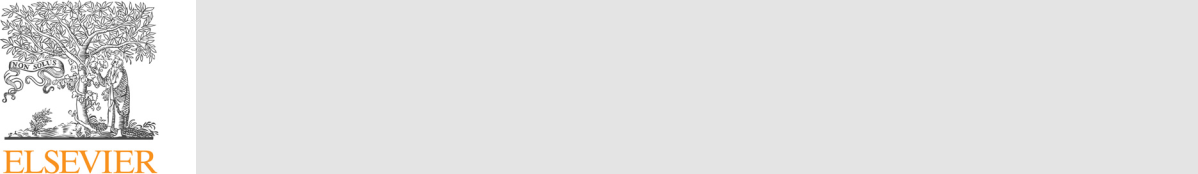
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Rapid recovery of the vegetation diversity and soil fertility after cropland T abandonment in a semiarid oak ecosystem: An approach based on plant  functional groups



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ABSTRACT

In many parts of the world, including the semi-arid Mediterranean areas, land abandonment has led to sig-nificant changes in vegetation composition, plant diversity as well as soil fertility. In this study, new approaches were presented on how the understory plant functional group diversity and composition changed after land abandonment in Zagros oak forests (Quercus brantii Lindl.) in western Iran. In addition, the impact of land-use change on main soil properties were investigated. The diversity and nutrient status of the three stages of the secondary succession of abandoned agroforestry systems were compared: croplands after a short period of abandonment (~5 years), croplands after a long period of abandonment (~15 years) and oak forests re-presenting the ‘climax’ stage. The plant species were classified in four functional groups (annual forb, annual grass, perennial forb, and perennial grass). The diversity indices were computed for each group and each stage. Results showed that the Shannon-Wiener diversity and Margalef richness of all functional groups significantly increased with time from the shortly abandoned croplands to the forest. Shortly after abandonment, annuals (especially annual forbs) were dominant whereas the abundance of the perennials increased after 15 years of abandonment and in the ‘climax’ forest. The soil content in lime decreased along the successional stages (from 52.7% to 26.4%) and was strongly negatively correlated with the diversity of the perennial forbs. In contrast, the soil total nitrogen and aggregate stability increased with succession (respectively from 0.04% to 0.19% and from 0.49 mm to 0.92 mm) and were strongly positively correlated with the diversity of this group. Recovery in soil fertility (and in particular, total nitrogen), provided suitable conditions for the establishment of a wide range of plant functional groups, which in turn increased the species diversity. The relatively fast recovery of soil fertility and plant diversity of abandoned agricultural lands indicated that the reestablishment of the forest vegetation could rely mostly on natural processes.

1. Introduction

Forests are subject to various threats worldwide despite their high diversity ([de Groot et al., 2016](#page1)). Over the last three centuries, land use change of 12 million km2 of forests and 5.6 million km2 of rangelands to other land uses has been a serious ecological challenge. This has led to adverse eﬀects on the services and sustainability of natural ecosystems and their biodiversity ([Reidsma et al., 2006; Moges et al., 2017;](#page1)



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[Depauwet al., 2019](#page1)). In many parts of the world, including the semi-arid Mediterranean forests of Zagros in western Iran, forest areas were largely converted in agricultural and pastoral lands and more recently (during the 20th century) a part of these areas were abandoned ([Romero-Calcerrada and Perry, 2004; Castellanos et al., 2005; San](#page1) [Roman Sanz et al., 2013](#page1)). Main reasons for agricultural abandonment were the low income from traditional agriculture, population migration from rural areas to cities and, in the case of Iran, the nationalization of

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forest areas and pastures ([Valipour et al., 2014](#page1)) Land abandonment can lead to formations of various vegetation types: from degraded forma-tions due to land erosion, which is quite frequent in semi-arid ecosys-tems, to scrublands or sometimes to naturally-established forests ([Prévosto et al., 2011; Sheﬀer, 2012; Zakkak et al., 2018](#page1)). Un-fortunately, in many areas, the status of the land and the vegetation succession pathways which are the back-bone of eﬃcient and eﬀective reforestation programs are not well known. These knowledge gaps could pose further risk of land degradation or even desertification in the coming decades ([Castellanos et al., 2005; San Roman Sanz et al., 2013;](#page1) [Heydari et al., 2014](#page1)). It is noteworthy that a cause of land abandonment can be due to a loss of soil fertility after too intensive or inappropriate farming practices. This is the case for some agroforestry systems in semi-arid Mediterranean conditions. Agricultural practices can in fact remove significant part of the tree canopy and the soil fertility can be altered by mechanical operations such as plowing and by using in-tensive chemical inputs. In this way, it destroys the structure and function of the ecosystem by damaging many soil microorganisms, re-ducing organic matter and soil fertility and altering vegetation-soil in-teractions ([Brunet et al., 2011; Zhang et al., 2013; Nath et al., 2018;](#page1) [Sanou et al., 2019](#page1)). Under such conditions, previous studies reported reduction in species diversity and destruction of ecological nests of many plant and animal species ([Seeber and Seeber, 2005; Miedema](#page1) [et al., 2019](#page1)). For instance, [Boutin and Jobin (1998)](#page1) showed that, in the early years after the land use change, the vacant ecological nests were occupied by some opportunistic species (usually annual species) which can overcome stress by producing abundant seeds ([Grime, 1979; Dreber](#page1) [et al., 2011](#page1)). In contrast, the more specialized plant species, with narrow tolerance range to the variation of ecological factors, are often eliminated from the ecosystem following disturbance ([Paywell et al.,](#page1) [1997; Flinn and Vellend, 2005](#page1)). However, this process strongly depends on the basic environmental characteristics of the area (such as soil), the primary plant species composition and the dominant functional groups. The resulting changes may have diﬀerent eﬀects on the species diversity and future of forest and pasture ecosystems ([Thomaes et al., 2012;](#page1) [Jakovac et al., 2016; Krishnadas et al., 2018](#page1)).

Plant functional groups refer to a group of species that have some common ecological traits i.e. morphological and physiological char-acteristics which play a similar role in the ecosystem ([Deng et al.,](#page1) [2008](#page1)). These groups are capable of representing spatial and temporal variations of environmental factors ([Austin, 1990; Verburg and van](#page1) [Eijk-Bos, 2003](#page1)) and have similar eﬀects on major ecosystem processes ([Lavorel and Garnier, 2002; Deng et al., 2008](#page1)). Therefore, plant func-tional groups reflect more eﬃciently ecological processes from the plant individual level to the ecosystem level than traditional classifi-cation of plant communities ([Westoby and Wright, 2006](#page1)). Functional analysis is one of the approaches used to illustrate the complexities of diﬀerent ecosystems ([Zhang and Zhang, 2007](#page1)) although its perfor-mance in diﬀerent ecosystems still needs to be further studied. Plant species can be divided into functional groups based on a variety of characteristics such as life-form, growth rate, nitrogen fixation, seed size, etc. ([Poorter et al., 2006; Deng et al., 2008](#page1)). The advantage of using traits instead of species is that diﬀerent vegetation types or even diﬀerent flora can be compared and that traits are more closely related to the functioning of the plant communities. As a consequence, even if the floristic compositions diverge among communities, the analysis of functional traits can tell us if the vegetation dynamics follows or not a same general pattern ([Domingues et al., 2007; Kahmen and Poschlod.](#page1) [2008](#page1)).

Despite the widespread use of multivariate analyses to detect ve-getation patterns ([Arekhi et al., 2010; Heydari et al., 2013; Mirzaei](#page1) [et al., 2017; Haggerty et al., 2019](#page1)), few studies have investigated plant functional groups along environmental gradients using quantitative approaches ([Lyon and Sagers. 2002; Zhang and Zhang, 2007](#page1)). For ex-ample, many studies have been carried out around the world on the impact on vegetation of land use change of forest to agriculture and of

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agricultural abandonment based on floristic views ([Tárrega et al., 2009;](#page1) [Prévosto et al., 2011; Holmes and Matlack, 2018](#page1)) while less studies have addressed these questions using plant functional groups ([Piekarska-Stachowiak et al., 2014; Li et al., 2016](#page1); [Lohmann et al.,](#page1) [2018](#page1); [Ribeiro et al., 2019](#page1)).

Climax vegetation of Zagros forests in western Iran include semi-arid, deciduous, xerophyte and cold oak forests. The Iranian oak forest is known as a unique habitat for some dominant, valuable plant and animal species ([Sagheb-Talebi et al., 2014; Fathizadeh et al., 2017](#page1)). The Zagros forests oﬀer a variety of ecosystem services such as timber, water, soil conservation, carbon storage and wildlife habitat, as well as various economic, social and cultural benefits to people ([Sagheb-Talebi](#page1) [et al., 2014](#page1)). The historical dependency of local communities on these forests, population growth and economic development (beginning in the early 1990s) have caused a significant level of deforestation in the area over the last thirty years, especially as a result of land use change to arable lands. Some parts of the natural forest were also changed to “agroforestry systems” combining a reduced forest cover with cereal cultivation. However, many of these lands were abandoned after some time due to reduced fertility or migration of farmers to cities ([Heidarlou](#page1) [et al., 2019](#page1)).

A volume of studies are available related to the floristic composition and eﬀects of disturbances on the species dynamics and diversity, dis-tribution and community structure in the semi-arid Zagros oak forests ([Pourreza et al., 2014; Heydari et al., 2017](#page1)) but those studies have not provided a comprehensive understanding for the restoration of semi-arid Zagros oak forests. Further, they were unable to specify which functional groups were most aﬀected by the land use change or de-gradation, or which group played a more prominent role for the de-termination of the climax community needed for a successful restora-tion program. As a consequence, actions are still lacking for the restoration of the degraded semi-arid Mediterranean forests of the Za-gros experiencing a pressing ecological need for human well-beings. Looking into it, this study was framed to present a new approach on how the understory plant functional group diversity and composition changed after diﬀerent land abandonment periods. It intended to compare the soil and vegetation attributes in three stages of the sec-ondary succession following the abandonment of the agroforestry sys-tems (~5 years of abandonment, ~15 years of abandonment, and oak forests which represent the ‘climactic’ stage). This study seeks to answer the following questions:

1- Do the diﬀerent functional groups based on growth form and life-span (perennial and annual forbs, grasses) show diﬀerent responses to certain soil properties following short-term (~5 years) and long-term (~15 years) abandonment?

2- Is the diversity of herbaceous species diﬀerently aﬀected by land use change and plant functional groups?

3- What are the most important soil properties in segregating these diﬀerent types of land-uses (undisturbed control forest, short-term and long-term abandonment from agriculture)?

2. Materials and methods

2.1. Site description

The study region is the Southern Zagros forests in the western Iranian province of Ilam. The study area (3.83 km2) was originally covered by oak forests (Quercus brantii Lindl.) and had been converted by the natives into traditional wheat farming (cereal cultivation under canopy or between natural trees/shrub). Some of these fields have been abandoned in diﬀerent years for various reasons, such as low pro-ductivity in particular due to a loss of soil fertility and farmer migration to the city.

For this study, three land uses ([Fig. 1](#page1)) were selected:

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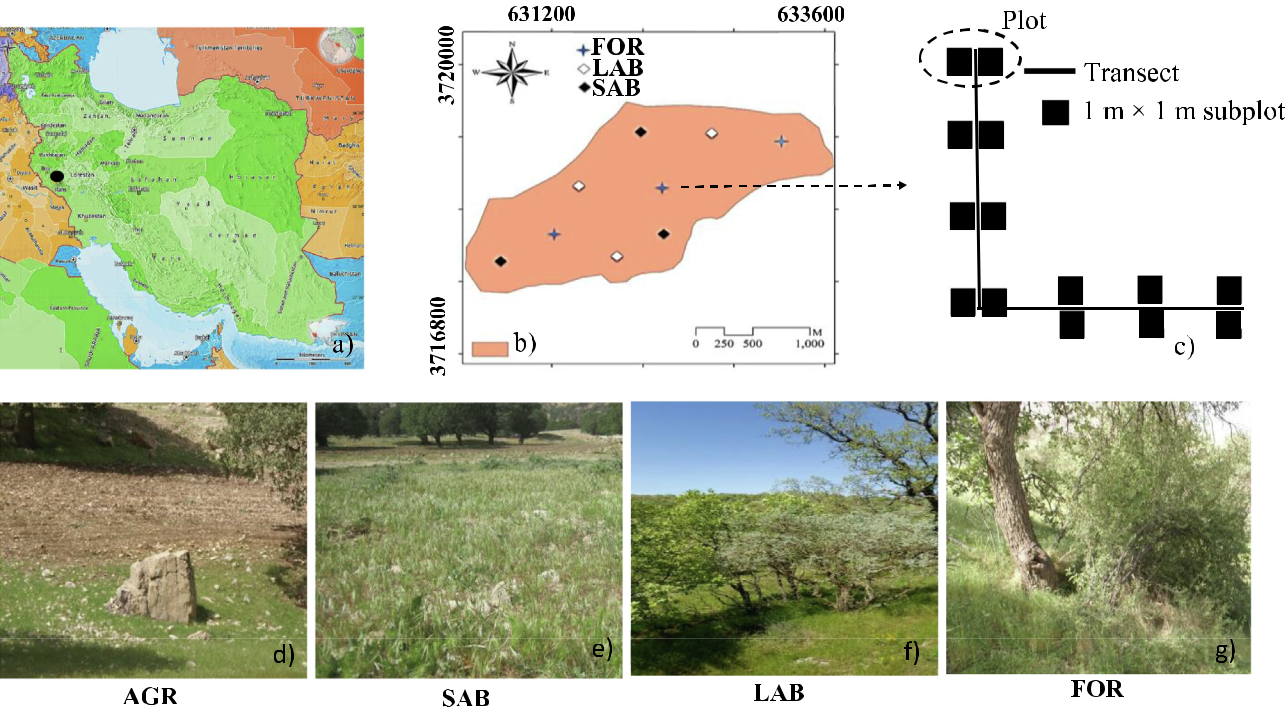


Fig. 1. (a) Location of the study area (●, Ilam province) in Iran, (b) map of the study area with the sampled areas, (c) sampling design, (d) agricultural plot (AGR), (e) plot after short-term abandonment from agriculture (SAB), (f) plot after long-term abandonment from agriculture (LAB) and (g) forest plot (FOR).

1. Undisturbed control forests (“FOR”). These forests are character-ized by a density of 85 tree ha−1, a tree height of 7.6 ± 2.1 m and exhibit coppice mode of sprouting dominated by the oak clumps. The tree cover is low (< 30%) and the understory is composed of a shrub layer.
2. Rainfed wheat agrosystem after 15 years of abandonment from 1999 to 2014 (“LAB”: long-term abandonment) and,
3. Rainfed wheat agrosystem after 5 years of abandonment from 2009 to 2014 (“SAB”: short-term abandonment).

Long-term climatic data (1999–2015, Ilam synoptic station) for the study area, indicated an average annual precipitation of 621.3 mm and a mean annual temperature of 17 °C. The dry period begins in May ending in October and the wet period extends from November to April. According to the classification system of [de Martonne (1925)](#page1), the cli-mate of this region is Mediterranean type ([Fathizadeh et al., 2017](#page1)). The dominant soils in this region are Inceptisols (Soil Survey Staﬀ 2014) with a clay loamy texture, having mean pH of 7.3 and mean soil depth of 30–40 cm ([Heydari et al., 2017](#page1)).

2.2. Experimental design and vegetation measurements

We selected three areas of 2–4 ha in each land use types (three re-plicates × three land use types) separated by a distance ranging from 800 to 1600 m and characterized by similar physiographic conditions (flat area or with a slope < 10% and 1450 m a.s.l). In each area, two perpendicular transects of 30 m length were randomly placed and seven plots composed of two subplots of 1 m2 were distributed along the transects (three plots in each transect and one plot where the transects met)) ([Tárrega et al., 2009](#page1)) leading to a total of 3 × 3 × 7 = 63 plots and 126 subplots. In each subplot, all species were recorded and a cover percentage was given to each species during the period of peak vege-tative growth i.e. May and June. All plant species were identified and named according to the available literature ([Ghahreman, 2000;](#page1) [Mozaﬀarian, 2008](#page1)). The plant species were classified in four functional groups: annual forbs, annual grasses, perennial forbs and perennial

grasses. All statistics were computed at the plot level (n = 63).

The species richness (SRmg), diversity (H′) and evenness (J′) were calculated using following equations ([Margalef, 1958; Shannon and](#page1) [Weaver, 1949; Pielou, 1966](#page1)):

*SR* mg=( *S* −1)/ln *N*

*s*

*H* ′= −∑ *pi* ln *pi*

*i*=1

* = *H* ′/ln(*S*)

In these equations; SRmg = Margalef's richness, H′ = Shannon–Wiener index, E = Pielou evenness, pi = proportion of cover of species ‘i’, N = total number of individuals and S = total number of species.

In this study, we calculated the herbaceous diversity indices ac-cording to types of life form (forbs and grasses) and life span (annual and perennial). These plant traits were selected because they are in-formative on species phenology, morphology, competitive ability and taxonomy ([Diekmann and Falkengren-Grerup, 2002; Verma et al.,](#page1) [2014](#page1)).

2.3. Soil sampling and laboratory analysis

To investigate the physical and chemical attributes of soils, three soil samples in each plot were collected in May 2013 at three random points to a depth of 20 cm with a cylindrical auger (diameter: 7 cm). The three soil samples were mixed together to obtain one composite soil sample per plot. Another undisturbed soil sample was sampled to de-termine bulk density (BD) in the 0–15 cm mineral layer ([Blake and](#page1) [Hartge, 1986](#page1)). The air-dried soil samples were sieved through 2-mm mesh in order to remove diﬀerent debris and roots prior to soil physical and chemical analyses. The hydrometer method used to assess soil texture ([Bouyoucos, 1962](#page1)). Soil organic carbon (SOC) was determined using dichromate oxidation based on the Walkley–Black method ([Nelson and Sommers, 1982](#page1)). Soil pH and electrical conductivity (EC) were determined by electrometrically (in H2O, 2:1 v/m) and

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Table 1

Results of the two-way ANOVA describing the eﬀects of plant functional groups (PFG), Land uses (LU) and their interaction on diversity, richness and evenness of understory vegetation. Significant p-values at p < 0.05 are indicated in bold.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | Shannon diversity index | |  |  |  | Margalef richness index | |  | Pielou evenness index | | |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Source |  | df | Meansquare | F-value | P-value |  | Meansquare | F-value | P-value | Meansquare | | F-value | P-value | |
|  |  | |  |  |  |  | |  |  |  | |  |  |  |
| Plant functional groups (PFG) | 3 | | 31.63 | 44.44 | 0.000 | 59.77 | | 40.22 | 0.001 | 1.69 | | 16.87 | 0.001 |  |
| Land use types (LU) | 2 | | 20.62 | 28.97 | 0.000 | 39.68 | | 26.70 | 0.000 | 3.61 | | 35.94 | 0.008 |  |
| PFG × LU | 6 | | 2.20 | 3.10 | 0.001 | 2.90 | | 1.95 | 0.000 | 1.31 | | 13.10 | 0.000 |  |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

conductivity probe in filtered extracts ([Kalra and Maynard, 1991](#page1)) re-spectively. Soil cation exchange capacity (CEC) was measured following extraction in buﬀered sodium acetate (NaOAc, at pH 8.2; [Sumner and](#page1) [Miller, 1996](#page1)). Kjeldahl digestion procedure employed to determine total nitrogen (TN) ([Bremner, 1996](#page1)). Mineral phosphorus (as ortho-PO4-2), was measured according to [Bray and Kurtz (1945)](#page1) approach. Finally, available potassium (K) and lime content (as the total neu-tralizing value (TNV)) were determined following ammonium acetate (pH = 7) extraction and titration with NaOH ([Black, 1986](#page1)), respec-tively. Soil aggregate stability (mean weight diameter; MWD) was computed according to the following equation:

([Shepherd et al., 2001](#page1)):

*MWD* =∑*in*=1 *xi* × *wi*

where: xi = mean diameter of each size class (2, 2–1, 1–0.25, and 0.25–0.053 mm) measured according to the hydrometer method, and wi = proportion of each size class to the total sample.

2.4. Statistical analysis

Prior to statistical analysis, Kolmogorov–Smirnov and Levene's tests were employed respectively to test the normality and homoscedasticity assumptions of the data. The transformation of the variables were done when necessary to assure the assumptions of homoscedasticity and normality of residuals. The eﬀects of the Plant Functional Groups (PFG), Land Uses (LU) and their interaction on Shannon-Wiener di-versity, Margalef richness and Pielou evenness of understory vegetation were tested with a two-way analysis of variance (ANOVA). One-way ANOVA was employed to investigate the eﬀect of land uses on soil properties. Duncan's test was used to separate the means of the de-pendent variables that diﬀered significantly among treatments. Boxplots were drawn using the ggplot2 package in R software. The relationships between diversity indices of diﬀerent plant functional groups and soil factors were analyzed by computing the Pearson cor-relation coeﬃcients. Discriminant function analysis (DFA) ordination was run to explore best predictor of the land uses. Entry and removal of soil variables were accomplished using tests of the associated F-statis-tics. Then, a matrix of pairwise F-ratios for each pair of land uses was used based on the selected soil variables following each step (stepwise method). Scores were calculated for each discriminant function (DF) and visualised by plotting DF2 against DF1. The associated classifica-tion matrix was used to obtain the predictive accuracy of the dis-criminant functions ([Heydari et al., 2017](#page1)). In addition, diﬀerences in vegetation composition between diﬀerent land uses were visualized using NMDS (non-metric multidimensional scaling) according to Bray–Curtis dissimilarities. All analyses were performed with the R 3.6.0 statistical software ([R Core Team, 2019](#page1)).

3. Results

The aboveground vegetation of FOR, LAB and SAB was represented by 48, 38 and 14 species respectively. The Asteraceae and Poaceae were dominant families in FOR and LAB. Poaceae and Brassicaceae were dominant families in SAB. There were 16 species only observed in FOR

such as Gladiolus segetum ker-Gawl, Helianthemum salicifolium, Malabila porphyrodiscus, Tragopogon longirostris, Taraxacum montanum, Trifolium scabrum. Also six species including Cephalaria dichaetophora Boiss, Neslia apiculata, Taeniatherum crinitum, Carthamus oxyacantha M Bieb, Cephalaria syriaca, Astragalus adscendens were exclusive to LAB. In ad-dition, seven species including Scariola orientalis, Sinapis arvensis, Vaccaria grandiflora, Avena wiestii Steud, Fumaria bracteosa, Lolium ri-gidum Gaudin, Picnomon acarna Cass were belonging to SAB. Four species i.e., Galium aparine L., Papaver dubium L., Vicia sativa L. and Cardaria Draba (L.) Desv. were common among the land uses.

3.1. Species diversity

The Shannon-Wiener diversity, Margalef richness and Pielou even-ness of understory vegetation were significantly aﬀected by the plant functional groups, the land uses, and their interactions ([Table 1](#page1)).

The values of Shannon-Wiener and Margalef richness were sig-nificantly highest for annual forbs and lowest for perennial grasses in all the land uses except at SAB where this trait was absent ([Fig. 2](#page1)). In LAB and FOR, the two indices followed the similar pattern: A-forb > P-forb > A-grass > P-grass. Similarly, Pielou evenness was sub-stantially lowest for perennial grasses in the LAB and FOR ([Fig. 2](#page1)) while it was also highest for annual forbs in the SAB. It also changed ac-cording to the following pattern A-forb = P-forb > A-grass > P-grass.

3.2. Change in soil properties by land uses

Mean values of each studied soil variable for each land use type are shown in [Table 2](#page1). Among these soil variables, TNV, BD, EC and sand content were the highest in SAB and the lowest in FOR whereas the reverse was true for SOC, TN, P, K and clay. Values for CEC, MWD and silt were intermediate in LAB and significantly lower in SAB.

3.3. Most eﬀective soil factors in separating the successional stages

Stepwise discriminant analysis showed that a combination of TN, TNV, MWD and sand content best-separated successional stages ([Table 3](#page1)). The other soil attributes were removed from the model.

Further, evaluation of the pairwise F-ratio matrices for each pair of land uses showed that land uses were significantly separated at the second step. Based on to the selected variables, two significant func-tions were obtained with respective eigenvalues of (λ1 = ) 9.236 and (λ2 = ) 2.574, which explained 85.9% and 8.1% of the total variance, respectively. Interestingly, according to the standardized coeﬃcients of each soil attributes, TN (0.876), TNV (−0.457) and MWD in function 1, versus sand content (−0.955) in function 2, were the best variables to separate land uses. Interestingly, stepwise discriminant analysis showed that a combination of TN, TNV, MWD and sand content best dis-criminated the land uses while SOC, P, K, CEC, BD, clay and silt con-tents were removed from the model ([Table 3](#page1)). Formation of distinct clusters in the ordination diagram indicated diﬀerences among the land uses ([Fig. 3](#page1)). Stepwise discriminant analysis showed 97% accuracy in delineating these groups due to the soil predictors. Respective land uses classification accuracies ranged from 95% each for FOR and LAB to

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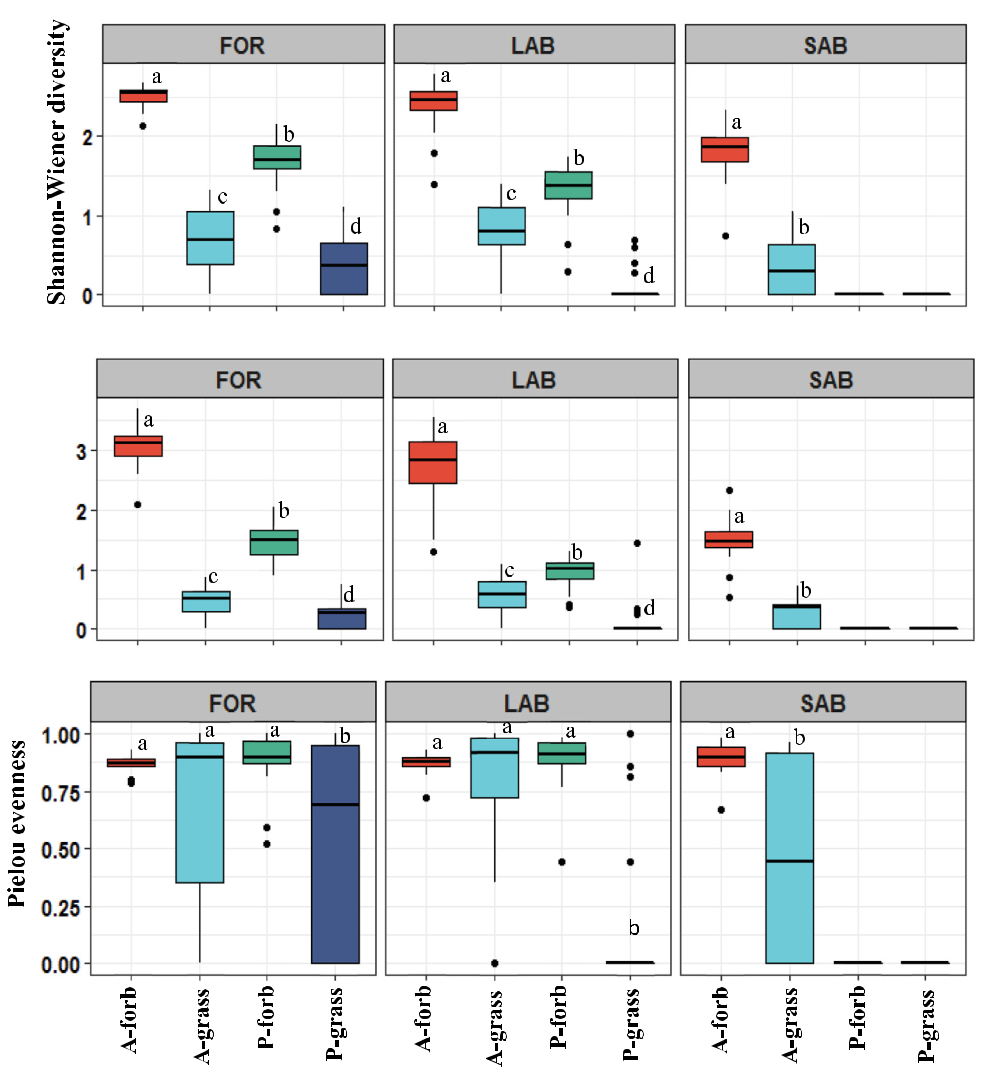


Fig. 2. Box-plot comparing means of Shannon-Wiener diversity, Margalef richness and Pielou evenness according to the plant functional groups and land uses. Means with the same letters are not significantly diﬀerent between land uses for plant functional groups based on Duncan's multiple range test (p < 0.01); A: annual, P: perennial, FOR: forest, SAB: short-term abandonment from agriculture and LAB: long-term abandonment from agriculture.

Table 2

Results from one-way analysis of variance (ANOVA) and Duncan's multiple-range test for means comparison of diﬀerent land uses eﬀect on soil properties (mean ± SE).

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Soil variable | F-value | P-value | FOR | |  |  | LAB | |  |  | SAB | |  |  |
|  |  |  |  | |  | |  | |  | |  | |  | |
| SOC (%) | 503.2 | < 0.001 | 1.97 | | ± 0.02 a | | 1.56 | | ± 0.06 b | | 0.44 | | ± 0.02 c | |
| TN (%) | 575.8 | < 0.001 | 0.19 | | ± 0.002 a | | 0.16 | | ± 0.005 b | | 0.044 | | | ± 0.002c |
| P (mg kg−1 dry soil) | 170.5 | < 0.001 | 20.18 | | | ± 0.29 a | 18.5 | | ± 0.30 b | | 13.71 | | | ± 0.15 c |
| K (mg kg−1 dry soil) | 65.2 | < 0.001 | 400.3 | | | ± 21.18 a | 320.8 | | | ± 5.5 b | 183.3 | | | ± 8.7 c |
| (dS/m) EC | 17.3 | 0.031 | 0.12 | | ± 0.001b | | 0.13 | | ± 0.002 b | | 0.19 | | ± 0.001 a | |
| TNV (%) | 94.7 | < 0.001 | 26.36 | | | ± 1.09 c | 35.25 | | | ± 0.79 b | 52.69 | | | ± 0.96 a |
| CEC (mol+kg−1) | 54.3 | < 0.001 | 18.89 | | | ± 0.32 a | 18.74 | | | ± 0.36 a | 14.32 | | | ± 0.38 b |
| Bulk density (gcm−3) | 32.4 | < 0.001 | 0.92 | | ± 0.04 a | | 1.07 | | ± 0.05 b | | 1.35 | | ± 0.02 c | |
| MDW (mm) | 77.1 | < 0.001 | 0.92 | | ± 0.025 a | | 0.86 | | ± 0.026 a | | 0.49 | | ± 0.027 b | |
| Clay (%) | 2.74 | 0.042 | 30 | ± 0.61 a | | | 27 | ± 0.62 b | | | 24 | ± 0.64 c | | |
| Silt (%) | 14.1 | < 0.001 | 25 | ± 1.12 a | | | 24 | ± 0.78 a | | | 20 | ± 0.86 b | | |
| Sand (%) | 16.9 | < 0.001 | 45 | ± 1.23 c | | | 49 | ± 0.99 b | | | 56 | ± 1.05 a | | |

Within rows, means with the same letters do not significantly diﬀer (p < 0.01); SOC, soil organic carbon, TN: total nitrogen, P: Mineral phosphorus, K Available potassium, TNV: total Neutralizing Value, CEC: cation exchange capacity and MWD: mean weight diameter of soil aggregates; forest (FOR), long-term abandoned from agriculture (LAB) and short-term abandoned from agriculture (SAB).

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Table 3

Standardized canonical coeﬃcient of soil attributes in each function.

|  |  |  |
| --- | --- | --- |
| Soil attributes | Function |  |
|  | 1 | 2 |
|  |  |  |
| TN | 0.876 | 0.089 |
| TNV | − 0.457 | −0.060 |
| MWD | 0.349 | −0.218 |
| Sand | − 0.132 | −0.955 |

Abbreviations: TN, total nitrogen; TNV, total neutralizing value; MWD, soil aggregate stability (mean weight diameter).

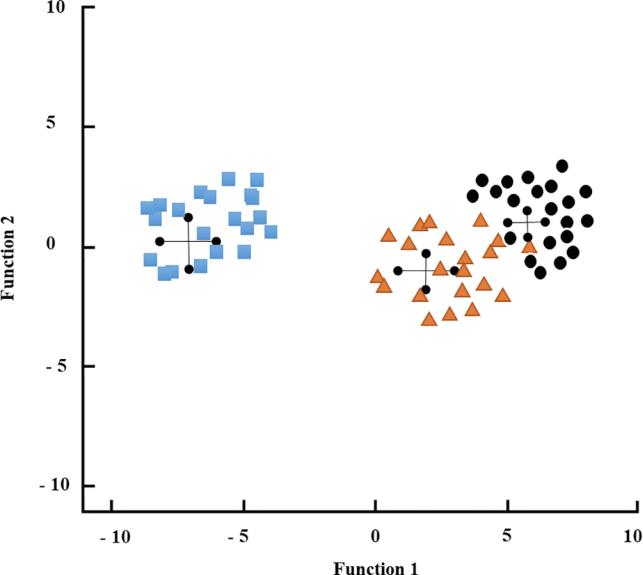


Fig. 3. Scatter plot of the first two discriminant functions values for each land use; FOR: forest, SAB: short-term abandonment from agriculture and LAB: long-term abandonment from agriculture.

Table 4

Classification matrix and its accuracy (%) using stepwise discriminant function analysis (DFA) for groups categorised using visual indicators, with predicted groups that were classified on the basis of selected soil attributes (TN, TNV, MWD and sand).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Land uses | Predicted group membership |  |  |  |
|  | FOR | LAB | SAB |  |
| Original group | FOR | 95.2 | 4.8 | 0 |
|  | LAB | 4.8 | 95.2 | 0 |
|  | SAB | 0 | 0 | 100 |

Abbreviations: forest (FOR), long-term abandoned from agriculture (LAB) and short-term abandoned from agriculture (SAB); 96.8% of original grouped cases correctly classified.

100% for SAB ([Table 4](#page1)).

3.4. Relationships between soil properties extracted by discriminate analysis with plant species functional groups diversity indices

Across the land use types, the TN and MDW showed strong positive correlations with the diversity indices of perennial forbs, while TNV caused strong negative impact on the diversity indices of this functional group. Evenness showed a negative and neutral relationship for annual forbs and annual grasses, respectively. In addition, a significant nega-tive relationship was observed between TNV and diversity indices of all PFG (except for evenness of annual forb). In addition, there was no significant relation between sand content and Margalef richness and Shannon diversity indices of all PFG ([Fig. 4](#page1)).

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3.5. Diﬀerences in vegetation composition among functional groups

Results of the non-metric multidimensional scaling (NMDS) showed that the understory vegetation composition of the study areas was significantly segregated along the first axis (NMDS axis 1, F-value = 3133 and P-value < 0.001) and the second axis (NMDS axis 1, F-value = 8.8 and P-value < 0.001). This indicated strong and con-sistent diﬀerences in the vegetation composition (Bray–Curtis dissim-ilarity). Along the first axis, SAB is separated from the other two land uses (LAB and FOR) by a clear distance ([Fig. 5](#page1)) illustrating the sig-nificant impact of long-term cultivation under oak forest canopy on understory vegetation composition. In contrast, both FOR and LAB were close together in the two-dimensional space of NMDS ([Fig. 5](#page1)a). Values of the Shannon Wiener diversity index in NMDS ordination diagram showed that diversity of perennial and annual forbs had the highest role in structuring the FOR and LAB, respectively ([Fig. 5](#page1)a, [Table 5](#page1)) whereas for structuring the SAB, the contribution of annual forbs were domi-nant. In addition, the contribution of perennial grasses in diversity was slightly higher in FOR than in LAB whereas annual grasses were more present in LAB than in FOR. The lowest diversity was observed in SAB where only annual forbs and grasses were present ([Fig. 5](#page1)a, [Table 5](#page1)). The analysis of the contribution of the diﬀerent functional groups in plant composition showed that these groups had similar contribution in plant composition of both FOR and LAB but not SAB ([Fig. 5](#page1)b).

4. Discussion

4.1. Plant functional group diversity following land abandonment

The results showed that long-term abandonment and forest (sec-ondary succession) increased diversity, richness and evenness of all functional groups compared to short-term abandonment. The absence of any human disturbances over a long time period was beneficial to vegetation diversity as it was also reported in other ecosystems ([Gustavsson et al., 2007; Plieninger et al., 2014](#page1)). With time, probably migration and dispersal rates of seeds in the abandoned areas increased ([Lozada et al., 2007; Baskin and Baskin, 2014](#page1)) and favored the di-versification of the plant communities.

Plant functional group diversity was also influenced by agricultural practices such as plowing which can inhibit the seed germination and recruitment of annual and perennial species ([Uchida and Ushimaru,](#page1) [2014](#page1)). Thus, such species associated with long-lasting soil seed banks cannot be restored in the short term after land abandonment ([Heydari](#page1) [et al., 2013](#page1)). In fact, a decline in seed density after land abandonment is often observed ([González-Rivas et al., 2009](#page1)). Moreover, some authors have also emphasized the high levels of soil nutrients in arable lands, which persist during the first years of abandonment, and that can en-hance intraspecific and interspecific competition limiting species es-tablishment ([Bernhardt-Römermann et al., 2008; Dölle et al., 2008,](#page1) [Prévosto et al., 2011](#page1)). More directly, the presence of crop residues can also inhibit the germination and establishment of plant species due to the modification of the microclimatic conditions of the soil (in parti-cular light extinction) and also due to allopathic eﬀects ([Teasdale and](#page1) [Mohler, 2000; Pärtel et al., 2005](#page1)). These processes could explain why species diversity of the diﬀerent functional groups was reduced even after 5 years of abandonment.

We also found that short-term abandonment only caused recovery of annuals and so diversity, richness and evenness of such functional groups increased. The dominance of annual functional groups is in line with the colonization hypothesis ([Brown and Southwood, 1987](#page1)) that states that annual grasses and forbs accumulate in shorter time than the plants having other traits in the abandoned lands. For example, annual grasses such as Bromus tectorum and Avena wiestii and annual forbs such as Galium aparine, Sinapis arvensis and Fumaria asepala are among the most abundant annual species present in the area shortly after land abandonment. [Tasser et al (2007)](#page1) stated that secondary succession

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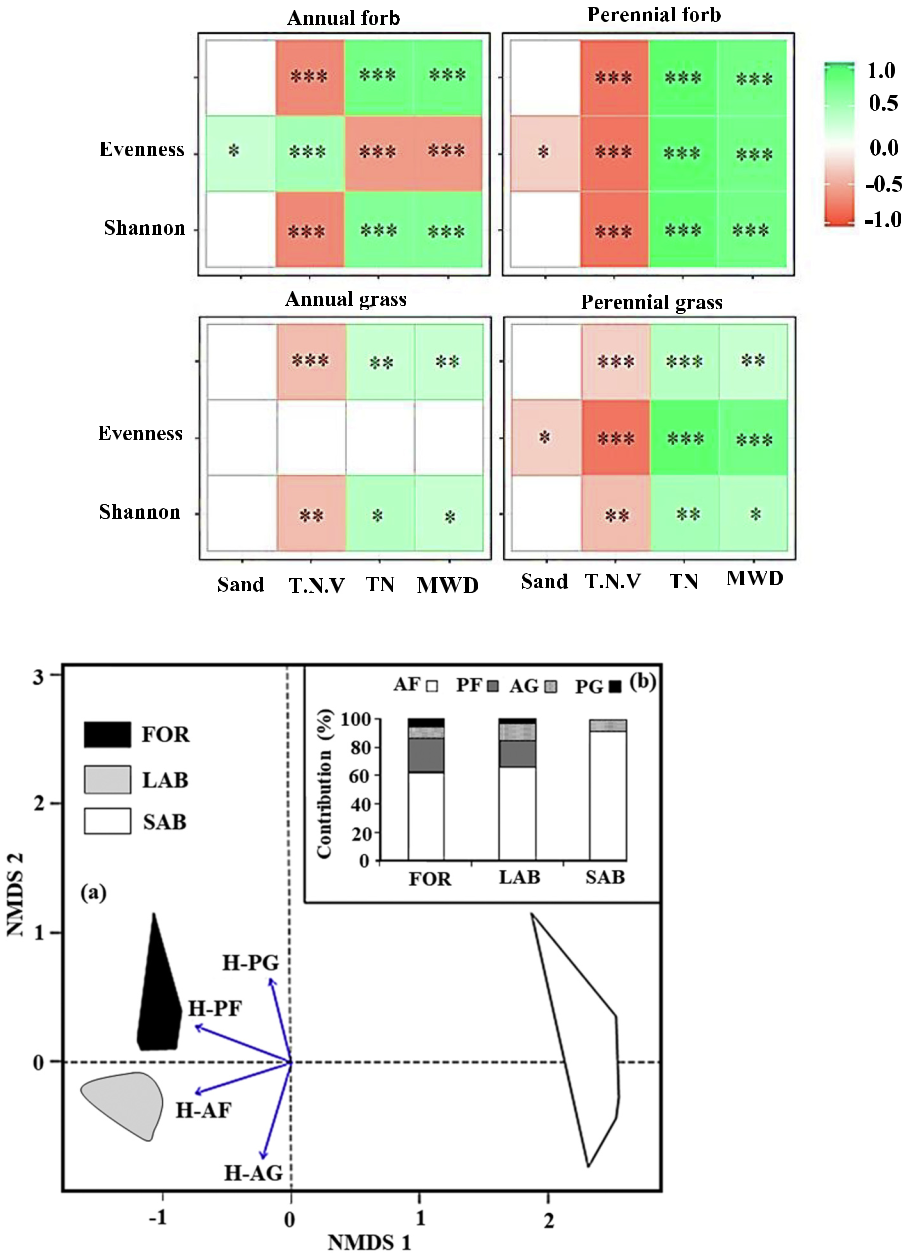


Fig. 5. NMDS ordination (stress = 0.073) of vegetation composition (a) and contribution (b) of diﬀerent plant functional groups including AF: annual forb, PF: perennial forb, AG: annual grass and PG: perennial grass in semi-arid oak forest in Zagros ecosystem. The length and direction of the arrows represent the importance of Shannon-Wiener diversity of each plant functional groups (H-PF: Shannon diversity of perineal forb, H-AG: Shannon diversity of annual grass, H-PG: Shannon diversity of perineal grass and H-AF: Shannon diversity of annual forb) in vegetation composition of each land uses (FOR: forest, SAB: short-term abandonment from agriculture and LAB: long-term abandonment from agri-culture), significance level of P < 0.05.

begins quickly after land abandonment and noted that dense grass communities can establish within the 1–3 years after abandonment. In line with our results, [Fensham (1999)](#page1) also noted the prevalence of annual forbs and grasses after a short time following agriculture abandonment.

The predominance of annual forms, that we observed in the early post-abandonment years, can be explained by the high production of small highly dispersible seeds ([Fenner et al., 2005; Heydari et al., 2013](#page1)) and the slow establishment of perennial plants ([Meiners et al., 2002;](#page1) [Fensham et al., 2016](#page1)).

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Fig. 4. Correlation between the most eﬀective soil properties extracted by discriminate analysis with plant species functional groups diversity indices; T.N.V: total Neutralizing Value, TN: total nitrogen and MWD: mean weight diameter of soil aggregates; blank square represent no significant correlation, significant positive and negative correlation in-dicated by green and red color respectively; \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001.

Table 5

The correlation between Shannon diversity index of diﬀerent plant functional groups and first and second axis of NMDS.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Shannon diversity | NMDS 1 | NMDS 2 | r2 | p |
|  |  |  |  |  |
| H-AF | −0.95402\*\*\* | −0.29974 | 0.8069 | 0.001\*\*\* |
| H-PF | −0.93359\*\*\* | 0.35833 | 0.8221 | 0.001\*\*\* |
| H-AG | −0.29483 | −0.9555\*\*\* | 0.7901 | 0.001\*\*\* |
| H-PG | −0.23209 | 0.97270\*\*\* | 0.5815 | 0.001\*\*\* |

H-PF: Shannon diversity of perineal forb, H-AG: Shannon diversity of annual grass, H-PG: Shannon diversity of perineal grass and H-AF: Shannon diversity of annual forb.

Our results showed that the presence of perennial species increased after 15 years of abandonment. The higher share of annual plants in the soil seed banks will guarantee their faster establishment in the short-term abandoned land and occupy much of the ecological niches. After their death, nutrients are added to soil favoring the establishment of the perennials ([Zobel et al., 2000](#page1)). Therefore, it can be concluded that perennials require long-term land abandonment for their establishment. It is evident by the occurrence of the highest and lowest values of the diversity indices for the perennial functional group (forbs and grasses) in the climax forest and long-term abandonment land-use types, re-spectively. The present findings supported the observation of [Brown](#page1) [and Southwood (1987) and Fensham et al. (2016)](#page1). Moreover, the pre-sent results confirmed that the plant functional based diversity analysis is necessary to understand the recovery of vegetation after agricultural abandonment in semi-arid oak forest ecosystem. Similar approaches were also successfully tested in diﬀerent terrestrial ecosystems sub-mitted to disturbances such as fire and land use changes ([Kazanis and](#page1) [Arianoutsou, 2004; Jangid et al., 2011; Torres et al., 2017; González-De](#page1) [Vega et al., 2018](#page1)).

4.2. Change in vegetation composition after abandonment

We found that plant composition widely diﬀered among the short-term, long-term abandonment and climatic forest. The similarity of the floristic composition between the forest and long-term abandonment land-use types confirms the positive eﬀect of protecting the oak forest ecosystem against the human disturbances on the long-term. This si-milarity results from the fact that environmental conditions (in parti-cular light and nutrients) are deeply modified by the establishment of a

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woody cover ([Dölle et al., 2008; Heydari et al., 2017](#page1)). However, even 15 years after abandonment, there are still diﬀerences remaining in vegetation composition between these two land-use categories. It must be noted that such diﬀerences in plant composition, reflecting land-use legacies, can persist over a very long period or even can be everlasting ([Dupouey et al., 2002](#page1)).

4.3. Influence of land abandonment on soil properties and soil–plant functional groups relationships

Our results showed that soil properties were largely influenced by cropland abandonment and land-use changes. The mean weight dia-meter of soil aggregates (MWD) and the total nitrogen (TN) increased along the successional stages, from recently abandoned croplands to the forest system, while the lime content decreased. MWD depends on ag-gregate stability which results from the interactions between primary particles and organic constituents to create stable aggregates. This process is aﬀected by various factors such as soil environmental con-ditions, management and land uses history ([Chhina et al., 2019](#page1)). In particular, the depletion of soil organic matter by agricultural practices can alter the stability of soil aggregates ([Zhao et al., 2017](#page1)). For in-stance, [Caravaca et al. (2004)](#page1) found that soil aggregate stability was significantly reduced in cultivated soils compared to forest soils in semiarid conditions.

Nitrogen content was the lowest and lime content the highest five years after cropland abandonment. A result also found by [Ayoubi et al.](#page1) [(2011)](#page1) who studied the change of soil properties from agricultural to forested lands in northern Iran. The higher lime content in the short-term abandonment could be due to the presence of carbonated soil layers not far from the surface in this region ([Sagheb-Talebi et al.,](#page1) [2014](#page1)) which could have been mixed with the upper soil layers during plowing operations. In contrast, in the forest, many processes including activities of the microorganisms and the roots of trees cause the dis-solution and leaching of lime, the transfer of lime to the depth and the reduction of surface lime ([Binkley and Fisher, 2013](#page1)).

The percentage of sand was also significantly higher in short-term abandonment than in the long-term abandonment. Cultivation and til-lage practices in our study region have caused a gradual degradation of the upper soil layers, which were also more prone to severe wind and water erosion ([Baumhardt et al., 2015](#page1)). Eroded soils in agricultural lands or in lands with a low abandonment history (< 5 years) exhibited a reduced percentage of fine soils particles (such as silt) while coarser particles such as sand were more abundant ([Zhao et al., 2005; Lobe](#page1) [et al., 2001](#page1)). Previous studies have shown that the loss of the fine fraction of soil (clay and silt) can deplete soil organic carbon and soil nutrients such as nitrogen and phosphorus ([Su and Zhao, 2003; Zhao](#page1) [et al., 2005](#page1)). These results are consistent with ours, namely a significant reduction of nitrogen and lower clay and silt contents shortly after abandonment. Besides, the increase in soil nutrients recorded in forest soils could be partially related to an increase in annual organic matter inputs ([Fortier et al., 2019; Wapongnungsang and Tripathi, 2018](#page1)). In accordance with our results, [Lucas-Borja et al. (2019)](#page1) showed that some soil properties, such as organic matter, nitrogen and C:N ratios, were similar in farmlands after 15 years of abandonment and in forested areas. Enrichment in soil nutrients observed in the late forest stages of the succession can be also accompanied by an improvement of soil water retention. For instance, [Lesschen et al (2008)](#page1) recorded after 15 years of abandonment an increase of the soil water-retention capa-city, hydraulic conductivity, infiltration, and reduction of the runoﬀ and erosion. However, such changes are not systematic and higher soil water repellency as well as lower soil hydraulic conductivity have been detected in forest soils compared to agricultural soils ([Lucas-Borja et al.,](#page1) [2019](#page1)). This indicates that changes in soil properties are also dependent of numerous factors such as the nature and intensity of the agricultural practices.

We found a positive correlation between nitrogen and aggregate

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stability and the diﬀerent plant functional groups, except for annual forbs evenness (negative correlation). Nitrogen is one of the most im-portant nutrients for establishment and growth of plant species ([Binkley](#page1) [and Fisher, 2013](#page1)). It represents a key role in increasing the diversity of diﬀerent plant functional groups ([Knops and Tilman, 2000; Ma et al.,](#page1) [2014](#page1)). Similarly, soil aggregate stability is strongly linked to soil or-ganic matter and nutrient availability and positive relationships are frequently observed between these factors and plant diversity ([Perroni-Ventura et al., 2006; Eskelinen et al., 2009; Lange et al., 2015;](#page1) [Tahmasebi et al., 2017](#page1)). The improvement of soil fertility after long-term abandonment has provided suitable conditions for the establish-ment of a wide range of plant functional groups, which in turn has increased species diversity. A negative relationship was found between diversity and richness of all functional groups with lime content (T.N.V). Lime is detrimental to plants: it changes the soil pH and re-duces the availability of micronutrients; zinc, manganese and P ([Marschner, 2011; Keys et al., 2018](#page1)). Therefore, higher lime content in soils of recently abandoned farmlands can negatively influence the di-versity of the diﬀerent functional groups whereas diversity is improved in the later stages of succession due to decreasing lime content. We found also positive correlations of TN and MDW with the diversity in-dices (except evenness with annual forbs). Previous studies also showed improvement of soil fertility (in particular N and C stocks) with higher plant diversity (e.g. [Fornara and Tilman, 2008; De Deyn et al., 2009](#page1)). For instance, it was found that species richness increased N stock and decreased N leaching. Potential explanations were a better reallocation of N from deeper to upper soil layers and more eﬃcient N recycling and mineralization ([McKane et al., 1990; Cong et al., 2014](#page1)). Soil infiltration capacity was also found to be better determined by plant functional groups diversity through a higher soil macroporosity ([Pérès et al., 2013;](#page1) [Su et al., 2018](#page1)).

5. Conclusion

In this study, our functional groups were eﬀective to discriminate the diﬀerent stages of succession. Growth-form is a simple trait but was proved to eﬃciently capture patterns of variation in several important functional traits and to be a robust predictor of responses to dis-turbance. The increase of diversity indices based on functional groups in the successional stages after abandonment was concomitant with improvement of soil fertility. This finding indicates that a higher functional diversity in abandoned croplands is connected to a higher rate of ecological processes. These processes in our study were mainly reflected by the increase in total soil nitrogen and higher aggregate stability. Therefore, the use of functional indices is eﬀective in re-vealing underlying soil mechanisms, which could have hardly been detected by simple taxonomic approaches.

From an applied perspective, we showed that the restoration of plant diversity and soil fertility occurred on a relatively short term after abandonment. Therefore, land degradation, which resulted from tra-ditional agricultural practices, was reversible and can rely mostly on natural processes. This indicates that no management actions are re-quired and that the simple protection against any human disturbances (e.g. intense grazing, wildfires) is suﬃcient to recover the main eco-system functions. However, restoration actions could be requested in case of too intense agricultural practices leading to a degradation dif-ficult to reverse or to speed up the natural restoration process.

CRediT authorship contribution statement

Mehdi Heydari: Conceptualization, Methodology, Software, Validation, Formal analysis, Resources, Data curation, Writing - original draft, Funding acquisition, Visualization, Supervision, Project admin-istration, Funding acquisition. Nasim Zeynali: Data curation, Writing - original draft. Masoud Bazgir: Methodology, Supervision. Reza Omidipour: Software. Mehrdad Kohzadian: Data curation. R. Sagar:

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Investigation, Writing - review & editing. Bernard Prevosto:

Investigation, 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 influ-ence the work reported in this paper.

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