Science of the Total Environment 905 (2023) 166990

Contents lists available at ScienceDirect

Science of the Total Environment

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

Echoes of the past: Agricultural legacies shape the successional dynamics of protected semi-natural dry grasslands

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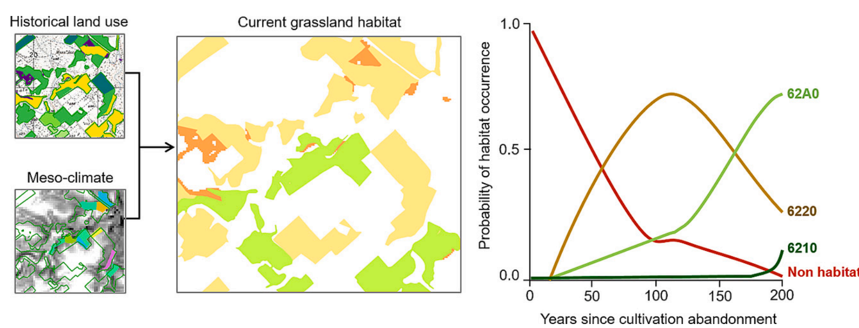
HIGHLIGHTS

- We investigated the role of time since cultivation abandonment as a driver of grassland succession.
- We integrated information on the past agricultural land use with the main abiotic constraints
- Successional patterns highlight spontaneous grassland recovery in agro-pastoral systems.
- Land use history and current environment shape the distribution of protected grasslands.
- Information on past land use changes can support habitat conservation.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Fernando A.L. Pacheco

Keywords:
Grassland ecology
Habitats Directive
Plant succession
Cultivation abandonment
Land use history

ABSTRACT

European semi-natural dry grasslands are among the most endangered terrestrial ecosystems, being recognised as habitats of community interest by the EU Habitats Directive. The occurrence and preservation of these habitats depend on a combination of anthropogenic and natural factors, although little is known regarding the role of past land-use changes. Here, we investigated the role of time since cultivation abandonment as a major driver of grassland successional dynamics in the Mediterranean agro-pastoral system of Alta Murgia, southern Italy. By integrating cartographic information on the past agricultural land-use with the main abiotic constraints (patch area, slope and aspect), we used generalised additive mixed models to test for the probability of occurrence of current grassland habitat types along time since cultivation abandonment (10 to 200 years). Our results disclosed the successional sequence of grassland plant communities since crop abandonment in the study area, highlighting that the distribution of semi-natural grassland communities largely depends on land use history besides current environmental patterns. Among the habitat types protected under the EU Habitats Directive, we highlighted that xero-thermic communities may represent an intermediate step of grassland succession after cultivation abandonment, while more mesic perennial communities indicate a late successional stage. These successional dynamics are further modulated by mesoclimatic conditions associated with slope and aspect,

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https://doi.org/10.1016/j.scitotenv.2023.166990
Received 24 June 2023; Received in revised form 8 September 2023; Accepted 9 September 2023
Available online 12 September 2023

especially in case of long-standing pastures that were not historically affected by agricultural transformations. Our findings can contribute to a deeper understanding of dynamics relevant to spontaneous vegetation recovery in open environments, which is a prerequisite for setting up effective grassland conservation and restoration actions. Furthermore, our results underline the value of integrating historical maps and current information for the assessment of habitat conservation status.

1. Introduction

Semi-natural dry grasslands of the Western Palearctic region are home to extremely diverse plant and animal communities, containing the global maxima of plant species diversity at smaller spatial scale (Wilson et al., 2012; Roleček et al., 2019). Grasslands provide invaluable functions relevant to the preservation of both agricultural and natural ecosystems, including the regulation of water supply and erosion, carbon storage, climate mitigation and pollination (Lemaire et al., 2011; Bengtsson et al., 2019; Bond, 2021). Nonetheless, semi-natural grasslands are among the most endangered terrestrial ecosystems worldwide, in turn raising concern for the conservation of the numerous species they sustain, e.g., the remarkable set of bird and insect communities uniquely depending on grassland habitats (Vickery et al., 2000; Haddad et al., 2009; Warren et al., 2021). Grassland habitat loss and degradation is primarily due to land use changes associated with agricultural intensification, abandonment and urbanization (Habel et al., 2013; Dengler et al., 2014). As a consequence of their impressive biodiversity and implicit vulnerability to anthropogenic pressures, semi-natural dry grasslands are recognised as habitats of community interest within the Annex I of the European Union (EU) Habitats Directive (HD), which thus grants for their legal protection and identifies these habitats as key to the implementation of the Natura 2000 (N2K) network. Although the HD builds on an extensive classification of vegetation, it can hardly handle the complexity of semi-natural habitats' dynamics along the continuum from natural to cultural (Ejrnæs et al., 2003; Troiani et al., 2016). Besides, evidence suggests that the stages of succession that follow agricultural abandonment may actually lead to the formation of very different grassland plant communities, in turn corresponding to different legally protected habitat types according to the HD (Calaciura and Spinelli, 2008; San Miguel, 2008). The occurrence and preservation of European semi-natural dry grasslands are known to depend on a set of anthropogenic factors, e.g., grazing, cutting and fire, preventing natural succession towards forest climax vegetation (Calaciura and Spinelli, 2008; San Miguel, 2008). The quantification of the effects of such factors in determining a specific stage in vegetation succession is often variously combined with an understanding of the role of local natural conditions (Hobbs et al., 2007; Svenning and Sandel, 2013). On the sidelines of the consideration of biotic-driven and abiotic-driven changes, past conditions are often disregarded in vegetation studies (Bruun et al., 2001; Cousins and Eriksson, 2002; Lindborg and Eriksson, 2004; Purschke et al., 2012). A delayed response to environmental changes can represent a major challenge to biodiversity conservation in semi-natural grasslands, e.g., providing evidence for unpaid extinction debts across different trophic levels (Bommarco et al., 2014; Poniatowski et al., 2018; Löffler et al., 2020; Deák et al., 2021). Nonetheless, environmental changes in past times are known to act as major drivers of current vegetation and biodiversity patterns, even considering changes over >200 years (Koerner et al., 1997; Lunt and Spooner, 2005; Gustavsson et al., 2007). Since the Middle Age, the use of natural resources through extensive activities has been the main force that shaped European landscapes (Antrop, 2005; De Aranzabal et al., 2008). However, due to the deep socio-economic changes that have occurred after the World War II, traditional use of natural resources was widely discontinued in rural areas of Europe (Antrop, 2004; Mazzoleni et al., 2004), inducing changes both at landscape and plant community levels (Poschlod and WallisDeVries, 2002; Mottet et al., 2006; Bracchetti et al., 2012; Daskalova and Kamp, 2023).

The Mediterranean Basin, in particular, is one of the world's regions where the effects of land abandonment are most evident (MacDonald et al., 2000; Weissteiner et al., 2011; Molina et al., 2023). Such effects have been widely documented in terms of encroachment by shrublands or forests (e.g., Lasanta-Martínez et al., 2005; Petanidou et al., 2008; Bracchetti et al., 2012). However, the succession on abandoned fields may also lead to the formation of semi-natural dry grasslands, where the soil is sufficiently poor in nutrients and colonisation sources are available in the seed bank or from neighbouring habitats (Pywell et al., 2002; Ruprecht, 2006; Winsa et al., 2015). Cultivation abandonment is listed among the main drivers of secondary succession in dry biomes (Carpenter et al., 1986; Agami et al., 1998; Dana and Mota, 2006), as the Mediterranean, where grasslands represent an important component of plant succession even long after cultivation abandonment (Debussche et al., 1996; Valverde-Asenjo et al., 2020; Molina et al., 2023). Hence, cultivation abandonment combined with extensive management, i.e. grazing or mowing, may prove effective in the spontaneous recovery and maintenance of semi-natural grasslands in abandoned fields (Gibson and Brown, 1992; Pywell et al., 2002). A deeper understanding of patterns and dynamics that can effectively favour spontaneous recovery is increasingly needed, especially considering the serious constraints affecting the setup of active restoration of species-rich grassland communities (Albert et al., 2019; Török et al., 2021; Mudrák et al., 2023).

By integrating the current knowledge on the ecological requirements of Mediterranean dry grassland plant communities (Mucina et al., 2016), we hypothesised that: i) grassland types dominated by annual and xero-thermic species can establish earlier after cultivation abandonment, while more mesic perennial communities indicate a late successional stage, and that ii) successional dynamics are further modulated by mesoclimatic and edaphic conditions associated with slope and aspect, possibly complementing the effects of past agricultural transformations. Hence, in our study system, we investigated the role of time since abandonment as a major driver of the transition among different grassland habitat types listed in the HD, i.e. from "Pseudo-steppes with grasses and annuals of the *Thero-Brachypodietea*" (HD code: 6220) to "Eastern sub-Mediterranean dry grasslands (*Scorzoneretalia villosae*)" (HD code: 62A0) or "Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*)" (HD code: 6210) (Biondi et al., 2012).

2. Materials and methods

2.1. Study area

We conducted our study in the Murgia Alta N2K site (IT9120007), in southern Italy, a calcareous plateau covering 126,000 ha and partly designated as a National Park since 2004 (Fig. 1). Ranging from 285 to 680 m a.s.l., Alta Murgia is characterised by its deep and compact platform of Cretaceous limestone, with very shallow and rocky soils and total lack of surface watercourses. The climate is typically sub-Mediterranean, with mean annual variation from 7 °C of January to 25 °C of July/August (Forte et al., 2005). Rainfall is concentrated in autumn-winter season, with average values of 570 to 700 mm/year and snow occasionally occurring above 500 m a.s.l. With the exception of residual patches of semi-deciduous oak forests and conifer plantations, the upper part of Alta Murgia is widely characterised by a typical Mediterranean agro-pastoral landscape dominated by cereal crops and semi-natural dry grasslands, being one of the most important areas for the conservation of open ecosystems in the Western Mediterranean Basin (Mairota et al., 2013b).

As with most grasslands of the Mediterranean region, dry grasslands of Alta Murgia have developed through centuries of grazing, cutting and light burning regime, and are mainly maintained by extensive sheep grazing. Grasslands are partially listed in Annex I of the Habitats Directive (HD), namely as "Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*)" (HD code: 6210), "Eastern sub-Mediterranean dry grasslands (*Scorzoneretalia villosae*)" (62A0) and "Pseudo-steppes with grasses and annuals of the *Thero-Brachypodietea*" (6220). In the study area, 6210 habitat is mainly represented by *Brachypodium rupestre* communities (order *Brachypodietalia pinnati*, class *Festuco-Brometea*), while 62A0 code is attributed to meso-xeric rocky grasslands belonging to the endemic alliance *Hippocrepido glaucae-Stipion austroitalicae* (order *Scorzoneretalia villosae*, class *Festuco-Brometea*) (Tarantino et al., 2021). 6220 habitat includes a diversified set of Mediterranean xero-thermic communities belonging to the orders *Brachypodietalia distachyi* (class *Stipo-Trachynietea distachyae*) and *Cymbopogono-Brachypodietalia ramosi* (class *Lygeo sparti-Stipetea tenacissimae*) (Tarantino et al., 2021). During the last three decades, grasslands have been subjected to a combination of anthropogenic impacts that locally accelerated processes of habitat degradation, fragmentation and loss (Mairota et al., 2013a). Dry grasslands currently cover ~35,100 ha (28 % of the total area of the N2K site) and represent what remains from the ~80,000 ha existing at the beginning of the XX century (Mairota et al., 2013a; Tarantino et al., 2023). Most dramatic habitat loss had occurred in the 90's, due to the replacement of rocky pastures with arable crops for durum wheat production, also associated to a widespread soil transformation caused by rock graining (Mairota et al., 2013a). Due to the actual maintenance of traditional pastoral systems, and considering the local environmental constraints (i.e. widespread low fertility, aridity), impacts associated with the encroachment by woody plants only play a minor role in the loss and degradation of grassland ecosystems (Mairota et al., 2013b; Tarantino et al., 2019).

With the exception of cereal crops, arable surface of Alta Murgia is mainly covered by permanent cultivations, mostly vineyards and traditionally managed olive and almond groves. These traditional cultivations, that were still widespread in large portions of the territory at the beginning of the XX century, have been largely discontinued from the second half of the century, due to the unsuitability of local growing conditions (e.g., steep areas, rocky and thin soil layers) for recent cultivation techniques and economic yield requirements (Shelef et al., 2016).

2.2. Current and past land cover

We assessed current grassland cover and past land use by coupling a remote sensing approach on satellite imagery with visual interpretation of aerial photographs and historical maps (Fig. 2). We derived the current extent of semi-natural herbaceous communities from multi-season Sentinel-2 imagery processing (year 2021; Copernicus Open Access Hub of the European Space Agency), through a data-driven pixel-based classification algorithm, as detailed in Tarantino et al. (2023). During spring 2021–2023, we carried out field surveys for habitat identification and mapping across the study area, consisting in 351 phytosociological relevés (square plots of 1 to 100 m^2) and 127 validation plots (quick surveys checking for dominant species), also accounting for the spatial extent of surveyed homogeneous communities within a grassland patch. Surveyed plant communities were then ascribed to HD habitat types according to Biondi et al. (2012). Considering the lack of information relevant to habitat quality in past times, in our study we did not consider information on grassland condition, as required for the assessment of habitat conservation status of HD habitats. Based on field data and interpretation of most recent available orthophotos (year 2019; https://pugliacon.regione.puglia.it/), we classified grassland polygons, or polygon portions, according to the current prevailing HD grassland habitat, i.e. semi-natural dry grasslands on calcareous substrates (HD code: 6210), pseudo-steppe with grasses and annuals of the *Thero-Brachypodietea* (HD code: 6220), Eastern sub-Mediterranean dry grasslands (HD code: 62A0), or non-protected herbaceous vegetation (HD code: no habitat). Taking into account that these grassland communities frequently occur in hardly distinguishable fine-scale vegetation mosaics (Tarantino et al., 2021), we estimated the overall proportion of habitat cover in the field, then we considered the most abundant habitat type (covering >50 % of the polygon) as a proxy descriptor of the patch vegetation. For the purpose of this study, we excluded 1864 ha of grasslands falling within conifer plantations, oak woods, quarries or highly anthropized areas, as these represent specific cases restricted to peculiar ecological conditions in the study area.

For each polygon, we detected past land uses by combining information from historical cartography (IGM - Istituto Geografico Militare 1:25.000, mapped in 1947–1958), and recent orthophotos (years

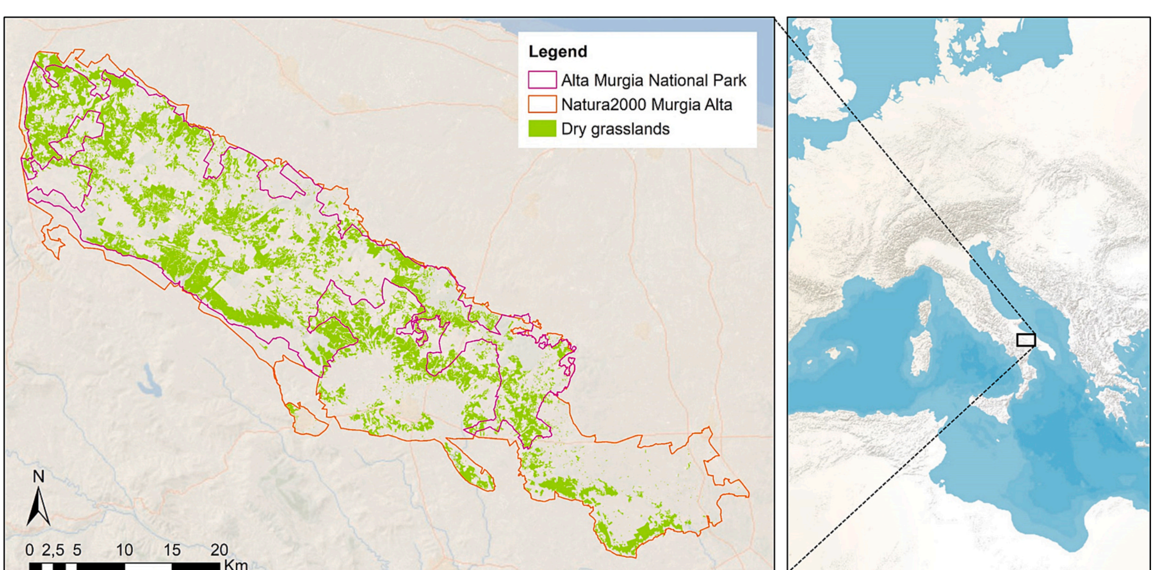

Fig. 1. On the left, map of study area showing the distribution of dry grasslands within the protected area of Alta Murgia National Park and N2K Murgia Alta site. On the right, location of the study area in southern Italy.

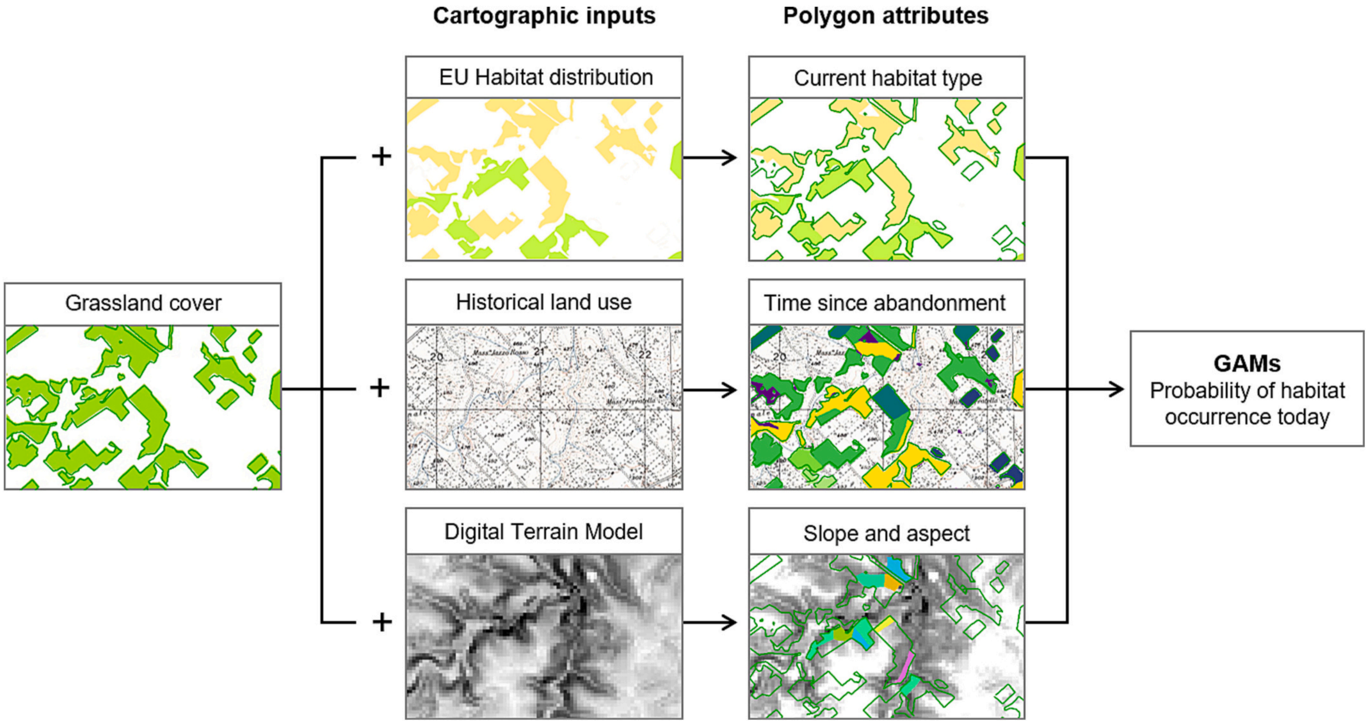

Fig. 2. Diagram of the approach used to combine cartographic information representing the variables tested for assessing the probability of habitat occurrence in the study area.

2011–2019). IGM cartography, relevant to aerial photographs and field surveys for the identification of topographic units, provides an accurate classification of the main permanent agricultural land use categories for the period 1947–1958, i.e., olive and almond groves, other fruit orchards and vineyards (https://www.igmi.org/). For those patches that did not display agricultural features in the period 1947–1958, we additionally used orthophotos and field observations to detect rural architectures representing signs of older agricultural use (i.e., traditional stonewalls, '*trulli*', '*specchie*'), mainly built in the area before the XX century (Ruggiero et al., 2019). We further used orthophotos and field observations to estimate time of cultivation abandonment before 2011, based on the conservation status and occurrence of planted tree rows.

Therefore, for each polygon, we were able to match the time since cultivation abandonment, identifying five temporal categories: <10 years (still cultivated after 2011), 20–30 years (cultivated in 1958, persisting tree rows in orthophotos), >60 years (cultivated in 1958, no persisting tree rows in orthophotos), >100 years (unknown land use in 1958, signs of former agricultural use), >200 years (unknown land use in 1958, no recognizable signs of former agricultural use). Such an approach, despite not being completely free of errors, is key to test hypotheses on the past of agrocosystems, particularly in Italian Karst landscapes that are strongly characterised by a rich and complex history of human settlements (Burri et al., 1999). Based on a regional Digital Terrain Model (https://pugliacon.regione.puglia.it/), we detected grassland surfaces with slopes >20 %, considering their aspect as cardinal quadrant (North, East, South, West, or none when the slope < 20 %). We did not test the effects of elevation, both because of its negligible variation in the area, and since we could not assign a single value to larger grassland polygons that encompass a wide elevation range. Similarly, we excluded the possibility to test the effects of grazing and light burning, as information on their spatial distribution is only partially available for the area and, in any case, does not allow for mapping their effects in the past. However, these are not deemed to be factors limiting grassland recovery in the studied landscape, as sheep grazing and fire are known to be constant and widespread since ancient times through the whole study area (Caballero et al., 2009; Perrino and Wagensommer, 2013).

Since we aimed at analysing landscape changes at patch (i.e., polygon) level, we preliminary tested whether patches belonging to different temporal or land cover classes differed in their spatial covariation, i.e. whether patches were spatially clustered due to e.g., non-considered factors. We used the package *landscapemetrics* (Hesselbarth et al., 2019) to calculate the Euclidean Nearest-Neighbor (ENN) aggregation metric (as in Katna et al., 2023), and then run a Kruskal-Wallis test to assess differences among classes, and a Pearson correlation test between time since abandonment and ENN values across all land cover classes. Since we retrieved no significant result (all $p > 0.05$), we considered patches in our study area as genuinely independent sampling units.

2.3. Statistical analyses

To verify our hypothesis on the role of time since cultivation abandonment in driving the current vegetation in the study area, we tested for differences in the occurrence of grassland habitat types (6210, 62A0, 6220, no habitat) along time since cultivation abandonment (10 to 200 years), by using generalised additive models (GAMs) according to the expected non-linear response to, e.g., categorical ordinal variables (time since cultivation abandonment). A binomial error distribution and a logit link function were adopted. For each habitat type we used its occurrence as dominant vegetation (categorised as 1 = dominant, 0 = absent or non-dominant) within each patch as response variable.

To account for our second hypothesis, regarding the combined effects of environmental conditions, we integrated time since cultivation abandonment with information on slope aspect and patch size as model predictors. As such, model formula for each habitat (H) in each patch consisted in the following terms:

$$H_i = S(t_i) + AS_i + P_i + \epsilon_i$$

where $S(t_i)$ is the smoothing spline of time since abandonment, AS is aspect slope as category variable with 5 states (North, East, South, West, none), and finally patch area (P). We preliminary checked whether fitting time since abandonment as smoothed variable in a GAM model increased model performance, by also running the same model without the smooth (i.e. assuming a linear relationship with time since abandonment in an equivalent GLM) and comparing models' values of Akaike's information criterion (AIC) as fitting indicator; such assessment resulted in smoothed factors systematically increasing model performance (δAIC > 4; Table S1 in Supplementary materials), which were thus retained for further considerations. For categorical variables, we also run a likelihood test (with the *anova* function) between the full model including all variables, and the same model run without the categorical variable of interest, in order to infer a general value of significance for the given variable, separately for each response variable. Similarly, variance partitioning among variables was assessed by computing models with and without the variable of interest and by comparing values of adjusted R^2, so that we considered the increase in explained variance as an indicator of each variable's importance. The effect of each predictor, and its direction, was considered significant when $p < 0.05$ and the confidence interval did not encompass 0. Tests were run in R 4.2.1, using the *gam* package (Hastie and Hastie, 2015).

3. Results

Overall, we selected 4992 dry grassland polygons, with surfaces ranging from 0.01 to 534.31 ha, on average, 6.62 (±24.64) ha (Fig. S1 in Supplementary materials). According to HD definition of habitat types, 0.2 % were dominated by semi-natural dry grasslands on calcareous substrates (HD code: 6210), 57.3 % by Eastern sub-Mediterranean dry grasslands (62A0), 37.0 % by pseudo-steppe with grasses and annuals of the *Thero-Brachypodietea* (6220), and 5.4 % by no recognizable HD type (non-habitat) (Fig. 3). 6210 habitat was mainly represented by small patches with *Brachypodium rupestre* communities, while 62A0 code was attributed to meso-xeric rocky grasslands generally dominated by *Stipa austroitalica*. 6220 habitat included a set of xero-thermic communities, alternatively indicated by high cover of annual (e.g., *Brachypodium distachyon*, *Stipellula capensis*) or perennial grasses (e.g., *Hyparrhenia hirta*, *Dactylis glomerata* subsp. *hispanica*), and geophyte-rich degraded pastures (e.g., with *Asphodelus ramosus*). Further observed herbaceous communities that could not be attributed to HD habitat categories were represented by nitrophilic and sub-nitrophilic communities, either grass-rich with annual (e.g., *Dasypyrum villosum*, *Triticum vagans*) and perennial grasses (e.g., *Elymus repens*), or characterised by a high cover

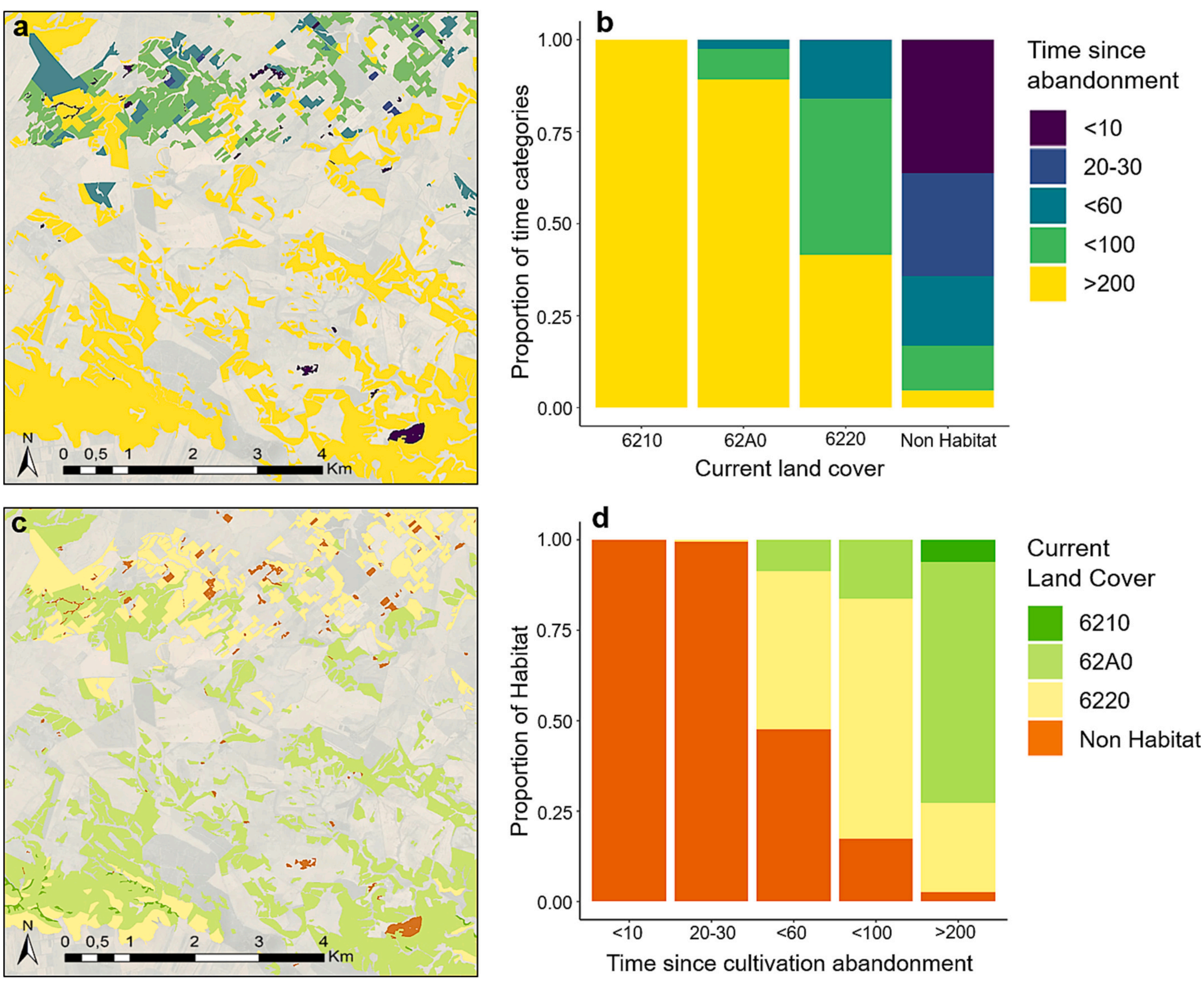

Fig. 3. Maps of the central portion of N2K Murgia Alta, showing: (a) the variation of time since cultivation abandonment; (c) the current distribution of grassland habitats. Bar-plots showing: (b) the proportions of categories of time since cultivation abandonment for each grassland habitat; (d) the proportions of grassland habitats for each time category.

of nitrophilic forbs (e.g., *Ferula communis*, *Silybum marianum*).

Considering time since the last land-use change, the grassland surface of Murgia Alta is largely characterised by old pastures, including pastures older than 200 years (68.0 %) or 100 years (22.2 %). A smaller portion of grassland surface occurs in formerly cultivated areas, namely >60 years (6.9 %), 20–30 years (1.2 %) or <10 years (1.7 %) before this study (Fig. 3).

Habitat occurrences in the study area were variously associated with the considered predictors, i.e. time since cultivation abandonment, patch area and slope aspect (Table 1). Nonetheless, the probability of observing all grassland types was mainly driven by time since cultivation abandonment, which in all cases was the first factor contributing to explain the observed variability in our landscape - e.g., consistently featuring the highest values of explained variance in all models (ranging between 18 and 56 %), albeit with different patterns among types. Both 6210 and 62A0 habitats were positively driven by time since cultivation abandonment (Table 1), with 6210 favoured by north-facing slopes and 62A0 on all slope orientations except south-facing slopes (Fig. 4). Conversely, 6220 grasslands and no-habitat grasslands were negatively driven by time since cultivation abandonment, thus prevailing in areas that were cultivated until most recently (Table 1). In particular, 6220 habitat shows a bimodal response to cultivation abandonment, since this habitat increases its probability of occurrence along with time since cultivation abandonment, which decreases in older pastures that were not cultivated for >100 years (Fig. 4). When considering slope aspects, the probability of observing 6220 habitat tends to decrease along with time since cultivation abandonment in steeper slopes, with the exception of south-facing slopes, which preserve the stability of 6220 habitat patches even in case of very old pastures (Fig. 4). No-habitat grasslands quickly decrease with time since cultivation abandonment, regardless of the slope orientation (Fig. 4). Patch extent only showed significantly negative effects on 6210 and no-habitat grasslands, indicating that these vegetation types most frequently occur in small patches in the study area (Table 1).

4. Discussion

4.1. Past land use and grassland habitats

Our study discloses the role of past agricultural land use as a predominant driver of present-day vegetation in a Mediterranean agro-pastoral ecosystem, highlighting that the distribution of semi-natural grassland communities largely depends on land use history, even more than on current patch size and main mesoclimatic patterns. Overall, the considered methodological approach underlines the value of integrating information from remotely-sensed land cover, historical maps and field observations for the implementation of quantitative baselines needed for the monitoring of habitat quality in a protected area (Nagendra et al., 2013; Lucas et al., 2015; Mairota et al., 2015). In particular, by integrating information on the past land use with the main ecological constraints associated with slope aspects, our reconstruction allows to disclose the successional sequence of grassland plant communities since crop abandonment throughout the Murgia Alta N2K site. While synanthropic herbaceous communities quickly colonise agricultural areas after abandonment, the probability to reach dry grassland vegetation belonging to HD habitat types increases with time. This finding was not unexpected, since oligotrophic vegetation generally needs longer times to develop on agricultural soils (Pywell et al., 2002; Ruprecht, 2006; Valkó et al., 2018). Nonetheless, evidences of the capability of agricultural fields to turn into semi-natural grasslands are encouraging in a grassland recovery perspective, with the purpose of understanding spontaneous dynamics, considering the serious constraints associated with active restoration activities (Valkó et al., 2018, 2022; Tölgyesi et al., 2022; Fantinato et al., 2023). In the study area, abandoned fields were already shown to spontaneously develop into xeric annual semi-natural grasslands within a few years (Labadessa et al., 2020), given that source populations of colonising species and dispersal are supported by spatial proximity to focal sites (Pywell et al., 2002; Öster et al., 2009; Winsa et al., 2015). However, encroachment after land abandonment was proven to be naturally limited also by abiotic constraints in many dry areas of the Mediterranean Basin (Houssard et al., 1980; Escarré et al., 1983; Valverde-Asenjo et al., 2020).

Our results are in line with our hypotheses, highlighting that, among the habitat types protected under the EU Habitats Directive, the xero-thermic communities of 6220 habitat can represent an intermediate step of grassland succession, as they can gradually colonise abandoned fields in a few decades, but then tend to disappear after longer time since cultivation abandonment. Such a dynamic feature of xero-thermic plant communities is widely acknowledged in vegetation studies (e.g., Verdú et al., 2000; Bagella et al., 2016; Molina et al., 2023), though its consideration is frequently misleading in conservation assessments, since transient dynamics are seldom integrated by authorities in conservation issues (Leroux et al., 2007; Pressey et al., 2007). As hypothesised, these successional dynamics are further modulated by slope orientation, since the occurrence of this habitat is significantly more stable in pastures along south-facing hillsides even when they were not disturbed by agricultural practices for centuries. In fact, 6220 habitat includes herbaceous plant communities adapted to typical dry Mediterranean climate conditions, i.e. with warmer winter temperatures and prolonged summer drought, noticeably occurring along southern slopes of Alta Murgia plateau (Perrino and Wagensommer, 2013). Based on such a twofold feature of xero-thermic community dynamics, the occurrence of this grassland type can be alternatively explained as a result of anthropogenic or climatic factors. However, it is also important to account for the complexity of 6220 habitat definition, as this habitat includes a highly diverse set of annual and perennial plant communities featuring different ecological requirements, e.g., in terms of soil depth and nutrient availability (Biondi et al., 2012). Hence, as our results consider these grasslands overall, further studies may disclose differential dynamics within the diversity of 6220 communities, in function of their specific adaptation to the variable combination of natural and anthropogenic conditions. As an example, in our study area, this can be the case of *Stipellula capensis* communities, which are frequently associated with post-cultural fields, or discontinuous *Hyparrhenia hirta* communities, which are locally prevailing on south-facing rocky slopes.

Patches with longer continuity of pastoral land use due to century-long grazing tradition and cultivation abandonment show higher probability to host sub-Mediterranean grasslands of the 62A0 and 6210 habitats. In particular, 62A0 habitat features the species-rich endemic communities dominated by *Stipa austroitalica*, which locally characterise

Table 1
Estimated variance explained by time since cultivation abandonment, patch area and slope on the probability of occurrence of different types of grassland habitats in the N2K site Murgia Alta site.

Predictor	6210		62A0		6220		No habitat	
	Explained variance	p	Explained variance	p	Explained variance	p	Explained variance	p
Time since cultivation abandonment	0.210	<0.001	0.342	<0.001	0.181	<0.001	0.561	<0.001
Patch area	0.001	<0.001	0.010	<0.010	0.001	<0.010	0.018	<0.001
Slope	0.180	<0.001	0.100	<0.001	0.142	<0.001	0.089	<0.010
Total variance explained	39.1 %		45.2 %		42.4 %		66.8 %	

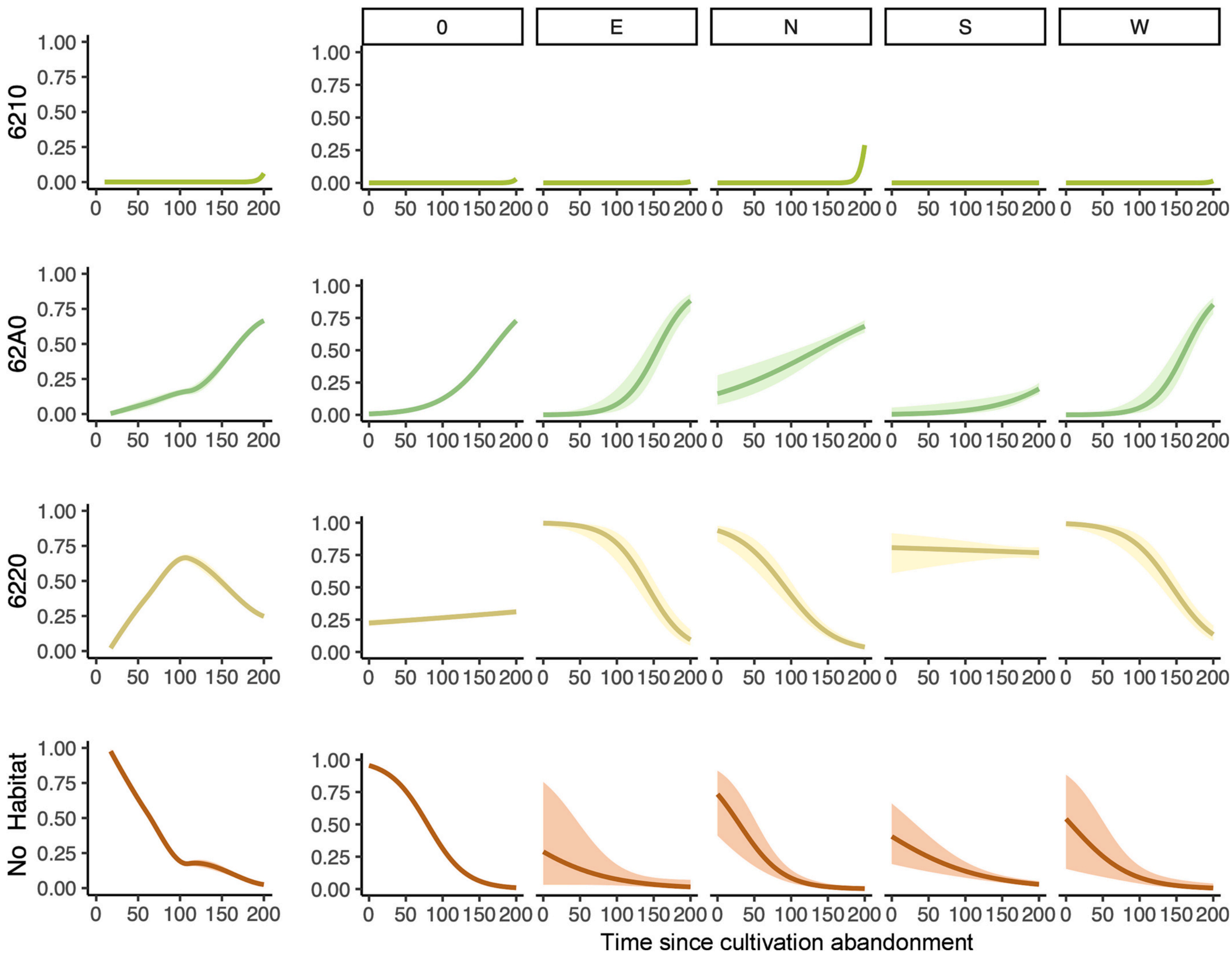

Fig. 4. Relationships between time (years) since cultivation abandonment and probability of occurrence of grassland types (6210, 62A0, 6220, no habitat), overall (on the left) and for each slope category (0 = slope < 20 %, E = East, N = North, S = South, W = West), in the N2K site Murgia Alta site. Shaded areas indicate 95 % confidence intervals.

all those surfaces where forest vegetation is strongly limited by current environmental conditions (Forte et al., 2005). Hence, our findings provide further indication that this type of grassland represents the latest stage of vegetation succession in most of the Alta Murgia calcareous plateau, as a consequence of a set of long-standing natural and anthropogenic factors currently hampering the formation of expected forest vegetation (Bianco, 1962).

Conversely, meso-xeric communities of the 6210 habitat only cover 0.2 % of the considered grassland surface and mostly occur in small patches, thus being considered the rarest grassland type in the study area. The observed surface of 6210 habitat is much lower than the 33,987.90 ha reported within the official fact sheet of the N2K site 'Murgia Alta' (see: https://natura2000.eea.europa.eu). This contradiction stems from the fact that the locally widespread communities belonging to 62A0 habitat were formerly ascribed to the 6210 habitat in the official HD data. In fact, similarly to 62A0 grasslands, this habitat requires longer periods to recover after cultivation abandonment, but the occurrence of 6210 is locally limited to peculiar edaphic and mesoclimatic conditions taking place at the foothills of north-facing slopes and dolinas. In fact, if compared to the other dry grassland communities occurring in the study area, this habitat type is locally represented by less drought-resistant communities dominated by *Brachypodium rupestre*. Due to its limited coverage in the area, in turn implying a restricted range of plant and animal species herewith associated (e.g., the relictual population of the butterfly *Brenthis hecate*; Labadessa et al., 2021), the preservation of this habitat should be locally counted among conservation priorities of the Alta Murgia protected area. Such a deeper understanding of local ecological requirements and distributional patterns of grassland habitats is underpinning for setting up local conservation actions, e.g., for the identification and prioritisation of sites and strategies for their effective restoration.

4.1.1. *Limitations and opportunities*

In the study area, our results suggest that spontaneous grassland recovery in cultivated fields mostly depends on time since cultivation abandonment, given a widespread field proximity to semi-natural grasslands and a continuation of moderate grazing and fire regime. While acknowledging that grazing and burning may play a key role for the maintenance of semi-natural grasslands in abandoned fields (Gibson and Brown, 1992; Pywell et al., 2002), we assumed a negligible variation of these factors at the selected temporal and spatial scales in our case study. More in-depth studies are though needed to understand the role of grazing and fire regime for the preservation of the studied grasslands, e.g., in limiting the encroachment by woody species.

In our study, information was derived by categorical vector maps, due to the need for considering homogeneous spatial units that could best inform on the medium- to large-scale patterns, in turn avoiding the noise of fine-scale variations in mosaic vegetation. This limitation gives opportunities for further exercises integrating a pixel-based approach, at an appropriate scale, which is most suitable to deal with metrics relevant to landscape- and niche-driven limitations for grassland recovery, e.g., those relevant to plant dispersal abilities, measured abiotic conditions, and patch connectivity (Soons et al., 2005; Jakobsson et al., 2016; Kapás et al., 2023).

We also acknowledge that secondary succession may follow different pathways according to local meso-climatic features and soil conditions. Therefore, we underline the need for studies relevant to successional dynamics at lower spatial and temporal scales, e.g., by investigating inter-annual changes at plant community level, as well as to the modelling of restoration opportunities in function of the effects of most recent and impactful land management, e.g., stone shattering (Mairota et al., 2013a).

Furthermore, our findings on the effects of past land use changes aim at promoting insights on the potential direct and indirect effects of socio-economical and historical changes on vegetation dynamics, as information about changes in human population, livestock numbers and agricultural policies may as well have contributed to the observed dynamics.

5. Conclusions

Our results indicate a strong role of time since cultivation abandonment in shaping current grassland vegetation in a Mediterranean agro-pastoral landscape. From an applicative point of view, this finding contributes to a deeper understanding of dynamics relevant to spontaneous vegetation recovery, in turn representing a prerequisite for setting up effective grassland conservation and restoration actions.

Information on the extent and dynamics of EU-listed grassland habitats is key to fulfilling the main objective of the HD reporting (art. 17), as well as to assess the success of the protection measures implemented within the Natura 2000 network. Namely, according to the last available HD Report (https://nature-art17.eionet.europa.eu/article17/habitat/summary/), all the considered grassland types have been evaluated as in either inadequate or bad conservation status in at least one of the bioregions where they occur, mostly with declining trends. This strongly suggests that a deeper understanding of grassland habitats dynamics, such as in our case study, is key to predict their future occurrence in anthropogenic landscapes and, consequently, to design proper conservation actions.

CRediT authorship contribution statement

Rocco Labadessa: Conceptualization, Methodology, Investigation, Formal analysis, Writing – original draft, Writing – review & editing. **Leonardo Ancillotto:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **Maria Patrizia Adamo:** Funding acquisition, Project administration, Supervision, Writing – original draft, Writing – review & editing. **Luigi Forte:** Supervision, Writing – original draft, Writing – review & editing. **Saverio Vicario:** Methodology, Writing – original draft, Writing – review & editing. **Luciana Zollo:** Funding acquisition, Project administration. **Cristina Tarantino:** Funding acquisition, Project administration, Supervision, Writing – original draft, Writing – review & editing.

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 made available on request.

Acknowledgements

We thank six anonymous reviewers who kindly provided suggestions that improved the first version of this manuscript. This study was carried out within the project "Monitoraggio di habitat e specie nel Sito Murgia Alta, code A0605.34" funded by "POR Puglia 2014-2020, Asse VI, Azione 6.5", the project "NewLife4Drylands – LIFE20 PRE/IT/000007" funded by the "LIFE Preparatory project – Programme for the Environment and Climate Action" of the European Commission, and the project "European long-term ecosystem, critical zone and socio-ecological systems research infrastructure PLUS – eLTER PLUS" funded under the programme "H2020-EU.1.4.1.2. - Integrating and opening existing national and regional research infrastructures of European interest", grant agreement n. 871128.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.166990.

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