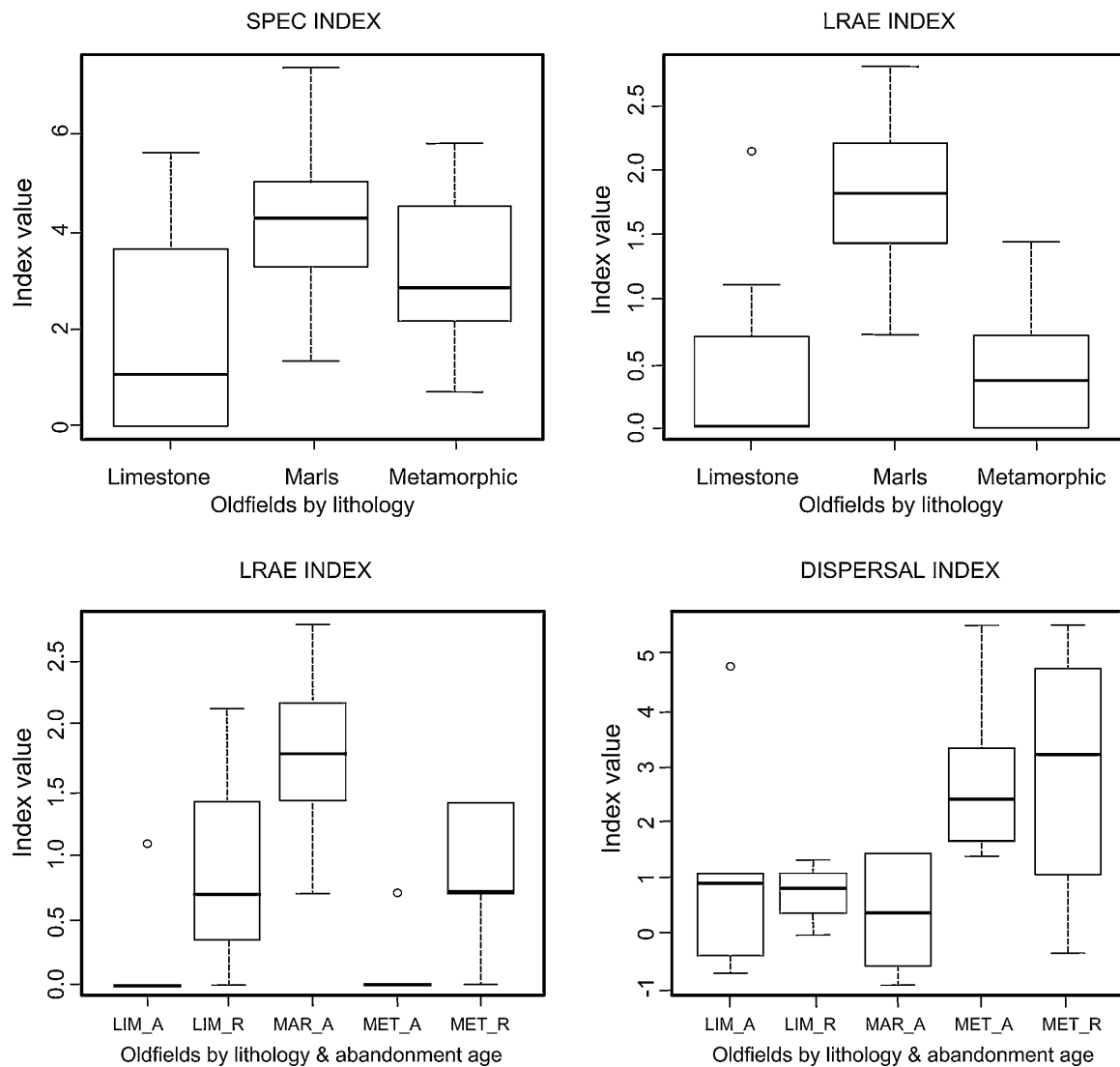


Fig. 7. Box-plots representing breeding bird conservation value and functional (dispersal) indexes displaying significant differences (Kruskal–Wallis non parametric analysis of variance) among lithology and lithology x abandonment age.

- The values of OM were very low in cultures over marls (0.87%), and were even lower after abandonment (0.71%). In limestones, the OM content was still low (1.46%), and increased slightly with abandonment (1.63%). In metamorphic soils OM content was also low (1.66), but in that case it increased considerably after abandonment (3.5%).
- The Cation exchange capacity decreased in MAR soils, but was enhanced in LIM and especially in MET ones, related with the increase in OM and aggregate stability.
- Macronutrients increased in all cases, generally, in MET and LIM substrates, but decreased in MAR ones (with the exception of Mg). The C/N relationship improved with abandonment, especially in MET oldfields where a higher OM content, more organic soils and a better developed plant cover were found.
- Micronutrients also increased with abandonment, with the exception of Cu, in MET areas. On the contrary, all of them decreased in LIM areas, as occurred in MAR ones with the exception in that case of Mn, that showed a slight increase.

To conclude, as expected from their sensitivity to degradation (e.g., Verstraeten et al., 2003; Sougnez et al., 2011) there seems to occur an improvement of soils in metamorphic and limestone lithologies, and a worsening in marly ones. Agricultural use

modifies the physical properties of soils and often causes their gradual degradation (Trabaquini et al., 2013), a trend that can be naturally reversed after abandonment.

4.1.2. Evidences of erosion

The results show how, both in MET and LIM, abandonment does not imply an intensification of erosive processes with respect to those detected in areas under active cultivation. But in MAR, erosion due to piping processes has led to a situation of badland development (Romero-Díaz et al., 2012). The degree of erosion among pilot areas, is undoubtedly related to the extent of improvement of edaphic conditions and to the establishment of plant cover (Verstraeten et al., 2003; Lesschen and Cammeraat, 2007a). However, in MAR, erosion processes are enhanced by topographical modifications during the cultivation phase (Cerdà et al., 1995).

4.1.3. Infiltration capacity

Usually, after abandonment, the first rainfall events generate a surface blocking effect in the soil, so that at tensions close to the gravitational value, there was a reduction in the rate of infiltration with respect to cultivated soils, except in the more clayey soils of MET areas, stressing the role of texture in these processes (Ruiz-Sinoga et al., 2011). Absolute values also show that variability.

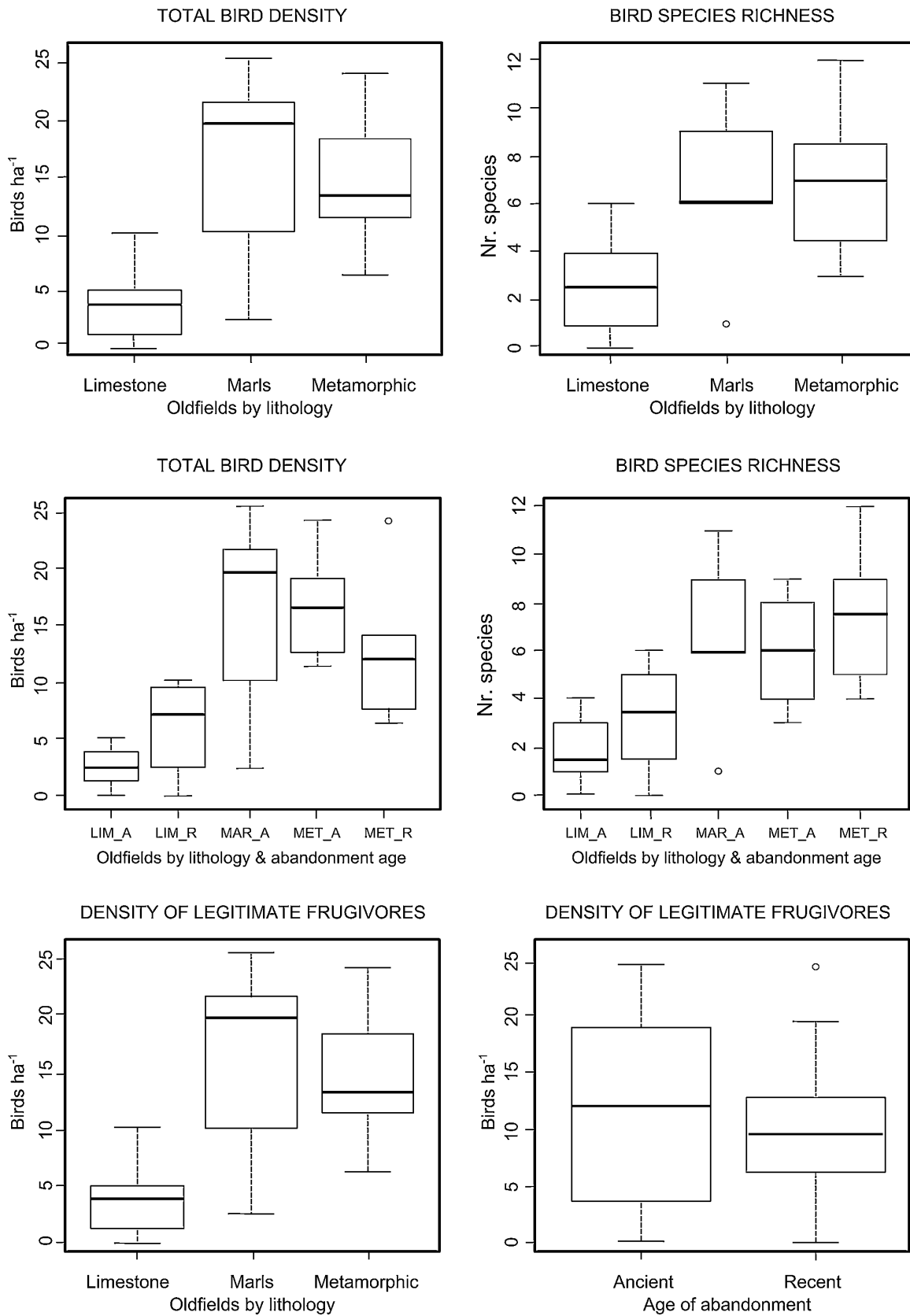


Fig. 8. Box-plots representing wintering bird community indexes displaying significant differences (Kruskal–Wallis non parametric analysis of variance) among lithology and abandonment age classes (and their combination).

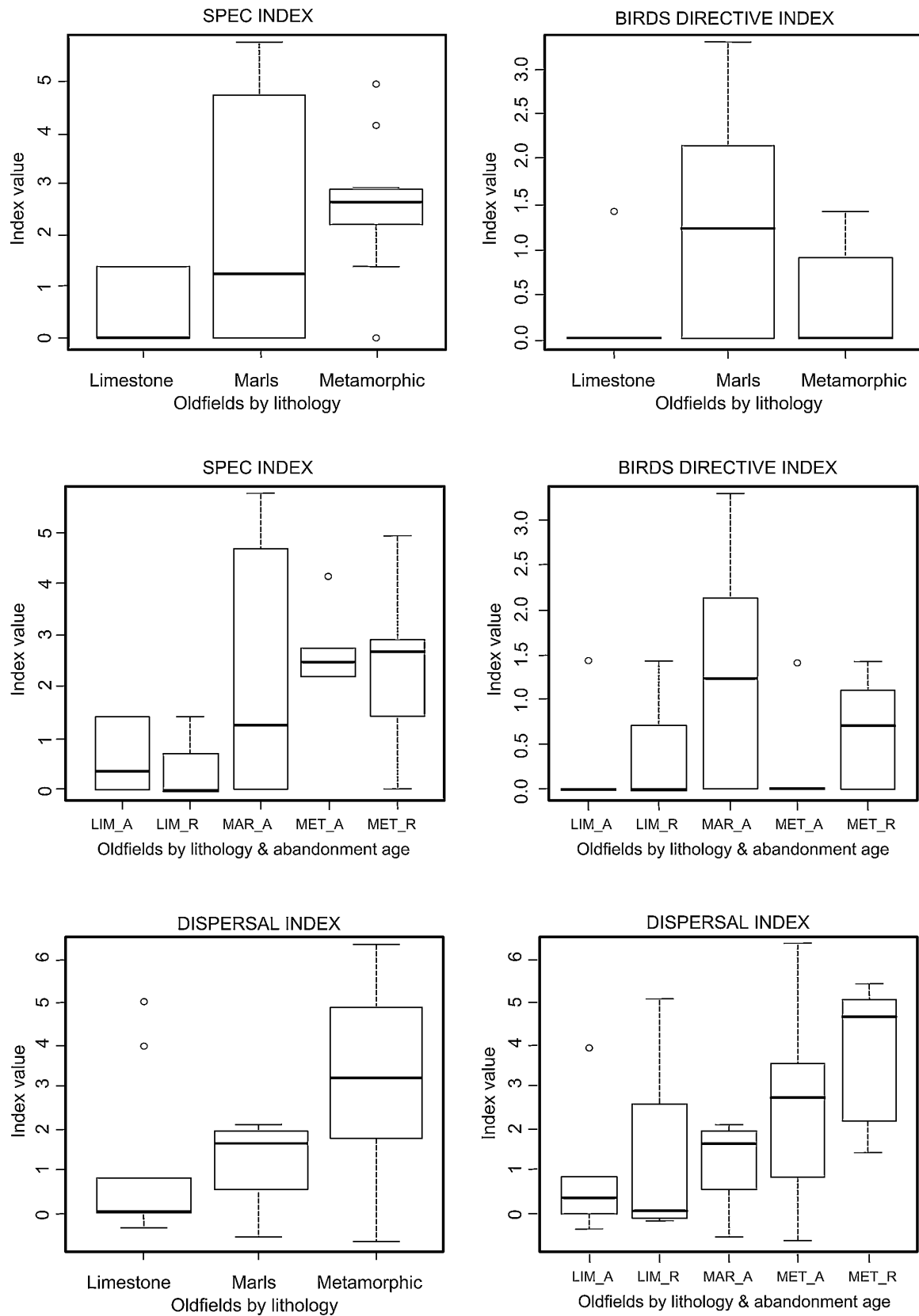


Fig. 9. Box-plots representing wintering bird conservation value and functional (dispersal) indexes displaying significant differences (Kruskal–Wallis non parametric analysis of variance) among lithology and lithology x abandonment age classes.

Table 6

Summary of the biophysical features and indicators that characterize the main differences in recovery status (soil and biota), functionality, conservation value and environmental fragility of the three pilot areas studied. In soil properties and erosion evidences, '+' indicates improvement or increase, and '-', worsening or decrease after abandonment (with respect to equivalent cultivated soils). WSE=weak sheet erosion; SSE=strong sheet erosion; R and G=Rill and Gully erosion.

		Lithology			
		Marls	Limestones	Metamorphic	
Flora	Composition	Lowest species richness	Intermediate species richness (increasing in ancient abandonment)	Highest species richness (chamaephytes and nanophanerophytes); = in both ages, but species turnover	
		Dominance of small shrubs (non-endozoochorus)	Strictly progressive succession pattern		
	Structure	Steppic physiognomy; >50% bare soil (AA)	Bare soil <40% (AA); Dominance of small shrubs and chamaephytes	Bare soil <40% (AA); Dominance of small shrubs and chamaephytes	
		Dominance of tussockforming and other perennial grasses	More annuals	More tree canopy	
	Function	High occurrence of positive interactions (facilitation)	Higher occurrence of negative interactions (inhibition/competition)	High occurrence of positive interactions (facilitation, perch effect)	
Conservation value		Intermediate herbivory	Intense herbivory (-)	Lower herbivory	
		Effective dispersal of fleshy-fruited species	Safe site effect (margins)	Effective dispersal of fleshy-fruited species	
		High for frequency of Red Data Book species <i>Genista cinerea</i> (RBWP)	Lowest	High for frequency of management-regulated species (RBWP + use)	
Fauna	Composition	Higher density (winter)	Intermediate density and species richness	Maximum density (breeding) and species richness	
		Species seasonal turnover			
	Structure	Dominance of steppic and open-habitat species maintained in ancient abandonment stages	Transition from open agricultural mosaic to scrubland communities	Transition from agricultural mosaic to scrubland and open woodland communities	
	Function	High winter dispersal potential	Lower dispersal potential	Higher forest bird component	
Conservation value		High for SPEC and RBBS (breeding) and marginally for BDIR (wintering)	Lower in most cases (higher in recent abandonment)	High winter dispersal potential	
				Higher for winter SPEC	
Soils	Apparent density	-	+	+	
	Texture	+silt -sands	+silt -sand	+clays, -sand +gravel more compensated fractions	
	Stability of aggregates	+	+	+	
	Organic matter	Very low Decreases after abandonment	Low Increases after abandonment	Low Increases considerably after abandonment	
	Cationic exchange capacity	-	+	++	
	Macro-nutrients	-	+	+	
	Micro-nutrients	-	-	+	
	Infiltration capacity	Very low	Intermediate	High	
	Erosion	Grade	High	Intermediate	Low
		Evidences	-WSE +SSE ++R&G, piping	-WSE +SSE	-WSE -SSE

In MAR, that situation occurs at any suction tension and proportionally to the time since abandonment, which implies a greater capacity for the generation of runoff. Combined with the greater difficulty for plant recolonization (given the low OM content and the terracing of plots), this has led to a higher erosion potential with the formation of pipes and gullies, and to huge soil losses (Romero-Díaz et al., 2011b).

In LIM, the area of recent abandonment had a higher macroporosity and hence, a greater infiltration capacity, similar to that of the cultivated area, with a tension of -2 cm and even higher than -6 cm. This situation indicates that, with increasing time since abandonment, soil compaction becomes greater, and also agrees with the fact that erosion is not very evident, due to the scarce potential for runoff generation in recent oldfields and to the establishment of a denser shrub cover in ancient ones. In limestone substrates, Cerdà (1997b, 1998); Cerdà (1997b, 1998) equals lower infiltration to soil degradation.

In MET_AR, an attempt of cultivation five years ago can have prevented changes in porosity during such a short time interval, which explains the similar behavior of recently abandoned and actively cultivated fields. MET_AA is, among the three lithologies, the area where a greater infiltration is allowed at -6 cm suction, which recalls the influence of features of an advanced state of plant colonization (roots and microfauna holes), and the role of the more clayey texture of its soils (Cerdà, 1998).

4.2. Biodiversity changes

4.2.1. Flora and vegetation indicators

The main qualitative and quantitative differences between pilot areas are related to lithology rather than to abandonment age. MAR oldfields, even in the ancient stage studied, had lower woody plant richness and poorer structural development (Table 6), leading to a percent of bare soil higher than 50%, compared to 34–35% in the ancient oldfields of other substrates. Opposed to this, but also

directly related to the stronger physical stress (Pugnaire et al., 2004), facilitative interactions were favored, and most of the plant cover corresponded to tussock-forming and other perennial grasses (especially *L. spartum* among the former, and *B. retusum* among the latter).

In LIM and MET, percent bare soil was still high as correspond to semiarid areas, but it is 15–16% lower on average, plant cover being dominated by small shrubs and chamaephytes. Higher values of protective cover types like plant litter and rock were also recorded in these substrates. Annuals' cover was always significantly higher in recent oldfields, with minimum values – as expected from the competition with woody plant components – in MET_AA. The cover of forbs and other annual plant species could play some role in the protection of soil against erosion (Cerdà et al., 1995; Obando, 2002; Blanco-Canqui et al., 2006; El Kateb et al., 2013), which should be assessed in more detail in the context of oldfield management.

The colonization by fleshy-fruited nanophanerophytes seems more limited in LIM than in MET oldfields, although their structural contribution was very small in any substrate, probably due to the limiting semiarid climate (Navarro et al., 1993; Lesschen and Cammeraat, 2007b) and to historical degradation processes. Landscape-scale degradation seems to be affecting the local pool of late-successional shrub species (Table 5). This was evident in MAR, where the only fleshy-fruited species recorded in reference forest areas (*A. horridus*, a chamaephyte), was well distributed in the ancient abandoned areas. Its trophic role can even be more relevant than its structural contribution, given the partial frugivorous character some typical bird species of these areas (Richardson, 1965; Hodar, 1995). In LIM, however, these species are scarce even in ancient oldfields (only colonized by *Rhamnus lycioides* and marginally by *Pistacia lentiscus*), suggesting that there are barriers to their dispersal or establishment. Moreover, we usually found *R. lycioides*, an efficient colonizer of oldfields (Bonet, 2004; Pausas et al., 2006), seeking refuge in stone-reinforced field margins of the limestone areas, avoided by our sampling design (personal observations). Such microsite selection and the dominance of some smaller shrubs inside the fields (e.g., *Anthyllis cytisoides*), are regarded as indicators of the prevalence of inhibitory effects. MET oldfields seemed to supply more favorable microsites for shrub colonization (Rühl and Schnittler, 2011) and less inhibitory effects.

Only marly substrates exerted a positive effect on the relative frequency of perennial herbaceous species (tussock- or mat-forming plants like *S. tenacissima*, *Lygeum spartum* and *B. retusum*). In MET, these non-woody life forms had to share space and interact with a higher diversity of woody species. Their poorer performance in LIM recalls the suggested inhibitory effects of earlier-colonizing small shrubs, since *S. tenacissima* and *B. retusum* are widespread around the pilot area in forest and dry grassland communities. In MAR, perennial grasses can take advantage of their clonal vegetative growth mode (Bonet, 2004; Pueyo et al., 2010), overcoming the limitations posed by physical stress (water shortage, substrate erodibility). This allows them to play a relevant physiognomical and functional role, affecting plant and animal biodiversity and exerting some control on physical processes, which make them key components of restoration strategies (De Baets et al., 2009; Cortina et al., 2011).

The significantly higher richness of facilitator species in MAR can reflect the high environmental stress experienced under the overall restrictive conditions of semiarid areas, enhanced by their specific geomorphological and edaphic post-abandonment features (Navarro et al., 1993; Cerdà et al., 1995). Although generally important in compositional terms, chamaephytes and small shrubs increased their structural contribution as physical conditions became more favorable, with maximum values in MET.

Both perennial grasses and chamaephytes are key components of semiarid Mediterranean vegetation (Navarro et al., 1993; Palacio, 2006; Pueyo et al., 2010; Cortina et al., 2011; Zapata and Robledano, 2014).

Oldfield colonization, as a result of the activity of dispersal agents (namely frugivorous birds) in combination with microsite suitability and other forces involved (predation, competition . . .), seems to occur at different speeds depending on the species considered. Establishment appears as a slow process (characteristic of semiarid areas, Obando, 2002; Pugnaire et al., 2006; Cañadas et al., 2010), conditioned by the availability of propagule sources and by the efficacy of favorable (perch effects, passive and active facilitation) and negative forces (physical limitations, biological interactions: predation, competition). Negative physical conditions (soil degradation, erosion, water shortage) are particularly strong in marls compared to more resistant lithologies (Faulkner et al., 2003; Bellin et al., 2011), but positive forces and interactions (vegetative growth, bird dispersal, facilitation) seem reasonably effective and managers can take advantage of them (Vallejo et al., 2005). Only in LIM, an apparent biological blockage of succession could be occurring, since physical conditions and propagule supply are not necessarily worse there. Such an arrestment has been demonstrated in other Mediterranean communities dominated by pioneer shrubs (Acácio et al., 2007), being attributed to an unattractiveness to dispersers (birds), or to a failure of seedling establishment due to competition from the established vegetation (Mendoza et al., 2009). In our case, it can be explained by the dominance of competitive or inhibitory species (Haase et al., 1997; Bonet, 2004), although other factors (e.g., herbivory) can also be invoked (Tzanopoulos et al., 2007).

4.2.2. Ornithological indicators

Compositional and structural indicators describe bird assemblages dominated by species of open spaces and with poorly structured vegetation. The contribution of forest-dwelling species was only significant in MET. The effect of time since abandonment on bird assemblages was apparently important, modifying the influence of soil type on vegetation characteristics, and thus appearing nested within the effects of lithology. Some ornithological indexes, both in summer and winter, were significantly higher in recent than in ancient oldfields. In the former the availability of open space and pioneer colonizing vegetation provide habitat and resources for a variety of non-specialist forest species (Sirami et al., 2007, 2008; Vallecillo et al., 2008).

In general, conservation value indexes (SPEC, RBBS, BDIR) and the functional one (DISP) delivered opposite results, with higher values of the former usually found in MAR (except for SPEC in winter), and of the last one in MET. Since the exception is mainly related to the abundance of a forest-dwelling species (*P. cristatus*), the expectations of conservation value peaking in steppe-like habitats are confirmed. Ornithological interest is also expected to increase at intermediate levels of disturbance (or recovery), particularly if oldfields in different successional stages coexist in the landscape. These habitat mosaics are of great value for birds due to the coexistence of species of Mediterranean origin together with some of more steppic character, with greater affinity for semiarid desert-like landscapes (Blondel et al., 2010; Ambarli and Bilgin, 2014). An increase in the effectiveness of bird dispersal (which can be self-reinforced by the presence of colonizing shrubs) could work against the maintenance of such mosaics, with the risk of a loss of ornithological value. In any case, given the particular dynamics of oldfields in the ecogeographical context studied, open habitats can last for an undefined period (in MAR), and succession can be stopped at intermediate stages dominated by non-endozoochorous shrubs (in LIM).

However, the functional value of shrubby habitats for birds and other vertebrates (López and Moro, 1997; Mangas et al., 2008; Pita et al., 2009) in Mediterranean mosaic landscapes, should not be underscored. This is particularly relevant for bird species with larger home ranges including the oldfields, but not recorded in the point-count surveys (e.g., raptors, corvids). Two pilot areas (LIM and MET) take part of habitat mosaics relevant for these species, being included in Natura 2000 sites (SCI and/or SPA), and the third one (MAR) lies close to this protected network. Thus, ornithological value should also integrate the functional contribution to larger spatial units. Regarding this role, the relative abundance of keystone species like rabbit (*Oryctolagus cuniculus*) should be assessed, given its influence on vegetation and its trophic value for top predators (Delibes-Mateos et al., 2007).

4.3. Integrated assessment

Our pilot areas reflected the net local expression of positive (soil amelioration, plant facilitation, animal-mediated dispersal) and negative (erosion, soil degradation, inhibition) forces, which can be described with several physical and biological indicators (Table 1) and integrated into a management framework. Vegetation development was expected to increase with the availability of propagule sources, disperser activity, passive and active facilitation, and to be limited by inhibition and herbivory (Haase et al., 1997; Bonet, 2004; Tzanopoulos et al., 2007). From a functional perspective, natural reforestation was expected to progress as the positive interaction linkages between plants and animals develop (Debussche et al., 1996; Bonet, 2004), i.e., as ecosystem service providers (e.g., vertebrate dispersers) increase in the community (Sekercioglu, 2006).

Most of the responses indicated in Table 1 were confirmed. Particularly, a desertification and steppization trend (Le Houérou, 2002; Bonet, 2004; Cortina et al., 2011) in MAR soils, due to their low inherent fertility and their proneness to agricultural degradation (Cerdà et al., 1995; Romero-Díaz et al., 2007). Although this trend was accompanied by a floristic impoverishment, high ornithological value and some floristic singularity were retained. On the opposite, soil improvement and vegetation progress occurred in LIM and MET areas, but signs of dispersal limitation (Mendoza et al., 2009) and of arrested succession (Bonet, 2004; Santana et al., 2010) were also displayed. Marly areas exhibited lower plant cover and structure, even after a long abandonment time, but their colonization by endozoochorous species (*A. horridus*), seemed effective in the mid-term. This could be related to the relative importance of facilitation (e.g., by tussock grasses; Barberá et al., 2006), and to the activity of frugivores. Although the representation of frugivores decreased along the physical stress gradient, they were still reasonably effective in MAR. In turn, establishment success did not always improve with vegetation structural development (i.e., with age since abandonment). The limitations to dispersal seem rooted rather in the source (local pool of colonizers) or in the destination (biotic filters), than in the efficacy of dispersal agents. Restoration could require the active reintroduction of some shrub species (at least to create colonization foci) and the removal of negative biotic interactions.

In general, our results gave support to the responses that can be expected from physical and biological gradients, although modulated by landscape and local context. Within the lithological framework, succession appeared contingent, and the syndromes described probably represent only a few of the multiple pathways of renaturalization. The speed and direction of vegetation recovery in semiarid areas can vary considerably and not necessarily in relation to soil type (Dana and Mota, 2006). In limestone substrates, succession is often more progressive than in our study areas (López-Bermúdez et al., 1998; Lesschen et al., 2008b), while

in metamorphic ones it can be slowed or arrested (Pugnaire et al., 2006; Padilla et al., 2011). In any case, the frequent occurrence of divergent physical and biological trajectories, calls for an integration of biodiversity in the assessment of oldfield recovery.

The various recognizable gradients and syndromes also provide a broader framework for the selection of conservation or restoration measures, and for the definition of the spatial scale at which they should be applied (Navarro et al., 2006). The intensity of management should also be tuned to the strength of physical degradation forces and biotic interactions. Corrective management (physical protection, revegetation) can be applied to the areas with most urgent and severe erosion impacts (Cortina et al., 2011), but acknowledging the need to keep some moderate disturbance, either to maintain low or sparsely-vegetated areas, or to actively break inhibitory forces when necessary. On the basis of the spatial distribution of vegetation cover and erosion evidences, such dual management can be performed at field scale (within plots), or at whole farm or catchment level, where different successional stages can coexist spatially.

5. Conclusions and management recommendations

Considering the huge research effort made in the Spanish Southeast on the geomorphological and edaphic consequences of land management (e.g., García Ruiz and López Bermúdez, 2009; Romero-Díaz, 2010; Romero-Díaz et al., 2011a; Calatrava et al., 2011; Sougnez et al., 2011), and the parallel research on the ecology of vegetation and other biota (e.g., Francis, 1990; Padilla, 1997; Obando, 2002; Navarro et al., 2003; Cañadas, 2008; Armas et al., 2011) it is surprising that very few studies have attempted to integrate these two aspects (Cañadas et al., 2010), whose management may require trade-offs between conflicting interventions (Marta-Pedroso et al., 2007).

Biodiversity plays a key functional role in the preservation of the ecogeomorphological integrity of abandoned farmland. Apart from the most obvious protective function of vegetation cover, microbiological activity, plant species interactions, or animal-mediated dispersal, can help to stabilize soil processes and speed secondary succession. It is advisable to take advantage of these ecological interactions in the restoration of oldfields (Méndez et al., 2008). We have to seek a management framework which can reconcile classic restoration solutions (based on uniform prescriptions for agricultural land reforestation) and totally passive natural rewilding mechanisms. Fortunately, restoration paradigms within which physical degradation only could be stopped through an increase in plant cover (particularly tree cover) are being challenged (Martínez-Fernández and Esteve, 2005; Cortina et al., 2011). In turn, the natural reforestation approach is gaining support against strategies of active restoration or maintenance, on the basis of its lower costs and higher benefits for biodiversity (Navarro and Pereira, 2012).

Natural recovery, however, is not generally applicable since it can deliver undesirable results in either of the studied dimensions. In the same way that classical reforestation techniques may not be suitable for semiarid Mediterranean areas (Romero-Díaz and Belmonte-Serrato, 2008), subject to strong climatic stress and physical limitations, passive re-naturalization may be insufficient to revert the geomorphological and edaphic processes triggered by previous cultivation techniques (i.e., terracing), particularly in the less coherent substrates (Albaladejo et al., 1995; Cerdà et al., 1995). Similarly, it could fail to provide enough disturbance (i.e., herbivore activity) to maintain the desired habitat and landscape heterogeneity.

Our study has revealed how in limestone and metamorphic areas, erosion and soil degradation are less obvious (Verstraeten et al., 2003; Sougnez et al., 2011). After a long period without agricultural use, concentrated erosion is absent and soil properties

improve (especially in metamorphic soils) due to a significant increase in naturally-developing plant cover. By contrast, in marly lithologies the abandonment has very negative effects, with soil characteristics worsening and erosion processes increasing (López-Bermúdez and Romero-Díaz, 1989; Romero-Díaz et al., 2007). Given that the physical threats affecting marly oldfields are the result of the interaction between substrate erodibility, topographic modifications (terracing) and natural vegetation patchiness (Bonet, 2004; Puigdefábregas, 2005), they would need specific, localized management measures (within-field intervention), rather than widespread revegetation projects that can eliminate open habitat of high wildlife and scenic value. In the more resistant lithologies, there is no specific need to accelerate succession, but a landscape-scale management delivering a wildlife-friendly mosaic (Pons et al., 2003; Pita et al., 2009; Sánchez-Oliver et al., 2014). In an intermediate position of this management gradient, limestone areas would also need some disturbance-based management in case that succession is arrested or colonization inhibited. Under a rewilding paradigm (Navarro and Pereira, 2012), such disturbance could be delivered by wild fauna (Sandom et al., 2013) or by extensive cattle (Robles et al., 2009). On the opposite, refuge-based (creating favorable microsites) or facilitation-mediated (taking advantage of nurse effects) management has to be applied if excess herbivory is confirmed (both at within-field scale).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2014.08.006>.

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