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# Traditional ploughing is critical to the conservation of threatened plants in Mediterranean olive groves

Ana Júlia Pereira [a,*], Miguel Porto [b,c,d,e], Otília Correia [a], Pedro Beja [b,c,d,e]

[a] *cE3c, Centre for Ecology, Evolution and Environmental Changes & CHANGE–Global Change and Sustainability Institute, Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal*
[b] *CIBIO/InBIO, Research Centre in Biodiversity and Genetic Resources, Associate Laboratory, University of Porto, Vairão, Portugal*
[c] *CIBIO/InBIO, Research Centre in Biodiversity and Genetic Resources, Associate Laboratory, Instituto Superior de Agronomia, Universidade de Lisboa, Lisboa, Portugal*
[d] *BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, University of Porto, Vairão, Portugal*
[e] *Estação Biológica de Mértola (EBM), CIBIO, Mértola, Portugal*

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ABSTRACT

Arable plant diversity has been dramatically declining due to agriculture intensification, with several arable species currently included in national Red Lists. This is particularly relevant in the case of plant communities of the traditional Mediterranean agricultural systems. Despite the current knowledge about the factors affecting this diversity, it is not clear how these communities, which have likely evolved under the pressure of ploughing for millennia, depend on this regular soil disturbance. This is an important issue nowadays, because current management practices focused on the conservation of the ground vegetation cover, to protect soil and other biological groups, often exclude ploughing. In this paper, we test the hypothesis that traditional ploughing is favourable to more specialist arable plants, predictably more dependent on the regular soil disturbance. We address this issue in a Mediterranean agricultural system, the traditional olive groves of Southern Portugal, which is characterized by the annual ploughing of soil. A total of 90 plots containing 1350 sampling quadrats were sampled, and all plant species identified. We categorized plants in four target groups of conservation interest, and then used a joint species distribution model to model their occurrence in relation to three management practices: ploughing, cultivation and low-intensity grazing, using abandoned olive groves as reference level. Results suggest that ploughing is a key factor for the maintenance of arable plant diversity. Ploughing had a positive effect on the occurrence of rare arable plants, archaeophytes and on several Red listed species. In order to conserve these high value plant communities and endangered plant species, we recommend incentivizing ploughing using reduced tillage techniques (e.g. chisel ploughing) on these traditional Mediterranean agricultural systems.

## 1. Introduction

Arable plant species, generally called weeds, are the set of wild plants found in agroecosystems, and have been dramatically declining in the more developed and populated areas of the Holarctic since the middle of the XX century due to agriculture intensification (Albrecht et al., 2008; Richner et al., 2015; Storkey et al., 2012). The exponential increase in the use of herbicides and fertilizers, the strong mechanization of agriculture and the landscape homogenization, led not only to the impoverishment of arable plant communities in terms of richness (Andreasen et al., 2018; Baessler and Klotz, 2006; Chamorro et al., 2016; Fried et al., 2009; Meyer et al., 2013; Richner et al., 2017; Sutcliffe and Kay, 2000), but also to a shift in composition driven by the resistance to herbicides (Baucom, 2019) and the tolerance to fertilizers (Storkey et al., 2010). These changes affected both the field species that can thrive with the pressure of regular cultivation, and those that live in the field edges and other marginal habitats that integrate the traditional landscape mosaic (Fried et al., 2009; Recasens et al., 2020).

Currently, several arable plant species are considered rare (Albrecht et al., 2016; Bergmeier and Strid, 2014), including arable archaeophytes: plants from the Irano-Turanian region that spread all over Europe and the Mediterranean Basin, alongside with the expansion of agriculture from the Far East, since the Neolithic (Meyer, 2020). As a consequence, some arable plant species are already assessed as

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* Correspondence to: cE3c, Faculdade de Ciências, Universidade de Lisboa, Edifício C2, 5º piso, sala 2.5.14, Campo Grande, Lisboa 1749-016, Portugal.
*E-mail address:* ajpereira@ciencias.ulisboa.pt (A.J. Pereira).

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threatened in the Red Lists of many European countries, (for a review see Albrecht et al., 2016; Metzing et al., 2018; Munoz, 2017). Furthermore, the loss of this plant diversity (Carmona et al., 2020; Tarifa et al., 2021), may provoke cascading effects on the biotic interaction networks (Bretagnolle and Gaba, 2015; Martínez-Núñez et al., 2019) and on the ecosystem services provided by them, like pollination and pest control (Marshall et al., 2003; Twerski et al., 2022).

A series of studies have shown that the diversity of arable plant communities at field scale is determined by factors like crop type (Perronne et al., 2015), past crop sequence (Mahaut et al., 2019), nitrogen inputs (Rotchés-Ribalta et al., 2016) and tillage system (Armengot et al., 2016). At a larger scale, arable plant diversity tends to be positively related to landscape heterogeneity (Gaba et al., 2010; Solé-Senan et al., 2014). Despite the current knowledge about the multiple factors that affect the diversity of arable plant communities and about the negative impacts of agriculture intensification, little is known about how these communities depend on the traditional management practices that have been in place for centuries but that are being abandoned nowadays, namely the mechanical and regular disturbance of soil by ploughing with traditional techniques (Palmer, 1998). In particular, it is still unclear what are the effects of the exclusion of ploughing on specialist arable plants and on those sharing an evolutionary history side by side with the onset of agriculture, like the arable archaeophytes. These are predictably more dependent on the regular soil disturbance and possibly more vulnerable to the abandonment of this traditional tillage practice, or its replacement by other management practices that do not disrupt soil and tend to maximize the ground vegetation cover, like no tillage and other conservation agriculture practices such as, direct seeding, mowing or extensive grazing (Barroso et al., 2015; Carpio et al., 2020; Tarifa et al., 2021; Terzi et al., 2021).

Indeed, no tillage practices, that strictly avoid or minimize soil disturbance (Derpsch et al., 2014), which are gradually being implemented to minimize soil disturbance and erosion (Panettieri et al., 2020), and to boost arthropod populations (Rey et al., 2019), may change the floristic composition of the communities (see Radić Lakoš et al., 2014; Simoes et al., 2014), and the proportion of life forms leading, for example, to the reduction of annual plants (see Simoes et al., 2014; Terzi et al., 2021). More importantly, these practices may filter out from the community those species with specific traits, including regenerative traits, that have been positively selected by ploughing, favoured, directly or indirectly, by soil disturbance, like secondary dormancy processes (Torra et al., 2018), light germination requirements (Chauhan et al., 2012; Cordeau et al., 2015; Royo-Esnal et al., 2015) and physical dormancy release by tegument scarification (Crawley, 2004). As a consequence, excluding ploughing from the fields could eventually lead to the local extinction of several arable species, including rare and threatened species (Recasens et al., 2020). Despite this, the studies addressing the effects of conventional versus traditional and versus conservation tillage practices have been focused on the overall composition patterns (Bilalis et al., 2001; Dorado and López-Fando, 2006; Plaza et al., 2011), rather than on the particular effects on specialist arable species, which, until now, have been overlooked and mostly based on experimental studies (for example Albrecht and Mattheis, 1998; Bilalis et al., 2001; Lang et al., 2021; Torra et al., 2018).

In this study, we explore the effects of ploughing on the arable plant species compared to the absence of this traditional practice, using abandoned agricultural systems as a proxy of no tillage and other non-disruptive soil practices. We hypothesize that the cyclical soil disturbance is favourable to the arable plant communities, by promoting the occurrence of specialist arable plants that have evolved under the pressure of ploughing, while, by the contraire, non-disruptive soil practices select against these specialist plants.

To do this, we investigated the effects of traditional ploughing and other low-intensity management practices, compared to no tilled and abandoned systems, on the diversity of arable plant communities, of a Mediterranean agricultural system, characterized by the annual ploughing of soil. In the Mediterranean region, the declining trend of arable plant diversity is particularly serious because arable plant communities are very rich (Bergmeier and Strid, 2014). The species pool of these communities encompass not only arable archaeophytes and other wide distribution arable weeds, but also narrow distribution species, including endemic plants and other climatic or edaphic endemisms, which are apparently restricted to traditional agroecosystems, like the traditional olive groves or rainfed annual crops (Meyer and Bergmeier, 2020; Recasens et al., 2020).

The study system comprises the traditional olive groves of Southern Portugal, which are an important habitat and refuge for arable plant communities, including several threatened species according to the Red List of Vascular Plants of Continental Portugal (Carapeto et al., 2020), that are undergoing a severe decline due to agriculture intensification (Moreira et al., 2019). Our main goal was to understand the role of this traditional practice in the maintenance of the diversity of arable plant communities and its effects on rare arable species, using a Joint Species Distribution Model. Following our hypothesis, we expect that the traditional ploughing of soil increases specialist arable species richness, being determinant for the maintenance of rare arable species populations.

## 2. Materials and methods

### 2.1. Study area

The study was conducted in Portugal, in the region of Alentejo (38° 1'N, 7° 51'W; Fig. 1). The climate is Thermo-Mediterranean with a mean annual air temperature (Tp) of 19 °C, ranging between 9,5 °C (Tmin) and 24 °C (Tmax), and a mean annual precipitation (Pp) of 612 mm (Monteiro-Henriques et al., 2016), circa of 75% occurring between October and April. This region is a rural and mostly flat territory, covered by a mosaic of large areas of grasslands, low-density evergreen oak woodlands ('Montado'), and rainfed and irrigated agricultural areas with annual and perennial crops such as cereal, sunflower, vineyards and olive groves.

A large scale intensification of farming started in this region during the 1990's, as in other regions of Portugal and Spain, stimulated by market mechanisms and the European Union (EU) Common Agricultural Policy (CAP), and surged later (2000) by the implementation of a large irrigation reservoir in the Guadiana River (Morgado et al., 2022). These circumstances led to the fast conversion of non-irrigated agricultural areas into irrigated and very intensive cultures, mainly fast growing varieties of olive, which presently occupy 85000 ha, and were virtually absent 30 years before (Morgado et al., 2022). This strong land-use change was made mostly at the expenses of open rainfed annual crops (63%) and of traditional rainfed olive groves (21%) (Morgado et al., 2022), the so called Mediterranean olive groves, leading to a huge loss of valuable habitat for ground-nesting bird species (Morgado et al., 2020), and for rare arable and non-arable plant species (Carapeto et al., 2020; Moreira et al., 2019), respectively.

Our study system was the traditional Mediterranean olive groves occupying the basic soils (vertisols and luvisols) of Alentejo (Fig. 1). These agricultural systems present a similar structure as the other traditional olive groves of the Mediterranean Basin. Typically, they are rainfed permanent crops with a low density of olive trees (<150 trees ha$^{-1}$), usually old or very old trees (>50 years). The olive fruit is the main outcome of these cultures for the production of olive oil, but often they are cultivated together with wheat, legumes or sunflower, with low levels of nitrogen inputs. Ploughing is often done twice a year with a chisel plow or a disk plow, to a maximum depth of 15 cm, to prepare the soil for annual crop cultivation or just for clearing spontaneous weedy vegetation. The application of herbicides in order to control arable weeds it is not a common practice in these traditional systems, although this is a recurrent practice in nearby intensive production systems. Besides regular ploughing and cultivation, grazing by sheep is a common

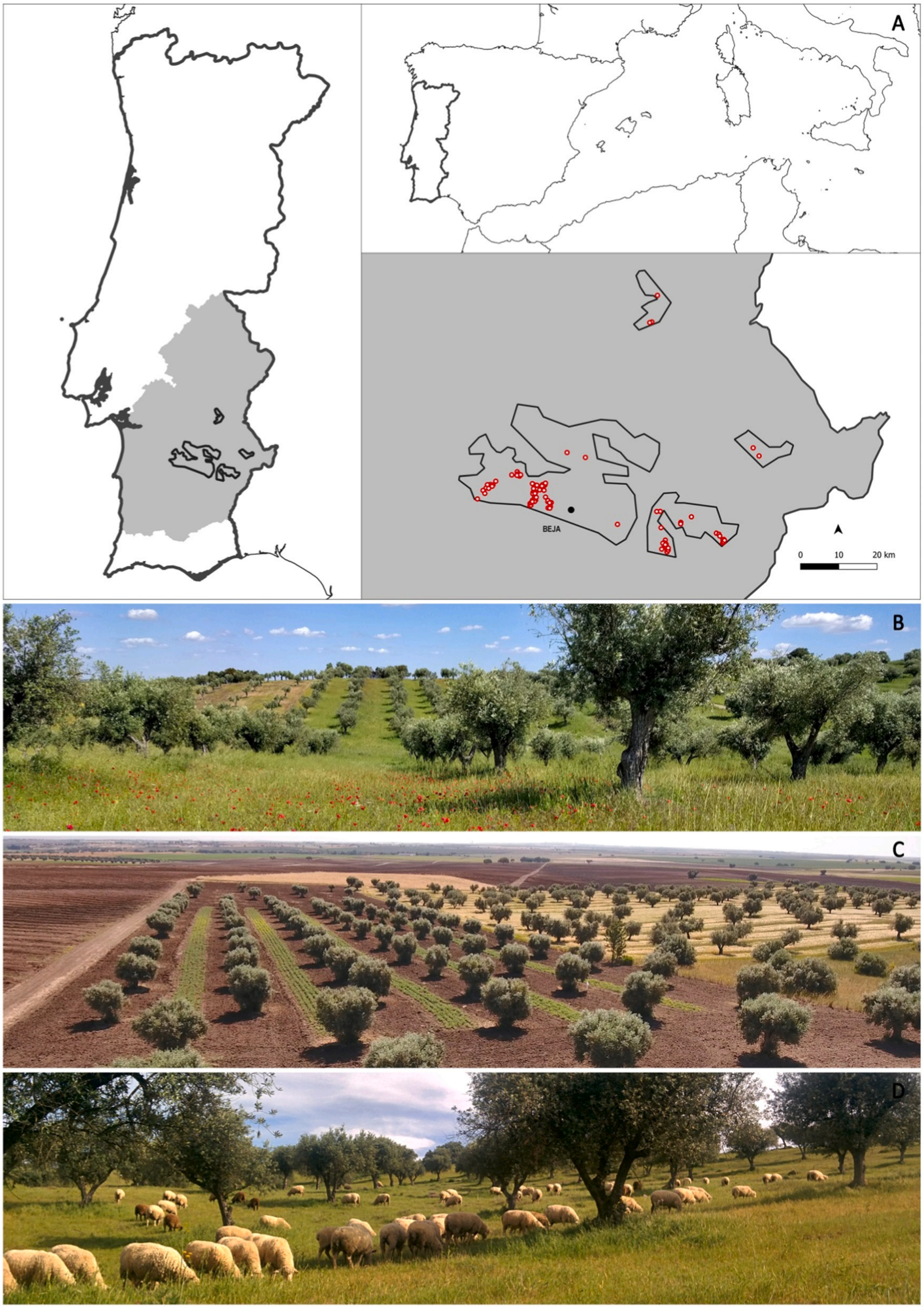

**Fig. 1.** A) Location of the study area (Southern Portugal). Red circles are the location of each olive grove (sampling plot; n=90). The black polygon around plots sets the limits of the vertisols and luvisols soils of Alentejo region; B) Ploughed olive groves with no annual crops; C) Olive groves with cultivated annual crops; D) Grazed olive groves by sheep.

practice in the olive groves of this region, usually, but not always, they are fenced. Moreover, several traditional olive groves are now abandoned and no longer ploughed or tilled, only being disturbed by occasional olive fruit harvesting. These sites, which are gradually being replaced by intensive cultures, have been abandoned due to the ageing of the rural population and the market competition by large scale producers (Pinto-Correia, 2021).

### 2.2. Sampling design

Traditional olive groves inside the study area were delimited in a GIS software (QGIS 3.20.3) over aerial imagery from 2016 to 2018 (Microsoft Bing Aerial and Google Satellite imagery). These groves are easily identified from aerial imagery due to their shape (usually rectangular), small dimension (<2 ha), typical low tree density (100–150 trees/ha) and orthogonal arrangement. Sampling plots were selected based on a 300×300 m grid layer, by selecting one olive orchard in every other grid cell, in a checker-board pattern, to guarantee a more even spatial arrangement. Prior to sampling, plots were checked in the field and excluded if: a) the land use has changed, b) the ground vegetation cover had been cleared by a recent ploughing or a stochastic event (e.g. fire), and c) the plot was being cultivated during the sampling year. Each excluded plot was replaced by a nearby alternative in the same grid cell.

In each sampling plot, 15 quadrats of one square meter were laid out in a regular manner around the centroid according to the scheme in Figure B1 (Appendix B). In each sampling unit, all plant species were recorded and identified to species level. When needed, plant material was collected for confirmation in the lab. A total of 90 plots and 1350 sampling units were sampled once. Sampling was carried out during spring (from April to May) for three consecutive years, 2018 (n=36), 2019 (n=32) and 2020 (n=22). Sampling was concentrated in the most favourable weeks for annual species, to minimize a possible effect of season.

### 2.3. Species groups

Prior to data analyses, species were categorized in four target groups: a) Archaeophytes, b) Narrow endemics, c) Rare arable plants and d) Red listed species. In a) we included species listed as agricultural archaeophytes in online databases (Euro+Med, 2006-) and the literature (Fanfarillo et al., 2020; Snir et al., 2015; Willcox, 2012; Zając et al., 2009). In b), we included the species endemic to the west Mediterranean region (from Italy westwards, including North Africa). In c), we included species classified as rare in the literature (Bergmeier and Strid, 2014; Metzing et al., 2018; Munoz et al., 2017; Storkey et al., 2012). In d), we included species classified in any of the three IUCN threat (CR, EN, VU) and near-threat (NT) categories, according to the Red List of the Vascular Plants of Continental Portugal (Carapeto et al., 2020). Some of the species were attributed to more than one group (species classification on Appendix A).

### 2.4. Management variables

We considered three binary variables to characterize management at the plot level, based both in field observations and on the series of aerial imagery (2003–2020) from Google Satellite. Ploughing (1/0) was assigned to plots where there was direct evidence of recent mechanical ploughing in the field (soil stripes, disturbed soil) and upon validation of the regularity of the ploughing events in the previous years through the aerial imagery series. Cultivation (1/0) was assigned to plots where there was evidence of recent crop cultivation, like straw and other crop vegetable debris and upon validation of the presence of crops in the previous years through the aerial imagery series. Grazing (1/0) was assigned to plots where sheep or their signs (e.g. fecal pellets, fences) were confirmed by direct field observations. Consequently, plots without any of these signs and without signs of any other management practice, were attributed to no tilled and abandoned plots, and taken as the reference level (triple zero) in the model. In the field these plots corresponded to olive groves with high herbaceous vegetation cover and compact soil, with occasional presence of shrubs. The inexistence of past ploughing events (≥4 years) was verified trough the aerial imagery series.

A categorical variable (Management') combining these three variables was considered for some analysis in order to classify the plots regarding their preponderant management type: 'ploughing', 'cultivation', 'grazing', and 'abandonment'.

### 2.5. Data analyses

#### 2.5.1. Management effects on species diversity

Species diversity was quantified using the standardized Hill numbers ($q$=0, 1, 2), at the plot level. These diversity indices, also called the equivalent or effective number of species, are a parametric family of diversity indices that differ among them by the parameter $q$ that determines the sensitivity to species relative abundances (Jost, 2006). Because they are expressed in units of effective numbers of species they can be directly compared across orders $q$ to extract information about dominance and other characteristics of the community (Chao et al., 2014). However, because measures of species diversity are highly sensitive to sampling effort, we standardized these indices to equal coverage using the R package iNEXT (Hsieh et al., 2016). Standardizing diversity indices by coverage is preferable to equal-effort standardization because it recognizes that different communities require different sample sizes in order to be equally well characterized, and hence, comparable (Roswell et al., 2021). The procedure consists in estimating the Hill numbers for the same 'reference' coverage, for all plots (by rarefying or extrapolating). The reference coverage was calculated as the minimum estimated coverage value obtained (via extrapolation) when doubling the sample size of all plots (in our case 0.945). This was suggested as being the value that allows the most robust comparisons across plots (Chao et al., 2012; Roswell et al., 2021).

To test differences in the total species richness and the richness by target groups we used a Linear Mixed Model (LMM), using the categorical variable 'Management' as the fixed effect and the category 'abandonment' as the reference level. To account for the eventual variation due to the sampling year, this factor was included in the model as random effect. The analyses were performed using the R package lme4 (Bates et al., 2015).

#### 2.5.2. Management effects on target groups and species

To test which species or groups of species were affected by the management variables, we used a joint species distribution model (JSDM). This class of models is a powerful analytical tool to analyse community ecology data because it explicitly acknowledges the multivariate nature of communities by assuming that the species respond jointly to the environment and to each other, thus allowing a better identification of assembly processes that are structuring communities (Ovaskainen et al., 2017). To fit our model, we used the Hierarchical Modelling of Species Communities framework (HMSC; Tikhonov et al., 2019), a type of JSDM that allows the simultaneous integration of community data with environmental covariates, species traits, phylogenetic data and also information about the spatio-temporal context of the samples.

For the community data matrix (Y matrix), we used the finest scale data, i.e., the presence-absence of species in each sampling unit (n=1350). Species occurring in two or less sampling plots (n=90) were excluded from analysis to minimize model convergence problems (55 species out of 274; Appendix A, column ́removed). The species membership in the four target species groups was coded with four binary variables, comprising the trait matrix (matrix T). The three binary management variables were included as the environmental matrix (matrix X), after checking that their pairwise Pearson correlations were not higher than 0.60.

The model was fit with a probit link function, assuming a Bernoulli distribution and the default priors distribution, as recommended for presence/absence data (Ovaskainen et al., 2017). To account for the hierarchical spatial and temporal structure of the sampling, we considered four random effects: 'year of sampling', 'sampling unit', 'plot' coded as factor, and also 'plot' included as a spatial random effect (via each plot's coordinates). To capture the effects of the residual variation associated with each random effect, these were modelled with a latent variable approach (π matrix; Ovaskainen et al., 2016), using two latent variables for the factor random effects and five for the spatial random effect.

We estimated the model coefficients and uncertainty by sampling their posterior distribution with five chains (Markov Chain Monte Carlo estimation), each running for 600,000 iterations with a burn-in of 500,000 and the remaining were thinned by a factor of 100 in order to yield 1000 posterior samples per chain and 5000 in total. To evaluate if MCMC estimation was a valid approximation of the posterior distribution, the chain convergence and their stationary distribution was visually inspected by their trace plots (Tikhonov et al., 2019). Model fit was evaluated through its explanatory power using the marginal Tjur coefficient of discrimination (Tjur, 2009), a measure of the effect size of the model that excludes the contribution of the random effects.

The contribution of each group of variables (fixed effects and the four levels of random effects) to the distribution of each species was assessed by variance partitioning of the estimated model, pooling together the three predictors as fixed effects. To discard the possibility that the amount of variance explained by the species grouping was not being spuriously inflated by the classification *per se*, independently of which species fall into each group (Wright et al., 2007), we compared the mean percentage of explained variance, for each species group, with the null expectation of 1000 random groupings of species of the same size.

## 3. Results

### 3.1. Overall diversity

A total of 274 taxa was recorded in the sampling plots (n=90), including 169 genera and 38 families (Appendix A). There were, on average, 55.5 species (±10.2 SD) per plot (standardized values by coverage). The average sample completeness was relatively high (mean coverage of 0.944), suggesting that samples were representative of the communities where they were drawn from.

The species pool comprised several Red listed species (n=15), including threatened and near threatened species (Table 1), and several Rare arable plants (n=36). The Archaeophytes constituted a group of 32 species and the Narrow endemics a group of 45 species. These groups were not mutually exclusive (Table B1; Appendix B).

**Table 1**
List of threatened and near threatened species according to the Red List of the Vascular Plants of Continental Portugal (Carapeto et al., 2020), their respective life form and distribution range.

| *Taxon* | Life form | Distribution range | Threat category |
|---|---|---|---|
| *Adonis annua* L. | annual | Wide distribution range | Vulnerable |
| *Adonis microcarpa* DC. | annual | Mediterranean | Vulnerable |
| *Anchusa puechii* Valdés | annual | Iberian Peninsula | Critically Endangered |
| *Bellevalia trifoliata* (Ten.) Kunth | perennial | Mediterranean | Critically Endangered |
| *Biarum mendax* P.C.Boyce | perennial | Iberian Peninsula | Endangered |
| *Bupleurum lancifolium* Hornem. | annual | Mediterranean | Near Threatened |
| *Cynara tournefortii* Boiss. & Reut. | perennial | Iberian Peninsula | Vulnerable |
| *Echium boissieri* Steud. | perennial | Iberian and North of Africa | Vulnerable |
| *Galium viscosum* Vahl | annual | Iberian and North of Africa | Vulnerable |
| *Linaria hirta* (L.) Moench | annual | Iberian Peninsula | Vulnerable |
| *Linaria ricardoi* Cout. | annual | Portugal | Endangered |
| *Linaria micrantha* (Cav.) Hoffmanns. & Link | annual | Mediterranean | Vulnerable |
| *Phlomis herba-venti* subsp. *herba-venti* L. | perennial | Wide distribution range | Near Threatened |
| *Scorzonera hispanica* L. var *crispatula* DC. | perennial | Wide distribution range | Near Threatened |
| *Vaccaria hispanica* (Mill.) Rauschert | annual | Wide distribution range | Vulnerable |

There were no significant differences regarding community species diversity (Hill numbers) in relation to the management type (Figure B2 and Table B2; Appendix B). In the same manner, there were almost no significant differences in the richness by target groups between management types (Figure B3 and Table B3; Appendix B), except for 'cultivation' and 'grazing'. Cultivation presented a higher richness of Archaeophytes in relation to Abandonment ($p$ value $<0.05$; Table B3; Appendix B) and Grazing presented a lower richness of Rare arable plants ($p$ value $<0.01$) and of Red listed species ($p$ value $<0.05$; Table B3; Appendix B).

### 3.2. Management effects on target groups

The explanatory power of the model to test the effects of management on target groups and species, was 0.184 considering only the fixed effects (mean marginal Tjur $R^2$), corresponding to a conditional Tjur $R^2$ of 0.389. Variance partitioning showed that management variables accounted for an average of 18.3% (individual species range 1.5–63.9%) of the explained variance, while the remaining variance was attributed to random effects at different scales, but mainly to the plot level (mean of 54%) and to the regional spatial variation (mean of 17%). Sampling unit and year of sampling represented only 6% and 7%, on average, of the explained variance.

For the species included in the Red listed group, the mean percentage of the variance explained by the fixed effects (management variables) was 25%, and was significantly higher than expected for random species groups of the same size (percentile 0.999 of the null expectation) (Figures B5 and B6; Appendix B). For the Rare arable plants group, the fixed effects explained on average 21% of the variance, also significantly higher than expected (percentile 0.961 of the null expectation). For the Archaeophytes and Narrow endemics groups, the percentage was 20%, which was not significantly higher than expected (percentiles 0.905 and 0.758, respectively) (Figures B5 and B6; Appendix B).

Management variables had a differential effect over the target groups. Ploughing had a significant overall positive effect on the average frequency of Rare arable plants and marginally significant on the Archaeophytes, but no significant effect on the average frequency of species of the Red listed group (Fig. 2). Grazing presented a significant negative effect on the frequency of Red listed species and on Rare arable plants, but no effect was observed on the Archaeophytes. In turn, cultivation presented a significant negative effect on Red listed species, but no effect on either Archaeophytes or Rare arable plants. No effect was observed on Narrow endemics for all analysed management variables.

### 3.3. Management effects at species level

Species responded to management quite differently individually. In relation to ploughing, 26% of the species analysed (n=219) responded positively, 16% negatively, and 58% did not respond. The response to grazing was considerably more negative: 31% responded negatively, 12% positively and 58% did not respond. Cultivation was rather neutral to the majority of the species: 16% responded negatively, 10% positively and 74% presented no response. Species responses were, however, correlated. There was a significant negative correlation between the response to ploughing and to cultivation, as measured by model coefficients (Pearson −0.24; 95% confidence interval [−0.36, −0.11]), i.e., species that were positively associated with ploughing (without crop cultivation) tended to be negatively associated with cultivation, and vice-versa. Contrarily, there was a significant positive correlation between the response to grazing and to cultivation (Pearson correlation 0.35; 95% confidence interval [0.23, 0.46]), but no significant

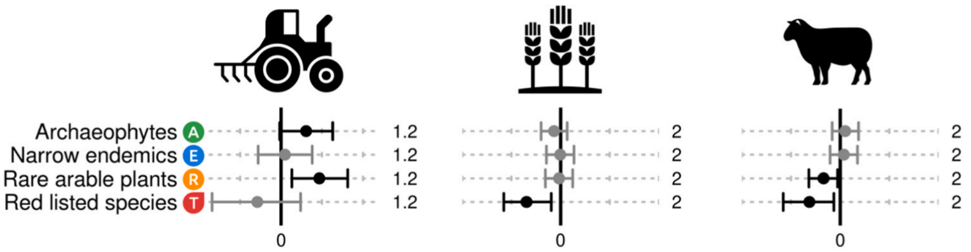

**Fig. 2.** Target group-level effects of management practices (Ploughing, Cultivation and Grazing) on the average frequency of species belonging to each of the four species groups. Abandoned sites were used as the reference level. Plots show the standardized regression coefficients (posterior mean and 95% credible intervals). The significant ($P<0.05$) and marginally significant ($P<0.10$) are coloured in black.

correlation between the response to ploughing and to grazing.

Although the target groups were significantly affected by the management factors, the individual species responses were quite variable (Fig. 3). A total of 18 out of 26 Archaeophytes responded positively to ploughing, while only 2 species responded negatively and 5 did not respond (Fig. 4). Likewise, a total of 19 out of 35 Rare arable plant species responded positively to ploughing, 5 species negatively and 11 did not respond (Fig. 4). Half of the species included in the Red listed group responded positively to ploughing (7 out of 14), 2 negatively and 5 did not respond. In fact, this variable response of the Red listed species to ploughing is due to the fact that this target group combine species that seem to be favoured by ploughing and species that seem to be favoured by no ploughing, like *Echium boissieri* and *Galium viscosum* (figure B4; Appendix B). The Narrow endemics presented a more neutral responses to ploughing, with no responses by 17 out of 31 species, while only 7 responded positively and other 7 negatively (Fig. 4).

Almost all Red listed species responded negatively to grazing (12 out of 14 species), and only 2 did not respond. Likewise, a total of 29 out of 35 Rare arable species responded negatively. The Archaeophytes and the Narrow endemics species were the less negatively affected by grazing, as only 6 out of 26 Archaeophytes and 11 out of 31 Narrow endemic species responded negatively.

The response of the Red listed species to cultivation is also noteworthy, with 9 out of 14 species responding negatively and the remaining species not responding. The Rare arable plants were also considerably affected by cultivation, with 13 out of 35 species negatively responding, while 22 did not respond. The Archaeophytes and the Narrow endemics species seemed the less affected by cultivation: 8 out of 26 and 7 out of 31 responded negatively, while the other species did not respond.

## 4. Discussion

The study clearly supports our hypothesis that the traditional ploughing of soil promotes the occurrence of specialist arable plants in the communities. In addition, we demonstrate that although arable plant diversity is strongly dependent on other local and landscape factors (here modelled as random effects), as also pointed out by other studies (Bourgeois et al., 2020; Rotchés-Ribalta et al., 2015a; Tarifa et al., 2021), the role of soil disturbance caused by ploughing on arable plant communities and on the promotion of rare arable diversity must not be neglected. Moreover, we found that even non-intensive practices like rainfed crop cultivation and low-intensity grazing had a detrimental effect on many of these species, highlighting their narrow ecological plasticity, contrarily to the main general idea about arable plants (Mahaut et al., 2020). These findings question the management practices focused on the protection of soil and of the ground herbaceous layer, which by nature exclude the soil disturbance, therefore, predictably, having negative effects on these specialist arable species.

Although we used abandoned agricultural systems as a proxy of no tillage practices, our results point towards what can be the effects of these conservation agriculture practices on the trajectory of arable plant communities and on the occurrence of specialist arable species, because the ecological conditions imposed by abandonment - undisturbed soils and maintenance of the ground cover vegetation - mimic the main management constraints imposed by no tillage by definition: to minimize or avoid soil disturbance and maximize soil surface cover (Derpsch et al., 2014; FAO, 2022).

### 4.1. Contrasting effects of management practices on target groups

The different low-intensity management practices had a differential effect on the occurrence of specialist arable plants (Archaeophytes, Red listed and Rare arable groups), although they did not affect the total species richness of the communities. Moreover, management practices presented contrasting effects, detrimental or beneficial, on target species and on target groups, except for the narrow endemics that did not respond to management factors. This differential effect is probably the result of the distinct disturbance regime resulting from each management, that filtered out from the community specific species or traits, and simultaneously, increased available niches for others (Booth and Swanton, 2002; Fried et al., 2012; Storkey et al., 2010).

Management with ploughing promoted on average the occurrence of specialist arable species, even though there was an important variability in the individual species responses. This positive response to ploughing is probably related to a common set of response traits that confer them the ability to thrive with the soil disturbance, such as short lifecycle, high seed production, seed persistence in the soil and secondary seed dormancy (Torra et al., 2018). In fact, these specialist arable species, regardless of their biogeographic origin, apparently present adaptations to soil disturbance that are either pre-adaptations or *de novo* adaptations acquired during a rapid adaptive evolution after the onset of agriculture (Vigueira et al., 2013).

Although cultivation was beneficial to some arable archaeophytes, several other specialist arable plants, including threatened species, were negatively affected. This was expected, because crop competition and mineral fertilization to increase crop yield are well known to be important determinants of arable community composition and a strong filter of these plants (Gaba et al., 2018; Kleijn and Van Der Voort, 1997; Meyer et al., 2013; Storkey et al., 2012). Even in extensively managed fields like those in our study, with low mineral fertilization inputs, several specialist arable plants were apparently outcompeted from cultivated fields probably due to crop competition by available soil nutrients (Blackshaw and Brandt, 2009; Rotchés-Ribalta et al., 2016) and access limitation to light, limiting the germination at the soil surface (Cordeau et al., 2015; Storkey et al., 2012). Furthermore, competition by the common arable plants may negatively affect the establishment and growth of specialist arable plants (Rotchés-Ribalta et al., 2016), for example, by reducing their biomass and seed production, an effect that was observed in experimental conditions (Epperlein et al., 2014).

Likewise, low-intensity grazing had a detrimental effect on the occurrence of the majority of specialist arable plants, suggesting that these species do not tolerate the ecological conditions, imposed by this management practice, like increase in nitrogen content and soil

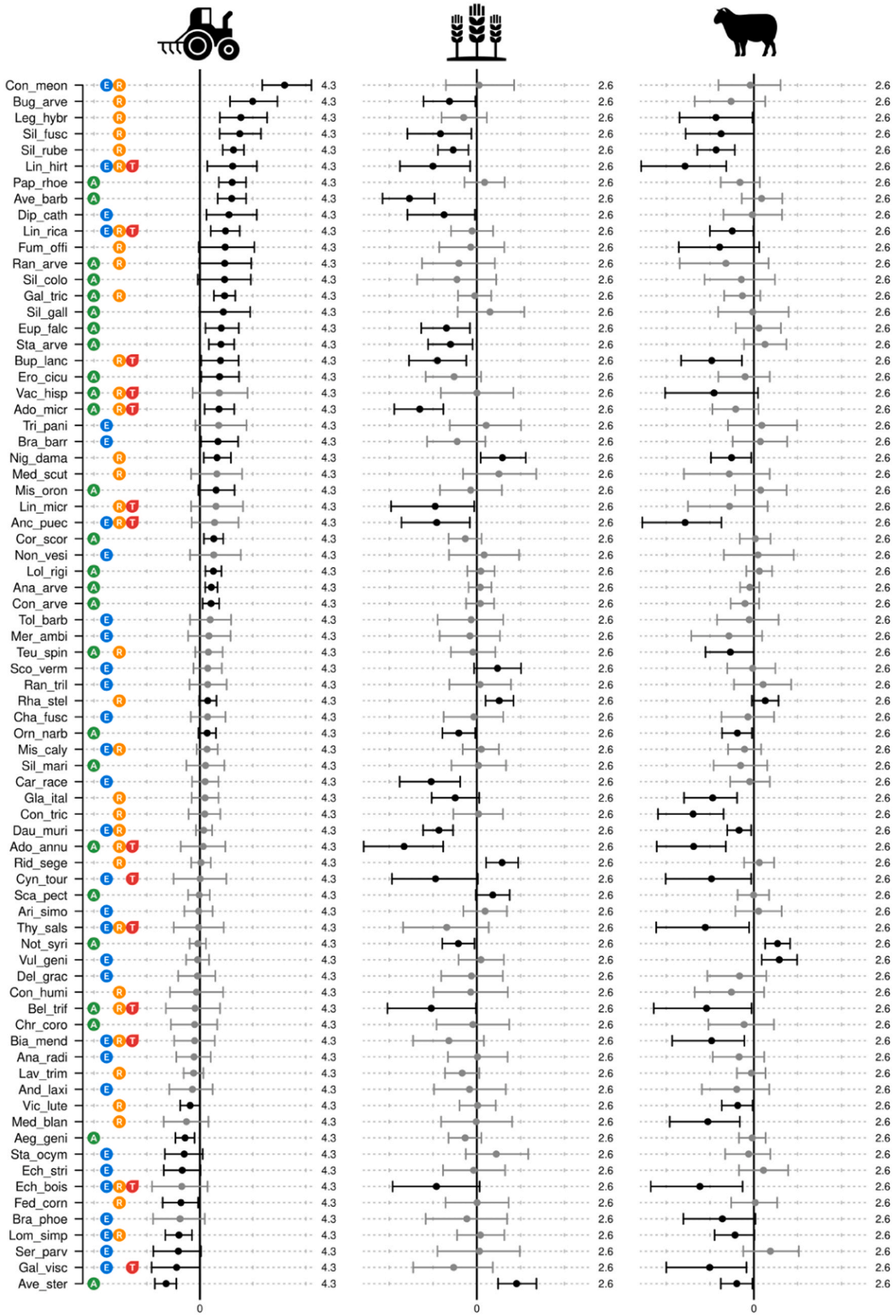

**Fig. 3.** Species responses to management practices (Ploughing, Cultivation and Grazing) considering Abandonment as the reference level. Plots show the standardized regression coefficient (posterior mean and 95% credible intervals). The significant (P<0.05) and marginally significant (P<0.10) effects are coloured in black. Species are sorted by the coefficent of the Ploughing variable. Only species belonging to at least one of the groups are shown. Group membership is represented by the icons: A - Archaeophytes; E - Narrow endemics; R - Rare arable plants; T - Red listed species.

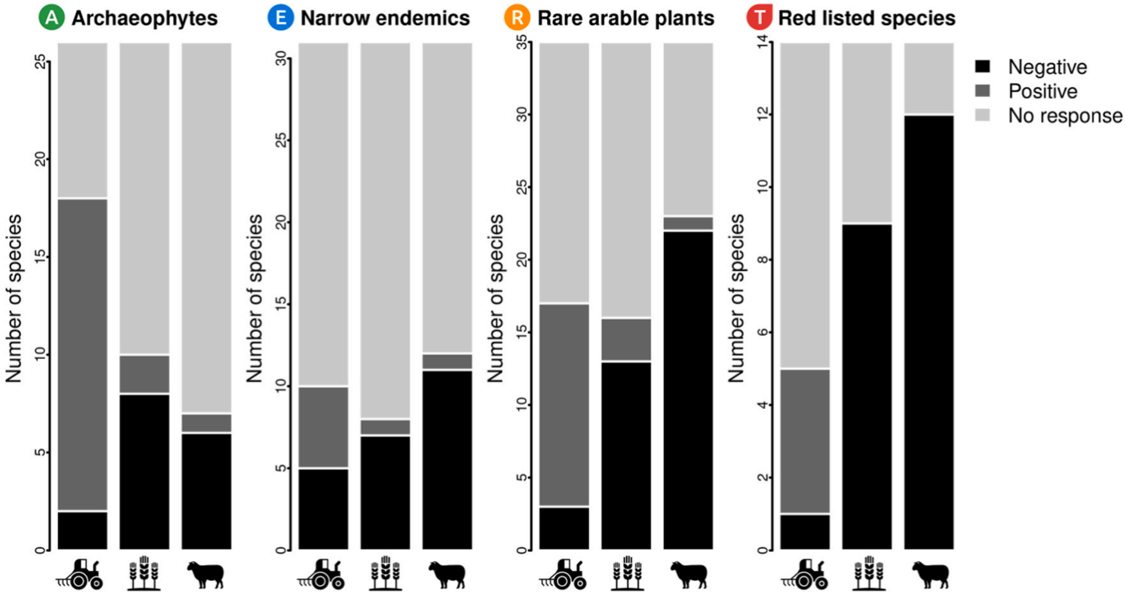

**Fig. 4.** Number of species that responded positively (dark grey), negatively (black) or showed no response (light grey) to the three management practices, in each species group. Responses are quantified by the estimated model coefficients. For the positive and negative effects, we only counted species whose coefficient was significant at a level of $p < 0.10$. Note that some species are counted in more than one group. Icons represent (from left to right): Ploughing, Cultivation and Grazing management practices.

compaction (Lenssen et al., 2013). Our findings, are supported by Rotchés-Ribalta et al. (2015a), that observed that grazing negatively affected the richness of specialist and rare arable species in a field study to compare farming practices on arable weed diversity, including grazing and tillage to control arable weeds. Barroso et al. (2015), also observed a shift in species composition imposed by grazing on an experimental study to compare different treatments to control weeds. This trend, however, may also be explained, by the absence of soil disturbance and not just by the grazing *per se*. Indeed, it is likely, that the interaction of both factors through the years, may had, substantially, altered the trajectories of these communities, leading to the decrease of arable plants over time, in particular of specialist and rare arable plants.

### *4.2. Traditional ploughing as a key factor to sustain rare arable diversity*

Our results suggest that the regular soil disturbance is a key factor for the maintenance of rare arable plants, with reported decline in Portugal but also in other areas of the Mediterranean region (e.g. *Buglussoides arvensis*, *Galium tricornuntum*, *Fumaria parviflora*, *Legousia hybrida*, *Ranunculus arvensis*), including threatened and near threatened species according to IUCN criteria (e.g. *Adonis microcarpa*, *Bupleurum lancifolium*, *Linaria hirta*, *Linaria ricardoi*, *Linaria micrantha*, *Vaccaria hispanica*).

Several experimental studies support our findings, Albrecht and Mattheis (1998), for example, showed that excluding tillage with ploughing from experimental treatments caused a large decrease on the number of rare arable plants in 90% of all sampling units. Also, Bilalis et al. (2001) detected a decrease in the richness of arable weeds, both perennial and annual, and a lower proportion of rare species under no tillage treatment in a field experiment. Likewise Torra et al. (2018), observed a higher emergence of rare arable plants on ploughed soils compared with non-disturbed soils, after sowing seeds according to two experimental treatments (tillage and no-tillage), concluding that most of the species analysed needed soil disturbance in order to germinate. In addition, Rotchés-Ribalta et al. (2015b) refer that the slight periodic soil disturbances tended to favour the presence of rare arable plants, when studying the local effects that determine their presence on arable fields.

By the contraire, the abandoned plots, our reference level in the model, apparently didn't ensure the niche requirements for the occurrence of several threatened archaeophytes and rare arable plants. This could be caused by a secondary succession process, triggered by the absence of soil disturbance, that led to the displacement of these arable annual species by perennial ones (Solé-Senan et al., 2018). According to Recasens et al. (2020), during this succession process, specialist arable plants, including rare species, are expected to disappear from the communities, due to seed burial (Solé-Senan et al., 2014) and competition for available niches (Hernández Plaza et al., 2015). However, we cannot disentangle the effect of other factor imposed by this condition, the one caused by the maintenance of ground vegetation cover, that may reduce the incident light reaching the soil surface, constraining the establishment of species that require light to germinate (Chauhan et al., 2012; Cordeau et al., 2015; Royo-Esnal et al., 2015).

Although we used abandoned traditional olives groves as a proxy of a no tillage situation, our results stress that the non-disturbance of the soil, as advocated by this practice, may contribute to the decline of rare annual arable species, as also emphasized by Recasens et al. (2020). Even if, the seed bank may buffer this declining trend at the community level (Rotchés-Ribalta et al., 2020), this may not be a safeguard for all rare arable species, since their seedling emergence pattern is variable across them (Torra et al., 2018) and seems to be dependent, directly or indirectly, of the disturbance of the soil, as our study and others (above) indicate.

### *4.3. To plough or not to plough - recommendations for the conservation of arable plant diversity*

Arable plant species present diverse ecological strategies (Perronne et al., 2014) but the long history of regular soil disturbance by ploughing (see Palmer, 1998) is likely to have been an important selective factor on their life history (Neve et al., 2009). Apparently, this has led to a rich community of soil disturbance-tolerant species, like the arable archaeophytes and other specialist arable plants (Bourgeois et al., 2019). Our results highlight the role of this traditional ploughing for the conservation of these specialist arable plants, and in particular of currently rare and threatened species of the arable plant communities of Mediterranean olive groves associated with basic soils.

However, the beneficial effects of ploughing on these plants may depend on the way ploughing is practised regarding the frequency and time of ploughing events and tillage techniques. Although we did not test it, more conventional techniques like mouldboard ploughing or other harsh soil inversion techniques may produce negative effects on arable plant communities, because they likely lead to seed bank depletion (Ball, 1992; Feledyn-Szewczyk et al., 2020; Gruber and Claupein, 2009), due to the deeper burying of seeds, which prevents germination (Critchley et al., 2006). Likewise, based on ours and other authors' results (Recasens et al., 2020; Rotchés-Ribalta et al., 2015b; Torra et al., 2018), conservation tillage practices like no tillage or other that do not disrupt soil and promote the ground vegetation cover (e.g. mowing, direct seeding and low-intensity grazing), may also restrict the establishment of these specialist arable plants because they require disturbance to break seed dormancy.

We think there has been a biased scientific discussion around the effects of ploughing without accounting for the consequences of excluding it for arable plant diversity and the cascading effects of losing this diversity (Bretagnolle and Gaba, 2015; Marshall et al., 2003). While it is true that despite weed diversity (richness), the abundance (cover) of weeds enhances pollination services (Bretagnolle and Gaba, 2015; Marshall et al., 2003), and that the overall weed diversity (richness) is positively related with the diversity of pollinators and other insects (Albrecht et al., 2020; Cano et al., 2022), the role of rare weeds in these networks is not yet clarified. For instance, specific weeds with specific flower traits may be an important food source for specialized pollinators (Carvell et al., 2007; Gibson et al., 2006; Rollin et al., 2016), so their loss may lead to declines in pollinator diversity. Therefore, conflicting views in respect to plough or not to plough the arable habitats of Europe and of the Mediterranean Basin region should be harmonized to properly design soil management strategies that, without compromising conservation agriculture objectives, like the protection of soil and minimize soil erosion, simultaneously ensure the conservation of arable plant diversity and of specialist and rare arable species.

In the case of the traditional agricultural systems focused on our study, and perhaps, to some extent, other rainfed extensive cultures (e.g. wheat), we recommend keeping and incentivizing ploughing using reduced tillage techniques (chisel and disk ploughing) or others that closely reproduce the traditional way of doing it (Palmer, 1998). We also urge not to replace this traditional practice for others that exclude soil disturbance, contrarily to what is advocated by other authors focused more on the protection of soil and on other biological groups (e.g. Rey et al., 2019; Tarifa et al., 2021), because, based on our results, ploughing is probably not replaceable by other low-intensity practices, and its substitution may promote the decline of these species.

However it is important to note, that although no tillage may reduce the proportion of rare annual plants, it apparently benefits threatened perennial plants, that do not tolerate the regular disturbance of soil by ploughing, which tend to occur in abandoned sites and other marginal habitats, like field edges (Fried et al., 2009; José-María et al., 2010), stressing the role of no tillage areas for the maintenance of these particular species in the agricultural mosaic.

Furthermore, we stress that our results and the inference about their consequences on these arable plant communities, with a specific biogeography and evolutionary history (Mediterranean Basin), cannot be extrapolated to other regions of the world with a completely different regional pool of arable weeds, even with similar macro climatic conditions, like other bioclimatic Mediterranean regions, for instance.

From a European perspective, Mediterranean agricultural systems, like the traditional olive groves, still constitute a significant reservoir of diversity of the arable flora and every effort must be made to preserve this arable habitat (Allen et al., 2006; Meyer, 2020, Recasens et al., 2020). Accordingly, we advise that future actions of European Union (EU) Common Agricultural Policy (CAP) should include eco-schemes or other financial instruments that directly support the conservation of arable plant diversity of traditional Mediterranean olive groves, in accordance with one of CAP's Specific Objective: to contribute to the protection of biodiversity, to the enhancement of ecosystem services and the preservation of habitats and landscapes. Specifically, this EU policy instrument should include Single Payment Schemes (SPS) to incentivize two main management practices: a) the traditional way of managing the 'weedy' ground vegetation cover through the regular ploughing with reduced tillage techniques, and b) the maintenance and promotion of marginal habitats (e.g. field edges). Directly subsidizing these High Nature Value Farming Systems (Loumou and Giourga, 2003), will help to ensure the conservation of arable plant diversity and threatened species populations.

## Authors contributions

AJP and PB conceived de idea; AJP and MP designed the methodology; AJP collected the data; MP and AJP analysed the data; AJP, MP, PB and OC led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data Availability

Data will be published in the Dryad repository upon acceptance.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2023.108775.

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