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 lanscape homogeneization, 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.

Keywords: oldfields; Mediterranean; semiarid; physical degradation; biodiversity; integrated assessment

Highlights:

- Abandonment of farmland is common in semiarid Mediterranean areas
- Physical and biodiversity features were assessed in oldfields of different lithology
- Biodiversity and physical conservation trajectories were often opposite or divergent
- Natural reforestation is a feasible but non-generalizable management option
- A framework is proposed for setting oldfield management mode, scale, and intensity

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 half of the Iberian Peninsula (García-Ruiz and Lana-Renault, 2011).

The effects of abandonment can be positive or negative (Kosmas et al., 2000; Zaragozí et al., 2012), depending on soil and climate. Under favorable climatic conditions for the maintenance of vegetation, soils may ameliorate over time, gaining organic matter inputs, enhancing microbial and faunal activity, improving their structure, increasing their infiltration capacity and reducing the erosion potential (Trimble, 1990). Under harsher conditions, abandoned crops are a favorable scenario for erosion (Navarro and Pereira, 2012). If plant colonization is not enough to generate a progressive 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 (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; Robles et al., 2009). 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).

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 centre 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 in areas with forest potential (Allué-Andrade, 1995), 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 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 (Sitzia 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 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:

(i) To characterize type-areas of agricultural abandonment on representative lithologies, through the examination and interpretation of physical and biodiversity indicators.

(ii) 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.

(iii) To make an integrated assessment of the post-abandonment trajectories and their consequences with reference to the expected trends of physical and biological change

(iv) 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. Case studies: abandonment type-areas on different lithological substrates

2.1. Pilot areas and general study design

Three pilot areas of the Region of Murcia (SE Spain) were selected, with different lithological substrate (Figure 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) (Figure 1). Each pilot area included at least three abandoned dryland almond 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. The surface of each discrete sampling area (lithology x 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: colour, 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, Potasium, Magnesium, Manganese, Iron, Zinc and Copper.

2.2.1. 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 along transects of 30 m long, with a separation of 1 m. 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.

2.2.2. Infiltration capacity of soils

Several infiltration trials were made with minidisk infiltrometers. Three trials were conducted in each type of soil and land use (cultivation, recent and ancient abandonment), 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 Ruíz-Sinoga et al. (2003). The minidisk infiltrometer consists of a graduated glass tube with an approximate lenght 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 minidisc 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.

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, in press): 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 m^2 (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, in press). 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.

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, 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.

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 tan 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 (Figure 2).

3.1.3. Infiltration capacity

The results display a great variability depending on the lithological characteristics of soils and time since abandonment (Figure 3). In general, infiltration rates are higher in cultivated areas than in oldfields. Specifically, in the marly soils (MAR), infiltration capacity 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 tan this value can be filled with water), the recently abandoned oldfields behave in a similar way tan active cultures, but in the ancient ones infiltration is slowed. However, when the suction tension is increased up to -6 cm, then it is the recent abandonment which behaves best in relation to infiltration. In MET, whatever the suction tension, cultures and recently abandoned areas behave in a similar way. The ancient abandonment areas, 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.

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3.2. Changes in biological indicators

3.2.1. Flora and vegetation

Values of vegetation and floristic indicators (mean±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 (Figure 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 where 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 (*A. 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 figures 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 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 (LRFS+use) is also enhanced in MAR compared with the two other types, and in MET over LIM ones. 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 (*Asparagus 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 that 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 (Figure 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 (Figure 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 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, Figure 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 (Figure 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 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; Figure 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 x 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 MAR and LIM, while the Bird Directive Index (BDIR) reached a marginally significant higher value in MAR (Figure 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 ones (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 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.
- 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.

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 (Ruíz-Sinoga et al., 2011). Absolute values also show that variability.

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 lead 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 (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 was reduced to 34-35% 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 abadoned 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*, usually 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, in press).

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, in press). 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 recomendations

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., 2006). 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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7. References

Acácio, V., Holmgren, M., Jansen, P., Schrotter, O., 2007. Multiple Recruitment Limitation Causes Arrested Succession in Mediterranean Cork Oak Systems. Ecosyst. 10, 1220-1230.

Albaladejo, J., Ortiz, R., Guillen, F., Alvarez, J., Martinez-Mena, M., Castillo, V., 1995. Erodibility of Agricultural Soils in the Semiarid Mediterranean Area of Spain. Arid Soil Res. Rehabil. 9(3): 219-226.

Ambarli, D., Bilgin, C. C. (in press). Effects of landscape, land use and vegetation on bird community composition and diversity in Inner Anatolian steppes. Agric. Ecosyst. Environ. DOI: http://dx.doi.org/10.1016/j.agee.2013.11.006

Aparicio, A., Albaladejo, R.G., Olalla-Tárraga, M.Á., Carrillo, L.F., Rodríguez, M.Á., 2008. Dispersal potentials determine responses of woody plant species richness to environmental factors in fragmented Mediterranean landscapes. For. Ecol. Manage. 255: 2894-2906.

Armas, C., Miranda, J.D., Padilla, F.M., Pugnaire, F.I., 2011. Special issue: The Iberian Southeast. J. Arid Environ. 75: 1241-1243.

Allué-Andrade, J.L. 1995. El Cambio Climático y los Montes Españoles. Cuadernos de la S.E.C.F., 2: 35-64.

Bellin, N., Vanacker, V., van Wesemael, B., Solé-Benet, A., Bakker, M.M. 2011. Natural and anthropogenic controls on soil erosion in the Internal Betic Cordillera (southeast Spain). CATENA 87, 190-200.

Barberá, G.G., Navarro-Cano, J.A., Castillo, V.M. 2006. Seedling recruitment in a semi-arid steppe: The role of microsite and post-dispersal seed predation. J. Arid Environ. 67, 701-714.

Blanco-Canqui, H., Gantzer, C.J., Anderson, S.H., 2006. Performance of Grass Barriers and Filter Strips under Interrill and Concentrated Flow. J. Environ. Qual. 35, 1969-1974.

Blondel, J., Aronson, J., Bodiou, J.-Y., Boeuf, G. 2010. The Mediterranean Region Biological Diversity in Space and Time. Oxford University Press, Oxford, 384 pp.

BIRDLIFE INTERNATIONAL. 2004. Birds in Europe. Population Estimates, Trends and Conservation Status. Birdlife Conservation Series, 12, Cambridge.

Bocio, I., Navarro, F.B., Ripoll, M.A., Jiménez, M.N., Simón, E.D., 2004. Holm oak (Quercus rotundifolia Lam.) and Aleppo pine (Pinus halepensis Mill.) response to different soil preparation techniques applied to forestation in abandoned farmland. Ann. For. Sci. 61, 171-178.

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.

Bonet, A., Pausas, J., 2004. Species richness and cover along a 60-year chronosequence in old-fields of southeastern Spain. Plant Ecol. 174, 257-270.

Bonet A., Pausas, J.G., 2007. Old field dynamics on the dry side of the Mediterranean Basin: Patterns and processes in semiarid Southeast Spain, in: Cramer V.A., Hobbs R.J., (Eds.). Old Fields: Dynamics and Restoration of Abandoned Farmland. Island Press, Washington DC, pp. 247–264.

Calatrava, J., Barberá, G.G., Castillo, V.M., 2011. Farming practices and policy measures for agricultural soil conservation in semi-arid Mediterranean areas: The case of the Guadalentín basin in southeast Spain. Land Degrad. Develop. 22, 58-69.

Calvo, J.F., Esteve, M.A., López-Bermúdez, F. (Coord.), 2000. Biodiversidad. Contribución a su conocimiento y conservación en la Región de Murcia. Servicio de Publicaciones de la Universidad de Murcia, Murcia.

Cañadas, E.M., 2008. Estudio de tierras agrícolas abandonadas en ambiente semiárido mediterráneo: vegetación, suelos y distribución espacial. Bases para la gestión. PhD Thesis, University of Granada.

Cañadas, E.M., Jiménez, M.N., Valle, F., Fernández-Ondoño, E., Martín-Peinado, F., Navarro, F.B., 2010. Soil–vegetation relationships in semi-arid Mediterranean old fields (SE Spain): Implications for management. J. Arid Environ. 74, 1525-1533.

Cerdà, A., Boix, C., Soriano, M.D., Calvo, A., Imeson, A.C., 1995. Degradación del suelo en una catena sobre margas afectada por el abandono del cultivo en un ambiente semiárido. Cuatern. Geomorfol. 9: 59-74.

Cerdà, A., 1998. The influence of aspect and vegetation on seasonal changes in erosion under rainfall simulation on a clay soil in Spain. Can. J. Soil Sci. 78, 321-330.

Coote, L., Dietzsch, A.C., Wilson, M.W., Graham, C.T., Fuller, L., Walsh, A.T., Irwin, S., Kelly, D.L., Mitchell, F.J.G., Kelly, T.C., O'Halloran, J., 2013. Testing indicators of biodiversity for plantation forests. Ecol. Indic. 32, 107-115.

Cortina, J., Amat, B., Castillo, V., Fuentes, D., Maestre, F.T., Padilla, F.M., Rojo, L., 2011. The restoration of vegetation cover in the semi-arid Iberian southeast. J. Arid Environ. 75, 1377-1384.

Cramp, S. (Ed.), 1998. The Complete Birds of the Western Paleartic. Oxford University Press, London.

Dana, E.D., Mota, J.F., 2006. Vegetation and soil recovery on gypsum outcrops in semi-arid Spain. J. Arid Environ. 65, 444-459.

De Baets, S., Poesen, J., Reubens, B., Muys, B., De Baerdemaeker, J., Meersmans, J., 2009. Methodological framework to select plant species for controlling rill and gully erosion: application to a Mediterranean ecosystem. Earth Surf. Process. Landf. 34, 1374-1392.

Debussche, M., Escarré, J., Lepart, J., Houssard, C., Lavorel, S., 1996. Changes in Mediterranean plant succession: old-fields revisited. J. Veg. Sci. 7, 519-526.

Delibes-Mateos, M., Redpath, S.M., Angulo, E., Ferreras, P., Villafuerte, R. 2007. Rabbits as a keystone species in southern Europe. Biol. Conserv. 137, 149-156.

Detsis, V., 2010. Placing land degradation and biological diversity decline in a unified framework: Methodological and conceptual issues in the case of the North Mediterranean region. Land Degrad. Develop. 21, 413-422.

El Kateb, H., Zhang, H., Zhang, P., Mosand, R., 2013. Soil erosion and surface runoff on different vegetation covers and slope gradients: A field experiment in Southern Shaanxi Province, China. Catena 105, 1-10.

Esteve-Selma, M.A., Martínez-Fernández, J., Hernández, I., Montávez, J.P., López, J.J., Calvo, J.F., Robledano, F., 2010. Effects of climatic change on the distribution and conservation of Mediterranean forests: the case of *Tetraclinis articulata* in the Iberian Peninsula. Biodiv. Conserv. 19(13): 3809-3825.

Faulkner, H., Ruiz, J., Zukowskyj, P., Downward, S., 2003. Erosion risk associated with rapid and extensive agricultural clearances on dispersive materials in southeast Spain. Environ. Sci. Policy 6, 115-127

Francis, C.F., 1990. Variaciones sucesionales y estacionales de vegetacion en campos abandonados de la provincia de Murcia, España. Ecología 4, 35-47.

Fuentes-Castillo, T., Miranda, A., Rivera-Hutinel, A., Smith-Ramírez, C., Holmgren, M., 2012. Nucleated regeneration of semiarid sclerophyllous forests close to remnant vegetation. For. Ecol. Manage. 274, 38-47.

García-Ruiz, J.M., 2010. The effects of land uses on soil erosion in Spain: A review. Catena 81, 1-11.

García-Ruiz, J.M., Lana-Renault, N., 2011. Una revisión de los efectos hidrológicos y erosivos del abandono de tierras en España. Geographicalia 59-60, 125-135.

Garcia Ruiz, J. M., López Bermúdez, F., 2009. La erosión del suelo en España. Sociedad Española de Geomorfología, Zaragoza, 441 pp.

Gil-Tena, A., Brotons, L., Saura, S., 2009. Mediterranean forest dynamics and forest bird distribution changes in the late 20th century. Glob. Change Biol. 15, 474-485.

Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J., Baraza, E., 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. Ecol. Appl. 14, 1128-1138.

Haase, P., Pugnaire, F.I., Clark, S.C., Incoll, L.D., 1997. Spatial pattern in Anthyllis cytisoides shrubland on abandoned land in southeastern Spain. J. Veg. Sci. 8, 627-634.

Hodar, J.A., 1995. Diet of the Black Wheatear Oenanthe leucura in two steppe shrub's zones of Southeastern Spain. Alauda 63, 229-235.

Huston, M., 1979. A General Hypothesis of Species Diversity. Am. Nat. 113, 81-101.

Herrera, C.M., 1984. A Study of Avian Frugivores, Bird-Dispersed Plants, and Their Interaction in Mediterranean Scrublands. Ecol. Monogr. 54, 1-23.

Jordano, P., 2000. Fruits and frugivory, in: Fenner, M. (Ed.), Seeds: the ecology of regeneration in plant communities, 2nd edition. CABI Publ., Wallingford, UK, pp. 125-166.

Kati, V., Devillers, P., Dufrêne, M., Legakis, A., Vokou, D., Lebrun, P., 2004. Testing the Value of Six Taxonomic Groups as Biodiversity Indicators at a Local Scale. Conserv. Biol. 18, 667-675.

Kosmas, C., Gerontidis, S., Marathianou, M., 2000. The effect of land use change on soils and vegetation over various lithological formations on Lesvos (Greece). Catena 40, 51-68.

Lasanta, T. 1989. Evolución reciente de la agricultura de montaña: El Pirineo aragonés. Geoforma Ediciones, Logroño, 220 pp.

Le Houérou, H.N., 2002. Man-Made Deserts: Desertization Processes and Threats. Arid Land Res. Manage. 16, 1-36.

Lesschen, J.P., Cammeraat, L.H., 2007a. Soil properties and types, in: Conditions for Restoration & Mitigation of Desertified Areas Using Vegetation (RECONDES). Review of Literature and Present Knowledge. European Commision. Directorate General for Research-Environment, pp. 71-78.

Lesschen, J.P., Cammeraat, L.F., 2007b. Effects of plants on soil properties, in: Conditions for Restoration & Mitigation of Desertified Areas Using Vegetation (RECONDES). Review of Literature and Present Knowledge. European Commision. Directorate General for Research-Environment, pp. pp. 135-141.

Lesschen, J.P., Cammeraat, L.H., Kooijman, A.M., van Wesemael, B., 2008a. Development of spatial heterogeneity in vegetation and soil properties after land abandonment in a semi-arid ecosystem. J. Arid Environ. 72, 2082-2092.

Lesschen, J.P., Cammeraat, L.H., Nieman, T., 2008b. Erosion and terraces failure due to agricultural land abandonment in a semi-arid environment. Earth Surf. Process. Landf. 33, 1574-1584.

López, J.J., 1999. Respuesta ambiental de las principales especies arbustivas en sistemas áridos y semiáridos mediterráneos: modelos y aplicaciones. Tesis Doctoral. Universidad de Murcia.

López, G., Moro, M.J., 1997. Birds of Aleppo pine plantations in south-east Spain in relation to vegetation composition and structure. J. Appl. Ecol. 34, 1257-1272.

López-Bermúdez F., Romero-Díaz M.A., 1989. Piping erosion and badland development in southeast Spain, in: Yair, A., Berkowicz, B. (Eds.), Arid and Semi-arid Environments-Geomorphological and Pedological Aspects. Catena Suppl. 14, 59–73.

López-Bermúdez, F., Romero-Díaz, A., Martínez-Fernandez, J., 1998. Vegetation and soil erosion under a semi-arid Mediterranean climate: a case study from Murcia (Spain). Geomorphology, 24, 51-58.

Luzuriaga, A. L., Sánchez, A. M., Maestre, F. T., Escudero, A., 2012. Assemblage of a Semi-Arid Annual Plant Community: Abiotic and Biotic Filters Act Hierarchically. PLoS ONE 7, e41270.

Madroño, A., González, C., Atienza, J.C. (Eds.), 2004. Libro Rojo de las Aves de España. Dirección General para la Biodiversidad-SEO/Birdlife, Madrid.

Mangas, J.G., Lozano, J., Cabezas-Díaz, S., Virgós, E., 2008. The priority value of scrubland habitats for carnivore conservation in Mediterranean ecosystems. Biodiv. Conserv. 17, 43-51.

Manzano, P., Malo, J.E., Peco, B., 2005. Sheep gut passage and survival of Mediterranean shrub seeds. Seed Sci. Res. 15, 21-28.

Maestre, F.T., Cortina, J., 2004. Are *Pinus halepensis* plantations useful as a restoration tool in semiarid Mediterranean areas? For. Ecol. Manage. 198, 303-317.

Maestre, F.T., Bowker, M.A., Puche, M.D., Belén Hinojosa, M., Martínez, I., García-Palacios, P., Castillo, A.P., Soliveres, S., Luzuriaga, A.L., Sánchez, A.M., Carreira, J.A., Gallardo, A., Escudero, A., 2009. Shrub encroachment can reverse desertification in semi-arid Mediterranean grasslands. Ecol. Lett. 12, 930-941.

Marín-Sanleandro, P., Sánchez-Navarro, A., Delgado-Iniesta, M.J., Fernández-Delgado Juárez, M., 2007. Relación entre la estabilidad estructural con los tipos y usos del suelo en el sureste de España, in: Romero-Díaz, A., Belmonte-Serrato, F., Alonso-Sarría, F., López-Bermúdez, F., (Eds.). Advances in Studies on Desertification, pp. 705-708.

Marta-Pedroso, C., Domingos, T., Freitas, H., de Groot, R.S., 2007. Cost–benefit analysis of the Zonal Program of Castro Verde (Portugal): Highlighting the trade-off between biodiversity and soil conservation. Soil Till. Res. 97, 79-90.

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. Veget. Sci. 13, 234-248.

Martínez-Fernández, J., Esteve, M.A., 2005. A critical view of the desertification debate in southeastern Spain. Land Degrad. Develop. 16, 529-539.

Martínez-Fernández, J., Esteve, M.A. (Coord.), 2010. Sostenibilidad Ambiental de la Región de Murcia. EDITUM, Murcia.

Méndez, M., García, D., Maestre, F.T., Escudero, A., 2008. More ecology is needed to restore mediterranean ecosystems: A reply to Valladares and Gianoli. Restor. Ecol. 16, 210-216.

Mendoza, I., Gómez-Aparicio, L., Zamora, R., Matías, L., 2009. Recruitment limitation of forest communities in a degraded Mediterranean landscape. J. Veg. Sci. 20, 367-376.

Moreira, F., 1999. Relationships between vegetation structure and breeding bird densities in fallow cereal steppes in Castro Verde, Portugal. Bird Study 46: 309-318.

Moreira, F., Russo, D., 2007. Modelling the impact of agricultural abandonment and wildfires on vertebrate diversity in Mediterranean Europe. Landsc. Ecol. 22, 1461-1476.

Nainggolan, D., de Vente, J., Boix-Fayos, C., Termansen, M., Hubacek, K., Reed, M.S., 2012. Afforestation, agricultural abandonment and intensification: Competing trajectories in semi-arid Mediterranean agro-ecosystems. Agric. Ecosyst. Environ. 159, 90-104.

Navarro, T., Nieto Caldera, J.M., Pérez Latorre A.V., Cabezudo, B., 1993. Estudios fenomorfológicos en la vegetación del sur de España. III. Comportamiento estacional de una comunidad de badlands. Acta Bot. Malacitana, 18: 189-198.

Navarro, F.B., Jiménez, M.N., Ripoll, M.A., Bocio, I., De Simón, E., 2003. Análisis de la riqueza florística en cultivos agrícolas abandonados de la Depresión de Guadix-Baza (Granada). Monogr. Fl. Veg. Béticas 13, 17-34.

Navarro, F.B., Ripoll, M.A., Jiménez, M.N., De Simón, E., Valle, F., 2006. Vegetation response to conditions caused by different soil-preparation techniques applied to afforestation in semiarid abandoned farmland. Land Degrad. Develop. 17, 73-87.

Navarro, L.M., Pereira, H.M., 2012. Rewilding Abandoned Landscapes in Europe. Ecosyst. 15, 900-912.

Obando, J.A., 2002. The impact of land abandonment on regeneration of semi-natural vegetation: A case study from the Guadalentín, in: Geeson, N.A. Brandt, C.J., Thornes, J.B. (Eds.) Mediterranean desertification: A mosaic of processes and responses. John Wiley and Sons, Chichester, pp. 269-276.

Ostermann, O.P., 1998. The need for management of nature conservation sites designated under Natura 2000. J. Appl. Ecol. 35, 968-973.

Otero, I., Boada, M., Badia, A., Pla, E., Vayreda, J., Sabaté, S., Gracia, C.A., Peñuelas, J., 2011. Loss of water availability and stream biodiversity under land abandonment and climate change in a Mediterranean catchment (Olzinelles, NE Spain). Land Use Policy 28, 207-218.

Padilla, A., 1997. Colonización vegetal en campos de cultivo abandonados en la provincia de Alicante. Tesis Doctoral, Universidad de Alicante.

Padilla, F.M., Miranda, J.d.D., Ortega, R., Hervás, M., Sánchez, J., Pugnaire, F.I., 2011. Does shelter enhance early seedling survival in dry environments? A test with eight Mediterranean species. Appl. Veg. Sci. 14, 31-39.

Palacio, S., 2006. Fenomorfología y estrategias funcionales de los principales tipos de caméfitos leñosos mediterráneos del Prepirineo. Pirineos 161, 159-170.

PAND, 2008. Programa de Acción Nacional contra la Desertificación. MMARM, Madrid, 208 pp.

Pausas, J.G., Carreras, J., Ferré, A., Font, X., 2003. Coarse-Scale Plant Species Richness in Relation to Environmental Heterogeneity. J. Veg. Sci. 14, 661-668.

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.

Peco B., Carmona C.P., de Pablos, I., Azcarate, F.M., 2012. Effects of grazing abandonment on functional and taxonomic diversity of Mediterranean grasslands. Agric. Ecosyst. Environ. 152, 27–32.

Pinheiro, J., Bates, D., Debroy, S., Sarkar, D., The R Development Core Team, 2013. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-109. http://cran.r-project.org/web/packages/nlme/index.html

Pita, R., Mira, A., Moreira, F., Morgado, R., Beja, P., 2009. Influence of landscape characteristics on carnivore diversity and abundance in Mediterranean farmland. Agric. Ecosyst. Environ. 132, 57–65.

Plieninger, T., Gaertner, M., Hui, C., Huntsinger, L., 2013. Does land abandonment decrease species richness and abundance of plants and animals in Mediterranean pastures, arable lands and permanent croplands? Environ. Evidence 2, 3.

Pons, P.; Lambert, B.; Rigolot, E., Prodon, R., 2003. The effects of grassland management using fire on habitat occupancy and conservation of birds in a mosaic landscape. Biodiv. Conserv. 12, 1843-1860.

Pueyo, Y., Kéfi, S., Díaz-Sierra, R., Alados, C.L., Rietkerk, M., 2010. The role of reproductive plant traits and biotic interactions in the dynamics of semi-arid plant communities. Theor. Popul. Biol. 78, 289-297.

Pugnaire, F.I., Armas, C., Valladares, F., 2004. Soil as a mediator in plant-plant interactions in a semi-arid community. J. Veget. Sci. 15, 85-92.

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.

Puigdefábregas, J., 2005. The role of vegetation patterns in structuring runoff and sediment fluxes in drylands. Earth Surf. Process. Landf. 30, 133-147.

Puigdefábregas, J., Mendizábal, T., 1998. Perspectives on desertification: western Mediterranean. J. Arid Environ. 39: 209–224.

R Development Core Team, 2009. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, URL: http://www.R-project.org (accessed on 01.09.2011).

Raevel, V., Violle, C., Munoz, F., 2012. Mechanisms of ecological succession: insights from plant functional strategies. Oikos 121, 1761-1770.

Reidsma, P., Tekelenburg, T., van den Berg, M., Alkemade, R., 2006. Impacts of land-use change on biodiversity: An assessment of agricultural biodiversity in the European Union. Agric. Ecosyst. Environ. 114, 86-102.

Rey-Benayas, J. M., Martins, A., Nicolau, J. M., Schulz, J. J., 2007. Abandonment of agricultural land: an overview of drivers and consequences. CAB Reviews: Persp. in Agric. Vet. Sci., Nutrition & N. Resour. 2007, 2, 057, 14 pp. http://www.cabi.org/cabreviews/?loadmodule=review&page=4051&reviewid=33805&site=167 [accessed on 28/03/2013]

Richardson, F., 1965. Breeding and feeding habits of the Black Wheatear *Oenanthe leucura* in Southern Spain. Ibis 107, 1-16.

Rivas-Martínez, S. 1983. Pisos bioclimáticos de España. Lazaroa 5, 33-43.

Robles, A.B., Ruiz-Mirazo, J., Ramos, M.E., González-Rebollar, J.L., 2009. Role of Livestock Grazing in Sustainable Use, Naturalness Promotion in Naturalization of Marginal Ecosystems of Southeastern Spain (Andalusia), in Rigueiro-Rodríguez, A., McAdam, J., Mosquera-Losada, M.R. (Eds.), Agroforestry in Europe, Springer Netherlands, pp. 211-231.

Romanya, J, Rovira, P., Vallejo, R., 2007. Análisis del carbono en los suelos agrícolas de España. Aspectos relevantes en relación a la reconversión a la agricultura ecológica en el ámbito mediterráneo. Ecosistemas 16 (1), 50-57.

Romero-Díaz, A., 2003. Influencia de la litología en las consecuencias del abandono de tierras de cultivo en medios mediterráneos semiáridos. Papeles de Geografía 38, 151-165.

Romero-Díaz, A., Marín-Sanleandro, P., Sánchez-Soriano, A., Belmonte-Serrato, F., Faulkner, H., 2007. The causes of piping in a set of abandoned agricultural terraces in Southeast Spain. Catena 69, 282-293.

Romero-Díaz, A., Belmonte-Serrato, F., 2008. Erosión en forestaciones aterrazadas en medios semiáridos: Región de Murcia. Editum y Real Academia Alfonso X El Sabio, Murcia, 191 pp.

Romero-Díaz, A., 2010. Procesos de erosión y desertificación en ambientes semiáridos, in: Pillet, F., Cañizares M.C., Ruíz, A.R. (Eds.), Territorio, paisaje y sostenibilidad. Un mundo cambiante. Ediciones del Serbal, pp. 195-223.

Romero-Díaz, A., Ruíz-Sinoga. J.D., Belmonte-Serrato, F., 2011a. Tasas de erosión hídrica en la Región de Murcia. Bol. Asoc. Geógrafos Españoles 56, 129-153.

Romero-Diaz, A., Marín-Sanleandro, P., Sanchez-Soriano, A., 2011b. Procesos de piping en el paraje de Los Brianes-Corvera, in: Hernández Bastida, J. (Coord.), Recorridos por el Campo de Cartagena. Control de la degradación y uso sostenible del suelo. Instituto Euromediterráneo del Agua, pp. 57-71.

Romero-Díaz, M.A., Robledano, F., Belmonte, F., Zapata, V., Ruiz-Sinoga, J.D., 2012. Influencia del abandono de cultivos en los procesos de degradación de suelos en la Región de Murcia, in: Gonzalez, E. (coord.), Avances de la Geomorfología en España 2010-2012, Santander, Univ. Cantabria, pp 587-590.

Ruíz-Sinoga, J.D., Lucas-Santamaría, B., Romero-Lopera, A., Noguera-Robles, M.J., Gallegos-Reina, A. Márquez-Carrero, J., Martínez-Murillo, J.F., 2003. Determinación de la conductividad hidráulica en laderas mediante el uso de infiltrómetros de minidisco a lo largo de un gradiente pluviométrico mediterráneo, in: Álvarez-Benedi, J., Marinero, P. (Eds.), Estudios de la zona no saturada del suelo, vol. 4, 143-152.

Ruíz-Sinoga, J.D., Martinez-Murillo, J. F., Gabarron-Galeote, M. A., Garcia-Marin, R., 2011. The effects of soil moisture variability on the vegetation pattern in Mediterranean abandoned fields (Southern Spain). Catena 85, 1-11.

Rühl, J., Schnittler, M., 2011. An empirical test of neighborhood effect and safe-site effect in abandoned Mediterranean vineyards. Acta Oecol. 37, 71-78.

Russo, D., 2007. Effects of land abandonment on animal species in Europe: conservation and management implications. Integrated Assessment of vulnerable ecosystems under global change in the European Union. European Commission, Directorate – General for Research Environment, Luxembourg: Office for Official Publications of the European Communities, 53 pp.

Sánchez-Gómez, P., Carrión, M.A., Hernández, A., Guerra, J., 2002. Libro Rojo de la Flora Silvestre Protegida de la Región de Murcia. Dirección General del Medio Natural, Región de Murcia, Spain.

Sánchez Gómez, P., Guerra, J. (Eds.), 2007. Nueva Flora de Murcia: Plantas Vasculares, 2nd ed. Diego Marín Librero Editor, Murcia, Spain.

Sánchez, A.M., Peco, B., 2002. Dispersal mechanisms in *Lavandula stoechas* subsp. pedunculata: autochory and endozoochory by sheep. Seed Sci. Res. 12, 101-111.

Sánchez-Oliver, J.S., Rey-Benayas, J.M., Carrascal, L.M., 2014. Differential effects of local habitat and landscape characteristics on bird communities in Mediterranean afforestations motivated by the EU Common Agrarian Policy. Eur. J. Wildl. Res. 60, 135-143.

Sandom, C.J., Hughes, J., Macdonald, D.W., 2013. Rewilding the Scottish Highlands: Do Wild Boar, *Sus scrofa*, Use a Suitable Foraging Strategy to be Effective Ecosystem Engineers? Restor. Ecolo. 21, 336-343.

Santana, V., Baeza, J. M., Marrs, R., Vallejo, R.V., 2010. Old-field secondary succession in SE Spain: can fire divert it? Plant Ecol. 211, 337-349.

Sekercioglu, C.H., 2006. Increasing awareness of avian ecological function. Trends Ecol. Evol. 21, 464-471.

Shochat, E., Abramsky, Z., Pinshow, B., 2001. Breeding bird species diversity in the Negev: effects of scrub fragmentation by planted forests. J. Appl. Ecol. 38, 1135-1147.

Sirami, C., Brotons, L., Martin, J.-L., 2007. Vegetation and songbird response to land abandonment: from landscape to census plot. Divers. Distrib. 13, 42-52.

Sirami, C., Brotons, L., Burfield, I., Fonderflick, J., Martin, J.-L., 2008. Is land abandonment having an impact on biodiversity? A meta-analytical approach to bird distribution changes in the north-western Mediterranean. Biol. Conserv. 141, 450-459.

Sirami, C., Nespoulous, A., Cheylan, J.-P., Marty, P., Hvenegaard, G.T., Geniez, P., Schatz, B., Martin, J.-L., 2010. Long-term anthropogenic and ecological dynamics of a Mediterranean landscape: Impacts on multiple taxa. Landsc. Urb. Plan. 96, 214-223.

Sitzia, T., Semenzato, P., Trentanovi, G., 2010. Natural reforestation is changing spatial patterns of rural mountain and hill landscapes: A global overview. For. Ecol. Manage., 259: 1354-1362.

Sougnez, N., van Wesemael, B., Vanacker, V., 2011. Low erosion rates measured for steep, sparsely vegetated catchments in southeast Spain. Catena 84, 1-11.

Suárez, F., Sainz, H., Santos, T., González, F., 1991. Las Estepas Ibéricas. MOPT, Madrid, 160 pp.

Trimble, S.W., 1990. Geomorphic effects of vegetation cover and management: Some time and space considerations in prediction of erosion and sediment yield, in: Thornes, J. (Ed.), Vegetation and Erosion, Processes and Environments. Wiley, London, pp. 55-65.

Tzanopoulos, J., Mitchley, J., Pantis, J.D., 2007. Vegetation dynamics in abandoned crop fields on a Mediterranean island: Development of succession model and estimation of disturbance thresholds. Agric. Ecosyst. Environ. 120, 370-376.

Valdecantos, A., Cortina, J., Vallejo, V.R., 2006. Nutrient status and field performance of tree seedlings planted in Mediterranean degraded areas. Ann. For. Sci. 63, 249-256.

Vallecillo, S., Brotons, L.S., Herrando, S., 2008. Assessing the response of open-habitat bird species to landscape changes in Mediterranean mosaics. Biodiv. Conserv. 17, 103-119.

Vallejo, R., Aronson, J., Pausas, J. G., Cortina, J., 2005. Restoration of Mediterranean woodlands, in: Van Andel, J. & Aronson, J. (Eds.), Restoration ecology: a European perspective. Blackwell Sci., Oxford.

Vallejo, V.R., Smanis, A., Chirino, E., Fuentes, D., Valdecantos, A., Vilagrosa, A., 2012. Perspectives in dryland restoration: approaches for climate change adaptation. New Forests 43, 561-579.

Van der Putten, W.H., Mortimer, S.R., Hedlund, K., Van Dijk, C., Brown, V.K., Lepä, J., Rodriguez-Barrueco, C., Roy, J., Diaz Len, T.A., Gormsen, D., Korthals, G.W., Lavorel, S., Regina, I.S., Smilauer, P., 2000. Plant species diversity as a driver of early succession in abandoned fields: a multi-site approach. Oecologia, 124: 91-99.

Verstraeten, G., Poesen, J., de Vente, J., Koninckx, X., 2003. Sediment yield variability in Spain: a quantitative and semiqualitative analysis using reservoir sedimentation rates. Geomorphology, 50, 327-348.

Wiens, J.A., 1989. The ecology of bird communities. Cambridge University Press, Cambridge, UK.

Zapata, V.M., Robledano, F. (in press). Assessing biodiversity and conservation value of forest patches secondarily fragmented by urbanization in semiarid Southeastern Spain. J. Nat. Conserv. http://dx.doi.org/10.1016/j.jnc.2013.11.002

Zaragozí, B., Rabasa, A., Rodríguez-Sala, J.J., Navarro, J.T., Belda, A., Ramón, A., 2012. Modelling farmland abandonment: A study combining GIS and data mining techniques. Agric. Ecosyst. Environ. 155, 124-132.

Zhang, R., 1997. Determination of soil Sortivity and Hydraulic Conductivity from the Disk Infiltrometer. Soil Sci., 61: 1024-1030.

Figure captions

Figure 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).

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

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

Figure 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 (LRFS) index; lower left, richness of facilitator/nurse plants; lower right, richness of inhibitor/competitor plants.

Figure 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.

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

Figure 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 abandonment age classes.

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Tables

Table 1. Expected positive and negative (+/-) 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	(-) Homogeneization and loss of open habitats	Expansion of sub-desert xerosteppes (Martínez-Fernández & Esteve, 2010) Shrub encroachment (Maestre et al., 2009; Nainggolan et al., 2012)
	(+) Mosaic heterogeneity	Increase of dense forest patches and connectivity (Nainggolan et al., 2012)
Soils	(-) Erosion and desertification	Important in less coherent soils (i.e. marls), intense sub-surface erosion phenomena (piping) (López-Bermúdez & Romero-Díaz, 1989; López-Bermúdez et al., 1998)
	(+) Edaphic recovery and improvement	More stable and even progressive situations in other substrate types (Faulkner et al., 2003; Bonet, 2004)
Soil water	(-) Availability and holding capacity	Increased consumption by vegetation, reduced infiltration (García-Ruiz & Lana-Renault, 2011; Otero et al. 2011)
	(+) Quality and regulation	Increase of holding capacity, improved quality (Navarro & Pereira, 2012; Zaragozí et al., 2012)
Biodiversity	(-) Decrease of non-forest components	Degradation of grasslands and loss of steppic animal components (Moreira, 1999; Moreira & Russo, 2007)
	(+) Increase of forest components	Increase of carnivores and forest birds, especially euro-siberian elements (Sirami et al., 2010; Pita et al. 2009)
Aestetic, cultural and socioeconomic aspects	(-) Loss of cultural value	Loss of scenic and cultural value associated to traditional management (Sitzia et al., 2010; Navarro & Pereira, 2012)
	(+) Increase of economic income	Increased attraction for ecotourism and hunting (Sitzia et al., 2010; Navarro & Pereira, 2012)

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 (ºC)	16 ºC	18 ºC	18 ºC
PET (mm)	800	950	950
Bioclimatic classification[1]	(Lower=warm) Mesomediterranean	(Upper) Termomediterranean	(Upper) Termomediterranean

(1) Rivas-Martínez (1983)

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; VC: Very common.

	BIRDS				**FLORA**	
VALUE	**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

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) **(MAR**)	Cultivated fields (C)	23.0	51.7	8.0	17.3	0.87	8.5
	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) **(LIM**)	Cultivated fields (C)	11.0	30.9	39.6	18.5	1.46	48.4
	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) **(MET**)	Cultivated fields (C)	10.5	27.9	26.6	35.0	1.66	38.7
	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

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 1x1 UTM squares).

	CORVERA (marls)			**LA MURTA (limestone)**				**LA FUENSANTA (metamorphic)**			
Especies:	**Forest (Model)**	**Forest (Local)**	**Ancient oldfields**	**Forest (Model)**	**Forest (Local)**	**Ancient oldfields**	**Recent oldfields**	**Forest (Model)**	**Forest (Local)**	**Ancient oldfields**	**Recent oldfields**
Rhamnus lycioides	+	-	-	+	+	+	-	+	+	+	+
Chamaerops humilis	+	-	-	+	-	-	-	+	-	-	-
Pistacia lentiscus	+	-	-	+	+	+	-	+	+	+	+
Quercus coccifera	+	-	-	+	-	-	-	+	+	+	-
Juniperus oxycedrus	+	-	-	+	-	-	-	+	+	+	-
Juniperus phoenicea	+	-	-	+	-	-	-	+	-	-	-

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&G= Rill and Gully erosion.

		LITHOLOGY		
		MARLS	**LIMESTONES**	**METAMORPHIC**
Flora	**Composition**	Lowest species richness Dominance of small shrubs (non-endozoochorus)	Intermediate species richness (increasing in ancient abandonment) Strictly progressive succession pattern	Highest species richness (chamaephytes and nanophanerophytes) = in both ages, but species turnover
	Structure	Steppic physiognomy >50% bare soil (AA) Dominance of tussock-forming and other perennial grasses	Bare soil < 40% (AA) Dominance of small shrubs and chamaephytes More annuals	Bare soil < 40% (AA) Dominance of small shrubs and chamaephytes More tree canopy
	Function	High occurrence of positive interactions (facilitation) Intermediate herbivory Effective dispersal of fleshy-fruited species	Higher occurrence of negative interactions (inhibition/competition) Intense herbivory (-) Safe site effect (margins)	High occurrence of positive interactions (facilitation, perch effect) Lower herbivory Effective dispersal of fleshy-fruited species
	Conservation value	High for frequency of Red Data Book species *Genista cinerea* (LRFS)	Lowest	High for frequency of management-regulated species (LRFS+Use)
Fauna	**Composition**	Higher density (winter) Species seasonal turnover	Intermediate density and species richness	Maximum density (breeding) and species richness
	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 Higher forest bird component
	Function	High winter dispersal potential	Lower dispersal potential	High winter dispersal potential
	Conservation value	High for SPEC and RBBS (breeding) and marginally for BDIR (wintering)	Lower in most cases (higher in recent abandonment)	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

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Figure captions

Figure 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).

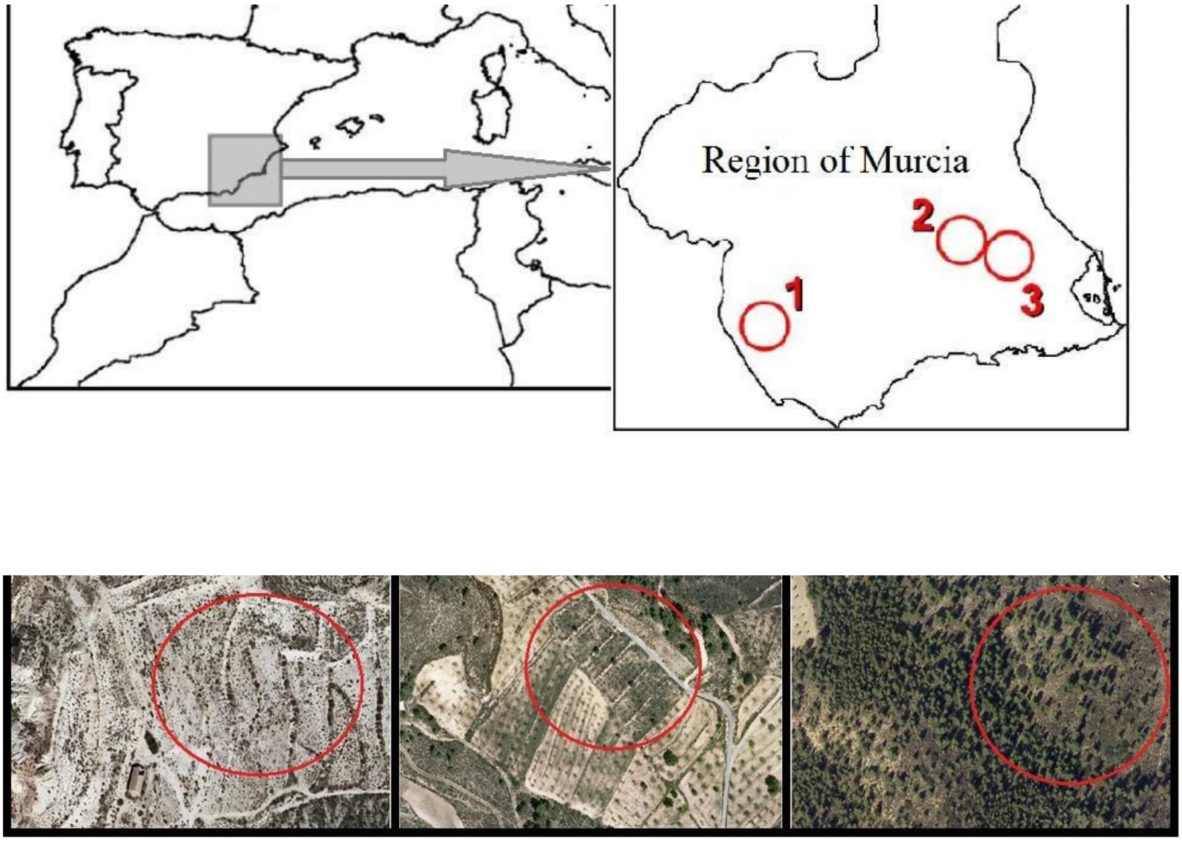

Figure 2. Examples of *piping* processes in oldfields of the pilot area of Corvera (MAR).

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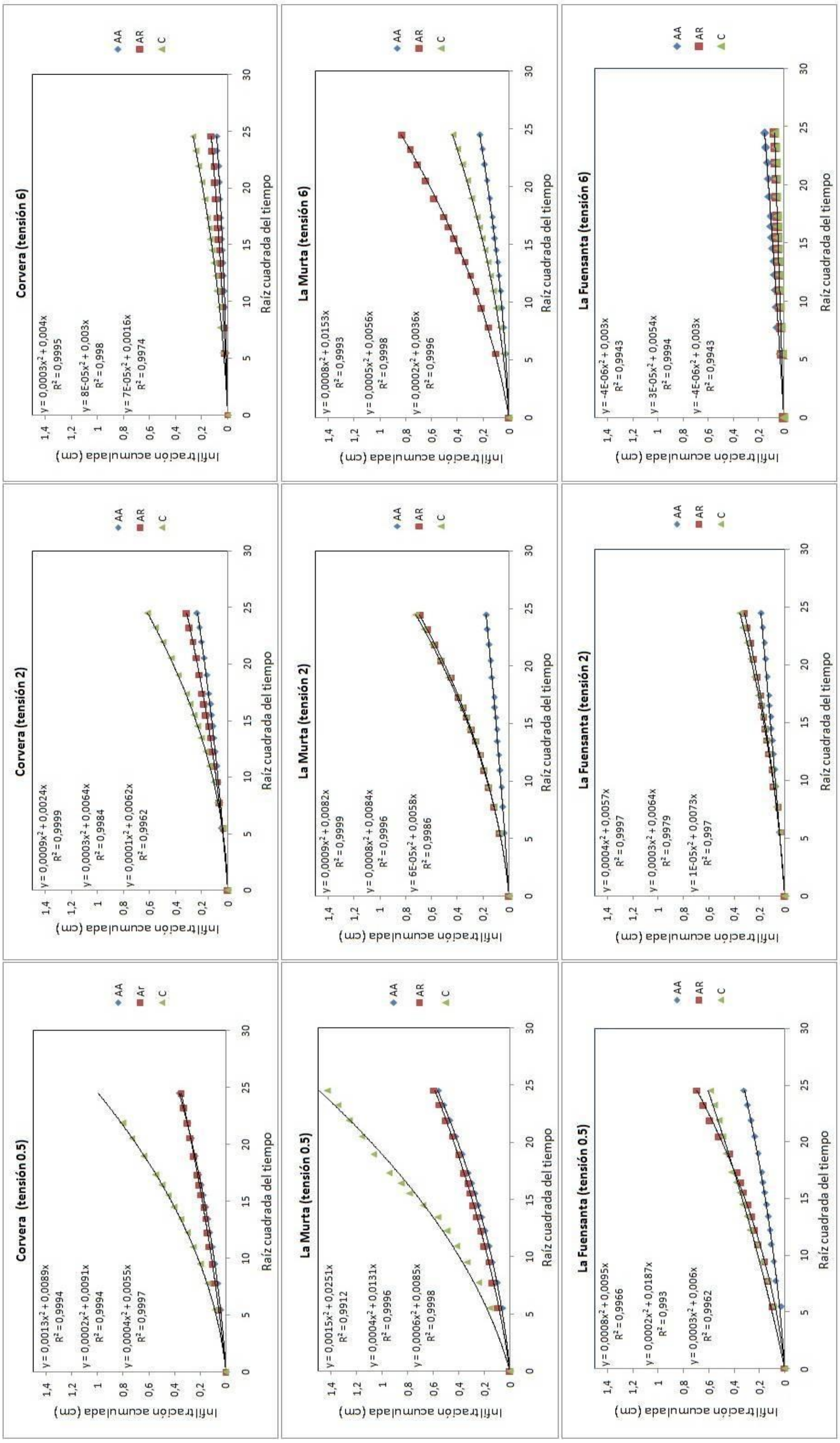

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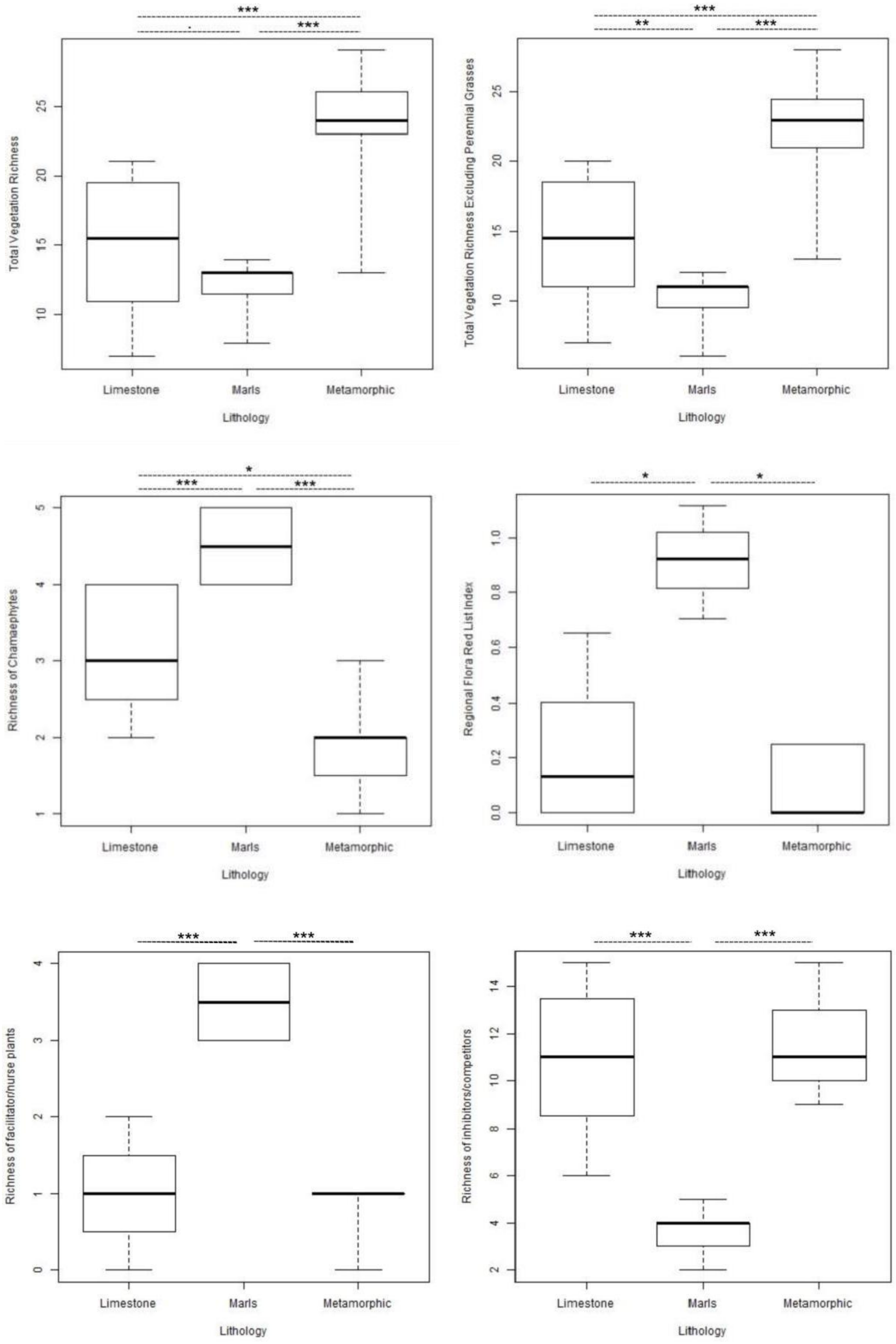

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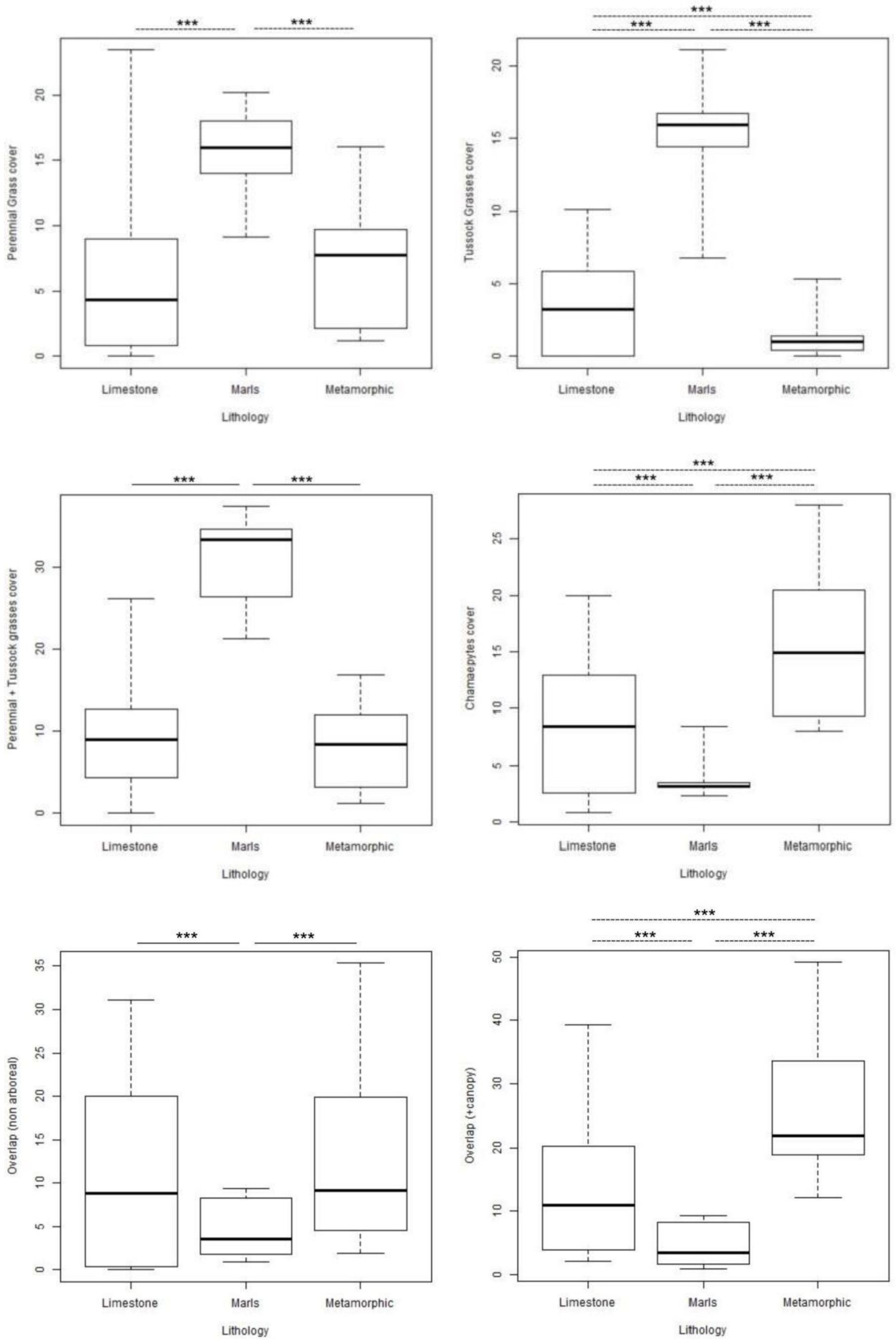

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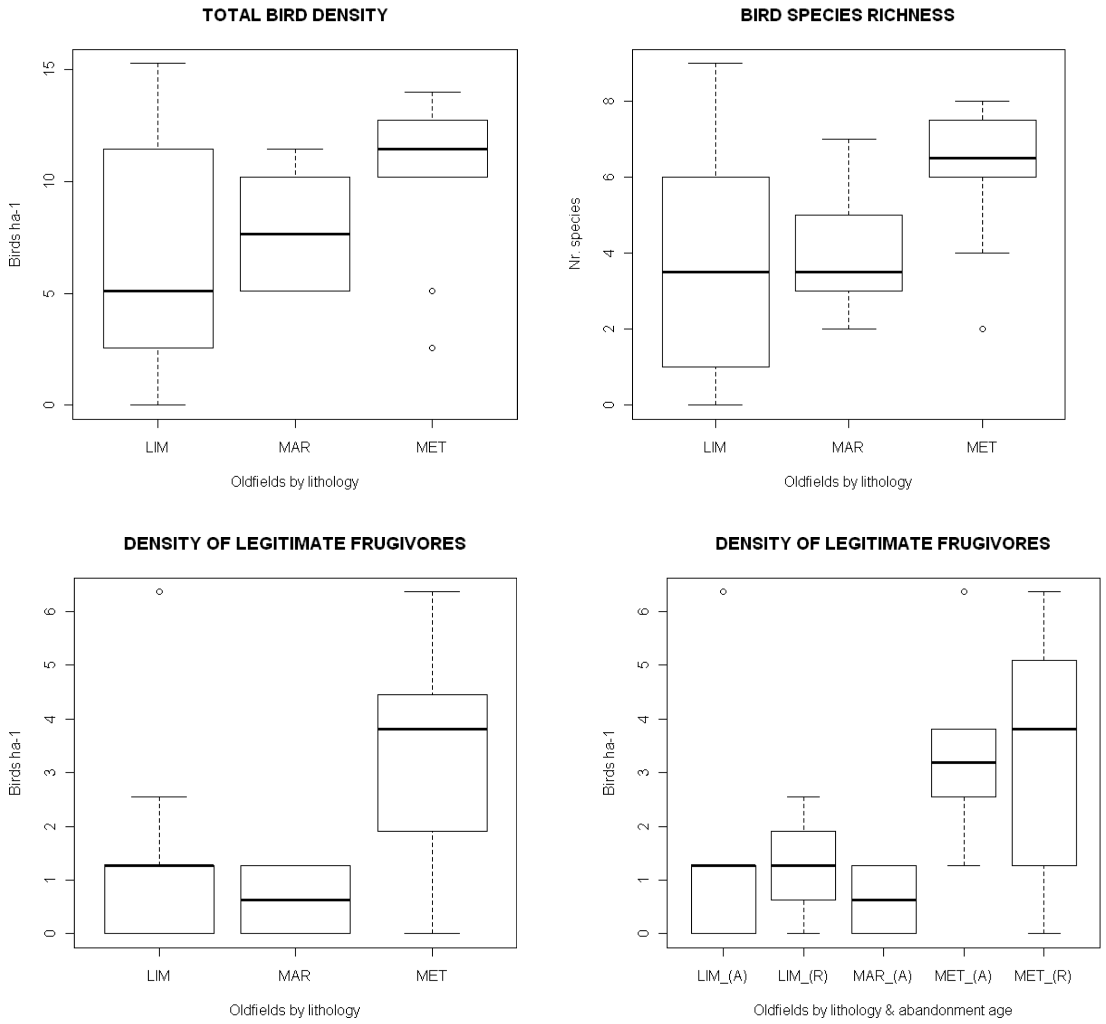

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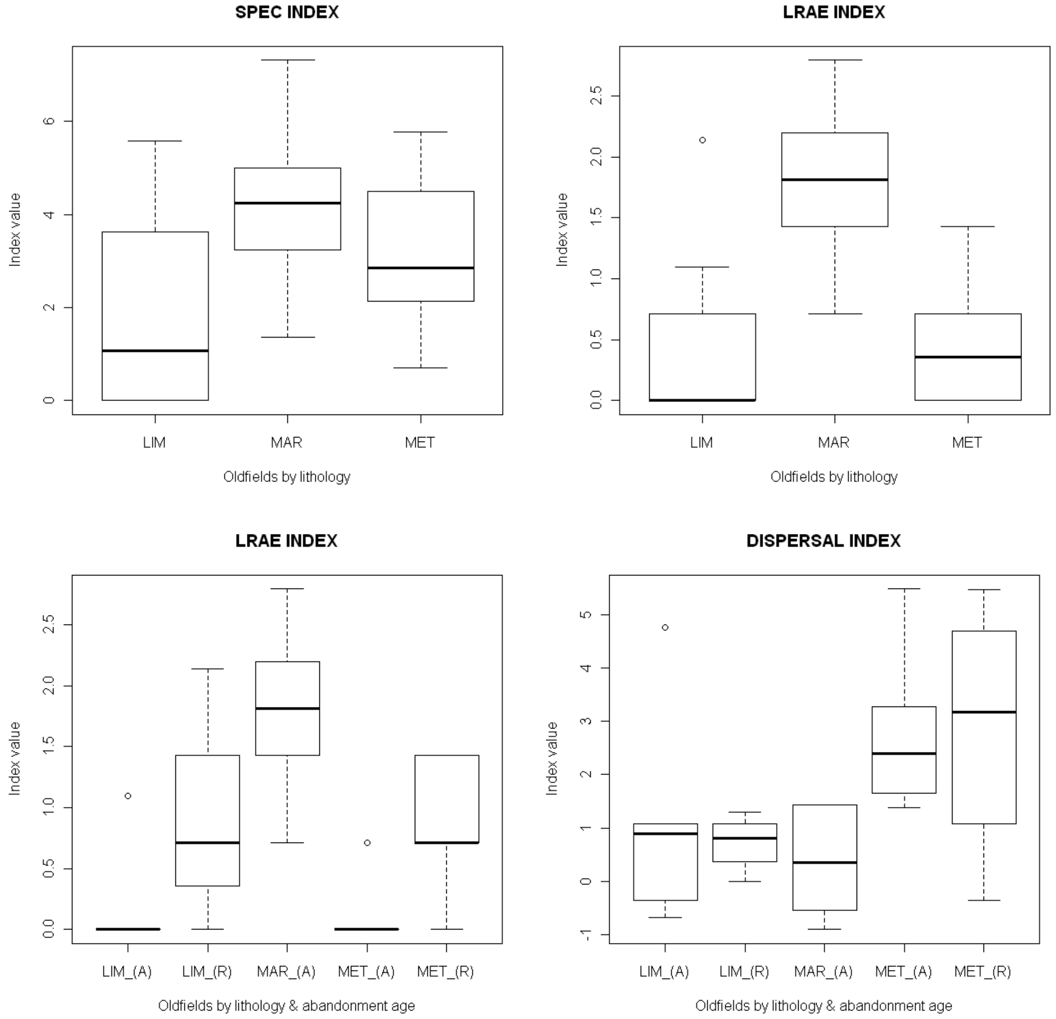

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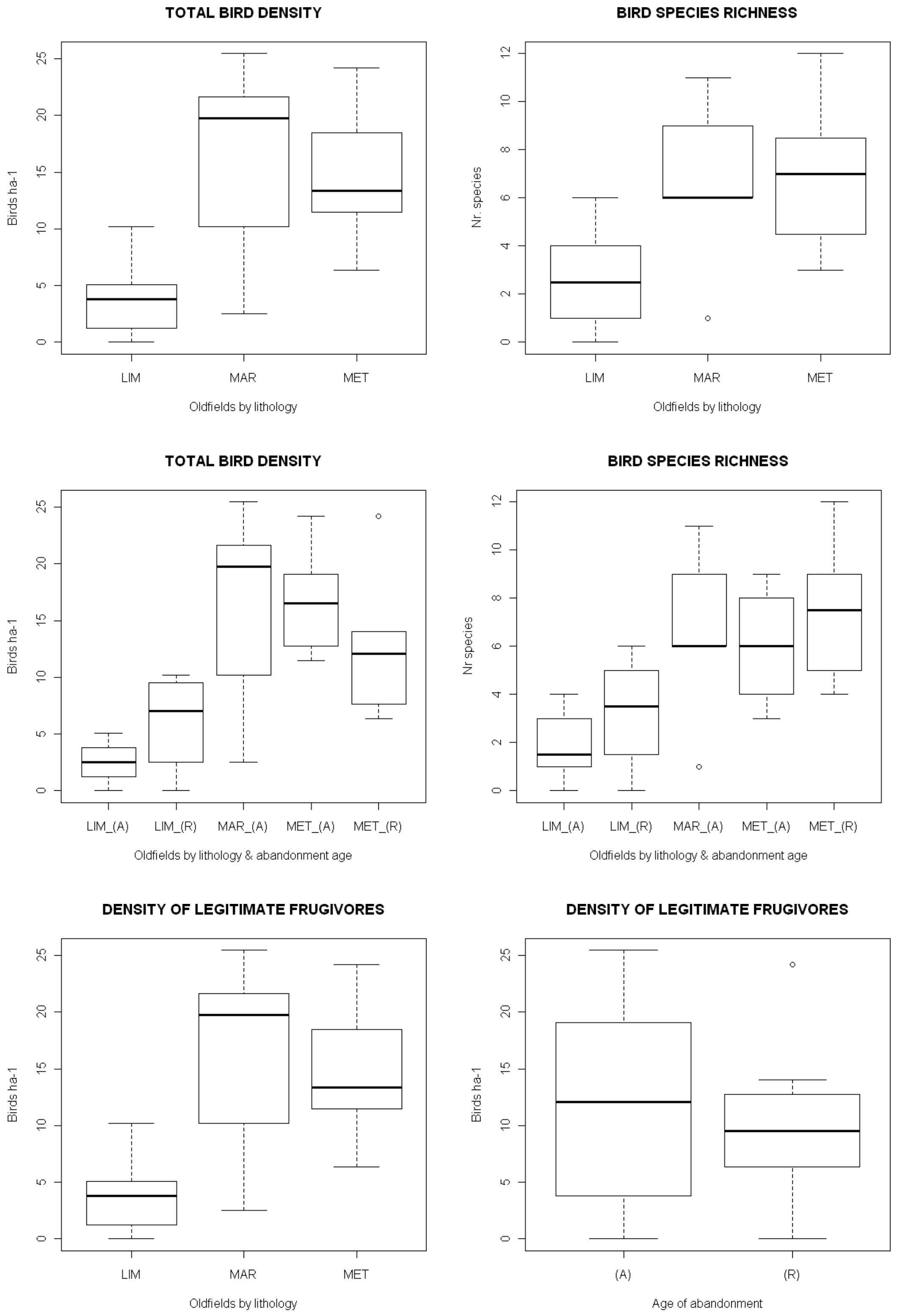
Figure 8. Box-plots representing wintering bird community indexes displaying significant differences (Kruskal-Wallis non parametric analysis of variance) among lithology and abandonment age classes.



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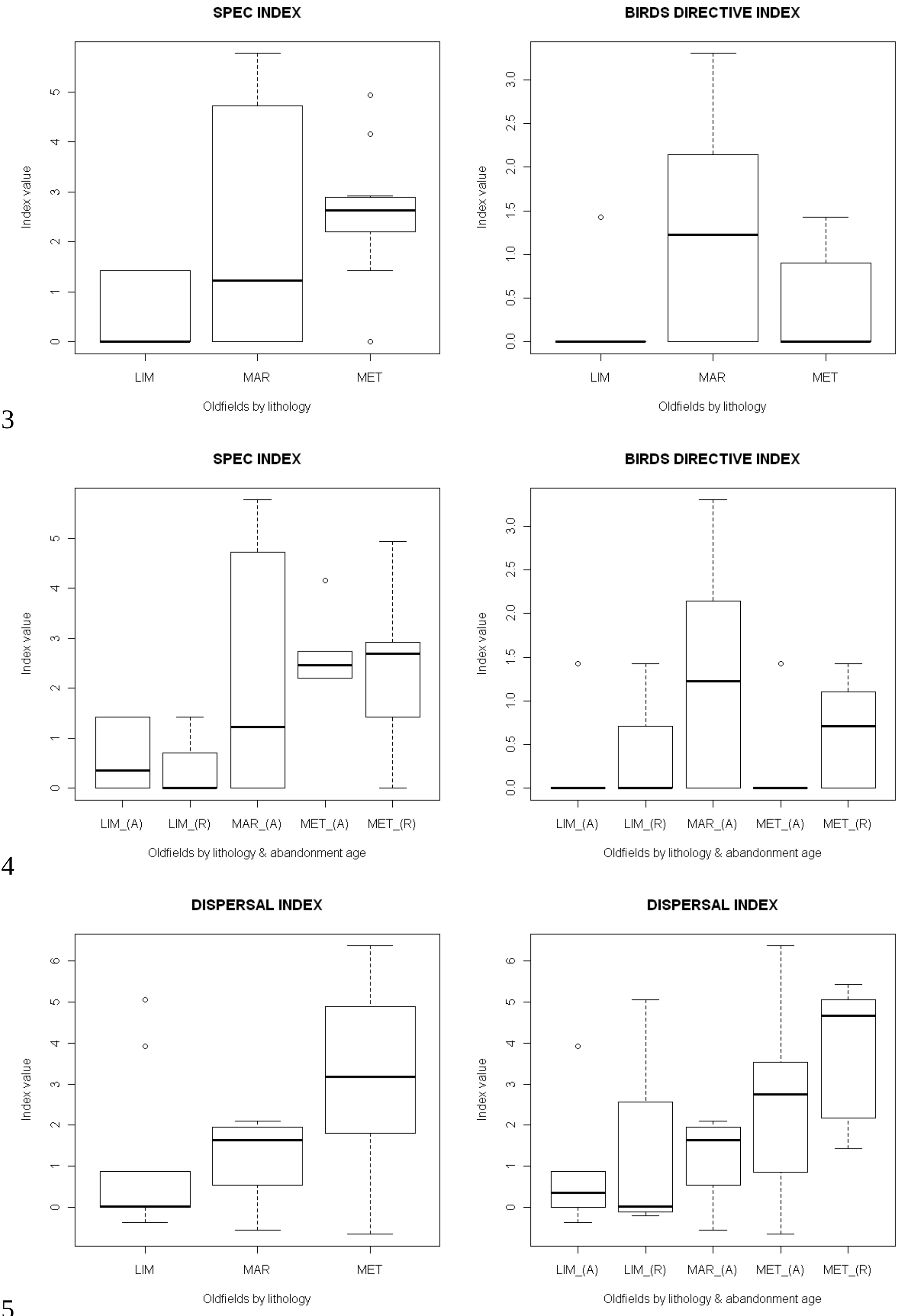

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Supplementary material

Annex 1. Full list of woody plant species represented in pilot areas classified according to the characteristics used for their structural and functional typification: Life forms: TRE=trees; CHA=chamaephytes; NFN=nanophanerophytes; CLI=climbers; SSH=small shrubs; PGR=perennial grasses. Main dispersal mode: ANE=anemochorous; BAR=barochorous (autochorous included; Raevel *et al*., 2012); ENZ=endozoochorous; ECZ=ectozoochorous. Main interaction mode: FA=nurse (facilitator); IC=inhibitor or competitor; NE=neutral or unknown. The table also includes the scores assigned to the species in the calculation of conservation value indexes. Characterization is made from the literature (Gómez-Aparicio *et al*., 2004; Aparicio *et al*., 2008; Bonet & Pausas, 2004; Manzano *et al*., 2005; Sánchez & Peco, 2002) and from personal observations of the species' mutual relationships in the study areas (due to variable effects, perennial grasses are not characterized regarding interaction mode).

Species	**Life form**	**Dispersal mode**	**Interaction mode**	**RARE index score**	**RBWP index score**
Anthyllis cytisoides	SSH	BAR+ENZ	IC	0	0
Artemisia barrelieri	CHA	ANE	IC	0	2
Artemisia campestris	CHA	ANE	IC	0	2
Asparagus acutifolius	CLI	ENZ	NE	0	2
Asparagus albus	CHA	ENZ	NE	0	2
Asparagus horridus	CHA	ENZ	NE	0	2
Brachypodium retusum	PGR	ECZ	-	0	0
Cistus albidus	SSH	BAR	IC	0	0
Cistus clusii	CHA	BAR	IC	0	0
Daphne gnidium	NFN	ENZ	NE	0	2
Dittrichia viscosa	SSH	ANE	IC	0	0
Dorycnium pentaphyllum	CHA	BAR	FA	0	0
Ephedra fragilis	SSH	ENZ	FA	0	2
Fumana ericoides	CHA	BAR	IC	0	2
Fumana laevipes	CHA	BAR	IC	0	4
Fumana thymifolia	CHA	BAR	IC	0	0
Genista cinerea	SSH	BAR	FA	4	6
Hammada articulata	SSH	BAR	FA	0	2
Helianthemum almeriense	CHA	BAR	IC	0	0
Helianthemum syriacum	CHA	BAR	IC	0	2
Helichrysum stoechas	CHA	ANE	IC	0	2
Juniperus oxycedrus	NFN	ENZ	IC	2+1	2
Lavandula stoechas	CHA	BAR+ENZ	IC	0+1	4
Lygeum spartum	PGR	ANE	-	0	0
Olea europaea var. sylvestris	NFN	ENZ	NE	0+1	0
Onobrychis stenhoriza	CHA	BAR	NE	0	4
Phagnalon rupestre	CHA	ANE	NE	0	2

Species	**Life form**	**Dispersal mode**	**Interaction mode**	**RARE index score**	**RBWP index score**
Phagnalon saxatile	CHA	ANE	NE	0	2
Phlomis lychnitis	CHA	ANE	NE	0	2
Pinus halepensis	TRE	ANE	IC	0+1	0
Pistacia lentiscus	NFN	ENZ	NE	0+1	2
Plantago albicans	CHA	BAR+ECZ	NE	0	2
Polygala rupestris	CHA	BAR	NE	0	2
Quercus coccifera	NFN	ECZ	IC	0+1	2
Retama sphaerocarpa	SSH	ANE+ENZ	FA	0	0
Rhamnus alaternus	NFN	ENZ	NE	2+1	4
Rhamnus lycioides	NFN	ENZ	NE	0+1	2
Rosmarinus officinalis	CHA	BAR	IC	0	0
Rubia peregrina	CLI	ENZ	NE	0	2
Salsola genistoides	SSH	ANE	FA	0	0
Santolina viscosa	CHA	ANE	IC	2+1	4
Satureja obovata	CHA	ANE	IC	0+1	2
Sedum sediforme	CHA	BAR	NE	0	0
Staehelina dubia	CHA	ANE	NE	0	4
Stipa tenacissima	PGR	ANE	-	0	0
Teucrium capitatum	CHA	BAR	IC	0	2
Teucrium carolipaui	CHA	BAR	IC	0	4
Teucrium rivasii	CHA	BAR	IC	2	6
Thymelaea hirsuta	SSH	BAR	IC	0	2
Thymus hyemalis	CHA	BAR	IC	0+1	2
Thymus mastichina	CHA	BAR	IC	0+1	4

Annex 2. List of woody plant species represented in pilot areas showing their representation in oldfields of different age and in their corresponding peripheral reference (forest) areas. Presence values are based only on the inclusion in sampling plots. For fleshy-fruited nanerophytes and spontaneous trees, their observation outside samples is denoted (P).

Area	COR_A	COR_F	MUR_R	MUR_A	MUR_F	FUE_R	FUE_A	FUE_F
Lithology	MAR	MAR	LIM	LIM	LIM	MET	MET	MET
Age since abandonment	Ancient	Forest	Recent	Ancient	Forest	Recent	Ancient	Forest
Year	2011-13	2013	2011-13	2011-13	2013	2011-13	2011-13	2013
Anthyllis cytisoides		+	+	+	+	+	+	+
Artemisia barrelieri			+	+		+	+	
Artemisia campestris	+		+	+	+	+	+	+
Asparagus acutifolius				+	+	+	+	P
Asparagus albus						+	+	P
Asparagus horridus	+	+	+	+	+	+	+	P
Brachypodium retusum	+	+			+	+	+	+
Cistus albidus						+	+	+
Cistus clusii					+			
Daphne gnidium						+	+	P
Dittrichia viscosa			+	+		+		
Dorycnium pentaphyllum		+	+	+	+	+	+	+
Ephedra fragilis					+			
Fumana ericoides		+		+		+	+	
Fumana laevipes							+	
Fumana thymifolia	+	+		+	+	+	+	+
Genista cinerea	+	+	+	+	+			
Hammada articulata	+							
Helianthemum almeriense	+	+	+	+	+	+	+	+
Helianthemum syriacum	+	+	+	+	+	+	+	
Helichrysum stoechas			+	+		+	+	+
Juniperus oxycedrus							+	P
Lavandula stoechas						+	+	
Lygeum spartum	+		+	+		+	+	
Olea europaea var. sylvestris		+		+	+	+	+	P
Onobrychis stenhorriza		+						
Phagnalon rupestre	+			+	+	+	+	
Phagnalon saxatile	+	+	+	+	+	+	+	+
Phlomis lychnitis						+	+	+
Pinus halepensis		+		P	+	+	+	+
Pistacia lentiscus				P	P	+	+	+
Plantago albicans	+		+	+		+	+	
Polygala rupestris					+	+	+	+
Quercus coccifera							+	+
Retama sphaerocarpa	+							
Rhamnus alaternus					+			
Rhamnus lycioides				+	+	+	+	+
Rosmarinus officinalis				+	+	+	+	+
Rubia peregrina						+	+	+
Salsola genistoides	+	+						
Santolina viscosa			+	+				
Satureja obovata	+		+	+	+	+	+	
Sedum sediforme	+					+	+	+

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Area	COR_A	COR_F	MUR_R	MUR_A	MUR_F	FUE_R	FUE_A	FUE_F
Lithology	MAR	MAR	LIM	LIM	LIM	MET	MET	MET
Age since abandonment	Ancient	Forest	Recent	Ancient	Forest	Recent	Ancient	Forest
Year	2011-13	2013	2011-13	2011-13	2013	2011-13	2011-13	2013
Staehelina dubia						+	+	+
Stipa tenacissima				+	+	+	+	+
Teucrium capitatum		+	+	+	+	+	+	+
Teucrium carolipaui				+				
Teucrium rivasii				+				
Thymelaea hirsuta	+		+	+	+	+		
Thymus hyemalis	+	+	+	+	+	+	+	+
Thymus mastichina						+		
Total woody species richness (excluding those marked with ‘P’)	**18**	**16**	**18**	**28**	**25**	**37**	**37**	**21**

Annex 3. Mean values of compositional and structural variables based on flora and vegetation samples from the studied oldfields.

		MEAN±SE				
Var description:		**COR_A**	**MUR_A**	**MUR_R**	**FUE_A**	**FUE_R**
Lithology		Marls	Limestone	Limestone	Metamorphic	Metamorphic
Abandonment age		Ancient	Ancient	Recent	Ancient	Recent
Year		2011-13	2011-13	2011-13	2011-13	2011-13
TOTAL RICHNESS	R_TOT	18.00±0.67	28.00±0.62	18.00±0.74	37.00±0.80	37.00±1.82
TOTAL RICHNESS (excluding perennial grasses)	R_EPG	16.00±0.67	26.00±0.63	17.00±0.69	34.00±0.78	34.00±1.53
Richness of Nanophanerophytes	R_NFN	0.00±0.00	2.00±0.13	0.00±0.00	6.00±0.35	4.00±0.64
Richness of Small shrubs	R_SSH	5.00±0.19	4.00±0.35	4.00±0.19	2.00±0.00	4.00±0.31
Richness of Chamaephytes	R_CHA	11.00±0.60	19.00±0.46	13.00±0.55	24.00±0.48	23.00±0.84
Richness of Climbers	R_CLI	0.00±0.00	1.00±0.13	0.00±0.00	2.00±0.16	2.00±0.32
Richness of Trees (spontaneous)	R_TRE	0.00±0.00	0.00±0.00	0.00±0.00	1.00±0.00	1.00±0.00
Richness of Perennial grasses	R_PGR	2.00±0.00	2.00±0.16	1.00±0.16	3.00±0.25	3.00±0.32
Mean frequency of of Nanophanerophytes	MF_NFN	0.00±0.00	0.09±0.00	0.00±0.00	0.31±0.02	0.18±0.04
Mean frequency of of small shrubs	MF_SSH	0.45±0.02	0.53±0.06	0.42±0.04	0.41±0.05	0.18±0.08
Mean frequency of of Chamaephytes	MF_CHA	0.22±0.05	0.32±0.01	0.30±0.03	0.32±0.01	0.31±0.03
Mean frequency of of Climbers	MF_CLI	0.00±0.00	0.02±0.02	0.00±0.00	0.39±0.05	0.22±0.08
Mean frequency of trees (spontaneous)	MF_TRE	0.00±0.00	0.00±0.00	0.00±0.00	0.83±0.00	0.33±0.00
Mean frequency of of Perennial grasses	MF_PGR	0.87±0.04	0.38±0.04	0.04±0.03	0.15±0.03	0.10±0.04
Richness of Anemochorous species	R_ANE	6.00±0.26	10.00±0.46	8.00±0.33	11.00±0.31	12.00±0.27
Richness of Barochorous species	R_BAR	8.00±0.33	12.00±0.38	7.00±0.41	12.00±0.33	13.00±0.71
Richness of Endozoochorous species	R_ENZ	1.00±0.00	4.00±0.16	1.00±0.18	9.00±0.35	8.00±1.06
Richness of Ectozoochorous species	R_ECZ	1.00±0.00	0.00±0.00	0.00±0.00	2.00±0.18	1.00±0.18
Richness of Anemochorous and endozoochorous species	R_ANE+ENZ	1.00±0.19	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Richness of Barochorous and endozoochorus species	R_BAR+ENZ	0.00±0.00	1.00±0.00	1.00±0.00	3.00±0.13	2.00±0.18
Richness of Barochorous and ectozoochorus species	R_BAR+ECZ	1.00±0.16	1.00±0.19	1.00±0.19	1.00±0.13	1.00±0.13
Mean frequency of Anemochorous species	MF_ANE	0.47±0.04	0.31±0.02	0.32±0.03	0.32±0.01	0.32±0.03
Mean frequency of Barochorous species	MF_BAR	0.24±0.02	0.36±0.02	0.30±0.05	0.42±0.02	0.28±0.03
Mean frequency of Endozoochorous species	MF_ENZ	0.75±0.03	0.12±0.01	0.06±0.03	0.30±0.01	0.17±0.04
Mean frequency of Ectozoochorous species	MF_ECZ	0.80±0.06	0.00±0.00	0.00±0.00	0.22±0.06	0.08±0.04
Mean frequency of Anemochorous and endozoochorous species	MF_ANE and ENZ	0.05±0.02	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Mean frequency of Barochorous and endozoochorus species	MF_BAR and ENZ	0.00±0.00	0.94±0.04	0.65±0.02	0.19±0.08	0.13±0.10
Mean frequency of Barochorous and ectozoochorus species	MF_BAR and ECZ	0.08±0.05	0.27±0.13	0.29±0.13	0.02±0.02	0.48±0.12
Richness of facilitator/nurse plants	R_FA	4.00±0.19	2.00±0.19	2.00±0.19	1.00±0.00	1.00±0.16
Richness of inhibitors/competitors	R_IC	7.00±0.32	17.00±0.45	12.00±0.53	19.00±0.55	18.00±0.23
Richness of neutral/unknown	R_NE	5.00±0.33	7.00±0.25	3.00±0.25	15.00±0.46	15.00±1.46
Mean frequency of facilitator/nurse plants	MF_FA	0.43±0.02	0.15±0.01	0.04±0.03	0.67±0.05	0.42±0.09
Mean frequency of inhibitor/competitor species	MF_IC	0.26±0.04	0.42±0.02	0.41±0.03	0.35±0.02	0.33±0.02
Mean frequency of neutral/unknown species	MF_NE	0.23±0.06	0.13±0.03	0.22±0.09	0.30±0.01	0.20±0.03
Bare soil cover (%)	C_BS	51.20±2.00	35.57±1.38	36.48±2.33	34.42±1.45	39.04±2.38

				MEAN±SE		
Var description:		**COR_A**	**MUR_A**	**MUR_R**	**FUE_A**	**FUE_R**
Rocks cover (%)	C_RO	0.27±0.17	1.92±0.40	0.50±0.12	1.62±0.22	4.73±0.49
Leaf litter cover (%)	C_LL	8.14±1.63	26.56±4.83	26.74±8.01	28.41±2.84	19.29±3.99
Perennial grass (*Brachypodium*) cover (%)	C_PG	15.66±1.23	5.11±1.44	6.69±2.86	3.78±1.77	10.00±0.95
Tussock grasses (*Stipa*, *Lygeum*) cover (%)	C_TG	15.26±1.43	6.30±0.80	0.34±0.34	0.84±0.14	1.56±0.61
Chamaephytes cover (%)	C_CH	3.76±0.69	12.30±1.84	4.63±1.40	17.28±2.28	14.21±2.34
Shrubs cover (%)	C_SH	4.14±0.31	16.13±2.04	9.26±3.90	28.89±2.52	5.31±0.79
Lichens and mosses cover (%)	C_LM	0.17±0.11	0.73±0.41	0.45±0.43	0.09±0.04	0.39±0.13
Annuals cover (%)	C_AN	6.06±2.19	12.44±4.83	20.66±9.01	1.21±0.50	15.80±5.83
Tree canopy cover (%)	C_TC	0.00±0.00	1.42±0.63	4.57±1.29	12.88±0.82	13.31±1.44
Perennial+Tussock grass cover (%)	C_BS	30.92±1.98	11.42±1.03	7.03±3.15	4.62±1.78	11.56±1.09
Overlap of non arboreal cover	OV_NA	4.65±1.23	17.06±3.24	5.75±3.78	16.54±3.30	10.32±4.25
Overlap (including canopy)	OV_TOT	4.65±1.23	18.48±3.26	10.32±4.33	29.41±3.86	23.64±4.46
Regional Flora Red List Index	LRFS	0.92±0.05	0.32±0.08	0.07±0.05	0.21±0.03	0.00±0.00
Reg. Flora Red List+Use Index	LRFS+USE	1.08±0.06	0.58±0.10	0.15±0.07	1.31±0.07	0.56±0.07
Regional Flora Rarity Index	RARE	3.48±0.13	4.26±0.21	2.70±0.20	4.78±0.25	4.12±0.31

Annex 4. Results of GLMMs relating floristic and vegetation variables with lithology and age classes considered separately (in the case of marly substrates, only ancient oldfields were sampled). In each column, the positive or negative effect of the first class of the predictor with regard to the second is indicated by the sign of the coefficient, and significance levels as 0.001 (***), 0.01 (**), 0.05 (*) and 0,1 (.).

			Lithology			**Age**
Variable	**Description**		**MAR-MET**	**MET-CAL**	**MAR-CAL**	**REC-ANT**
R_TOT	Total plant species richness	P-value	***	***	.	*
		Intercept	-0,67	0,44	-0,23	-0,17
R_EPG	Total woody plant species richness (excluding perennial grasses)	P-value	***	***	**	.
		Intercept	-0,78	0,43	-0,35	-0,14
R_NFN	Richness of nanophanerophytes	P-value	-	***		
		Intercept		1,92		
R_SSH	Richness of small shrubs	P-value	***	*	.	
		Intercept	0,87	-0,49	0,38	
R_CHA	Richness of chamaephytes	P-value	***	*	***	
		Intercept	-0,89	0,25	-0,65	
R_CLI	Richness of climbers	P-value	-	**		
		Intercept		3,21		
R_PGR	Richness of perennial grasses	P-value		*	*	*
		Intercept		0,73	0,98	-0,71
MF_NFN	Mean frequency of nanophanerophytes	P-value	-			
		Intercept				
MF_SSH	Mean frequency of nanophanerophytes	P-value				
		Intercept				
MF_CHA	Mean frequency of small shrubs	P-value				
		Intercept				
MF_CLI	Mean frequency of chamaephytes	P-value				
		Intercept				
MF_PRG	Mean frequency of perennial grasses	P-value	**		*	**
		Intercept	3,2		2,58	-2,55
R_ANE	Richness of anemochorous species	P-value	***	***	***	
		Intercept	-3,5	1,88	-1,63	
R_BAR	Richness of barochorous species	P-value	**			**
		Intercept	-2,56			-0,36
R_ENZ	Richness of endozoochorous species	P-value				
		Intercept				
R_ECZ	Richness of ectozoochorous species	P-value	***	***		*
		Intercept	-1,79	1,52		-1,41
R_ANE+ENZ	Richness of anemochorous and endozoochorous species	P-value				
		Intercept				
R_BAR+ENZ	Richness of barochorous and endozoochorous species	P-value				
		Intercept				
R_BAR+ECZ	Richness of barochorous and ectozoochorous species	Intercept				0,85
		Intercept				
MF_ANE	Mean frequency of anemochorous	P-value				

			Lithology			**Age**
Variable	**Description**		**MAR-MET**	**MET-CAL**	**MAR-CAL**	**REC-ANT**
	species					
		Intercept				
MF_BAR	Mean frequency of barochorous species	P-value				
		Intercept				
MF_ENZ	Mean frequency of endozoochorous species	P-value	.		**	.
		Intercept	1,89		2,92	-1,59
MF_ECZ	Mean frequency of ectozoochorous species	P-value	*			
		Intercept	1,34			
MF_ANE+ENZ	Mean frequency of anemochorous and endozoochorous species	P-value				
		Intercept				
MF_BAR+ENZ	Mean frequency of barochorous and endozoochorous species	P-value		*		
		Intercept		-1,82		
MF_BAR+ECZ	Mean frequency of barochorous and ectozoochorous species	P-value				.
		Intercept				1,5
R_FA	Richness of facilitator/nurse speces	P-value	***		***	***
		Intercept	1,38		1,25	-1,16
R_IC	Richness of inhibitor/competitor species	P-value	***		***	
		Intercept	-1,5		-1,1	
R_NE	Richness of neutral/indifferent species	P-value	***	***		
		Intercept	-1,18	1,36		
MF_FA	Mean frequency of facilitator/nurse speces	P-value		*	.	
		Intercept		2,02	1,87	
MF_IC	Mean frequency of inhibitor/competitor species	P-value				
		Intercept				
MF_NE	Mean frequency of neutral/indifferent species	P-value				
		Intercept				
C_BS	Bare soil cover	P-value	***		***	
		Intercept	0,33		0,35	
C_RO	Rock cover	P-value	***	***	*	**
		Intercept	-2,46	0,96	-1,5	0,7
C_LL	Leaf litter cover	P-value	***		***	
		Intercept	-1,07		-1,18	
C_PG	Cover of perennial grasses	P-value	***		***	
		Intercept	0,82		0,97	
C_TG	Cover of tussock grasses	P-value	***	***	***	***
		Intercept	2,54	-1,01	1,52	-2,06
C_CH	Cover of chamaephytes	P-value	***	***	***	
		Intercept	-1,43	0,62	-0,81	
C_SH	Cover of shrubs (including endozoochorous sps)	P-value	***	**	***	***
		Intercept	-1,41	0,29	-1,12	-0,81
C_LM	Cover of lichens and mosses	P-value				
		Intercept				

			Lithology			**Age**
Variable	**Description**		**MAR-MET**	**MET-CAL**	**MAR-CAL**	**REC-ANT**
C_AN	Cover of annuals	P-value	*	***	***	***
		Intercept	-0,33	-0,66	-1,00	1,02
C_TC	Cover of tree canopy	P-value	-	***	-	***
		Intercept		1,47		0,62
C_P_TG	Cover of perennial and tussock grasses	P-value	***		***	***
		Intercept	1,34		1,2	-0,52
OV_NA	Cover overlap (>100%) excluding trees	P-value	***		***	***
		Intercept	-1,06		-0,89	-0,46
OV_TOT	Cover overlap (>100%) including trees	P-value	***	***	***	
		Intercept	-1,74	0,61	-1,13	
LRFS	Regional Flora Red Data Book Index	P-value	*		*	.
		Intercept	2,19		1,57	-2,65
LRFS+USO	Reg. Flora Red Data Book+use Index	P-value		.	*	*
		Intercept		0,94	1,1	-1,05
RARE	Flora Rarity Index	P-value				
		Intercept				

Annex 5. Results of GLMMs relating floristic and vegetation variables with lithology x age classes considered together. Only the variables with significant results in previous analyses (for lithology and age classes independently) were tested, and only those with significant results are presented. A negative coefficient indicates a change in the sense left cathegory<upper cathegory, and a positive one in the opposite sense. Significance levels as in Annex 4.

Dependent variable		MAR_A	CAL_A	CAL_R	MET_A	MET_R
R_FA (Richness of facilitator/nurse species)	**MAR_A**					
	CAL_A	* -0,84				
	CAL_R	*** -1,94	. -1,09			
	MET_A	** -1,25				
	MET_R	*** -1,54				

		MAR_A	CAL_A	CAL_R	MET_A	MET_R
C_TC (Cover of tree canopy)	**MAR_A**					
	CAL_A					
	CAL_R		*** 1,17			
	MET_A		*** 2,02	*** 1,03		
	MET_R		*** 2,24	*** 1,06		

		MAR_A	CAL_A	CAL_R	MET_A	MET_R
C_AN (Cover of annuals)	**MAR_A**					
	CAL_A	*** 0,71				
	CAL_R	*** 1,22	*** 0,5			
	MET_A	*** -1,61	*** -2,33	*** -2,83		
	MET_R	*** 0,95	. 0,23	* -0,26	*** 2,57	

Annex 6. Full list of the bird species recorded in oldfields, showing their scores in different conservation assessments, and their functional classification (regarding frugivory).

			INDEX SCORES			
SPECIES	**BREEDING**	**WINTERING**	**SPEC**	**DAVES**	**LRAE**	**DISP**
Aegithalos caudatus	+	+	0	0	0	1
Alectoris rufa	+	+	4	0	2	0
Anthus pratensis		+	0	0	0	0
Carduelis cannabina	+	+	4	0	0	-1
Carduelis carduelis	+	+	0	0	0	-1
Carduelis chloris	+	+	0	0	0	-1
Columba livia/domestica		+	0	0	0	0
Emberiza cirlus	+	+	0	0	0	0
Erithacus rubecula		+	0	0	0	4
Ficedula hypoleuca	+		0	0	0	4
Fringilla coelebs	+	+	0	0	0	-1
Galerida sp	+	+	2	2	0	0
Lanius meridionalis	+	+	0	0	2	0
Lanius senator	+		4	0	2	0
Loxia curvirostra	+	+	0	0	0	0
Miliaria calandra	+		4	0	0	0
Motacilla alba		+	0	0	0	0
Oenanthe hispanica	+		4	0	2	0
Oriolus oriolus	+		0	0	0	0
Parus ater		+	0	0	0	-1
Parus cristatus		+	4	0	0	1
Parus major	+	+	0	0	0	-1
Passer domesticus	+	+	2	0	0	0
Petronia petronia	+		0	0	0	0
Phoenicurus ochruros		+	0	0	0	4
Phylloscopus collybita		+	0	0	0	1
Serinus serinus	+	+	0	0	0	-1
Streptopelia decaocto	+	+	0	0	0	0
Streptopelia turtur	+		2	0	4	0
Sturnus unicolor	+		0	0	0	0
Sylvia atricapilla		+	0	0	0	4
Sylvia conspicillata	+		0	0	2	4
Sylvia melanocephala	+	+	0	0	0	4
Sylvia undata	+	+	4	4	0	4
Turdus merula	+	+	0	0	0	4
Upupa epops	+		2	0	0	0

This is the Author Accepted Manuscript of the following article: 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. Agriculture, Ecosystems and Environment, 197, 222-242*, which has been published in final form at* https://doi.org/10.1016/J.AGEE.2014.08.006

Annex 7. Summary of densities of breeding bird species (individuals/ha), and derived community indices (total abundance, species richness, conservation value and dispersal potential). Mean values (±SE) are shown for each lithology x age class, except for total species richness.

Area	**COR_A**	**MUR_A**	**MUR_R**	**FUE_A**	**FUE_R**
Lithology	**Marls**	**Limestone**	**Limestone**	**Metamorphic**	**Metamorphic**
Abandonment age	**Ancient**	**Ancient**	**Recent**	**Ancient**	**Recent**
Year	**2011-13**	**2011-13**	**2011-13**	**2011-13**	**2011-13**
Lithology+abandonment age	**Marls_A**	**Limes_A**	**Limes_R**	**Metam_A**	**Metam_R**
Aegithalos caudatus	0.00±0.00	0.00±0.00	0.00±0.00	2.12±1.07	0.21±0.21
Alectoris rufa	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.21±0.21
Carduelis cannabina	0.42±0.42	0.21±0.21	0.95±0.95	0.00±0.00	0.00±0.00
Carduelis carduelis	0.42±0.42	0.21±0.21	0.32±0.32	0.64±0.43	0.00±0.00
Carduelis chloris	0.21±0.21	0.00±0.00	0.00±0.00	0.85±0.63	0.64±0.28
Emberiza cirlus	0.00±0.00	0.00±0.00	0.00±0.00	0.21±0.21	0.64±0.28
Ficedula hypoleuca	0.00±0.00	0.00±0.00	0.00±0.00	0.21±0.21	0.00±0.00
Fringilla coelebs	0.00±0.00	0.21±0.21	0.00±0.00	0.42±0.27	0.00±0.00
Galerida sp	2.12±0.63	0.42±0.27	0.64±0.37	0.21±0.21	0.85±0.42
Lanius meridionalis	0.21±0.21	0.42±0.42	0.00±0.00	0.00±0.00	0.00±0.00
Lanius senator	1.27±0.46	0.00±0.00	0.95±0.32	0.21±0.21	0.85±0.27
Loxia curvirostra	0.00±0.00	0.00±0.00	0.00±0.00	0.21±0.21	0.00±0.00
Miliaria calandra	0.00±0.00	0.00±0.00	0.00±0.00	0.85±0.42	0.64±0.28
Oenanthe hispanica	1.91±0.55	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Oriolus oriolus	0.00±0.00	0.00±0.00	0.00±0.00	0.21±0.21	0.00±0.00
Parus major	0.00±0.00	1.70±0.42	0.64±0.64	1.27±0.46	0.64±0.43
Passer domesticus	0.21±0.21	0.00±0.00	0.00±0.00	0.42±0.27	0.00±0.00
Petronia petronia	0.00±0.00	0.00±0.00	0.00±0.00	0.21±0.21	0.21±0.21
Serinus serinus	0.42±0.27	0.00±0.00	0.64±0.64	0.21±0.21	0.42±0.27
Streptopelia decaocto	0.00±0.00	0.00±0.00	0.95±0.61	0.21±0.21	0.00±0.00
Streptopelia turtur	0.00±0.00	0.00±0.00	0.32±0.32	0.00±0.00	0.21±0.21
Sturnus unicolor	0.00±0.00	0.64±0.64	0.95±0.61	0.00±0.00	0.00±0.00
Sylvia conspicillata	0.42±0.27	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Sylvia melanocephala	0.00±0.00	1.06±0.39	0.64±0.37	1.49±0.51	1.70±0.42
Sylvia undata	0.00±0.00	0.42±0.42	0.64±0.64	1.06±0.61	1.06±0.51
Turdus merula	0.21±0.21	0.21±0.21	0.00±0.00	0.64±0.28	0.64±0.28
Upupa epops	0.00±0.00	0.21±0.21	0.00±0.00	0.00±0.00	0.00±0.00
TOTAL BIRD DENSITY	7.85±1.11	5.73±2.10	7.64±2.89	12.31±0.71	8.91±1.71
DENSITY OF LEGITIMATE FRUGIVORES	0.64±0.28	1.70±0.97	1.27±0.52	3.40±0.71	3.40±0.97
% LEG FRUG DEN/TOTAL DENSITY	9.58±4.58	23.61±8.72	12.78±4.75	27.84±5.26	32.08±7.65
MEAN BIRD SPECIES RICHNESS	4.00±0.73	3.33±1.23	4.25±1.55	6.67±0.33	5.83±0.98
TOTAL BIRD SPECIES RICHNESS	15	15	15	24	18
SPEC Index	4.23±0.80	0.96±0.58	2.84±1.29	3.08±0.59	3.41±0.77
Bird Directive (BDIR) Index	0.88±0.21	0.60±0.48	0.91±0.69	1.05±0.43	1.39±0.43
Spanish Bird Red Data Book (RBBS) Index	1.79±0.29	0.18±0.18	0.89±0.45	0.12±0.12	0.83±0.22
DISP Index	0.35±0.41	1.09±0.79	0.73±0.27	2.76±0.62	2.87±0.90

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Annex 8. Summary of densities of wintering bird species (individuals/ha), and derived community indices (total abundance, species richness, conservation value and dispersal potential). Mean values (±SE) are shown for each lithology x age class, except for total species richness.

Area	**COR_A**	**MUR_A**	**MUR_R**	**FUE_A**	**FUE_R**
Lithology	**Marls**	**Limestone**	**Limestone**	**Metamorphic**	**Metamorphic**
Abandonment age	**Ancient**	**Ancient**	**Recent**	**Ancient**	**Recent**
Year	**2011-13**	**2011-13**	**2011-13**	**2011-13**	**2011-13**
Lithology+abandonment age	**Marls_A**	**Limes_A**	**Limes_R**	**Metam_A**	**Metam_R**
Aegithalos caudatus	0.00±0.00	0.00±0.00	0.00±0.00	1.49±1.06	0.00±0.00
Alectoris rufa	0.42±0.27	0.00±0.00	0.00±0.00	0.00±0.00	0.21±0.21
Anthus pratensis	0.85±0.63	0.00±0.00	0.64±0.37	0.00±0.00	0.21±0.21
Carduelis cannabina	0.42±0.42	0.21±0.21	0.00±0.00	0.00±0.00	0.21±0.21
Carduelis carduelis	0.42±0.27	0.00±0.00	0.64±0.64	0.00±0.00	0.42±0.42
Carduelis chloris	1.70±0.42	0.00±0.00	0.32±0.32	0.00±0.00	0.00±0.00
Columba livia/domestica	2.55±2.08	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Emberiza cirlus	0.00±0.00	0.00±0.00	0.00±0.00	0.21±0.21	0.64±0.64
Erithacus rubecula	0.00±0.00	0.00±0.00	0.00±0.00	0.64±0.28	0.64±0.28
Fringilla coelebs	1.27±0.81	0.21±0.21	1.27±0.90	0.85±0.42	1.06±0.21
Galerida sp.	1.91±0.97	0.00±0.00	0.00±0.00	0.00±0.00	0.85±0.42
Lanius meridionalis	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.21±0.21
Loxia curvirostra	0.00±0.00	0.00±0.00	0.00±0.00	1.49±1.06	0.00±0.00
Motacilla alba	1.06±1.06	0.00±0.00	0.00±0.00	0.00±0.00	0.21±0.21
Parus ater	0.00±0.00	0.00±0.00	0.00±0.00	1.06±0.83	0.00±0.00
Parus cristatus	0.00±0.00	0.00±0.00	0.00±0.00	3.18±0.28	1.06±0.39
Parus major	0.00±0.00	0.00±0.00	0.00±0.00	4.03±0.69	1.49±0.39
Passer domesticus	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.64±0.64
Phoenicurus ochruros	1.06±0.39	0.00±0.00	0.95±0.32	0.64±0.43	2.12±0.42
Phylloscopus collybita	0.21±0.21	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Serinus serinus	3.18±0.28	0.85±0.42	1.27±0.90	1.27±0.66	0.85±0.42
Streptopelia decaocto	0.00±0.00	0.21±0.21	0.00±0.00	0.00±0.00	0.00±0.00
Sylvia atricapilla	0.00±0.00	0.21±0.21	0.00±0.00	0.00±0.00	0.21±0.21
Sylvia melanocephala	0.85±0.27	0.42±0.27	0.64±0.64	1.06±0.61	1.27±0.33
Sylvia undata	0.64±0.43	0.21±0.21	0.32±0.32	0.21±0.21	0.21±0.21
Turdus merula	0.00±0.00	0.21±0.21	0.00±0.00	0.64±0.43	0.21±0.21
TOTAL BIRD DENSITY	16.55±3.51	2.55±0.81	6.05±2.29	16.76±1.90	12.73±2.59
DENSITY OF LEGITIMATE FRUGIVORES	2.55±0.57	1.06±0.61	1.91±1.10	3.18±1.17	4.67±0.54
% LEG FRUG DEN/TOTAL DENSITY	14.31±3.68	23.61±12.25	31.70±22.99	18.46±6.65	45.17±10.27
MEAN BIRD SPECIES RICHNESS	6.50±1.38	1.83±0.60	3.25±1.25	6.00±0.97	7.50±1.18
TOTAL BIRD SPECIES RICHNESS	18	12	12	17	23
SPEC Index	2.16±1.02	0.59±0.29	0.36±0.36	2.70±0.31	2.44±0.67
Birds Directive (BDIR) Index	1.31±0.54	0.24±0.24	0.36±0.36	0.24±0.24	0.66±0.24
Spanish Bird Red Data Book (RBBS) Index	0.24±0.15	0.24±0.24	0.00±0.00	0.00±0.00	0.24±0.15
DISP Index	1.22±0.42	0.86±0.64	1.23±1.28	2.60±0.98	3.90±0.68

Annex 9. Summary of comparisons (Kruskal-Wallis non parametric analysis of variance) of the main ornithological indices among lithology and abandonment age classes. Comparisons between brackets show the result of global tests, significant paired comparisons carried out with the R package 'pgirmess' are shown below. Significance levels as in Annex 4.

	Breeding		
Index	**Lithology**	**Abandonment age**	**Lith & Abage**
Total bird density	[MET>MAR>LIM] (p=0.08)	NS	NS
Species richness	[MET>MAR,LIM]*	NS	[MET(A,R)> LIM(R),MAR>LIM(A)](p=0.12)
Density of legitimate frugivores	[MET>MAR,LIM]* MET>MAR*	NS	[MET(A,R)>LIM(R)>LIM(A),MAR]*
SPEC index	[MAR>MET>LIM] (p=0.05)	NS	[MAR>MET (A,R),LIM(R)>LIM(A)] (p=0.09)
BDIR index	NS	NS	NS
RBBS index	[MAR>MET>LIM]** MAR>MET* MAR>LIM*	NS	[MAR>LIM(R),MET(R)>LIM(A),MET(A)]* MAR>MET(A)* MAR>LIM(A)*
DISP index	[MET>LIM>MAR]** MET>LIM* MET>MAR*	NS	[MET(R)>MET(A)>LIM(A,R)>MAR]*

	Wintering		
Index	**Lithology**	**Abandonment age**	**Lith & Abage**
Total bird density	[MAR,MET>LIM]*** MAR>LIM* MET>LIM*	NS	[MAR>MET(A)>MET(R)>LIM(R)>LIM(A)]** MAR>LIM(A)* MET(A)>LIM(A)*
Species richness	[MET>MAR>LIM]*** MAR>LIM* MET>LIM*	NS	[MET(R)>MET(A),MAR>LIM(R)>LIM(A)]* MET(R)>LIM(A)*
Density of legitimate frugivores	[MAR,MET>LIM]* MET>LIM	A>R (p=0.08)	[MET(R)>MET(A)>MAR>LIM(R)>LIM(A)]* MET(R)>LIM(A)*
SPEC index	[MET>MAR>LIM]** MET>LIM*	NS	[MET(A,R)>MAR>LIM(A,R)]*
BDIR index	[MAR>MET,LIM] (p=0.11)	NS	[MAR>MET(R)>MET(A),LIM(A,R)] (p=0.19)
RBBS index	NS	NS	NS
DISP index	[MET>MAR>LIM]*	NS	[MET(R)>MET(A)>MAR>LIM(A,R)] (p=0.08)

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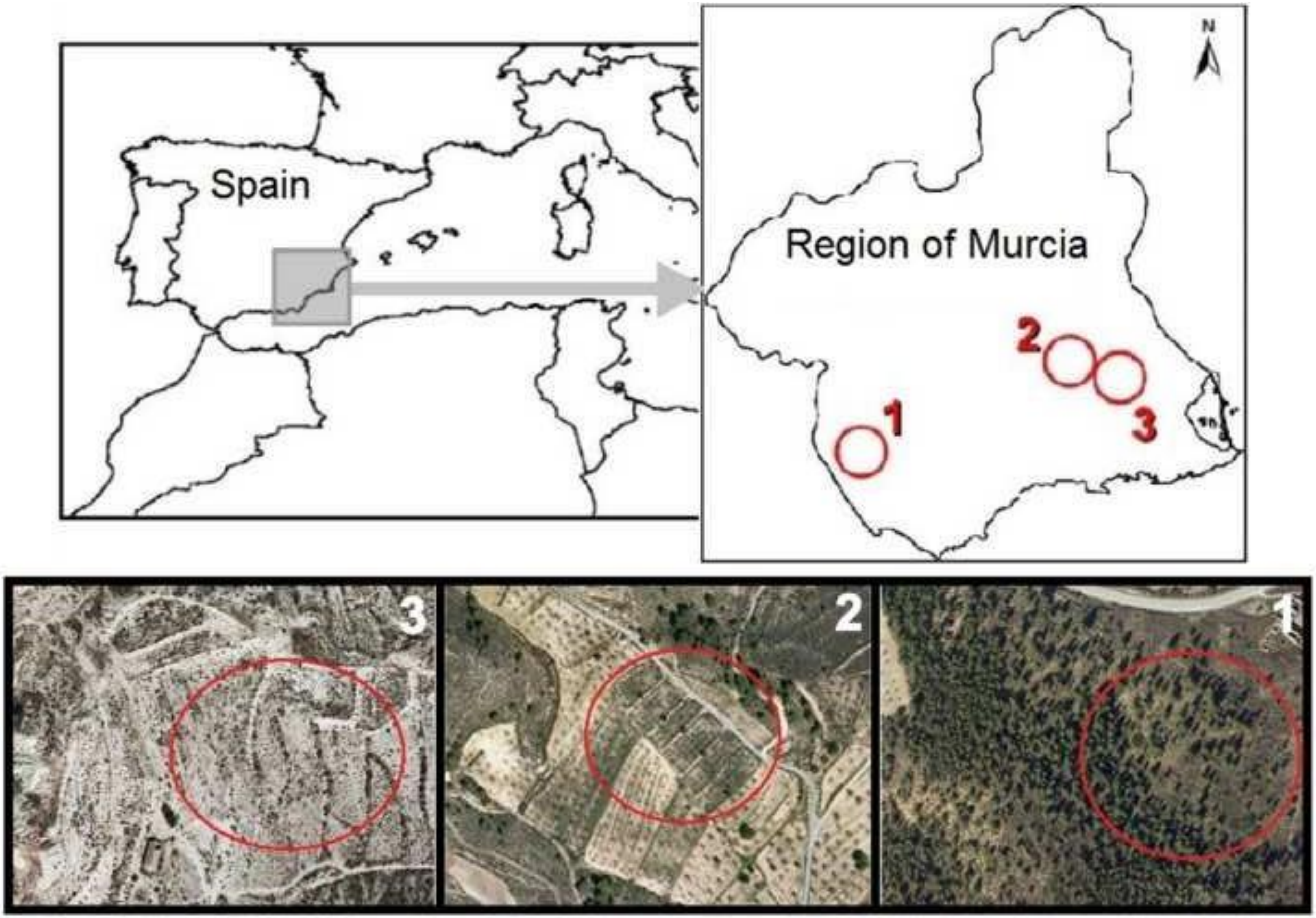

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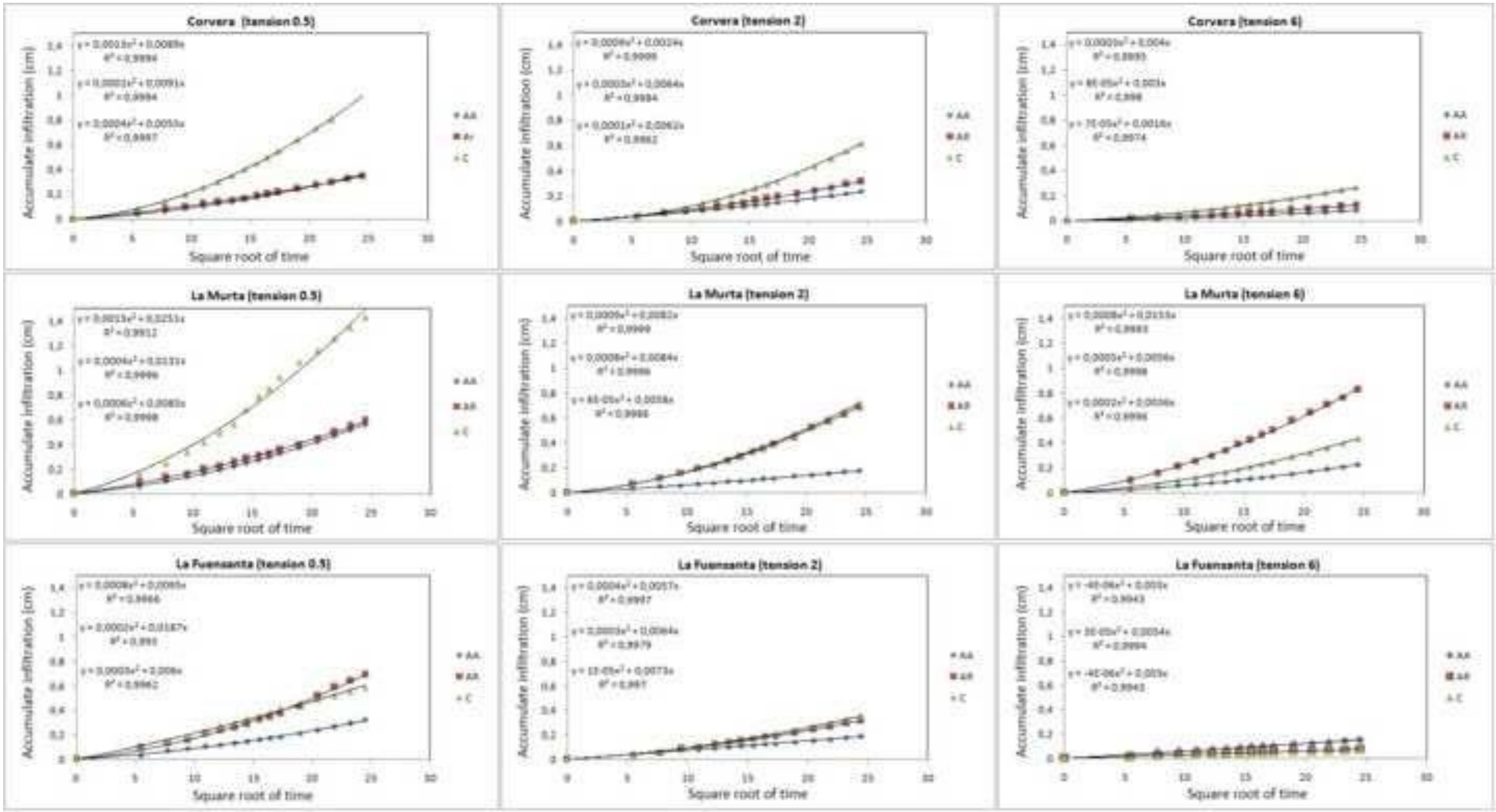
Figure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Corvera (tension 2)
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La Murta (tension 0.5)
La Murta (tension 2)
La Murta (tension 6)
La Fuensanta (tension 0.5)
La Fuensanta (tension 2)
La Fuensanta (tension 6)
Accumulate infiltration (cm)
Square root of time
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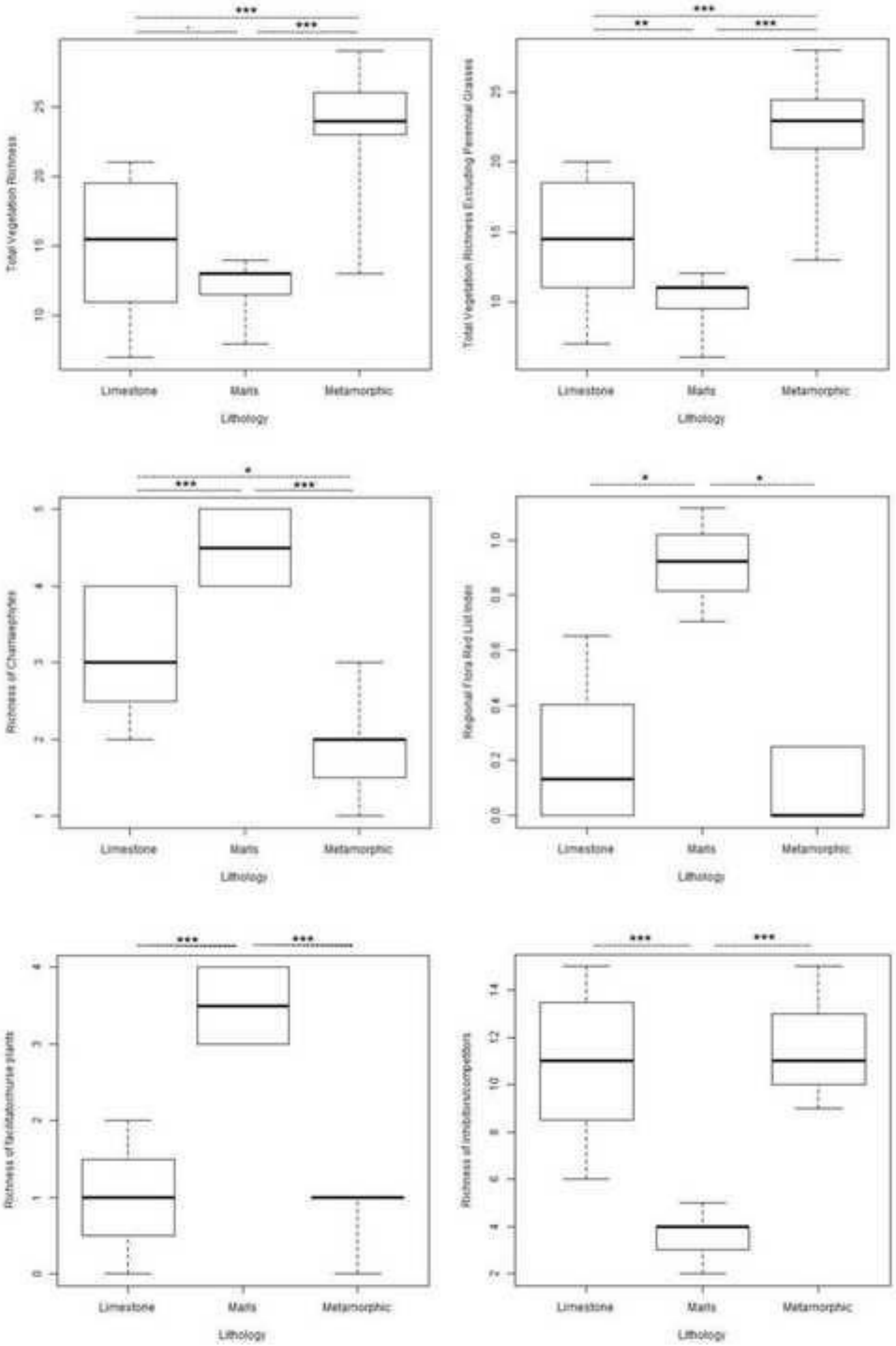

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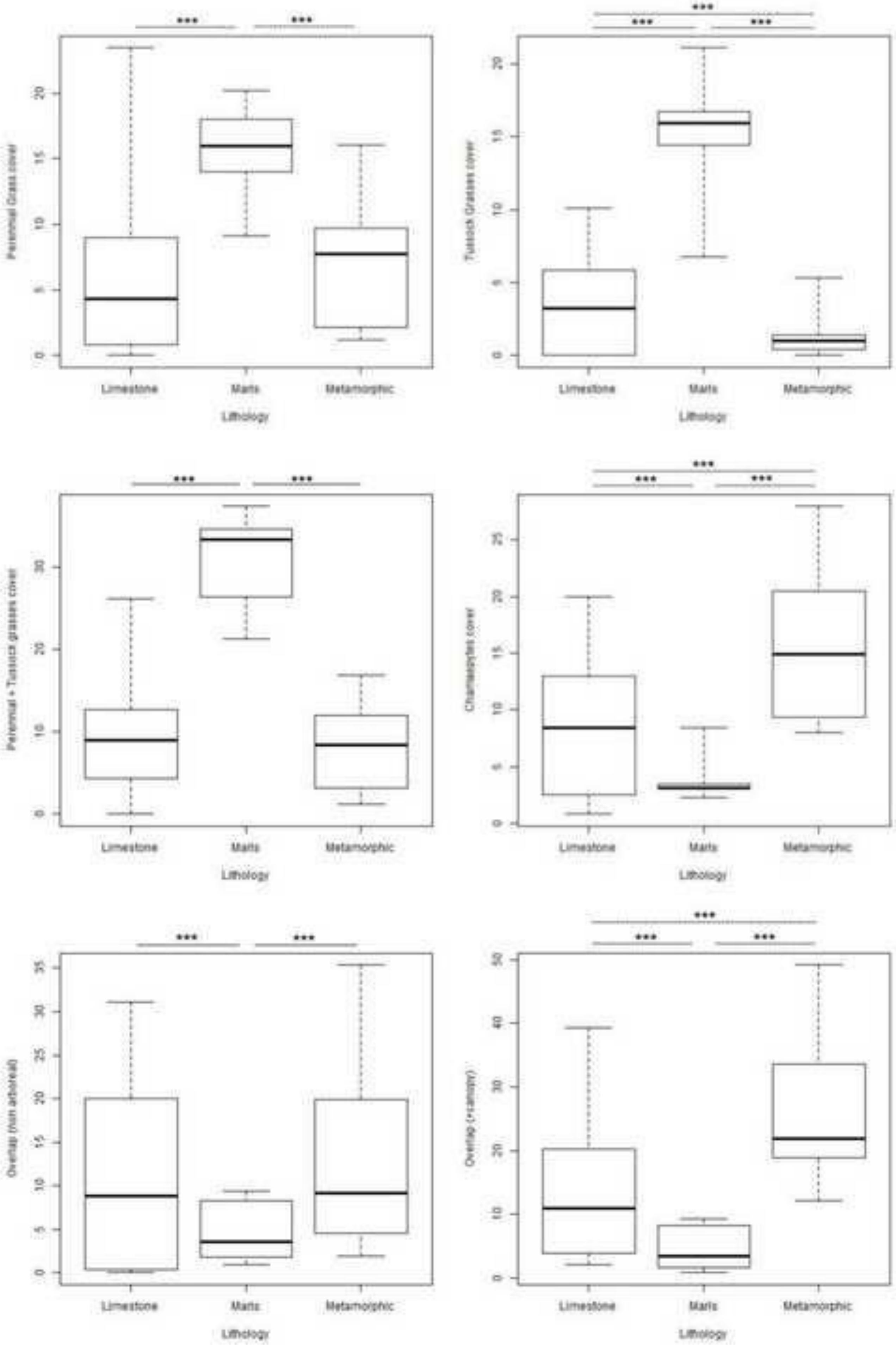
***
***
Perennial Grass cover
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Metamorphic
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Tussock Grasses cover
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Marls
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Lithology
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Perennial + Tussock grasses cover
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Chamaephytes cover
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Limestone
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Lithology
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Overlap (non arboreal)
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Marls
Metamorphic
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Overlap (+canopy)
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Limestone
Marls
Metamorphic
Lithology

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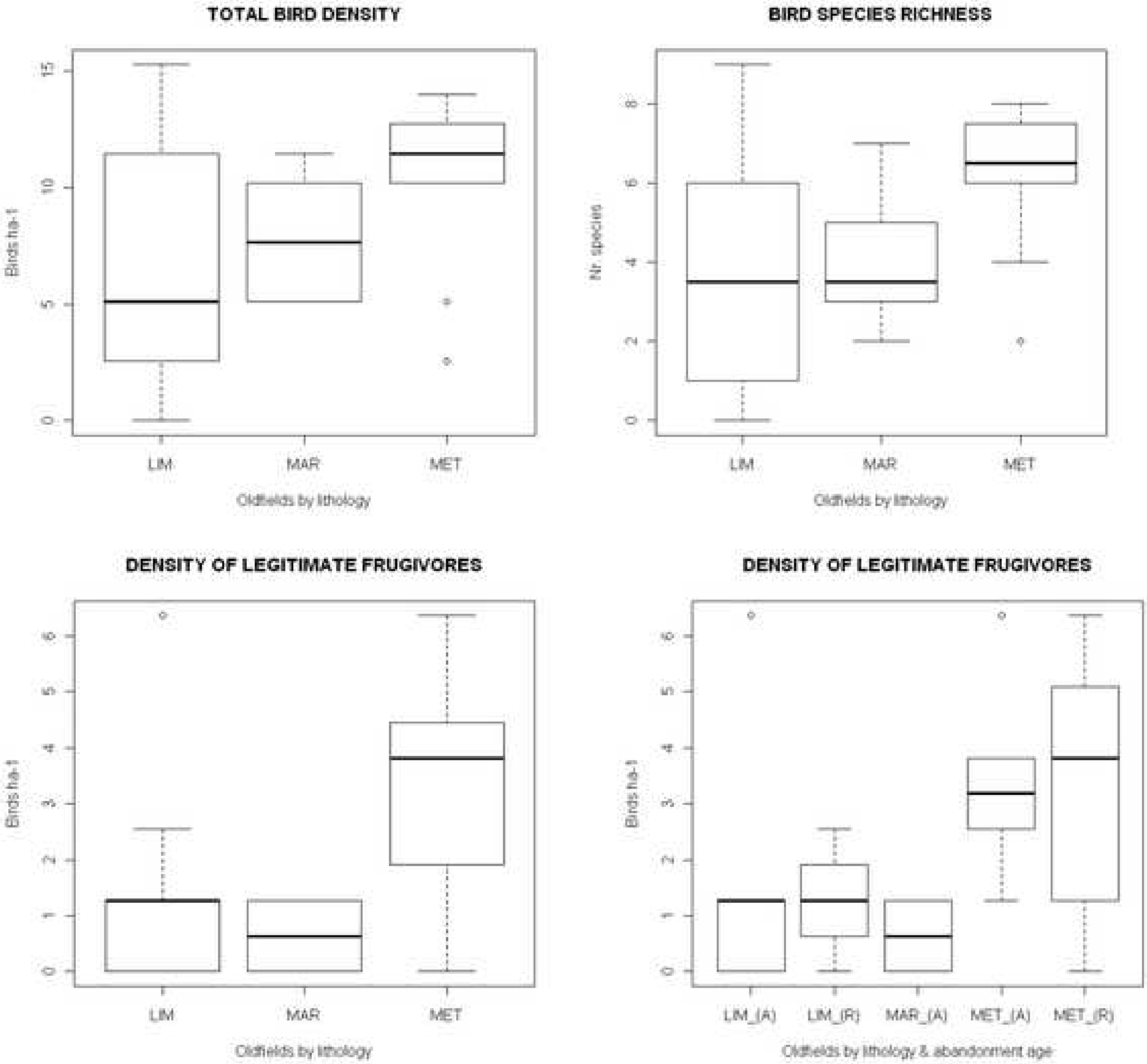

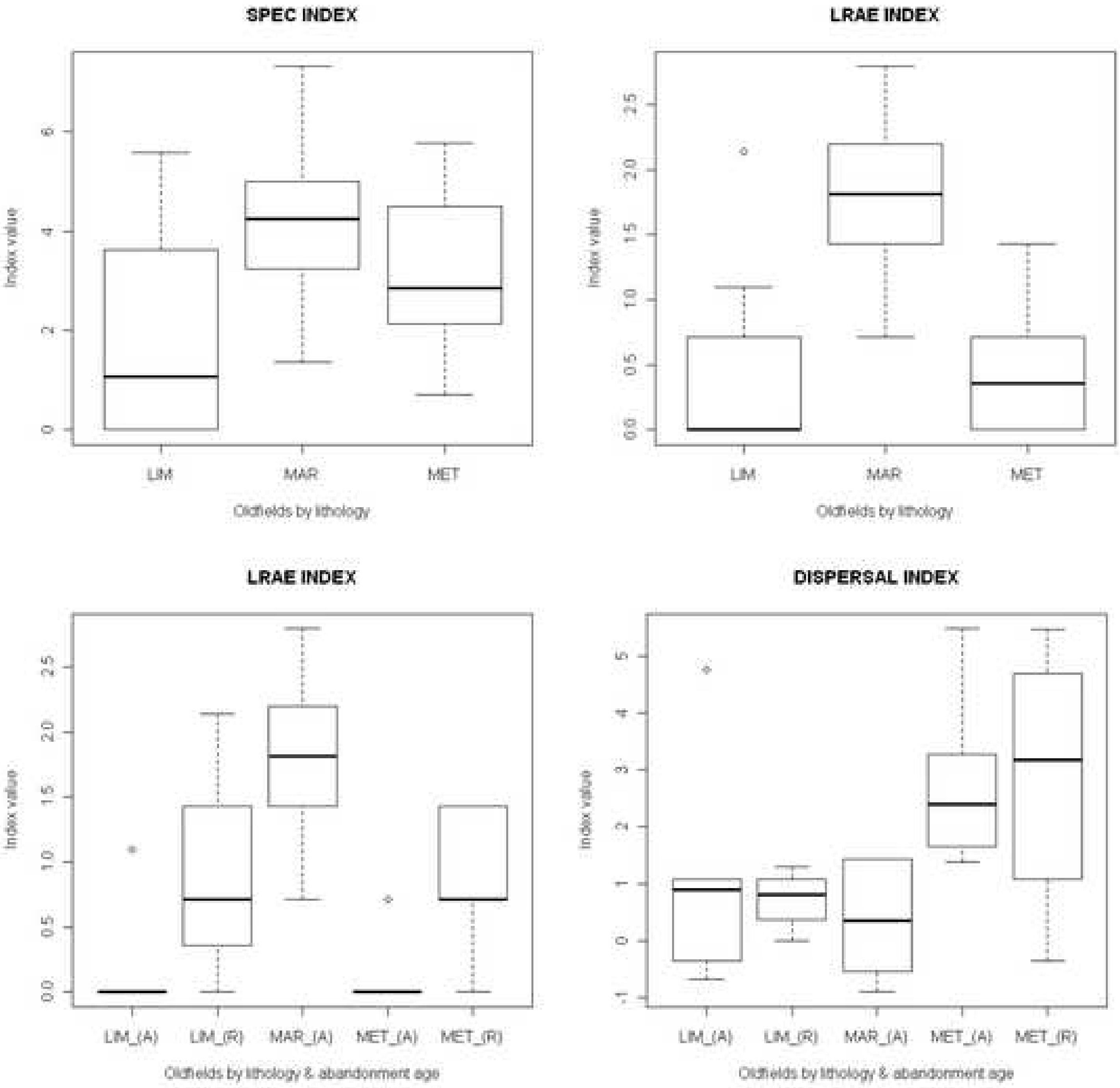
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Oldfields by lithology & abandonment age
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MET_(R)
Oldfields by lithology & abandonment age

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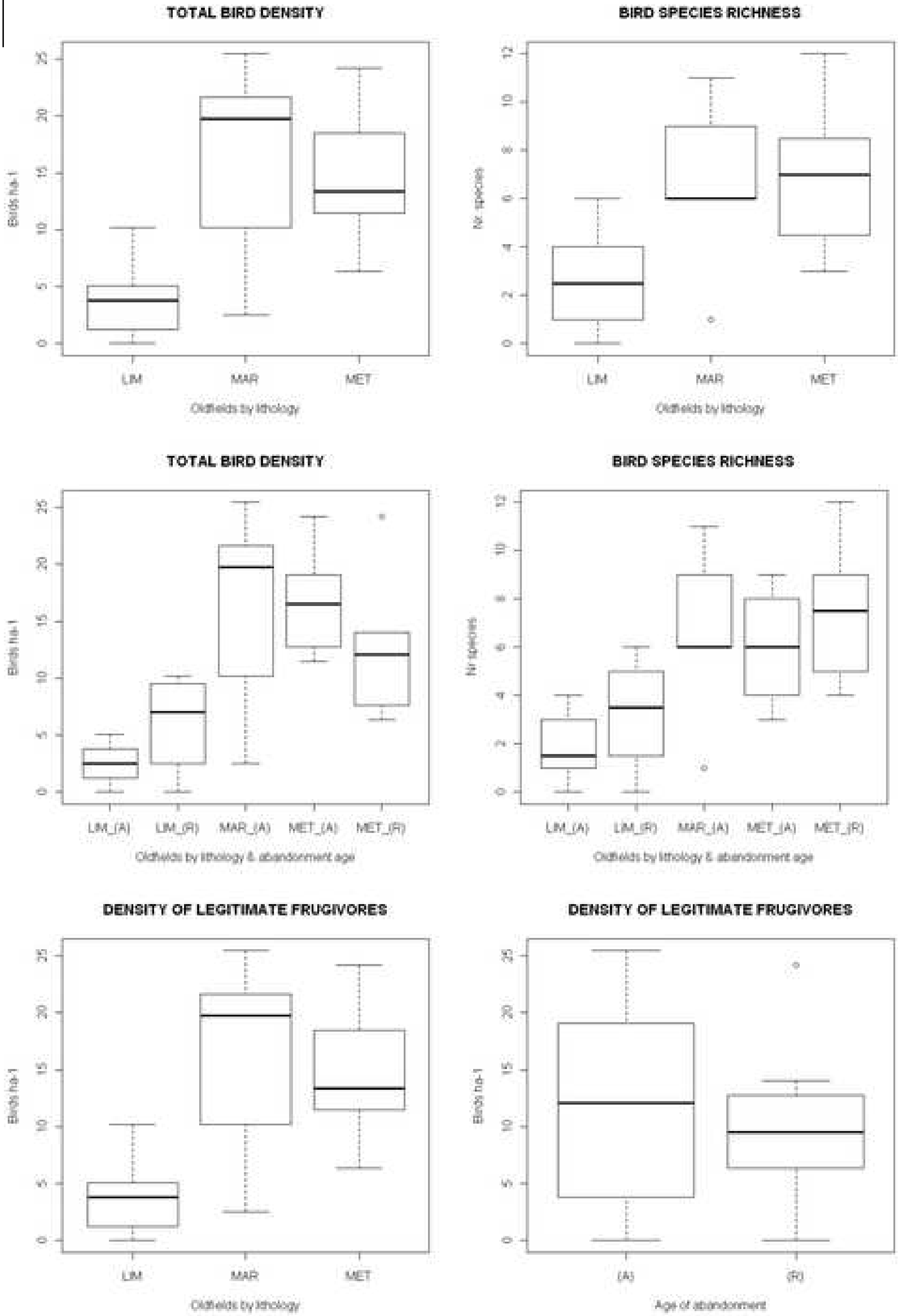

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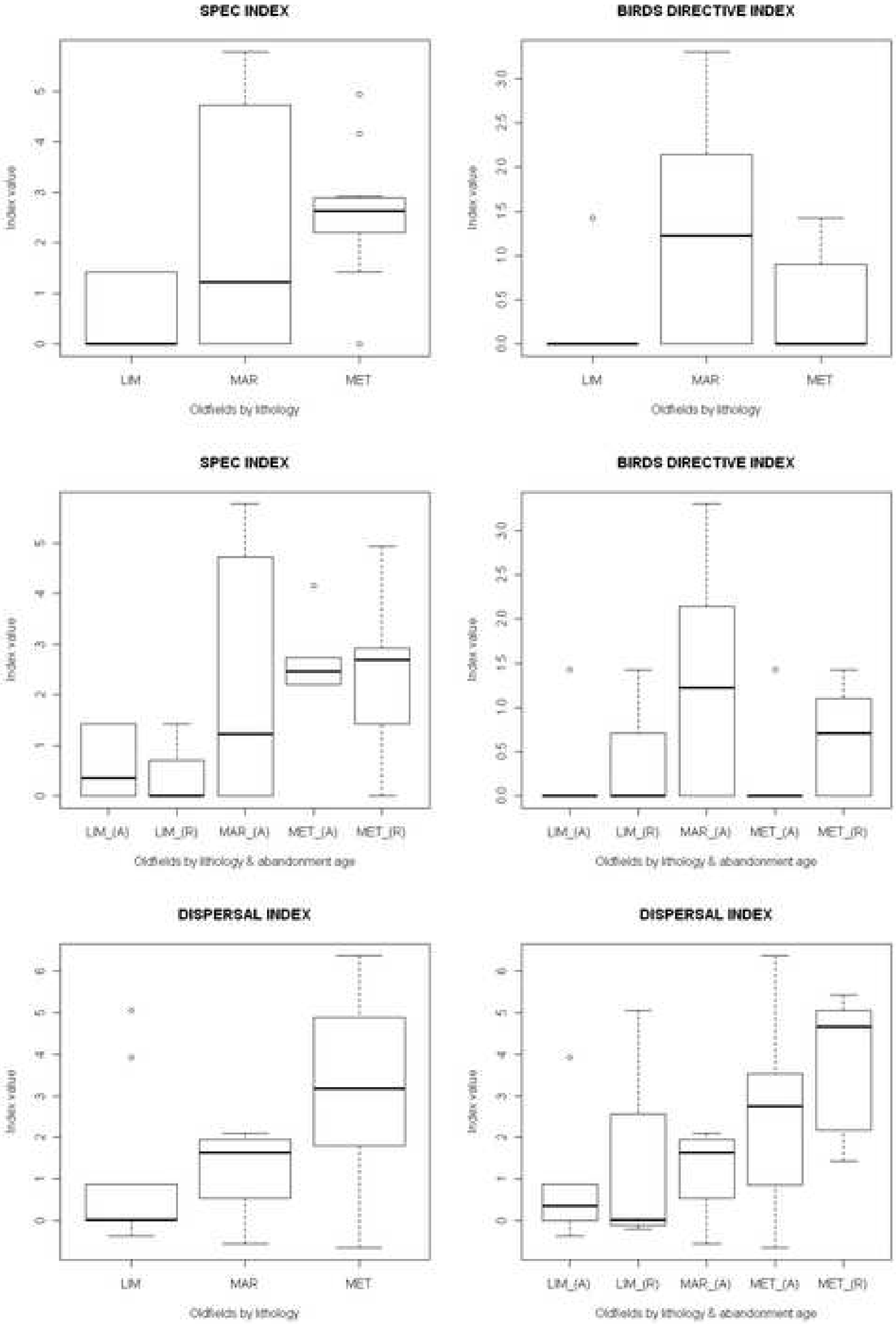
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Oldfields by lithology & abandonment age
BIRDS DIRECTIVE INDEX
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Oldfields by lithology & abandonment age

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