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# Effects of landscape fragmentation at a fine scale on Mediterranean mountain grassland plant diversity

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**Abstract**

European mountain grasslands are affected by abandonment and are being colonized by shrubs and forest. Grassland fragmentation is caused when the forest matrix grows, and surrounding grassland is split into fragments. Multiple studies have been done on grassland fragmentation but in anthropic matrices. Grassland isolation would not be a constraint for plant dispersion since the distance between grassland fragments is usually short. However, when they are abandoned, the surrounding forest can change the environmental characteristics and small fragments can disappear. We studied abandoned Mediterranean mountain grasslands in an oak forest matrix. We surveyed the grassland communities and their soil properties in multiple fragments of different sizes and isolation distances. We classified the grassland species into different groups by habitat preference and life form and calculated the landscape fragmentation variables. We analyzed the effect of fragmentation on the richness of the grassland groups and communities. Results showed that the fragmentation variables did not have any effect on the grasslands, except at the extreme ends of the gradient of the vegetation succession. The smallest grasslands favored perennial and wetter species over annual or drier species due to wetter soil conditions and less availability of light. Annual species are more abundant in southern aspect fragments with drier conditions across the fragments. The lack of connectivity among fragments is not a problem for grassland communities at a fine scale. Annual and drier grassland species remain even in the smallest fragments, but their conservation requires maintaining a minimum fragment size more than it does landscape connectivity.

**KEYWORDS**
communities, composition, edge effect, forest, habitat, richness

## INTRODUCTION

European mountains in the last decades have been transformed due to changes in land use and habitat diversity created or sustained by human activity (Kaligarič et al., 2006; MacDonald et al., 2000; Navarro & Pereira, 2012; Petanidou et al., 2008; Sluiter & de Jong, 2007). For example, mountain grasslands traditionally under livestock use have disappeared in favor of shrublands or forest (Chauchard et al., 2007; Flinn & Vellend, 2005). Such disappearance has a negative effect on grassland communities, causing a loss of floristic diversity (Gustavsson et al., 2007; Krahulec et al., 2001; Römermann et al., 2009). Decreasing fragment size and increasing isolation lead to lower grassland species richness and altered community composition (Bruun, 2000; Dainese et al., 2015; Köchy & Rydin, 1997; Krauss et al., 2004; Williams et al., 2006). The study of fragmentation effects on grasslands usually has been focused on agricultural landscapes, in matrices of anthropic origin, such as croplands, and at landscape scale (Cousins & Lindborg, 2008), or grassland mountain fragments of large size (Dainese et al., 2015). Nevertheless, forest succession due to the abandonment of traditional uses will make grasslands isolated at short distances within a natural forest matrix (Kirby & Watkins, 1998). Thus, grasslands managed with livestock and later abandoned caused the vegetation to form mosaics of forests–shrublands–grasslands (Bergmeier et al., 2010; Erdős et al., 2018).

Grassland plant diversity can be affected by two processes of fragmentation: a greater isolation among fragments and a modification of the environmental conditions in the fragments. The island biogeography theory predicts that species richness would increase with decreasing isolation among fragments and increase with increasing fragment sizes (Warren et al., 2015). At a local scale, isolation limits seed dispersal, which is an important factor in the colonization of habitats (Bullock, 2000; Roschewitz et al., 2005) and influences the dynamics among metapopulations (Cadotte, 2006; Levine & Murrell, 2003). The proximity between grassland fragments has a positive effect on the colonization of species due to the greater ease of seed dispersal (Brantley & Young, 2009; Ewers & Didham, 2006). In contrast, a reduction in floristic richness has been observed in forest glades due to isolation (Lanta et al., 2019; Sebek et al., 2015). Moreover, the contrast between grasslands and the surrounding matrix affects the dispersal movements of species. A hard matrix, that is, a matrix with very contrasting environmental conditions compared to the fragments, can be less permeable to species and reduce dispersal. Although a forest matrix can be a barrier for wind-dispersed seeds, it can also be inhabited by generalist plant species, making it a less harsh matrix than croplands, which are poorer in species richness (Öckinger et al., 2012). Nevertheless, some species may show difficulty in colonizing fragments of smaller size since the forest matrix modifies environmental conditions such as available light, microclimate, or soil nutrients (Bullock, 2000; Cole & Weltzin, 2005; Goldberg & Werner, 1983). Forest cover decreases the light below the trees (Martens et al., 2000), the temperature in the understory (Norris et al., 2011), and modifies soil nutrients such as carbon (Deng et al., 2013). For example, the reduction in available light when the forest grows alters the floristic composition of the gaps, promoting the presence of shade-loving species in the gaps and decreasing the composition and richness of generalist species (Naaf & Wulf, 2007).

No studies have verified the effects of the forest matrix on pasture fragmentation. In contrast with the landscape fragmentation studies, the grassland fragmentation by the forest is at a fine scale since the distances are short, but the environmental properties, such as the soil and light availability, in the forest can change in the smallest fragments (Flinn & Vellend, 2005). Knowing the effect of the fragmentation would help to know not only the composition of grasslands but also their dynamics due to any management. In turn, this information can be considered for designing rules to preserve them and the specialist species that make them up. Knowing the size of the grassland fragments or their degree of isolation at a fine scale is an important tool for their conservation.

In our study, we surveyed the grassland communities within the area of a natural Mediterranean mountain broad-leaved oak forest (*Quercus pyrenaica*) in the Sierra de Guadarrama (Madrid, Spain). Mediterranean grasslands are considered one of the most diverse habitats in Europe (Mucina et al., 2016). In the western Mediterranean mountains, grasslands are composed of annual species in the lower altitudes and drier soils and perennial species in the highest and wetter soils (Pilar Rodríguez-Rojo & Sánchez-Mata, 2004). In the Sierra de Guadarrama, broad-leaved oak forests are predominant at mid-elevations, but they were cleared and maintained as perennial grasslands of *Agrostis castellana* for livestock. Annual grasslands can also be found in drier and poorer soils. Nevertheless, these grasslands have been abandoned by livestock in recent decades, and the oak forests grew, decreasing and splitting the grasslands. The grasslands studied in this work have different sizes and degrees of isolation.

Our objective was to verify the effect of landscape fragmentation on the richness and composition of different grassland species groups. We hypothesized that species richness and composition would be (1) higher for annual or drier grassland species in larger fragments and (2) higher for perennials or wetter species in smaller fragments. (3) It is foreseeable that the fragmentation effects caused by isolation or connectivity do not influence the grassland diversity since the distances are short, but the size of the fragment does because the surrounding forest produces changes in some environmental parameters (Fahrig, 2013; Hanski, 2015). We expect smaller fragments to have a plant composition more like the forest fringe (perennial and wetter species) and less like the grassland community group (annual and drier species), which is promoted by the common management practices in these systems like livestock grazing or thinning.

# MATERIALS AND METHODS

## Study region, vegetation and sampling

The study was carried out in a mature, broad-leaved oak forest of *Q. pyrenaica* (approximately 300 ha) in the mountains of Sierra de Guadarrama (Madrid, Spain), 1200–1400 m above sea level (*Quercion pyrenaicae*, Mucina et al., 2016). Its climate is Mediterranean, with a mean annual temperature of 10.4°C and a mean annual precipitation of 802.1 mm, which is irregularly distributed and concentrated in winter. The soils are of acidic origin and their substrate consists of siliceous materials, such as granite, gneiss, schist, and quartzite. The forest has an understory of fern (*Pteridium aquilinum*), shrubs of Leguminosae (*Cytisus scoparius*, *Genista florida*, *Genista cinerascens*), and spiny small trees or shrubs (*Crataegus monogyna*, *Prunus spinosa*, *Rosa canina*, *Rubus corymbifera*, *Rubus micrantha*, *Rubus caesius*, *Rubus ulmifolius*, etc.) and a layer rich in shade-loving herbs (*Linarion triornithophorae*, Mucina et al., 2016). The forest presents gaps where grasslands and scrublands of different sizes and isolation appear. The habitats in the study site were mapped with 2017 aerial photography (PNOA, Spanish National Plan for Aerial Ortophotography) using QGIS (Figure 1). The grasslands are abandoned at present without any livestock. Although we do not have any information about when the grasslands were abandoned, a comparison between two aerial photographs (1956 and 2017 from PNOA, Spanish National Plan for Aerial Ortophotography) showed that the forest surface increased over that period (see comparison in Appendix S1: Figure S1). The grasslands showed a decrease of 36,898 to 12,122 ha (a reduction of 67.2% in 61 years).

Grasslands studied in this Mediterranean altitudinal region are dominated by *A. castellana* (*Festuco amplae–Agrostion castellanae*, Mucina et al., 2016). This species has a broad territorial distribution in Mediterranean Spain,

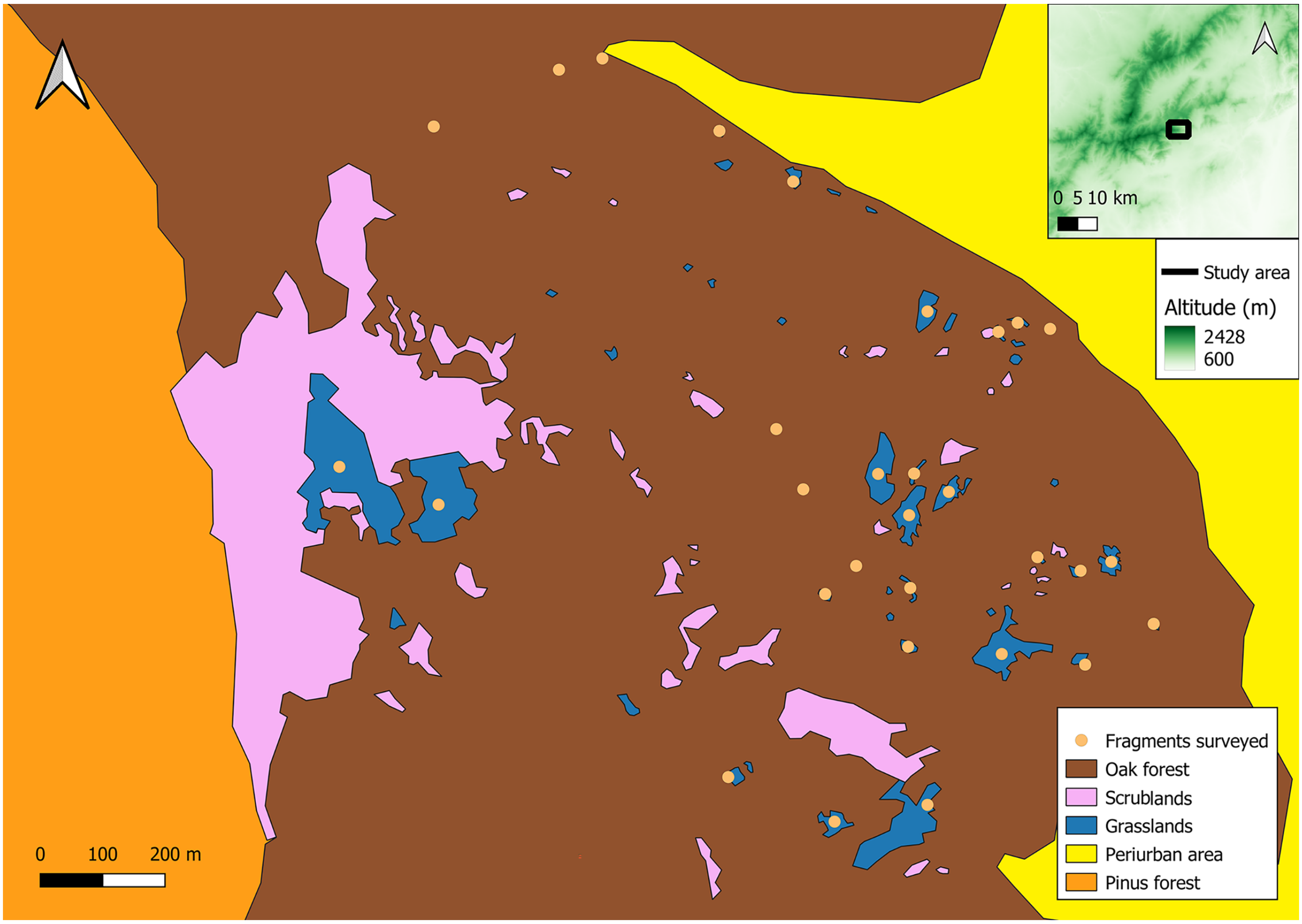

**FIGURE 1** Map of the habitats in the study area (−3.79345, 40.81289) and fragments surveyed.

showing a lower degree of hydromorphy than other related grassland communities, structured by *Arrhenaterum elatius* subsp. *bulbosum* (*Arrhenatherion elatioris*, Mucina et al., 2016). The development occurs in the ash mixed forest, with *Fraxinus angustifolia* and *Q. pyrenaica*, but also in the pure *Q. pyrenaica* forest and in the holm oak forests (*Quercus rotundifolia*). The phenological optimum of this species occurs at the beginning of summer. During this period, it is actively grazed by cattle and harvested for haymaking. By the end of summer, it dries out completely but regrows in autumn, although it does not produce stems. Thanks to its high productivity and the extensive distribution of *A. castellana*, it covers large areas. In zones with higher hydromorphism, *A. elatius* subsp. *bulbosum* becomes dominant, forming communities primarily managed for mowing. These communities differ from those dominated purely by *A. castellana* due to the presence of therophytes and the absence of hygrophilous species such as *Danthonia decumbens*, *Holcus lanatus*, or *Briza media*, among others. Intense livestock management or the use of fertilizers can lead to a shift toward grasslands dominated by *Poa bulbosa* or *Carex chaetophylla* (Sánchez-Mata et al., 2017).

We mapped the grassland fragments inside the forest using the 2017 aerial photographs. We visited all the fragments detected in the photographs to classify the fragments as scrublands or grasslands, as they can be confused in the aerial images. Grassland fragments were identified as open spaces without tree or shrub cover, where the predominant vegetation was herbaceous. In total, 50 fragments of grassland were mapped, from 100 to 20,000 $m^2$ (0.01–2 ha). The minimum distance separating a fragment from its nearest neighbor was 25 m. Fragments were classified into three categories according to their size: small, <250 $m^2$ (32 fragments); medium, 250–550 $m^2$ (8 fragments); and large, >1000 $m^2$ (10 fragments). To achieve a balanced survey among fragment sizes, vegetation surveys were carried out in 30 grassland fragments out of the 50 detected within the forest. We selected all the large (10 fragments) and medium (8 fragments) fragments. Among the smaller fragments, we selected 12 fragments that varied in size and distance from one another, to balance the survey with the rest of the categories. All herbaceous plant species in the fragments were estimated by a percentage cover (0%–100%) within plots (2 × 2 m) in each fragment. The number of plots in each fragment was established according to the fragment size: 1 for small, 5 for medium, and 10 for large, resulting in 152 plots across the 30 grassland fragments. Plots in medium and large fragments were distributed randomly, but with a minimum distance of 5 m between them and the edge of the forest (performed with QGIS program). The surveys were done once per plot in June 2020, and again in 2021, the peak season for grassland communities in this region.

The area of each grassland fragment (in square meters) was calculated, along with three measures of its landscape context: edge effect (perimeter/area ratio), percentage of grassland in a 500-m buffer around each fragment, and degree of connectivity with other areas of grassland in the system, based on the index developed by Hanski for the incidence function metapopulation model (Moilanen & Nieminen, 2002):

$$\mathrm{CI}_i = \sum \exp\left(-\alpha d_{ij}\right) A_j^{\beta}$$

where $A_j$ is the area of each fragment neighboring $j$ (in square meters), and $d_{ij}$ is the edge-to-edge distance (in meters) from the focal fragment $i$ to its neighboring fragment $j$. α is a species-specific parameter describing a species dispersal ability, and β is a parameter that describes the scaling of emigration by each fragment area. To be concordant with the radii used to estimate the proportion of habitat, we calculated Hanski's connectivity index with $\alpha = 2$ (average dispersal 500 m) and used $\beta = 0.5$, as recommended in Moilanen and Nieminen (2002).

We adopted *Flora iberica* as nomenclatural standard for vascular plants (Castroviejo, 2020). Plant species were classified into habitat preference groups according to the dominance values of EUNIS habitats classification level 2 in Chytrý et al. (2020) (see list of full species classification in Appendix S2: Table S1). We grouped them into five habitat preference groups. (1) Arable land and market gardens: fields of cereals and other forbs. These species groups are ruderals of arable or garden lands (hereafter referred as "Arable"). (2) Dry grasslands: dry lands dominated by grass or herbs, mostly not fertilized and with low productivity ("Dry"). (3) Mesic grasslands: lowland and montane mesotrophic and eutrophic pastures and hay meadows of the boreal, nemoral, warm-temperate humid and Mediterranean zones ("Mesic"). (4) Seasonally wet and wet grasslands: unimproved or lightly improved wet meadows and tall herb communities of the boreal, nemoral, warm-temperate humid, steppic and Mediterranean zones ("Mesic"). (5) Broadleaved deciduous forests and coniferous forests that we gathered in "Forest". We have also classified species according to their life form in therophytes (annuals); chamaephytes, hemicryptophytes and geophytes (perennials) (see list of full species classification in Appendix S2: Table S1). We classify the species by habitat preference group and life form as a way of characterizing the different strategies of the plant to the environmental requirements. Arable, Dry, Mesic and Wet habitat preference groups and annuals (therophytes) are favored by livestock presence and light availability. Arable, Dry and annuals also are indicators of drier grasslands, and Mesic, Wet and perennials (hemicryptophytes, geophytes, chamaephytes) are indicators of wetter grasslands. Forest group and geophytes are indicators of a community of forest vegetation.

Moreover, soil samples from the studied fragments were obtained on the same date. Five soil cores (7 cm in diameter and 20 cm in depth) per fragment were collected, and they were pooled into one sample. Roots and herbs were removed, and soil was air dried and sieved through a 2-mm mesh and then ground in a ball mill. The sieved soils were used for carbon and nitrogen concentration measurements. Soil carbon was measured as an indicator of forest succession, as it increases when tree cover impacts grasslands (Deng et al., 2013). Soil nitrogen was measured as an indicator of grazing activity, since livestock fertilize the ground (Proesmans et al., 2022). Finally, aspect and slope per fragment were taken from a Digital Terrain Model of 5-m resolution provided by the Spanish government (https://centrodedescargas.cnig.es/CentroDescargas/catalogo.do?Serie=LIDAR).

## Statistical analysis

The effects of fragmentation were analyzed using generalized linear mixed models (GLMMs) with richness as the response variable for every habitat preference group and life form (but we excluded chamaephytes since there were only two species in four plots) with a Poisson error distribution. As fixed effects, we tested the area of each fragment (as three categories: small, $<250$ m$^2$; medium, 250–550 m$^2$; large, $>1000$ m$^2$), percentage of buffer grassland and Hanski index (measures of the connectivity in the landscape), aspect (as a factor, north or south), the interaction between size and the rest of the predictors, slope (as a percentage), and nitrogen soil concentration (in milligrams per gram). To control for the repeated sampling of plots across dates (once per year = two surveys per plot in total), the year of survey nested in the plot was included as a random factor nested in the fragment. The relationships among the predictor effects were checked with Spearman correlations, and the edge effect and carbon soil concentration were not used since they have high positive and negative correlation, respectively, with the area (>0.8 Pearson correlation). The predictor variables were standardized, models were compared, and the best model according to the lowest Akaike information criterion (AIC) was selected. A post hoc Tukey's test was applied for pairwise comparisons between size fragments and aspect.

To test the effect of the fragmentation and quality variables on the species composition of the fragments, a redundancy analysis (RDA) was applied, and a test of significance of all constrained axes was performed using a Monte Carlo permutation test with 999 unrestricted permutations. Species abundance coverage data for RDA were square-root transformed at the plot scale to minimize the effects of dominant species. Predictor variables (fragment area, buffer, Hanski index, aspect, slope, nitrogen concentration in soil) were standardized, and the most significant were selected using a forward selection procedure, adding new variables following the order of their decreasing eigenvalues until the variables were nonsignificant ($p > 0.05$). We applied the RDA to learn the role of predictor variables in the community changes in the fragments. The retained variables in RDA were analyzed with a permutational multivariate ANOVA (PERMANOVA) based on the Bray–Curtis dissimilarity index, with 999 permutations for each predictor variable to determine the percentage of variance explained in the species composition. PERMANOVA pairwise multilevel comparisons were conducted to assess differences among fragment sizes in plant composition.

Statistical analyses were conducted with R (version R 4.1.0) and packages *lme4* (Bates et al., 2014) to test GLMMs, *MuMln* (Barton, 2016) for model comparison, and *vegan* (Oksanen et al., 2019) for RDA and PERMANOVA were used.

# RESULTS

We recorded a total number of 106 herbaceous plant species, of which 10 belonged to Arable, 38 Dry, 25 Mesic, 11 Wet, and 22 to Forest group; 39 were therophytes, 56 hemicryptophytes, 9 geophytes, and 2 were chamaephytes (in total 39 annuals and 67 perennials). Therophytes (annuals) were 9% of the Wet, 20% of the Mesic, 60% of the Dry, and 80% of the Arable group. Hemicryptophytes (perennials) were 34% of the Dry group, 59% of the Forest, 72% of the Mesic, and 90% of the Wet. Geophytes (perennials) were 27% of the Forest group.

Large and medium fragment sizes had higher species richness but were followed closely by smaller fragments (Table 1). Overall, the Dry group had the highest species richness, followed by Mesic and Wet. Arable and Forest groups were the poorest (Figure 2). When examined by fragment size, the Dry group is the richest in medium and larger fragments, while Wet and Mesic groups were richest in the smaller fragments. The Dry group is richest in south aspect fragments, whereas the rest of the groups have similar richness. Large fragments had a higher percentage of richness and abundance cover for the Dry and Mesic groups (Figure 3A,B). Dry group percentage of richness increased with fragment size, while abundance remained stable. Arable, Mesic and Wet groups had similar richness and percent cover across fragment sizes. The Forest group

**TABLE 1** Summary of the average and SD of richness of plant species (plot size of 4 $m^2$) and field variables per fragment size (number of fragments in parentheses).

| Variable | Small (12) | Medium (8) | Large (10) |
|---|---|---|---|
| Total plant richness | 13.38 ± 5.01 | 15.88 ± 5.24 | 15.86 ± 6.07 |
| Area ($m^2$) | 142.83 ± 42.93 | 378.73 ± 110.11 | 5230.44 ± 5927.54 |
| Buffer (%) | 1.86 ± 1.65 | 3.5 ± 1.65 | 3.02 ± 1.1 |
| Edge | 0.36 ± 0.06 | 0.26 ± 0.1 | 0.12 ± 0.05 |
| Hanski index | 85.36 ± 32.71 | 98.83 ± 43.19 | 119.07 ± 38.68 |
| Carbon soil (mg/g) | 61.2 ± 6.79 | 44.37 ± 15.01 | 36.75 ± 10.27 |
| Nitrogen soil (mg/g) | 4.6 ± 0.11 | 3.85 ± 1.15 | 4.24 ± 1.22 |
| Aspect (°) | 73.25 ± 32 | 108.48 ± 34.33 | 107.89 ± 29.4 |
| Slope (%) | 14.99 ± 4.55 | 11.98 ± 2.61 | 11.46 ± 4.27 |

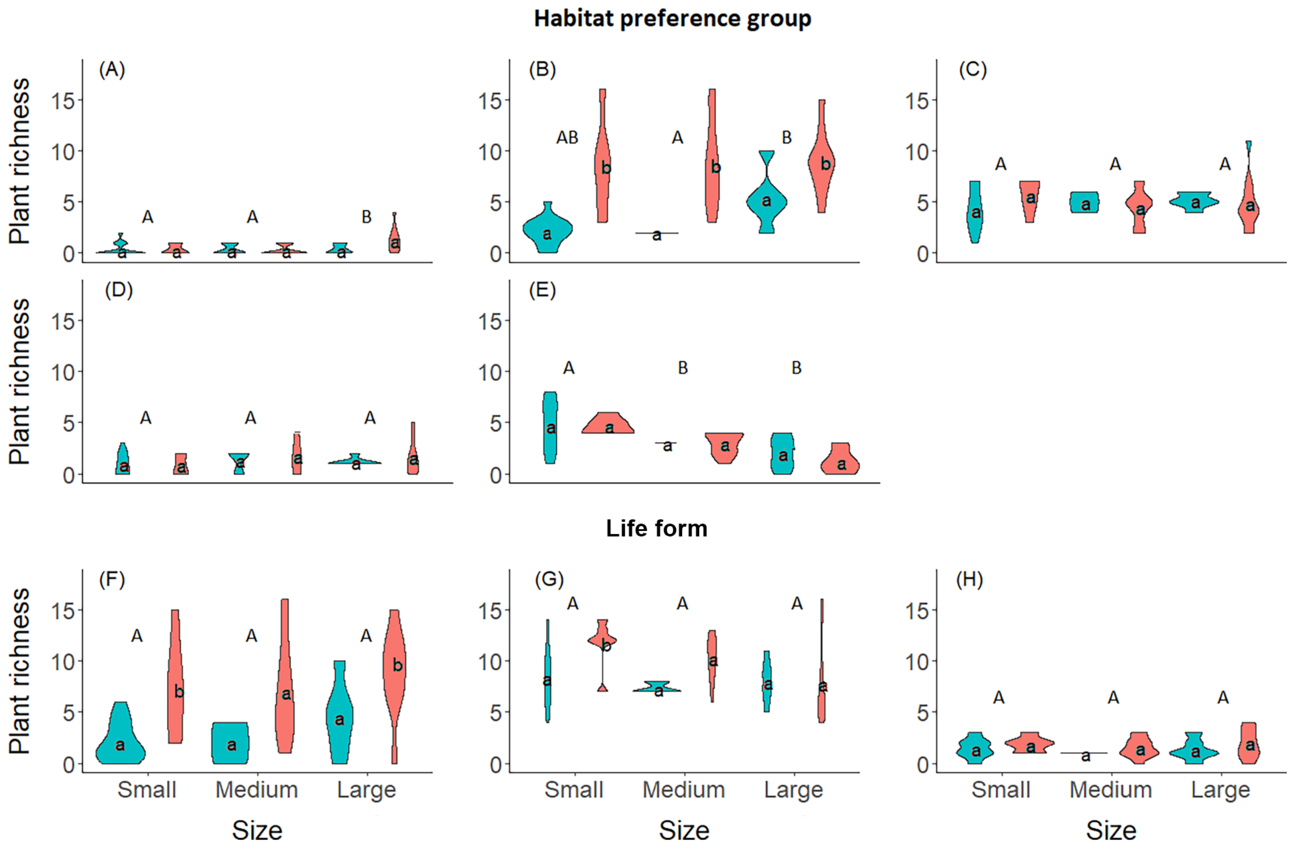

**FIGURE 2** Mean species richness per fragment size and aspect (blue: north, red: south), by habitat preference group: (A) Arable, (B) Dry, (C) Mesic, (D) Wet, (E) Forest; and by life form: (F) Therophyte, (G) Hemicryptophyte, (H) Geophyte. We excluded chamaephytes from the analyses. Different letters denote significant differences ($p < 0.05$) among fragment sizes (A, B, C) and aspect (a, b, c) after Tukey's test.

had the highest richness and abundance in the smallest fragments, decreasing with increasing fragment size. Therophytes make up almost half of the species richness in larger fragments, with descending richness in smaller fragments (Figure 3C). However, hemicryptophytes were more abundant than therophytes in larger fragments, with their abundance increasing in smaller fragments (Figure 3D). Geophytes and chamaephytes (perennials) had the lowest richness and abundance. Geophyte values were similar across fragment sizes, while chamaephyte values were similar in small and medium fragments but absent in large fragments.

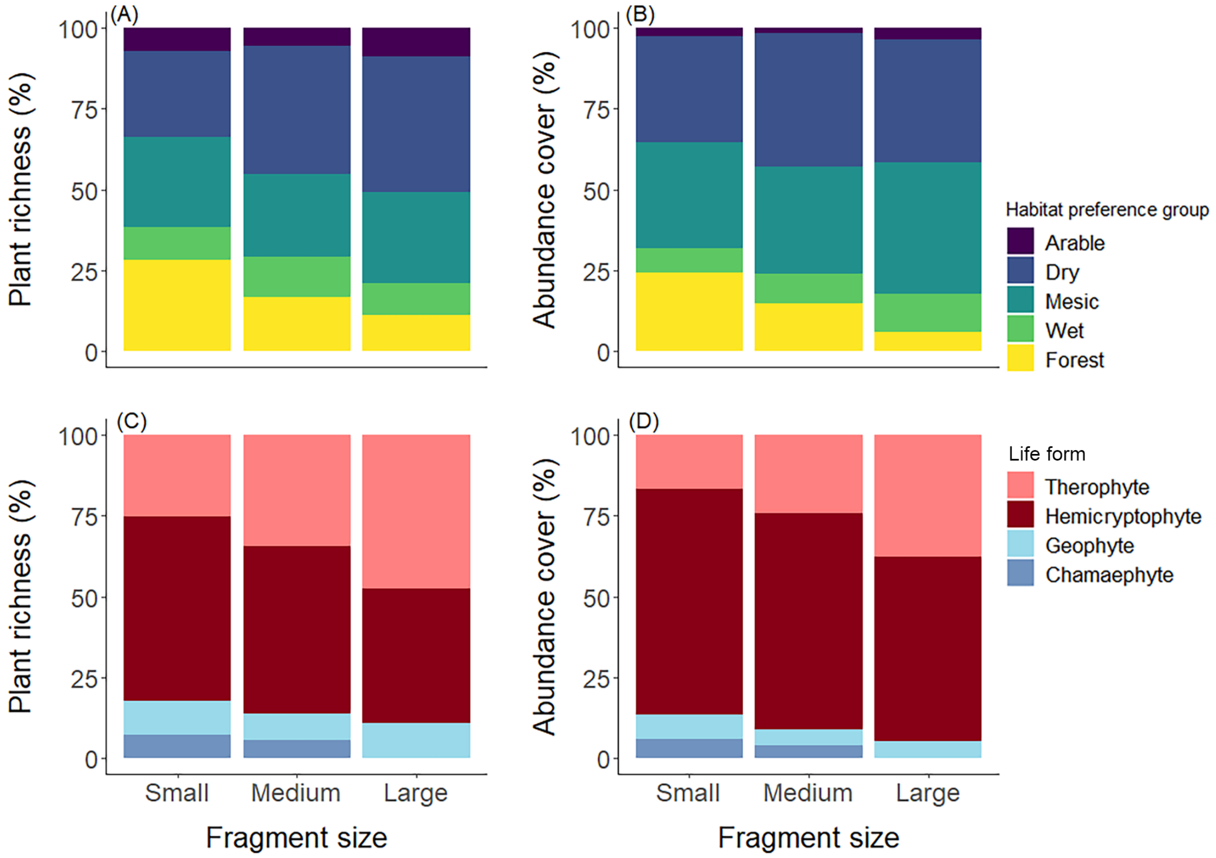

**FIGURE 3** Percentage of (A, C) richness and (B, D) abundance cover of habitat preference group and life form by fragment size.

## Fragmentation analysis

Buffer percentage and Hanski index were lower, while edge effect was greater, in the smallest fragments (Table 1). Soil carbon concentration was greater in the smallest fragments, decreasing with increasing fragment size. Nitrogen concentration in soil did not differ among fragments. Aspect and slope did not show a big difference among fragments, although the aspect in smaller fragments is more oriented to the north (<90°).

GLMMs indicated that fragment size is a predictor of richness in Arable and Forest groups and hemicryptophytes (perennials) species (Table 2). Connectivity variables (Buffer and Hanski index) and soil nitrogen did not significantly affect the richness in any habitat preference group or life form. Smaller fragments had a negative effect on species richness in the Arable group and a positive effect in the Forest group and for hemicryptophyte species. The north aspect had a negative effect on species richness for therophytes (annuals), and there was an interaction effect between aspect and fragment size on the Dry group. The Tukey test showed no significant differences in plant richness among fragment sizes within the Wet and Mesic groups. However, differences were found in the Dry group and between small/medium versus larger fragments in the Arable group and large/medium versus smaller in the Forest group (Figure 2). There were no significant differences in richness between north and south aspects for fragment sizes, except for the Dry group, which had the highest richness in south aspect fragments. The Tukey test showed no significant differences in richness among fragment sizes for any of the life forms. But there were significant differences in richness/aspect for the therophytes (highest in south aspect) and for hemicryptophytes (highest in south aspect) in the smaller fragments. Slope had a negative effect on Dry and Mesic groups and hemicryptophyte species but a positive effect on the Forest group, although the *p* value was lower than the rest of the predictors. Geophytes (perennials) were not affected by the predictor variables.

## Community analysis

The RDA model had a 20.55 $R^2$ total and 13.78 $R^2$ adjusted, and it was significant ($p < 0.001$; Figure 4). Aspect, fragment size, and buffer were the predictor

**TABLE 2** Results of the lowest Akaike information criterion (AIC), marginal ($R^2{}_m$) and conditional ($R^2{}_c$) generalized linear mixed models testing for effects of fragmentation of fragment size (Size), buffer, Hanski index (Index) and quality habitat of slope, aspect, and soil nitrogen (Nitrogen) for the richness of the habitat preference groups and life forms.

| | Habitat preference group | | | | | Life form | | |
|---|---|---|---|---|---|---|---|---|
| **Response variable** | **Arable** | **Dry** | **Mesic** | **Wet** | **Forest** | **Therophyte** | **Hemicryptophyte** | **Geophyte** |
| Size (small) | −0.27* | | | | 0.44*** | | 0.14* | |
| Aspect (north) | | | | | | −0.55*** | | |
| Size × Aspect | | −0.09** | | | | | | |
| Buffer | | | | | | | | |
| Index | | | | | | | | |
| Slope | | −0.17* | −0.16* | ns | 0.18* | | −0.12* | |
| Nitrogen | | | | | | | ns | |
| AIC | 97.66 | 244.74 | 208.77 | 156.01 | 191.07 | 284.82 | 253.32 | 150.46 |
| $R^2{}_m$ | 15 | 51 | 10 | 7 | 47 | 41 | 20 | |
| $R^2{}_c$ | 17 | 61 | 12 | 9 | 62 | 72 | 24 | |

*Note*: For each model effect, coefficient and significance levels (ns > 0.05, $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$) of the variables retained in the best model by AIC are displayed.

variables retained in the RDA model. Large and medium fragments followed the first axis, and the south aspect the second, with a positive effect of the buffer variable in the first axis. PERMANOVA showed that the fragment size explained 14.26% ($p < 0.001$), aspect 5.84% ($p < 0.001$) and buffer 3.80% ($p < 0.02$) of the community variation, and the pairwise multilevel comparisons indicated that the large and small fragments, as well as large with medium, were significantly different respectively ($p = 0.001$, $p = 0.003$), but not small with medium ($p = 0.072$).

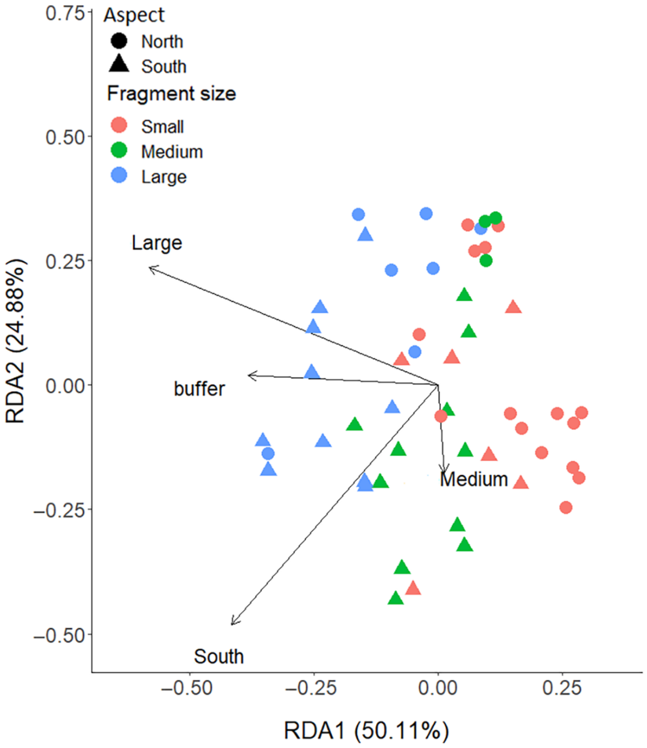

**FIGURE 4** Redundancy analysis (RDA) plot of the first two axes and their percentage of variance explained for the three sizes of grassland fragment groups. Only those variables extracted through Monte Carlo forward analysis are represented.

# DISCUSSION

## Fragmentation variable effects on grassland richness

This work shows the impact of fragmentation on grassland communities. Total species richness is very similar among fragment sizes but differs in plant composition. The total average richness is similar to other vegetation studies at matching altitudes in Sierra de Guadarrama (Pilar Rodríguez-Rojo & Sánchez-Mata, 2004; Rodríguez-Rojo and Sánchez-Mata, 2006). Annual species are more predominant in warmer and drier environments than perennials (Mesic, Wet, and Forest groups) in Mediterranean grasslands (Montalvo et al., 1993; Reed et al., 2021). These Mediterranean annual species avoid the summer drought and warm temperatures, blooming in spring and drying up in summer (Madon & Médail, 1997). Forest surrounding the smaller fragments can decrease the microclimate temperature and increase the relative humidity (Abd Latif & Blackburn, 2010). Thus, a drier environment is expected in larger fragments that favored annual plants, in comparison with smaller ones. Although Mediterranean annual species can persist when the landscape undergoes abandonment of traditional uses (Molina et al., 2023), Arable and Dry groups can be more sensitive to fragment size when the forest recovers and develops, altering environmental conditions due to reduced light and colder and wetter soils (van der Kamp et al., 2009). However, annual species can persist in smaller fragments even when the surrounding forest modifies environmental conditions, with a drier and warmer microclimate similar to that found on southern aspects. The northern aspect in Mediterranean mountains favors the growth of the forest due to lower stress caused by soil drought and high temperature (Améztegui et al., 2010). In contrast, the Mesic and Wet groups did not show differences in richness among fragment sizes or aspects. They are mainly conformed by hemicryptophytes (perennials) species, the predominant life form in the mid-mountain Mediterranean grasslands (Pilar Rodríguez-Rojo & Sánchez-Mata, 2004). Hemicryptophytes are also the predominant life form in the forest. Therefore, these species can be considered habitat generalists at this altitude since they can live in both grasslands and forest habitats, and the fragmentation effects of size or isolation are null or weak.

Connectivity variables did not affect the richness of different groups. Although the distance of seed herbaceous dispersion is usually very low (Soons & Ozinga, 2005), the short distance among fragments cannot be a problem for the dispersion of seeds within the forest. Therefore, the landscape configuration or meta-community dynamics are not a problem at this scale of study (Fahrig, 2013). Nevertheless, although species can reach the fragments, the grassland communities are filtered by environmental conditions such as light and soil characteristics. The smaller fragments have less availability of light due to the forest surrounding them, which modifies the grassland composition (Niu et al., 2016), and we expect their reduction to favor the perennial or wetter species. A null or weak effect of the fragment size or connectivity on grassland plant species has been observed for both specialist and generalist species at a regional scale (Gallé et al., 2022). However, we observed that fragment size affected the richness of the Arable, Dry, and Forest groups and the microenvironmental condition (south aspect) favored annual species. It points out that fragment size has a greater effect at a finer scale than regional scale due to changes in environmental and ecosystem properties at those scales.

## Soil properties

Soil carbon is higher in smaller fragments. The fall of leaves and branches of forest trees surrounding the grasslands raises the organic matter input and increases the soil carbon. This plant litter decomposition creates soil organic matter (Austin & Ballaré, 2010). Therefore, the evolution of grasslands into forests increases soil carbon during vegetation succession (Risch et al., 2008; van der Kamp et al., 2009; Deng et al., 2013; but see Guidi et al., 2014). This pattern in younger forests after the abandonment of grasslands has been observed previously in Mediterranean deciduous forest mountains (Alberti et al., 2008). This increase is also due to the edge effect of the surrounding forest that has been detected in the first maturation levels of forests (Risch et al., 2008; van der Kamp et al., 2009). This shows that the trees surrounding the grasslands can increase the soil carbon before the colonization of shrubs or trees if the fragment size is small enough and leaves and branches cover the fragment. Soil nitrogen did not show variation among size fragments, in contrast with other studies of abandoned grasslands in which the amount of soil nitrogen decreased (Alberti et al., 2008; Guidi et al., 2014).

## Fragmentation variable effects on grassland communities

The grassland composition showed a difference between small and medium versus large fragments, but not between small and medium. They are dominated by perennial species rather than large fragments (Figure 3C,D), indicating a threshold for species composition change at 500 $m^2$. The RDA plot showed an interaction between size and aspect, with large southern aspect fragments closer to small southern aspect fragments and the opposite for the northern aspect fragments. A greater composition of shade-tolerant perennial species has been observed in cleared abandoned forests (Lanta et al., 2019). The reduction in size modifies environmental conditions and ecosystem properties such as light and humidity when grasslands become very small. However, southern aspect can mitigate the environmental change with a drier and warmer microclimate. The buffer of grasslands showed weak positive effects on larger fragments. The lack of connectivity may disserve the open grassland communities (annual and drier species), but the variance explained was low.

## Limitations

Past landscape may better explain diversity than the present landscape due to extinction debt (Krauss et al., 2010). In this work, we did not have information about when livestock abandoned the territory. Grassland plant specialists are more sensitive to the past landscape than generalists due to the loss of connectivity in the past rather than a decrease in area (Krauss et al., 2010; Deák et al., 2021). Extinction debt in grassland plant specialists can be a long-term process, as extinction debt has been observed 40–100 years after a significant loss in grassland area and connectivity (Bommarco et al., 2014; Deák et al., 2021). We did not observe an effect of connectivity in our results, but the loss of connectivity in the past could affect present grassland diversity. Despite these limitations due to the lack of historical data, the current effects of fragmentation by area highlight the importance of analyzing fragmentation in Mediterranean mountain grasslands.

# CONCLUSIONS

From a conservation perspective, forest management can affect the conservation of grasslands, but only contrarily to the succession of grassland-forest community. This study shows how the richness of grassland species does not decrease with the reduction of fragment size or isolation, but it does with the composition favoring wetter and perennials and the decrease of drier and annual species (Hypotheses 1 and 2). Landscape connectivity is not a problem for the conservation of grasslands at a fine scale (Hypothesis 3); it does not require a mosaic of fragments or maintaining them in big sizes (medium fragments being approximately 250–500 $m^2$). Although perennial or wetter species are not affected by the fragmentation, annual or drier species suffer a reduction when the fragment is small or medium (less than 500 $m^2$). This work shows that annual or drier species can remain in those grasslands after the abandonment of traditional uses, probably because they are an important contingent of biodiversity in Mediterranean landscapes, being indicators of earlier succession in Mediterranean grasslands (Molina et al., 2023). However, the size of the fragment can modify the environmental conditions and improve or disserve their abundance and richness. Contrarily, the increase of fringe forest species and carbon soil in smaller grasslands is an indicator of their transformation into forests. Therefore, the conservation of grassland plant species in the area requires maintaining a minimum size of fragments (medium or large fragments are better), either with livestock or by clearing the forest.

## AUTHOR CONTRIBUTIONS

Jesús Sánchez Dávila contributed to the study conception and design with the help of Daniel Sánchez-Mata. Data preparation and data collection were performed by Jesús Sánchez Dávila and Daniel Sánchez-Mata. Data analyses were performed by Jesús Sánchez Dávila under the supervision of Rosario G. Gavilán. The manuscript was written by Jesús Sánchez Dávila with the help of Rosario G. Gavilán. All authors read and approved the final manuscript.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data (Sánchez Dávila, 2025) are available from Zenodo: https://doi.org/10.5281/zenodo.15854126.

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## REFERENCES

Abd Latif, Z., and G. A. Blackburn. 2010. "The Effects of Gap Size on Some Microclimate Variables during Late Summer and Autumn in a Temperate Broadleaved Deciduous Forest." *International Journal of Biometeorology* 54: 119–129.

Alberti, G., A. Peressotti, P. Piussi, and G. Zerbi. 2008. "Forest Ecosystem Carbon Accumulation during a Secondary Succession in the Eastern Prealps of Italy." *Forestry: An International Journal of Forest Research* 81: 1–11.

Améztegui, A., L. Brotons, and L. Coll. 2010. "Land-Use Changes as Major Drivers of Mountain Pine (*Pinus uncinata* Ram.) Expansion in the Pyrenees." *Global Ecology and Biogeography* 19: 632–641.

Austin, A. T., and C. L. Ballaré. 2010. "Dual Role of Lignin in Plant Litter Decomposition in Terrestrial Ecosystems." *Proceedings of the National Academy of Sciences of the United States of America* 107: 4618–22.

Barton, K. MuMIn: Multi-Model Inference. R Package Version 1.46.0.2022. https://CRAN.R-project.org/package=MuMIn

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2014. "Fitting Linear Mixed-Effects Models using lme4." arXiv.

Bergmeier, E., J. Petermann, and E. Schröder. 2010. "Geobotanical Survey of Wood-Pasture Habitats in Europe: Diversity, Threats and Conservation." *Biodiversity and Conservation* 19: 2995–3014.

Bommarco, R., R. Lindborg, L. Marini, and E. Öckinger. 2014. "Extinction Debt for Plants and Flower-Visiting Insects in Landscapes with Contrasting Land Use History." *Diversity and Distributions* 20(5): 591–99 Portico. https://doi.org/10.1111/ddi.12187.

Brantley, S. T., and D. R. Young. 2009. “Contribution of Sunflecks Is Minimal in Expanding Shrub Thickets Compared to Temperate Forest.” *Ecology* 90: 1021–29.

Bruun, H. H. 2000. “Deficit in Community Species Richness as Explained by Area and Isolation of Sites.” *Diversity and Distributions* 6: 129–135.

Bullock, J. M. 2000. “Gaps and Seedling Colonization.” In *Seeds: The Ecology of Regeneration in Plant Communities*, edited by M. Fenner, 375–395. Wallingford: CABI Publishing.

Cadotte, M. W. 2006. “Dispersal and Species Diversity: A Meta-Analysis.” *The American Naturalist* 167: 913–924.

Castroviejo, S. 2020. *Flora ibérica: plantas vasculares de la Península Ibérica e Islas Baleares* 1–784, Madrid: Real Jardín Botánico, CSIC.

Chauchard, S., C. Carcaillet, and F. Guibal. 2007. “Patterns of Land-Use Abandonment Control Tree-Recruitment and Forest Dynamics in Mediterranean Mountains.” *Ecosystems* 10: 936–948.

Chytrý, M., L. Tichý, S. M. Hennekens, I. Knollová, J. A. M. Janssen, J. S. Rodwell, T. Peterka, et al. 2020. “EUNIS Habitat Classification: Expert System, Characteristic Species Combinations and Distribution Maps of European Habitats.” *Applied Vegetation Science* 23: 648–675.

Cole, P. G., and J. F. Weltzin. 2005. “Light Limitation Creates Patchy Distribution of an Invasive Grass in Eastern Deciduous Forests.” *Biological Invasions* 7: 477–488.

Cousins, S. A. O., and R. Lindborg. 2008. “Remnant Grassland Habitats as Source Communities for Plant Diversification in Agricultural Landscapes.” *Biological Conservation* 141: 233–240.

Dainese, M., J. Lepš, and F. de Bello. 2015. “Different Effects of Elevation, Habitat Fragmentation and Grazing Management on the Functional, Phylogenetic and Taxonomic Structure of Mountain Grasslands.” *Perspectives in Plant Ecology, Evolution and Systematics* 17: 44–53.

Deák, B., Á. Bede, Z. Rádai, B. Tóthmérész, P. Török, D. Nagy, A. Torma, et al. 2021. “Different Extinction Debts among Plants and Arthropods after Loss of Grassland Amount and Connectivity.” *Biological Conservation* 264: 109372. https://doi.org/10.1016/j.biocon.2021.109372.

Deng, L., K.-B. Wang, M.-L. Chen, Z.-P. Shangguan, and S. Sweeney. 2013. “Soil Organic Carbon Storage Capacity Positively Related to Forest Succession on the Loess Plateau, China.” *Catena* 110: 1–7.

Erdős, L., G. Kröel-Dulay, Z. Bátori, B. Kovács, C. Németh, P. J. Kiss, and C. Tölgyesi. 2018. “Habitat Heterogeneity as a Key to High Conservation Value in Forest-Grassland Mosaics.” *Biological Conservation* 226: 72–80.

Ewers, R. M., and R. K. Didham. 2006. “Confounding Factors in the Detection of Species Responses to Habitat Fragmentation.” *Biological Reviews* 81: 117–142.

Fahrig, L. 2013. “Rethinking Patch Size and Isolation Effects: The Habitat Amount Hypothesis.” *Journal of Biogeography* 40: 1649–63.

Flinn, K. M., and M. Vellend. 2005. “Recovery of Forest Plant Communities in Post-Agricultural Landscapes.” *Frontiers in Ecology and the Environment* 3: 243–250.

Gallé, R., D. Korányi, C. Tölgyesi, T. Lakatos, F. Marcolin, E. Török, K. Révész, et al. 2022. “Landscape-Scale Connectivity and Fragment Size Determine Species Composition of Grassland Fragments.” *Basic and Applied Ecology* 65: 39–49.

Goldberg, D. E., and P. A. Werner. 1983. “The Effects of Size of Opening in Vegetation and Litter Cover on Seedling Establishment of Goldenrods (*Solidago* spp.).” *Oecologia* 60: 149–155.

Guidi, C., L. Vesterdal, D. Gianelle, and M. Rodeghiero. 2014. “Changes in Soil Organic Carbon and Nitrogen Following Forest Expansion on Grassland in the Southern Alps.” *Forest Ecology and Management* 328: 103–116.

Gustavsson, E., T. Lennartsson, and M. Emanuelsson. 2007. “Land Use More than 200 Years Ago Explains Current Grassland Plant Diversity in a Swedish Agricultural Landscape.” *Biological Conservation* 138: 47–59.

Hanski, I. 2015. “Habitat Fragmentation and Species Richness.” *Journal of Biogeography* 42(5): 989–993 Portico. https://doi.org/10.1111/jbi.12478.

Kaligarič, M., M. Culiberg, and B. Kramberger. 2006. “Recent Vegetation History of the North Adriatic Grasslands: Expansion and Decay of an Anthropogenic Habitat.” *Folia Geobotanica* 41: 241–258.

Kirby, K. J., and C. Watkins. 1998. *Ecological History of European Forests*. Wallingford: CAB International.

Köchy, M., and H. Rydin. 1997. “Biogeography of Vascular Plants on Habitat Islands, Peninsulas and Mainlands in an Eascentral Swedish Agricultural Landscape.” *Nordic Journal of Botany* 17: 215–223.

Krahulec, F., H. Skálová, T. Herben, V. Hadincová, R. Wildová, and S. Pecháčková. 2001. “Vegetation Changes Following Sheep Grazing in Abandoned Mountain Meadows.” *Applied Vegetation Science* 4: 97–102.

Krauss, J., A.-M. Klein, I. Steffan-Dewenter, and T. Tscharntke. 2004. “Effects of Habitat Area, Isolation, and Landscape Diversity on Plant Species Richness of Calcareous Grasslands.” *Biodiversity and Conservation* 13: 1427–39.

Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R. K., Helm, A., Kuussaari, M., Lindborg, R., et al. (2010). “Habitat Fragmentation Causes Immediate and Time-Delayed Biodiversity Loss at Different Trophic Levels.” *Ecology Letters*, 13(5), 597–605. Portico. https://doi.org/10.1111/j.1461-0248.2010.01457.x

Lanta, V., O. Mudrák, P. Liancourt, M. Bartoš, Z. Chlumská, M. Dvorský, Z. Pusztaiová, et al. 2019. “Active Management Promotes Plant Diversity in Lowland Forests: A Landscape-Scale Experiment with Two Types of Clearings.” *Forest Ecology and Management* 448: 94–103.

Levine, J. M., and D. J. Murrell. 2003. “The Community-Level Consequences of Seed Dispersal Patterns.” *Annual Review of Ecology, Evolution, and Systematics* 34: 549–574.

MacDonald, D., J. R. Crabtree, G. Wiesinger, T. Dax, N. Stamou, P. Fleury, J. Gutierrez Lazpita, and A. Gibon. 2000. “Agricultural Abandonment in Mountain Areas of Europe: Environmental Consequences and Policy Response.” *Journal of Environmental Management* 59: 47–69.

Madon, O., and F. Médail. 1997. “The Ecological Significance of Annuals on a Mediterranean Grassland (Mt Ventoux, France).” *Plant Ecology* 129: 189–199.

Martens, S. N., D. D. Breshears, and C. W. Meyer. 2000. “Spatial Distributions of Understory Light along the Grassland/Forest Continuum: Effects of Cover, Height, and Spatial Pattern of Tree Canopies.” *Ecological Modelling* 126(1): 79–93. https://doi.org/10.1016/s0304-3800(99)00188-x.

Moilanen, A., and M. Nieminen. 2002. "Simple Connectivity Measures in Spatial Ecology." *Ecology* 83: 1131–45.

Molina, J. A., J. P. Martín-Sanz, I. Valverde-Asenjo, A. Sánchez-Jiménez, and J. R. Quintana. 2023. "Mediterranean Grassland Succession as an Indicator of Changes in Ecosystem Biodiversity and Functionality." *Biodiversity and Conservation* 32: 95–118.

Montalvo, J., M. A. Casado, C. Levassor, and F. D. Pineda. 1993. "Species Diversity Patterns in Mediterranean Grasslands." *Journal of Vegetation Science* 4: 213–222.

Mucina, L., H. Bültmann, K. Dierßen, J.-P. Theurillat, T. Raus, A. Čarni, K. Šumberová, et al. 2016. "Vegetation of Europe: Hierarchical Floristic Classification System of Vascular Plant, Bryophyte, Lichen, and Algal Communities." *Applied Vegetation Science* 19: 3–264.

Naaf, T., and M. Wulf. 2007. "Effects of Gap Size, Light and Herbivory on the Herb Layer Vegetation in European Beech Forest Gaps." *Forest Ecology and Management* 244: 141–49.

Navarro, L. M., and H. M. Pereira. 2012. "Rewilding Abandoned Landscapes in Europe." *Ecosystems* 15: 900–912.

Niu, K., J.-S. He, S. Zhang, and M. J. Lechowicz. 2016. "Grazing Increases Functional Richness but Not Functional Divergence in Tibetan Alpine Meadow Plant Communities." *Biodiversity and Conservation* 25: 2441–52.

Norris, C., P. Hobson, and P. L. Ibisch. 2011. "Microclimate and Vegetation Function as Indicators of Forest Thermodynamic Efficiency." *Journal of Applied Ecology* 49(3): 562–570 Portico. https://doi.org/10.1111/j.1365-2664.2011.02084.x.

Öckinger, E., R. Lindborg, N. E. Sjödin, and R. Bommarco. 2012. "Landscape Matrix Modifies Richness of Plants and Insects in Grassland Fragments." *Ecography* 35(3): 259–267 Portico. https://doi.org/10.1111/j.1600-0587.2011.06870.x.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R.B., Simpson, G. L., and Solymos, P., Vegan: Community Ecology Package; R Package 2.5-6; 2019; https://github.com/vegandevs/vegan

Petanidou, T., T. Kizos, and N. Soulakellis. 2008. "Socioeconomic Dimensions of Changes in the Agricultural Landscape of the Mediterranean Basin: A Case Study of the Abandonment of Cultivation Terraces on Nisyros Island, Greece." *Environmental Management* 41: 250–266.

Pilar Rodríguez-Rojo, M., and D. Sánchez-Mata. 2004. "Mediterranean Hay Meadow Communities: Diversity and Dynamics in Mountain Areas throughout the Iberian Central Range (Spain)." *Biodiversity and Conservation* 13: 2361–80.

Proesmans, W., C. Andrews, A. Gray, R. Griffiths, A. Keith, U. N. Nielsen, D. Spurgeon, R. Pywell, B. Emmett, and A. J. Vanbergen. 2022. "Long-Term Cattle Grazing Shifts the Ecological State of Forest Soils." *Ecology and Evolution* 12(4) Portico. https://doi.org/10.1002/ece3.8786.

Reed, P. B., L. E. Pfeifer-Meister, B. A. Roy, B. R. Johnson, G. T. Bailes, A. A. Nelson, and S. D. Bridgham. 2021. "Introduced Annuals Mediate Climate-Driven Community Change in Mediterranean Prairies of the Pacific Northwest, USA." *Diversity and Distributions* 27: 2584–95.

Risch, A. C. R. C., M. F. J. F. Jurgensen, D. S. P.-D. S. Page-Dumroese, O. W. Wildi, and M. S. Schütz. 2008. "Long-Term Development of Above- and Below-Ground Carbon Stocks Following Land-Use Change in Subalpine Ecosystems of the Swiss National Park." *Canadian Journal of Forest Research* 38: 1590–1602.

Rodríguez-Rojo, M. P., and D. Sánchez-Mata. 2006. "Hay Meadow Communities (Arrhenatherion Koch 1926) Throughout the Iberian Central Range (Spain)." *Phytocoenologia* 36(2): 231–246. https://doi.org/10.1127/0340-269x/2006/0036-0231.

Römermann, C., M. Bernhardt-Römermann, M. Kleyer, and P. Poschlod. 2009. "Substitutes for Grazing in Semi-Natural Grasslands – Do Mowing or Mulching Represent Valuable Alternatives to Maintain Vegetation Structure?" *Journal of Vegetation Science* 20: 1086–98.

Roschewitz, I., D. Gabriel, T. Tscharntke, and C. Thies. 2005. "The Effects of Landscape Complexity on Arable Weed Species Diversity in Organic and Conventional Farming." *Journal of Applied Ecology* 42: 873–882.

Sánchez Dávila, J. 2025. "Field Data for 'Effects of Landscape Fragmentation at a Fine Scale on Mediterranean Mountain Grassland Plant Diversity'." Dataset. Zenodo. https://doi.org/10.5281/zenodo.15854127.

Sánchez-Mata, D., R. G. Gavilán, and V. de la Fuente. 2017. "The Sistema Central (Central Range)." In *The Vegetation of the Iberian Peninsula*, Vol. 1, edited by J. Loidi, 549–588. Cham: Springer International Publishing.

Sebek, P., R. Bace, M. Bartos, J. Benes, Z. Chlumska, J. Dolezal, M. Dvorsky, et al. 2015. "Does a Minimal Intervention Approach Threaten the Biodiversity of Protected Areas? A Multi-Taxa Short-Term Response to Intervention in Temperate Oak-Dominated Forests." *Forest Ecology and Management* 358: 80–89.

Sluiter, R., and S. M. de Jong. 2007. "Spatial Patterns of Mediterranean Land Abandonment and Related Land Cover Transitions." *Landscape Ecology* 22: 559–576.

Soons, M. B., and W. A. Ozinga. 2005. "How Important Is Long-Distance Seed Dispersal for the Regional Survival of Plant Species?" *Diversity and Distributions* 11: 165–172.

van der Kamp, J., I. Yassir, and P. Buurman. 2009. "Soil Carbon Changes upon Secondary Succession in Imperata Grasslands (East Kalimantan, Indonesia)." *Geoderma* 149: 76–83.

Warren, B. H., D. Simberloff, R. E. Ricklefs, R. Aguilée, F. L. Condamine, D. Gravel, H. Morlon, et al. 2015. "Islands as Model Systems in Ecology and Evolution: Prospects Fifty Years After MacArthur-Wilson." *Ecology Letters* 18(2): 200–217 Portico. https://doi.org/10.1111/ele.12398.

Williams, N. S. G., J. W. Morgan, M. A. McCarthy, and M. J. McDonnell. 2006. "Local Extinction of Grassland Plants: The Landscape Matrix Is More Important than Patch Attributes." *Ecology* 87: 3000–3006.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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