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Long-term cropland abandonment does not lead *per se* to the recovery of semi-natural herb communities deemed habitats of community interest

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Abstract – Abandoned croplands can be considered a new category of »scattered elements« of mountain landscapes. To gain a deeper understanding of the conservation status (sensu EEC Directive 92/43) of abandoned cropland in the northern Apennines, we used the concept of the social behavior type (SBT) of plant communities. SBTs refer to the behaviour and ecological attributes of species at a given observation level and allow the understanding of the plant community conservation status. We found that topographic and soil conditions drive species assemblage in pastures after crop abandonment, but that long-term abandonment does not lead *per se* to the recovery of the semi-natural grassland communities deemed worthy of conservation in the EEC Directive. It was mainly the lack of appropriate disturbance regimes that allowed the spread of dominant tall herbs, which, in turn, reduced site suitability for subordinate plants. Moreover, their spread fostered the presence of elements such as ruderals and fringe species. We concluded that these abandoned croplands had a good potential to develop into a Habitat as defined in the EU Directive but without appropriate management plans they would remain of low representativeness.

Keywords: abandonment, croplands, Ellenberg's indicator values, grassland recovery, management, protected habitats, social behaviour types

Abbreviations: AWC – available water capacity, CVRE – cross-validation relative error, DCA – detrended correspondence analysis, EIV – Ellenberg's indicator value, ISA – indicator species analysis, IV – indicator value, M – soil moisture, MRT – multivariate regression tree, N – soil nutrients content, R – soil chemical reaction, RDA – redundancy analysis, SBT – social behaviour type, T – air temperature.

Introduction

In a large part of Europe, the abandonment of traditional extensive farming activities has led to successional changes toward forest (Poschlod and WallisDeVries 2002), and the abandonment of hilly and mountain croplands to the formation of new herbaceous communities (Peroni et al. 2000); these abandoned areas can be viewed as new »scattered elements« in areas where forest recovery and expansion are underway as well as in agricultural landscapes, which are generally undergoing processes of intensified land use. In fact, in both cases, socio-economic and natural processes are threatening biodiversity and leading to homogeneous landscapes (Robinson and Sutherland 2002). The conservation and management of these new open ecosystems are key elements within the European agricultural policies (Rieger 2000, Rounsevell et al. 2005). Currently, the restoration of grassland on former croplands is a high priority of nature conservation (Stadler et al. 2007) and is one of the most frequent habitat restoration actions in central and northern Europe (Cramer et al. 2008).

Habitat (sensu 92/43/EEC Directive) protection entails regular monitoring, but before that, the target habitats must

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be properly defined and their conservation status assessed (Ejrnæs et al. 2004). However, Annex I of the Directive, building on an extensive classification of habitats, fails to specify how to discriminate between protected and non protected habitats along the continuum from natural to cultural, and there is not much help in the scientific literature in this regard (Ejrnæs et al. 2008). Significant contributions to solving this problem may be found in the phytosociological assessment of vegetation, since the phytosociological composition of a plant community (that is the presence of species belonging to different phytosociological units, such as classes, orders, etc.) reveals both its ecological and its dynamic conditions (Biondi 2011). Moreover, since the 92/43/EEC Directive defined habitats in phytosociological terms, the phytosociological assessment of vegetation would be a logical tool for habitat interpretation.

Another useful approach could be species grouping by social behavior types (SBTs) (Moola and Vasseur 2004, Gondard et al. 2006). SBTs derive from species behaviour and ecological attributes at a given observation level (Borhidi 1995). Social behaviour can be defined as the role that a plant species plays in the community considering species in regard to their auto-ecology, morphology and physiological performances (Alard and Poudevigne 2000). Therefore, assessment of an SBT provides information on the mechanisms underlying species assemblage and helps to clarify the ecological meaning of the species pool characterizing a certain plant community (Catorci et al. 2011a). Since the higher levels of phytosociological classification (class and order) group species that share wide ecological needs and dynamic features, they can be useful indicators of SBTs (Catorci et al. 2011a). In this way, it is possible to couple the phytosociological approach with the SBT assessment of a plant community, thus gaining a deeper understanding of its conservation status.

We focused on semi-natural dry grasslands that had taken over abandoned croplands in the hilly landscape of the Tuscan-Emilian Apennines, since this territory is undergoing strong processes of cropland abandonment and the reforestation of mountain slopes (Piussi and Pettenella 2000). In addition, only few studies have examined grassland recovery after field abandonment in a sub-Mediterranean climate in relation to conservation status as EU habitats. Such an assessment of how biotic and abiotic features affect the species assemblage might also provide key information for managing these ecosystems in order to achieve a favorable conservation status.

It has been argued that succession of abandoned fields leads to the formation of semi-natural communities whose floristic and structural features depend on such factors as resource availability (Ejrnæs et al. 2008), time since abandonment, and availability of seeds in neighbouring habitats (Pywell et al. 2002, Ruprecht 2006). Moreover, altitude and land form (Burrascano et al. 2013), soil features (Catorci and Gatti 2010), land use history (Catorci et al. 2011a) and disturbance type and intensity (Peco et al. 2006, de Bello et al. 2007, Kramberger and Kaligarič 2008, Catorci et al. 2012, Ribeiro et al. 2012) have proved to be crucial factors in determining grassland species composition. In particular, grazing animals facilitate the dispersal of seeds, create gaps for colonization (Gibson and Brown 1992, Bruun and Fritzbøger 2002) and foster species with resistance strategies to herbivory (Grime 2001).

Thus, we expected that in former cropland (abandoned nearly 20 years ago and previously ploughed every year) dynamic processes would lead to the formation of herbaceous communities with different species composition depending on the different abiotic conditions, but these processes are not sufficient *per se* to transform abandoned crops into semi-natural grassland communities included in Annex I of the Habitats Directive. We also postulated that the absence of disturbance allows the spread of competitive tall grasses and shrubs and thus affects the species composition, hindering the achievement of a favourable conservation status.

The specific research questions were: i) which environmental factors drive the species assemblage of plant communities after crop abandonment? ii) how do environmental features influence species composition of plant communities? iii) does the evaluation of the coenological composition of plant communities after crop abandonment provide insight significant for the assessment of their dynamic state and conservation status according the standards defined by the 92/43/EEC Directive?

Materials and methods

Study area

The study area (Fig. 1) is located in the south-eastern and south-western part of Bologna province (Italy), between 200 and 500 m a.s.l. From a bioclimatic viewpoint, the area is included in the sub-Mediterranean variant of the temperate continental and oceanic bioclimates (Pesaresi et al. 2014). The mean annual temperature is 13–14 °C. The annual rainfall is 800–900 mm. A period of drought stress occurs in summer; July is the driest month (average rainfall 40–50 mm), and winter cold stress occurs between early December and late February. The geological substratum consists of a mosaic of clays with chaotic structure (debris flow – mudflow), stone material, conglomerates and gravel,

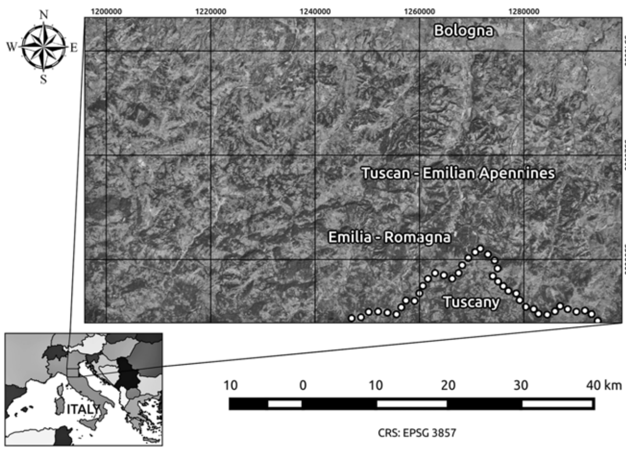

Fig. 1. Location of the study area in the south-eastern and south-western part of the Bologna province (Italy).

chalks, sandstones, marly, silty and flaky clays. Soils are generally deep (30–60 cm) with neutro-basic pH (6.5–7.5), mainly with sandy-loam and silty-clayey textures. The actual natural potential vegetation is referred to *Quercus pubescens* s.l. woods of the *Peucedano cervariae-Quercetum pubescentis* association and hop-hornbeam woods of the *Ostryo-Aceretum opulifolii* (Blasi 2010). The studied sites encompass former croplands (with wheat and alfalfa grown in rotation), where agricultural or pastoral practices have been absent at least for the last 20 years. All the study sites are characterized by herbaceous communities that are currently unmanaged.

Sampling design and data collection

We collected data in June-July 2013 in order to observe both the spring and the summer flowering species. Using a GIS, we overlaid the study area with a grid composed of 100 × 100 m macro-plots, each further divided into 100 plots (10 × 10 m). In each macro-plot we randomly selected one 10 × 10 m plot, excluding those that fell completely or partly on woods, brush and shrub vegetation, as well as those that fell in a buffer of 50 m from these vegetation types to avoid the edge effect. In all, we surveyed 100 plots. In each plot we recorded species cover values (percent values, visually estimated), altitude (m a.s.l.), slope aspect (azimuth degrees), slope angle (vertical degrees), outcropping rock cover and litter cover (percent values, visually estimated), soil depth (cm, five measurements per plot) and collected five soil sub-samples, taken within a depth of 30 cm and combined in one bulked sample.

To better characterize the plant communities from an ecological viewpoint, we assessed the Ellenberg indicator values (EIVs). We gathered EIVs from Pignatti (2005) and Guarino et al. (2012). EIVs proved to be useful in analyzing the drivers of vegetation change (i.e. McCollin et al. 2000, Klaus et al. 2012) especially when they are considered for comparison on a local scale (Godefroid and Dana 2007). In particular, we assessed air temperature (T), soil moisture (M), soil nutrient content (N), and soil chemical reaction (R).

To assess the dynamic and conservation state of the plant communities, we grouped species in SBTs. Species SBTs were assessed with respect to their regional synecology, following the most widely accepted phytosociological placement of each species (Ubaldi 2013, Biondi et al. 2014, Biondi and Pesaresi 2004, Biondi et al. 2005, Čarni 2005). We considered the following SBTs: SBT1, species of perennial semi-natural grassland usually undergoing herbivory (characteristic of *Festuco-Brometea* Br.-Bl. et Tx. 1943 class); SBT2, species of xeric grasslands (characteristic of *Tuberarietea guttatae* Br.-Bl., Roussine & Nègre 1952 and *Sedo-Scleranthetea* Br.-Bl. 1955 classes); SBT3, species of meadows (characteristic of *Molinio-Arrhenatheretea* Tx. 1937 class) usually undergoing soil nitrogen enrichment and annual cutting; SBT4, species of fringe habitats (i.e. species usually growing at the border of woody ecosystems and of forest clearings, characteristic of *Trifolio-Geranietea sanguinei* Müller 1962 class); SBT5, successional species (characteristic of *Rhamno-Prunetea* Rivas Goday & Borja ex Tüxen 1962, *Calluno-Ulicetea* Br.-Bl. & Tüxen ex Klika & Hadac 1944 and *Querco-Fagetea* Br.-Bl. & Vlieger in Vlieger 1937 classes); and SBT6, pioneer, ruderal, nitrophilous and semi-nitrophilous species growing in cultivated and uncultivated lands (characteristic of *Artemisietea vulgaris* Lohmeyer, Preising & Tüxen ex von Rochow 1951 and *Stellarietea mediae* Tüxen, Lohmeyer & Preising ex von Rochow 1951 classes). In this way we were able to assess the dynamic status of the plant communities (considering for instance SBTs 1, 2, and 3 versus SBTs 4 and 5) or the management-related impact on species composition (i.e. by assessing the abundance of SBTs 5 and 6), besides the relationship between environmental constraints and species composition. To assess the state of conservation of plant communities according the standards defined by the 92/43/EEC Directive, we consulted as a reference manual the »Italian Interpretation Manual of Habitats of the 92/43/EEC Directive« (Biondi et al. 2009). Species nomenclature followed Conti et al. (2005).

Data analysis

Aspect azimuth was first converted from the 0–360 compass scale to a linear (0–180) scale, giving northerly aspect a value approaching 0 and southerly aspect a value approaching 180. This transformation also converted east and west azimuth degrees so that they were equally distant from north. Moreover, as south-south-west-facing slopes are the warmest aspect, the aspect azimuth was shifted to a minimum on north-north-east slopes (22.5°) and a maximum on south-south-west slopes (202.5°).

Data on soil depth were averaged for each plot. Soil samples were analysed in the laboratory of the University of Bologna to determine the percentages of skeleton, sand, loam, and clay. In order to have a proxy for the soil water regimes, for each plot we calculated the soil available water capacity (AWC) using the software developed in Microsoft Office Excel 2000 by Armiraglio et al. (2003). AWC represents the maximum amount of available water the soil can provide. It mainly depends on soil texture and depth and, secondly, on soil specific weight and organic matter content (McRae 1991). The input variables processed were soil depth (cm), soil texture (percentage of sand, clay, loam, and percentage of skeleton), and a coefficient of water available for plants under a pressure of 0.05–15.00 bars, obtained from tabulated values (McRae 1991). Even though the outputs obtained are imprecise because they lack data on organic matter, nonetheless they offer a good proxy for comparing plots, because the estimation was based on soil depth and texture, and thus was independent of vegetation structure (i.e. vegetation cover, tiller density, canopy height, litter decomposition rate, etc.), which might alter the soil organic matter content.

To transform SBT binary data (presence/absence) into quantitative data (i.e. aggregated cover values of each SBT), we multiplied the »relevés × species cover« matrix by the »species × SBT« matrix to provide a »relevés × SBT cover« matrix, which formed the basis for the following analyses.

i) Environmental features driving the species assemblage after cropland abandonment

To assess the influence of macro-environmental variables on species assemblage, a constrained clustering using multivariate regression tree (MRT) analysis (De'ath 2002) with 100 iterations was executed on the »relevés × species« matrix constrained by the environmental variables (altitude, slope aspect, slope angle, AWC, outcropping rock cover, and litter cover). Prior to MRT analysis, species data were transformed using chord transformation (Legendre and Gallagher 2001). An overall error statistic (cross-validation relative error, CVRE) was computed for each test group and partition size (number of groups), to choose the optimal size of the tree. For each partition size, the mean and standard error of all CVRE estimates were computed. To provide a general overview of the ecological characteristics of the plant communities highlighted by MRT, we calculated mean, standard deviation, median, and 1st and 3rd quartiles for each environmental variable. We used the Shapiro-Wilk test to test the distribution normality of data. As data were not normally distributed, we ran the non-parametric Wilcoxon exact rank test to evaluate differences between groups at each step of clustering. Mean species cover values and species relative frequency in each group are reported in the On-line Suppl. Tab. 1.

To further assess the environmental features characterizing the groups of relevés emerging from MRT analysis, we first calculated the unweighted mean of T, M, N and R EIVs of the species present within each plot. Following Zelený and Schaffers (2012), we fitted mean EIVs, calculated for samples, onto a detrended correspondence analysis (DCA) ordination employing a permutation test that corrects the bias in the relationship between mean species EIVs and sample scores along ordination axes, introduced by the fact that mean EIV inherits compositional similarity among samples. Finally, we calculated the mean and median EIV for each group of relevés.

To perform MRT analysis, Shapiro-Wilk tests, Wilcoxon exact rank tests, and DCA we used the R software (version 2.15.2, R Core Team 2012) packages mvpart version 1.6-1 (mvpart function), stats version 2.15.2 (shapiro.test function), exactRankTests version 0.8-27 (wilcox.exact function), and vegan version 2.0-10 (decorana function), respectively. The R function used for projection of mean EIVs onto an ordination, with modified permutation test was envfit.iv (Zelený and Schaffers 2012).

ii) How do environmental features influence species and coenological composition of plant communities?

To understand how abiotic factors influence the species composition of plant communities, we performed indicator species analysis (ISA) to highlight the indicator species set (i.e. the species pool showing a preferential distribution among clusters) of each group (Dufrêne and Legendre 1997). To identify the indicator SBTs (aggregated cover values of species sharing the same SBT) for each group identified by MRT, we executed ISA on the »relevés × SBT cover« matrix using membership of MRT groups as grouping variable. To perform ISA we used labdsv version 1.6-1 (indval function) R-package. Finally, to better assess the status of grassland communities, we calculated the relative abundance of each SBT in every plant community considered (cover percent value of the considered SBT out of the total cover value of all the recorded SBTs in the plant community).

Results

i) Environmental features driving the species assemblage after cropland abandonment

MRT analysis generated a 3-leaved MRT with CVRE = 0.88 and standard error = 0.056 (Fig. 2), which was frequently selected as the best solution during the cross-validation iterations. The basic descriptive statistics of the environmental variables for each group highlighted by MRT and the statistical significance of differences between groups at each partition are shown in Tab. 1. The variable discriminating between the two branches in the first node of the 3-leaved MRT was rockiness. The relevés of the third leaf (T3.3) were characterized by the presence of outcropping rocks, while in the other groups rockiness was absent. Moreover, this group had lower AWC mean values and higher litter cover and altitude mean values than the group composed of T3.1 and T3.2. Differences between the two groups with regard to these variables were statistically significant (Tab. 1). The second partition was defined by altitude (Fig. 2). Group T3.1 included relevés located at altitudes higher than 290 m a.s.l. (mean value 418 m), with low

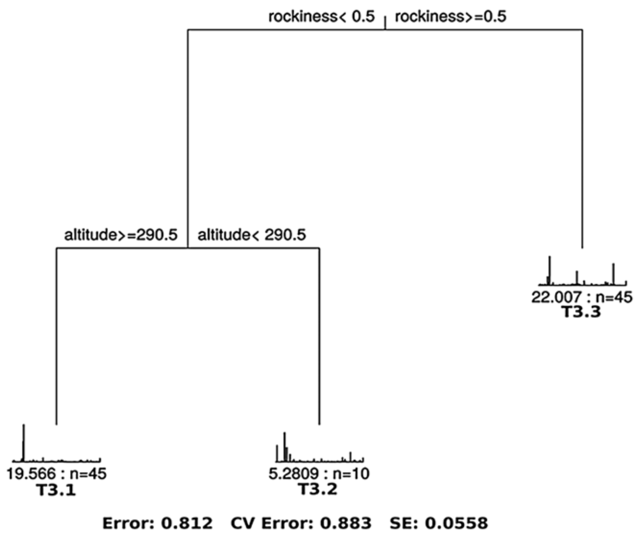

Fig. 2. The 3-leaved multivariate regression tree for the species data set, constrained by the explanatory variables data set. Rockiness (%) and altitude (m a.s.l.) discriminated the two branches of the tree. The threshold values shown for each partition of the tree correspond to the mean of the two limit values of the considered variables at the break between the branches. The relative abundances of the species are shown in histograms at the tips of the branches, with the species in the same order as in the input file. Under each histogram, the sum of squared errors for the group and the number of relevés in the leaf (n) are indicated. Below the tree, the residual error (Error), the cross-validation error (CV Error) and standard error (SE) are indicated.

Tab. 1. Descriptive statistics of the environmental variables for the groups highlighted by the multivariate regression tree analysis (T3.1, T3.2, and T3.3) and statistical significance of differences, as indicated by the results of Wilcoxon exact rank test (2-tailed), between the groups segregated in the 3-leaved multivariate regression tree. Aspect azimuth was converted from the 0–360 compass scale to a linear scale, giving northerly aspect a value approaching 0 and southerly aspect a value approaching 180; then it was shifted to a minimum on north-north-east slopes (22.5°) and a maximum on south-south-west slopes (202.5°). SD – standard deviation. * P < 0.05; ** P < 0.01; *** P < 0.001; n.s. – not significant.

Group	Statistics	Altitude (m a.s.l.)	Slope aspect (azimuth degree)	Slope angle (vertical degree)	Rockiness (%)	Litter (%)	Available water capacity (mm)
T3.1	mean	418.17	129.00	14.40	0.00	24.30	108.80
	SD	56.50	46.80	6.46	0.00	32.60	4.06
	1st quartile	384.00	67.50	10.00	0.00	0.00	105.92
	median	430.00	157.50	15.00	0.00	10.00	107.96
	3rd quartile	460.00	157.50	20.00	0.00	30.00	110.00
T3.2	mean	205.80	155.25	18.00	0.00	8.00	109.00
	SD	43.30	7.10	7.80	0.00	16.80	0.55
	1st quartile	201.00	157.50	15.00	0.00	0.00	107.60
	median	201.00	157.50	15.00	0.00	0.00	108.70
	3rd quartile	238.50	157.50	25.00	0.00	0.00	108.80
T3.3	mean	474.70	143.00	19.90	14.40	53.10	104.07
	SD	56.20	24.05	6.70	14.48	28.02	6.10
	1st quartile	454.00	112.50	15.00	5.00	30.00	100.96
	median	494.00	157.50	20.00	10.00	60.00	105.24
	3rd quartile	513.00	157.50	25.00	20.00	80.00	108.80
T3.1–T3.2 vs. T3.3		***	***	n.s.	***	***	***
T3.1 vs. T3.2		***	***	n.s.	n.s.	***	**

slope angles, while altitudes lower than 290 m, slightly higher AWC values and lower litter covers characterized relevés belonging to group T3.2 (Tab. 1). The first two axes of DCA based on the »relevés × species« matrix using mean randomized EIV values as constraining variables explained 77% of the constrained variance (52% explained by axis 1 and 25% by axis 2). Soil chemical reaction was strictly related to axis 1, while temperature was related to both axes. The combination of these two variables explained the separation of the three groups of plots, as indicated by the DCA scatterplot (Fig. 3). The differences in mean and median values of EIVs are in line with DCA results (Tab. 2). The T3.1 group was positively correlated with EIV soil reaction (i.e. with soils with higher pH), and characterized by a mean value greater than groups T3.2 and T3.3. The T3.2 group was positively correlated with EIV air temperature and characterized by higher mean T value than the other groups. Moisture and nutrient values showed very small differences among the three communities (Tab. 2).

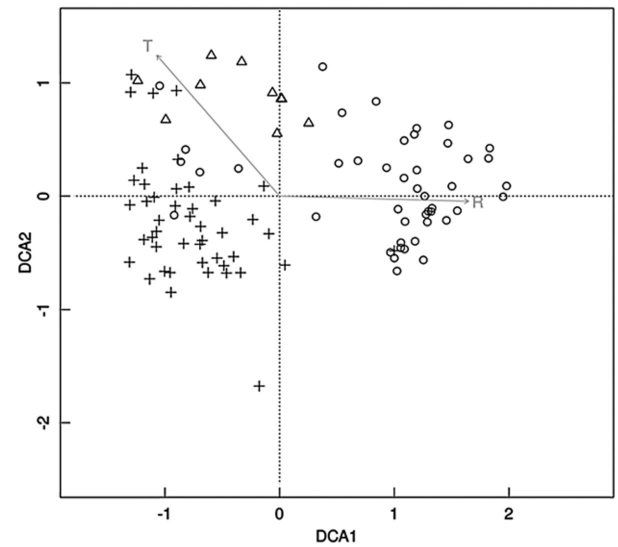

Fig. 3. Scatterplot of the detrended correspondence analysis (DCA) ordination executed on mean randomized Ellenberg indicator values and relevés data set. Sites are represented with different symbols to highlight the groups identified by multivariate regression tree analysis (circles – group T3.1; triangles – group T3.2; crosses – group T3.3). Only significant vectors (P < 0.05) have been represented (T – air temperature; R – soil chemical reaction).

ii) How do environmental features influence species and coenological composition of plant communities?

We recorded 209 species in the total set of relevés. The indicator species identified by ISA for groups highlighted by MRT analysis, as well as their mean abundances, are shown in Tab. 3. The first and second groups of the 3-leaved MRT included ten indicator species each; instead, the third was characterized by 17 indicator species. *Bromus erectus* Huds. dominated group T3.1, which also showed a high cover value of *Brachypodium rupestre* (Host) Roem. &

Tab. 2. Mean and median Ellenberg indicator values (EIVs) for air temperature, soil moisture, soil reaction, and soil nutrients of each group (T3.1, T3.2, and T3.3) emerging from the multivariate regression tree analysis.

Ellenberg indicator values	Group					
	T3.1		T3.2		T3.3	
	mean	median	mean	median	mean	median
air temperature	5.98	5.68	7.72	7.67	6.92	6.93
soil moisture	3.58	3.44	3.45	3.56	3.47	3.46
soil reaction	7.05	7.28	5.64	5.67	5.68	5.75
soil nutrients	3.75	3.68	3.73	3.62	3.54	3.52

Schult. The T3.2 group had higher values of *Avena sterilis* L. and *Triticum ovatum* (L.) Raspail, while *Bromus erectus* and *Sulla coronaria* (L.) Medik. dominated group T3.3 (Tab. 3, On-line Suppl. Tab. 1). ISA identified several coenological differences among groups (Tab. 4). SBT1, 3, 4, and 5 were indicators of the T3.1 community. SBT1, 2, and 6 were indicators of T3.2 community. SBT6 was indicator of T3.3 community (Tab. 4). The abundance (cover percentage) of each SBT with respect to the total cover value in the three groups is shown in Tab. 5.

Discussion

i) Plant community composition and site ecology

MRT analysis highlighted three main plant communities, linked to different environmental conditions (Fig. 2, Tabs. 1–2). This is consistent with previous research, which showed that in the sub-Mediterranean climate, landforms are key factors in determining plant species and communities distribution (Arévalo et al. 2012, Burrascano et al. 2013, Catorci et al. 2014b). In fact, sub-Mediterranean regions are characterised by summer drought stress with different intensities, depending on the elevation and landform factors (Somot et al. 2008). The main ecological factor behind these variables is the total solar radiation amount per unit area (Biondi et al. 2011). On south-facing slopes, the greater radiation in summer dramatically reduces the soil water content (Joffre and Rambal 1993), posing one more stress factor faced by plants in mountain areas (Catorci et al. 2014b). Landforms affect soil features (i.e. soil depth) as well (Cerdà et al. 1995). In detail, the T3.1 cluster grouped plots located on moderately steep slopes with southerly aspects (from east to west) (Tab. 1) and is dominated by competitive caespitose species, i.e. *Bromus erectus* (occurring in about 96% of plots with mean cover of 40.4%) and *Brachypodium rupestre* (occurring in 77.8% of plots with mean cover of about 23%). This community spreads in conditions that are not very dry, as highlighted by the lowest temperature EIV and the slightly higher AWC values (Tabs. 1–2). It is also noteworthy that the T3.1 group was positively correlated with soil reaction EIV and characterized by a mean value greater than the T3.2 and T3.3 groups, namely by the most basic pH among the considered clusters (Tab. 2, Fig. 3). In accordance with Catorci and Gatti (2010), these conditions allow the spread of species of SBT1 and

Tab. 3. Indicator species of the relevé groups highlighted by indicator species analysis for the 3-leaved multivariate regression tree and their respective indicator values (calculated by multiplying the relative abundance and the relative frequency of species in a group) and mean cover percentages, as highlighted by the indicator species analysis. Only significant indicator values ($P < 0.05$) higher than 30 are shown. Max group: group with maximum indicator value; P: proportion of indicator values obtained by randomized trials, equal to or exceeding the observed indicator value. The statistical significance (P) of the observed maximum indicator values was tested using permutation tests with 4,999 iterations.

Max group	Indicator species	Indicator value	P	Mean cover (%)
T3.1	*Brachypodium rupestre*	0.66	0.00	22.9
	Achillea collina	0.53	0.00	1.0
	Cota tinctoria	0.49	0.01	1.5
	Bromus erectus	0.44	0.01	40.4
	Vicia sativa	0.39	0.01	0.5
	Lotus corniculatus	0.35	0.01	0.6
	Fraxinus ornus	0.35	0.01	3.5
	Rubus ulmifolius	0.34	0.00	1.9
	Securigera varia	0.33	0.01	0.3
	Inula salicina	0.32	0.01	0.9
T3.2	*Triticum ovatum*	0.77	0.00	14.9
	Avena sterilis	0.64	0.00	32.1
	Scorpiurus subvillosus	0.47	0.00	2.7
	Hippocrepis comosa	0.46	0.00	0.5
	Calamintha nepeta	0.41	0.01	2.2
	Gladiolus italicus	0.38	0.00	0.1
	Potentilla recta	0.38	0.00	0.3
	Phalaris canariensis	0.35	0.00	0.4
	Trifolium campestre	0.35	0.04	1.5
	Crepis pulchra	0.30	0.02	0.3
T3.3	*Linum bienne*	0.85	0.00	3.7
	Hypochaeris achyrophorus	0.74	0.00	11.5
	Sonchus asper	0.68	0.00	0.7
	Picris hieracioides	0.67	0.00	0.7
	Allium schoenoprasum	0.65	0.00	0.4
	Sulla coronaria	0.63	0.00	19.0
	Potentilla hirta	0.54	0.00	0.6
	Daucus carota	0.50	0.00	0.9
	Althaea hirsuta	0.49	0.00	0.7
	Geranium dissectum	0.44	0.01	1.2
	Bartsia trixago	0.40	0.01	0.4
	Genista tinctoria	0.40	0.00	1.1
	Sonchus oleraceus	0.40	0.00	0.5
	Thymus longicaulis	0.39	0.02	0.7
	Ononis masquilleri	0.36	0.01	1.6
	Crepis vesicaria	0.33	0.02	0.3
	Filago pyramidata	0.31	0.03	0.4

SBT3 (Tab. 4), indicating the affinity of these plant communities with the sub-Mediterranean grasslands of the *Fes-*

Tab. 4. Indicator social behaviour types (SBTs) of the relevés groups (T3.1, T3.2, and T3.3) calculated by multiplying the relative abundance and the relative frequency of SBTs in a group, highlighted by Indicator species analysis for the 3-leaved multivariate regression tree. Only significant ($P < 0.05$) indicator values higher than 30 are shown. SBT1 – species characteristic of perennial pastures; SBT2 – species of xeric grasslands; SBT3 – species of meadows; SBT4 – species of fringe habitats; SBT5 – successional species; SBT6 – ruderal species. Max group: group with maximum indicator value; P – proportion of indicator values obtained by randomized trials, equal to or exceeding the observed indicator value. The statistical significance of the observed maximum indicator values was tested using permutation tests with 4,999 iterations.

Social behaviour type	Max group	Indicator value	P
SBT1	T3.1	0.546	0.000
	T3.2	0.471	0.002
SBT2	T3.2	0.540	0.003
SBT3	T3.1	0.500	0.006
SBT4	T3.1	0.390	0.012
SBT5	T3.1	0.342	0.004
SBT6	T3.2	0.729	0.000
	T3.3	0.497	0.015

Tab. 5. Percent abundance of each social behavior type (SBT) in each group of relevés (T3.1, T3.2, T3.3) highlighted by the multivariate regression tree analysis. SBT1 – species characteristic of perennial pastures; SBT2 – species of xeric grasslands; SBT3 – species of meadows; SBT4 – species of fringe habitats; SBT5 – successional species; SBT6 – ruderal species.

Social behaviour type	Group		
	T3.1	T3.2	T3.3
SBT1	62.7	18.6	28.3
SBT2	6.3	20.7	16.7
SBT3	3.7	1.9	1.4
SBT4	1.4	0.7	0.6
SBT5	10.2	6.2	5.4
SBT6	15.7	51.9	47.6

tuco-Brometea class (see Biondi and Galdenzi 2012), referred to the habitat »Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*)« (habitat code 6210, important orchid sites)]. According to the Italian interpretation manual of the 92/43/EEC Directive habitats (Biondi et al. 2009), this habitat includes perennial species-rich secondary grasslands dominated by hemicryptophytic grasses, from xeric to semi-mesophylous, mainly spread along the Apennine ridge. In the study case, however, as postulated by Grime (2001), the absence of disturbance allows a relatively high litter cover value (Tab. 1). Likewise, as stated by Bonanomi et al. (2013), the lack of disturbance enhances the spread of *B. rupestre* (Tab. 3, On-line Suppl. Tab. 1). This species is a dominant tall grass whose competitive success is related to its high tiller density and branching frequency (Pottier and Evette 2011), as well as to its capacity for clonal growth and clonal integration strategy (de Kroon and Bobbink 1997). These traits allow a rapid spread in the absence of disturbance, especially in productive conditions (Grime 2001). The invasion of *Brachypodium* species has a strong impact on the species composition of plant communities (Catorci et al. 2011a, b) and gives rise to the spread of fringe and successional species (Catorci et al. 2011a). Actually, SBT4 (species of fringe habitat) and SBT5 (successional species) are indicators of the T3.1 group (Tab. 4). Vegetation of the T3.1 community is also undergoing dynamic processes, as indicated by the presence among the indicator species of successional species such as *Fraxinus ornus* L. and *Rubus ulmifolius* Schott (Tab. 3), potentially leading to the formation of woody communities and to the loss of open habitats. Plots of the T3.2 group are located at the lowest altitudes and on markedly south-facing slopes (Tab. 1). The most abundant and frequent species are *Avena sterilis* (mean cover 32.1%, occurring in 90.0% of plots), *Triticum ovatum* (mean cover 14.9%, in 90.0% of plots), and *B. erectus* (mean cover 12.6%, in 80.0% of plots) (see On-line Suppl. Tab. 1). This community was positively correlated with temperature EIV and showed its highest mean value (Tab. 2). These harsh conditions may explain why SBT2 (species of xeric, grasslands) emerged as indicators. The indication of SBT6 (ruderal species) as well as their great cover values (Tab. 5) is consistent with the indication by ISA (Tab. 4) of several species of croplands and abandoned fields (e.g. *T. ovatum*, *Phalaris canariensis* L., *A. sterilis*, *Crepis pulchra* L., and *Scorpiurus subvillosus* L.). It indicates the incomplete evolution of the considered communities towards the kind of semi-natural grasslands indicated in the EU Directive. In particular, this herbaceous community seems to have a potential affinity for the *6220 habitat [Pseudo-steppe with grasses and annuals (*Thero-Brachypodietea*) because it hosts several species of the *Tuberarietea guttatae* class, even if the total cover value of SBT2 is not very high. The manual of interpretation of EU Habitats includes in this habitat Mediterranean and sub-Mediterranean xerophilous, mostly open, short-grass annual grasslands rich in therophytes and therophyte communities of oligotrophic soils on base-rich, often calcareous substrates. According to the Italian interpretation manual of the 92/43/EEC Directive (Biondi et al. 2009), this habitat encompasses vegetation types that differ considerably in physiognomy, floristic composition, ecological and structural features, sometimes very valuable from a naturalistic viewpoint, but more often trivial and very common in Mediterranean sectors of Italy.

The T3.3 cluster includes undisturbed plots of the steepest hilly southerly slopes, characterized by the highest rockiness and litter cover, and the lowest AWC values (Tab. 1), as well as by low soil moisture EIVs. The most abundant and frequent species were *Bromus erectus* (mean cover 25.9%, occurring in 97.8% of relevés), *Sulla coronaria* (mean cover 19.5% in 95.6% of relevés), and *Hypochaeris achyrophorus* L. (mean cover 11.8% in 93.3% of relevés). The xerophilous group of indicator species such as *Filago pyramidata* L., *H. achyrophorus*, *Thymus longicaulis* C. Presl, and *Potentilla hirta* L. (Tab. 3) suggests the presence of patches with shallow soils. On the other hand, the indication by ISA of *Sulla coronaria*, *Sonchus asper* (L.) Hill, *S. oleraceus* L., *Geranium dissectum* L., *Crepis vesicaria* L., *Daucus carota* L., as well as of SBT6 (pioneer, ruderal, nitrophilous and semi-nitrophilous species) (Tabs. 3–4), highlights both the past use of these areas as croplands and the absence of disturbance, suggested also by the highest litter cover value (Grime 2001). In fact, the abundance of these species is reduced by both grazing and mowing (Grime 2001). Moreover, litter can influence the processes of species assemblage within plant communities (Catorci et al. 2011b), reducing seed germination, establishment of individuals (Eriksson 1995) and growth of established plants (Facelli and Pickett 1991). On the other hand, the low cover value of dominant tall grasses (Tab. 3) such as *Brachypodium rupestre*, usually fostered by abandonment, may be due to the harsh condition of sites (Vitasović Kosić et al. 2011). The spread of geophytes, such as orchids (i.e. *Anacamptis pyramidalis* (L.) Rich., *Orchis morio* L., *O. coriophora* L.), as well as the relatively high cover value of SBT1 (28%) and of SBT2 (17%) that are typical of semi-natural dry grasslands belonging to the *Scorzonero-Chrysopogonetalia* (*Brometalia erecti*) order and the *Festuco-Brometea* class (Biondi and Galdenzi 2012), suggests the existence of ecological conditions that potentially could lead to xeric *Bromus erectus*-dominated community (which could be referred to the 6210 habitat). Finally, the not negligible cover value of successional species (SBT5 – 5–6%) in the T3.2 and T3.3 groups indicates the presence of dynamic processes leading to forest recovery and, therefore, the future loss of these open habitats.

ii) Conservation status of plant communities and management implications

The three communities highlighted by MRT analysis showed a different contribution of SBTs to the species pool (Tab. 5). It also emerged that after field abandonment, different environmental conditions drive the dynamic processes towards herbaceous communities that are likely to develop into EU habitats. However, in only one community (T3.1) did we observe a floristic composition clearly dominated by species of permanent pastures (namely, SBT1) as happens in the semi-natural dry grasslands of the Italian peninsula. In fact, in these communities the average cover value of *Festuco-Brometea* and/or *Molinio-Arrhenatheretea* species generally exceeds 70% (see Biondi et al. 2005). In the other groups (T3.2 and T3.3), species of semi-natural grasslands had a lower mean cover value (ranging from 41 to 46%), with a conspicuous contribution (17–21%) to the total abundance of species belonging to *Tuberarietea guttatae* and *Sedo-Scleranthetea* classes, especially in cluster T3.2, while species of *Artemisietea vulgari*s and *Stellarietea mediae* classes had a cover ranging from 48 to 52%. As a matter of fact, only grasslands of the T3.1 and T3.3 groups seem to have the potential to develop into dry grasslands belonging to the *Festuco-Brometea* class **(**6210 habitat), with inclusions, in grasslands belonging to the T3.3 group, of patches of the *Tuberarietea guttatae* class (6220 habitat). However, an open issue is the assessment of their degree of representativeness in comparison with the standards defined by the Italian manual of interpretation of EU habitats (Biondi et al. 2009). In fact, the studied grasslands spread on non-calcareous substrates instead of on limestone. On the other hand, it should be considered that pH values are quite neutro-basic, as indicated by the manual of interpretation.With regard to the plant community of the T3.2 group, it is difficult to evaluate its representativeness with respect to aspects of greater conservation interest of the 6220 habitat. We found that the abundance of SBT 4, 5 and 6 (encompassing species of fringe habitat, successional species, and pioneer, ruderal, nitrophilous and semi-nitrophilous species, respectively) is still high in any condition. Time after abandonment is considered a key issue in recovery of semi-natural grassland (Pywell et al. 2002, Ruprecht 2006), but probably these species (generally tall plants with ruderal-like ecological needs) are also able to persist in abandoned fields due to the absence of disturbance (Grime 2001).This means that the herbaceous plant communities considered fail to meet the floristic standards needed to ascribe them to the habitat *sensu* the 92/43/EEC Directive. Because of this, we can argue that the achievement of a favourable conservation status requires careful and deliberate management plans. In particular, sheep or cows should graze on grasslands belonging to the T3.3 group during the late spring and summer periods to reduce the abundance of dominant tall plants and enhance that of species with avoidance and tolerance strategies, which are species of the *Festuco-Brometea* class (Grime 2001). Sheep, in particular, are known as dispersal vectors for most of the species of the *Festuco-Brometea* class (Fischer et al. 1995), and thus they can facilitate the processes related to species spread in managed grasslands (Kaligarič et al. 2006). Grasslands of the T3.1 and T3.2 groups should be mown once a year in early summer, since late mowing allows the conservation of the maximum species richness (Catorci et al. 2014a). Moreover, fresh phytomass should be removed to avoid litter deposition and summer grazing can be useful to achieve a higher level of representativeness.

In conclusion, we found that the environmental factors driving the species assemblage in the sub-Mediterranean hilly landscape of the Tuscan-Emilian Apennines after crop abandonment are linked to topographic (rockiness and altitude) and soil (pH and AWC) conditions, which mainly determine the intensity and duration of water scarcity. Moreover, our results indicated that not all former croplands, notwithstanding their having undergone the same land use history, have the potential to achieve a high representative status of the EU Directive habitats (sometime because of unsuitable soil pH) and that long-term abandonment of croplands does not lead *per se* to the recovery of the semi-natural herb communities of the EU Habitats Directive in sub-Mediterranean climate. In line with Smith et al. (2000), the main reason of such a result may be found in the lack of appropriate disturbance regimes. The absence of disturbance has a further double effect. It allows the spread of woody successional species (shrubs and pioneer trees) and thus leads to forest recovery as well as the permanence of plants with ruderal-like ecological needs. Likewise, the absence of disturbance allows the spread of competitive species which, in turn, reduces the site suitability for non-dominant herbaceous plants (such as small-sized and early flowering species – Grime 2001), which are key elements of the grasslands referred to the 6210 priority habitat protected by the 92/43/EEC Directive. Moreover, the spread of competitive grasses (i.e. *Brachypodium rupestre*) fosters the presence of elements, such as fringe species, that are not characteristic of semi-natural disturbed grasslands (Catorci et al. 2011a). Finally, we can assert that the use of phytosociologically determined SBT of species is a very useful tool in understanding the conservation status of herbaceous communities undergoing successional processes along the continuum from cultural to natural, thus helping to solve a major problem in the EU Directive and habitat interpretation. Moreover, it gives information on the type of management required in order to achieve a better conservation status of habitats.

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