

How mowing restores montane Mediterranean grasslands following cessation of traditional livestock grazing

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This is an Accepted Manuscript of an article published by Elsevier in Agriculture, Ecosystems and Environment on 15 June 2020, available at:

<https://www.sciencedirect.com/science/article/pii/S0167880920300657?via%3Dihub>

<https://doi.org/10.1016/j.agee.2020.106880>

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Abstract

Traditional land-use cessation allows the spread of invasive tall-grass species and thus leads to a reduction in grassland biodiversity. We hypothesized that long-term multi-year mowing of invaded grassland fosters the recovery of its taxonomic diversity and functional composition by reducing the dominance of the tall grass species *Brachypodium rupestre*, and that this change increases the pasture feed value. In 2010, we fenced part of a grassland, abandoned for about 30 years, invaded by *Brachypodium rupestre* (1 hectare) in the central Apennine ridge (1,000-1,300 m a.s.l.), and cut it twice a year for six years; another area (1 hectare) was fenced and left unmown. Before the experiment started, we recorded species cover in 30 random sampling units (0.5 x 0.5 m) in the experimental area and in the unmown area. The sampling was repeated for the experimental area, every year for six years, except 2013, while it was done for the unmown area only at the end of the six years. We investigated the effect of the reduction of *Brachypodium rupestre* over time on taxonomic diversity indices, functional traits and pastoral value, using species accumulation curves and generalized linear mixed-effect modelling.

Twice-yearly mowing was effective in reducing the abundance of *B. rupestre* (mean cover $50.7 \pm 19.8\%$ Standard deviation to $9.0 \pm 7.2\%$), and in increasing significantly species richness (16.6 ± 3.0 to 26.8 ± 3.2), exponential Shannon (8.8 ± 2.8 to 14.4 ± 2.7), but not Shannon evenness (0.53 ± 0.1 to 0.54 ± 0.1). At the end of the treatment quite stable richness and diversity values were reached. Reduction of *B. rupestre* cover increased the pastoral value of the system ($39 \pm 12\%$ to $64 \pm 8\%$ of pabular species relative cover) and promoted the presence of species without vegetative propagation (17.8 ± 12.3 to 28.2 ± 10.9), with pleiocorms (25.4 ± 14.3 to 49.6 ± 17.9), rosettes (5.6 ± 5.6 to 16.6 ± 12.7) and hemirosettes (32.1 ± 15.8 to 47.7 ± 13.6), but caused a decrease in species whose clonal growth organs have prevalent vertical spread (123.9 ± 25.7 to 97.0 ± 23.3), reptant (60.3 ± 20.9 to 20.2 ± 10.4), and late flowering species (67.4 ± 19.9 to 46.3 ± 17.2). The decrease of *B. rupestre* and the increase in mowing frequency

reduced the abundance of species with clonal growth organs with prevalent horizontal spread (66.0 ± 19.5 to 17.9 ± 10.7), caespitose species (96.7 ± 20.9 to 43.6 ± 21.9), and grasses (94.0 ± 19.5 to 43.3 ± 22.0). Recurrent twice-yearly mowing seems to be appropriate in the restoration of sub-Mediterranean grasslands invaded by competitive species, facilitating the re-introduction of traditional grazing.

KEYWORDS: Grassland restoration; biotic interaction; functional ecology; pastoral value, grassland invasion; *Brachypodium rupestre*

Nomenclature Bartolucci et al. (2018)

1. Introduction

Historical, socio-economic and environmental contexts

The socio-economic changes following World War II, triggered a strong reduction in Mediterranean mountain farming and shepherding (Antrop, 2004; Mazzoleni, et al. 2004). Pastoral ecosystems are being lost or degraded at a very high rate all over Europe (Giarrizzo et al., 2017): more than five million hectares between 1990 and 2013 have been lost (<http://www.fao.org/faostat>). In the Italian peninsula, the changes were mainly linked to the strong depopulation of Mediterranean mountain areas (Catsadorakis, 2007) because of migration to the new industrial centers and large metropolitan areas with a progressive ageing of the population remained in the mountain lands. This process was so intense that numerous villages are today completely uninhabited and abandoned (Falcucci et al., 2007), and several pastoral systems evolved in shrubland and forest (Bracchetti et al., 2012) or were invaded by unpalatable tall grasses (Malatesta et al., 2019). However, there is an increasing interest worldwide for the Italian high-quality foods, so that in recent years a new economic interest is arousing in relation to the production of meat and cheese from semi-extensive Mediterranean mountain farms (Martins et al., 2017). Moreover, these habitats are encompassed in the EU Habitat Directive and are subject of public funding for their preservation and restoration (European Commission, 2018). As a result of this new economic and conservation interest, restoration of pastures is becoming a paramount issue, which requires a profound understanding of the mechanisms behind the coenological recovery processes, which is still largely lacking, especially in the sub-Mediterranean pastoral systems. These systems are affected by the sub-Mediterranean climate, a bioclimatic variant of the Mediterranean climate at the border between the Mediterranean and Temperate regions, and include the Mediterranean mountain areas, where winter cold stress and summer drought stress alternate with different intensities (Rivas-Martínez et al., 2011). Due to these characteristics, the sub-

Mediterranean systems are relatively unproductive, and plants manifest not only drought stress tolerance, but also frost resistance. In these systems, disturbance due to grazing and mowing can have different effects, depending on the variation of productivity and/or water availability (Carmona et al., 2012).

Because of the low productivity, the traditional semi-extensive farming activities focused on sheep breeding and meadows mowing (which, prior to abandonment was performed in June by hand scythe or small cutter bar), limited to the least steep and most productive areas. Since sub-Mediterranean grasslands provide adequate nutritional value for only part of the year, because the aboveground productivity peaks in late spring and drops in summer (Seligman, 1996), breeding was traditionally carried out by transhumance, moving flocks along routes stretching from lowland pastures near the sea, where animals graze during winter, to the montane pastures, in late spring-early autumn.

Effect of management cessation and grassland abandonment

The cessation of traditional semi-extensive farming or the decrease in herbage use, besides fostering the expansion of shrub-lands and forests, typically induces the invasion of coarse tall grasses (Louault et al., 2002) with competitive stress-tolerant strategies (Grime, 2001). This process generally reduces the overall feed value of pastures (i.e. Vitasović-Kosić et al., 2014), negatively affecting the economic sustainability of mountain farming and exacerbating the abandonment trend of the mountain areas (Catorci et al., 2014a; Scocco et al., 2018).

Several European species play this role in abandoned grasslands, such as *Deschampsia cespitosa* (Slovakia, Jendrišáková et al., 2011), *Calamagrostis epigejos* and *C. villosa* (Hungary, Házi et al., 2011; Alps, Niedrist et al., 2009), *Molinia coerulea* (central Europe, de Bello et al., 2012; Alps, Niedrist et al., 2009), *Bothriochloa ischaemum* (Hungary, Házi et al., 2011; Szentes et al., 2012) and *Brachypodium pinnatum* (south-eastern Europe: Pyrenees, Canals et al., 2017). In this regard, a cardinal species throughout the Italian peninsula is

Brachypodium rupestre (Host) Roem. & Schult. (Bonanomi et al., 2013), a competitive, stress tolerant coarse grass, 40-70 cm tall, whose flowering peak is in late spring-early summer. *B. rupestre* grows on clayey and calcareous soils (Dowgiallo and Lucchese, 1991) at a broad range of elevations, up to 1,200-1,300 m a.s.l.

The competitive behavior of perennial dominant species, among which *Brachypodium rupestre*, is related to a set of plant traits: tall canopies, high tiller density and branching frequency (Grime, 2001; Pottier and Evette, 2010), as well as the clonal growth and clonal integration strategy (de Kroon and Bobbink, 1997). These characteristics and properties allow individuals to maintain the coordination between resource acquisition and conservation, and to sustain dominance in a wide range of environmental conditions, through the rapid spread of clonal tussocks. In the final phases of invasion, coalescence of different patches often form nearly mono-dominant stands (de Kroon and Bobbink, 1997). In particular, *Brachypodium* species have silica-rich, tough and hairy leaves, which make the plant poorly palatable to domestic herbivores, minimizing the loss of resources (Canals et al., 2017); in fact, herbivores feed on them only in overstocking conditions (Catorci et al., 2014a). The cessation of herbivory fosters the enhancement of a vigorous belowground system; likewise, the lack of leaf consumption leads to the accumulation of a thick litter layer, which protects the young shoots arising in spring.

The increasing dominance of *Brachypodium* species leads to a modification of the coenological composition of pasture by the decrease of the grassland specialist taxa (early flowering taxa, small-sized plants, taxa with storage organs, etc.) and the increase of those typical of fringe communities and of nitrophilous habitats (tall herbs with late flowering strategies, species with runners and ability to form patches, etc.) (Catorci et al., 2011; Tardella et al., 2018).

Pasture restoration perspectives

Generally, grazing and mowing are the main management practices for grasslands, but sheep avoid feeding on *Brachypodium*, foraging on it only in conditions of high stocking rates. It has been found that this situation leads to the depletion of tussocks and improvement of *B. rupestre* palatability, but can harm animal welfare, as such a diet is associated with a sudden and marked increase of rumen keratinization (Catorci et al., 2014a) and lower absorption of nutrients. Thus, it is not very feasible to use sheep grazing as a method for grassland recovery (Scocco et al., 2013, 2016a,b). Fire, a possible management technique (Bond and Keeley 2005), is not allowed by the Italian law, while cattle avoid the plant at all. A viable method could be using horses, but to maintain a high stocking rate they should be fenced and the Italian law obliges to equip enclosed areas with canopies or structures designed to repair animals in adverse weather conditions. This is economically expensive and difficult to achieve in mountain areas, since traditionally horse breeding is done with a low number of animals free to graze in very wide territories to lower the cost of their management.

On the contrary, mowing is considered one of the most appropriate management types for ensuring the high conservation value of grasslands (Oroian et al., 2014; Tälle et al., 2014). It is a non-selective disturbance type (Kohler et al., 2005); however, it “selects” species that are taller than the cutter bar and species that are vulnerable to impact at the cutting date, for example, where seed-based reproduction is important, any species that has not yet completed flowering and seed production, leading to a complex trait-determined use of different temporal reproductive niches (Catorci et al., 2017). Several studies have shown that mowing fosters traits that allow resource allocation to leaves or underground storage organs (e.g. Klimeš and Klimešová, 2002; Craine, 2005). Because of these effects and since it reduces above-ground biomass and prevents litter accumulation (when hay is removed), mowing promotes the survival of light-demanding seedlings and low-growth species (Overbeck et al., 2003; Ilmarinen and Mikola 2009), and, in a not artificial community, leads to an increase in species richness and diversity, at least in formerly grazed or undergrazed systems of

temperate climates and productive conditions (Huhta et al., 2001; Bonanomi et al., 2006; Ruprecht et al., 2010; Hejzman et al., 2011; Valko et al., 2012).

In this regard, long-term studies have been performed in temperate climates (e.g. Bakker et al., 2002; Socher et al., 2013; Lepš, 2014), semi-arid steppe systems (Zhang et al., 2016; Valko et al., 2016), north-American prairies (Maron and Jefferies, 2001) or subtropical ones (e.g. Fidelis et al., 2012; Joubert et al., 2016; Fensham et al., 2017), but not in the sub-Mediterranean context, for which there is still a lack of knowledge about the effectiveness of mowing and the modalities of grassland restoration processes. In addition, the effect of mowing on plant traits has received relatively little attention (see de Bello et al., 2012) and few studies have employed both taxonomic and functional methodologies for a multi-approach evaluation of grassland restoration.

Given these considerations, we sought to define the effect of mowing activities on the species and functional composition of sub-Mediterranean productive grasslands invaded by *B. rupestre*. Mowing could be a viable methodology (expected to be economically supported by the European Union), at least in the earlier restoration phases, in order to allow the new use of pastures for the semi-extensive breeding of sheep and cattle. Because of this, in the course of a six year-long experiment, we assessed the variation of taxonomic diversity indices, trait abundance (related to reproductive features, space/time occupation besides acquisition and storage of resources) and pastoral value.

We hypothesized that recurrent disturbance (multi-year mowing) on abandoned grasslands invaded by *B. rupestre* fosters the recovery of taxonomic diversity by reducing the dominance of this species, and that this change is reflected in a shift in the species and trait composition over time, especially with regard to traits related to spatial and temporal niche partitioning and exploitation of resources. Also, mowing may influence the remobilization of nutrients from storage in belowground organs and, thus, should foster species with storage organs.

Our main questions were: i) does multi-year mowing reduce the abundance of *B. rupestre*? ii) do the effects of disturbance and of changes in *B. rupestre* features affect taxonomic richness and diversity and which of these drivers is the most effective? iii) How does multi-year mowing change the functional composition of grasslands on a fine scale, especially in regard to plant strategies linked to spatial and temporal niche occupation, and resource storage in belowground organs? iv) Does recurrent mowing influence the pastoral value of grasslands, so that it can facilitate the restoration of abandoned grasslands prior to re-establishment of traditional grazing activities?

2. Methods

2.1 Study area

The study site is located in the central Apennines (337398.00 m E, 4757200.00 m N, UTM coordinate system) and encompasses north-facing slopes with limestone bedrock, ranging from 1,000 to 1,300 m a.s.l. (Fig. 1). The climate is sub-Mediterranean (*sensu* Rivas-Martínez et al., 2011), characterized by the alternation of winter cold stress and summer drought stress. The mean annual rainfall is about 1,100 mm, and the average annual temperature 10-11°C. The soil has a neutral-sub acid pH, and its depth ranges from 20 to 40 cm. The soil texture is characterized by sand (8-10%), silt (32-35%) and clay (50-60%). Skeleton amount ranges from 45 to 50%, while total nitrogen from 6 to 7 g Kg⁻¹ (Catorci et al., 2012).

Non-invaded grasslands in similar environmental conditions were referred to the *Briza mediae-Brometum erecti brizetosum mediae* Biondi, Allegrezza et Zuccarello 2005 association, a highly diverse, thick-turf community, with aboveground productivity ranging from 170 to 190 g m⁻² of dry matter (Catorci et al., 2009). Such managed grasslands are characterized by several perennial grass species (*Bromopsis erecta*, *Festuca circummediterranea*, *Helictochloa praetutiana*, *Koeleria splendens*, *Dactylis glomerata*, *Cynosurus cristatus*, *Anthoxanthum odoratum*) associated with legumes (*Trifolium montanum*

subsp. *rupestre*, *T. ochroleucon*, *T. pratense*, *T. repens*, *Anthyllis vulneraria*, *Lotus corniculatus*, *Hippocrepis comosa*) and several forbs, sedges and chamaephytes (*Poterium sanguisorba* subsp. *balearicum*, *Carex caryophyllea*, *C. macrolepis*, *Luzula campestris*, *Pilosella officinarum*, *Salvia pratensis*, *Galium corrudifolium*, *Centaurea triumfetti*, *Helianthemum nummularium*, *Crepis lacera*, *Centaurea ambigua*, *Leontodon hispidus*, *Ranunculus* sp. pl., *Thymus* sp. pl.). Generally, these grasslands host a high number of species (usually about 70/80 species, with peaks over 90 taxa, every 100 square meters) with several endemisms (e.g. *Viola eugeniae*, *Phleum hirsutum* subsp. *ambiguum*, *Erysimum pseudorhaeticum*, *Potentilla rigoana*, *Campanula michrantha*) and orchids (e.g., *Dactylorhiza sambucina*, *Anacamptis morio*, *A. pyramidalis*, *Orchis mascula*, *O. pauciflora*, *Neotinea ustulata*, *Ophrys apifera*, *O. bertolonii*, *O. holosericea*, *O. sphegodes*, *Gymnadenia conopsea*). Their high conservation value has been recognized by the European Union's Habitats Directive (92/43/EEC), so that they are included in the 6210 habitat "Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*)", which is a priority habitat in important orchid sites. Beech woods of the *Fagetalia sylvaticae* order constitute the potential vegetation.

The study area has a centuries-old history of extensive grazing by sheep and, more recently cattle. Traditionally, grasslands are grazed by flocks between late spring and early autumn and, in the least steep or semi-flat slopes, hay is mown in early summer (Catorci et al., 2009). However, for at least the last 30 years, vast grassland areas, especially the steepest ones, have been undergrazed and are undergoing dynamic processes.

2.2 Sampling design and data collection

To reduce the macro-environmental variability among the sampling units, we selected slopes with elevation ranging from 1,000 to 1,300 m a.s.l.; aspect ranging from west–north–west to east–north–east; and slope ranging from 20° to 25°. To reduce variability due to

different management histories, we selected a territory inside the same ownership (Comunanza Agraria di Fematre).

Using remote sensing images and the QGIS software, we overlaid the chosen area with a grid of 100 m × 100 m and selected the cells of the grid with homogeneous aspect, slope angle and sward cover, in which *B. rupestre* cover exceeded 60%. Among the cells that matched these criteria, we selected two contiguous cells (1 ha each) characterized by homogeneous altitude (1,220-1,280 m a.s.l.), aspect (north–west-facing slope) and slope angle (25°). Soil depths ranged from 25 to 35 cm. In February 2010, these areas were fenced to avoid disturbance by domestic and wild mammalian herbivores. Since our aim was to study the recovery processes of abandoned and invaded grasslands, we did not include an area of traditionally managed grassland as a “reference state”, also because the whole district is largely abandoned or undergrazed (with several areas that change year by year the shepherding activities or the type of grazers), so that a geographical definition of what is under “traditional disturbance“ is nowadays impossible.

Previous research, not performed in the study area, demonstrated that vascular plant species richness was the highest when the grassland was mown twice a year and hay was removed (see Socher et al., 2013). Moreover, experimental research suggests the adequacy of summer mowing to avoid reallocation of nutrients to storage organs (Bobbink et al., 1989). Consequently, from 2010 to 2015, one area was mown twice yearly to remove the aboveground phytomass re-growth; this was done at the end of June, just before the *B. rupestre* flowering, and at the end of October. The sward was cut 2 cm above the soil level using a grass trimmer, and litter was removed by hand every year. The other area, used as a control, was left unmown and litter was not removed.

Considering the findings of previous studies on community assembly rules (e.g. Bartha et al., 2004; Wellstein et al., 2014), we assumed that fine-scale spatial resolution (0.5 m × 0.5 m) offered the most appropriate scale of study to detect the effect of biotic interactions. We

overlaid the two 100 m x 100 m fenced areas with a 5 m x 5 m grid and randomly selected 30 points at the crosses of the grid, both in the mown and in the unmown area; these points were the lower left-hand corners of 30 sampling units (0.5 m × 0.5 m). To avoid edge effects, we did not select random points within a belt of 5 m adjacent to the fences. In the experimental area, sampling was carried out in 2010, 2011, 2012, 2014, 2015, and 2016, while in the unmown area, sampling was performed in 2010, before the start of the experiment, and in 2016, six years after the start of the experiment. The random sampling was repeated every year to avoid temporal autocorrelation of the observations.

The site selection procedure strongly reduced the environmental variability among the sampling units, limiting problems related to pseudoreplication (Hurlbert, 2009). The distance among the sampling units was at least 5 m; however, their size (0.25 m²) and their number per area (30), compared with the extent of each area (1 ha) ensured that they were on average much more than 5 m apart, limiting problems related to spatial autocorrelation.

In each sampling unit, we visually estimated and recorded plant species and litter cover (percentage of the surface covered by all the individuals of each species, and by litter). Relevés were gathered in late June, immediately before the experimental area was mown.

To understand how the functional composition of the community was affected by mowing activities, we selected some traits related to space occupation (horizontal and vertical architecture, and vegetative propagation), temporal niche exploitation (timing of flowering) and resource storage strategies (storage organs). A description of each trait, with a list of the respective states and data sources, is provided in Appendix A (Table A). All traits were treated as categorical variables.

Finally, to understand whether recurrent mowing improved the pastoral value of restored grasslands, we classified each species, based on the synthetic index of Roggero et al. (2002), which follows an ordinal scale, from 0 to 5. This index takes into account species' nutritional value, palatability, taste, digestibility and resistance to grazing. In this study, we grouped

species in two classes: species whose specific index value ranged from 2 to 5 (i.e. from mediocre to excellent fodder plant, since plant selection does not depend only on the plant species but also on the type of grazer, the stocking rate and the grazing period); and species whose value was 0 or 1 (toxic or refused; occasionally consumed).

2.3 Data analysis

2.3.1 Preliminary data analysis

To investigate the community response to the variation of *Brachypodium rupestre* cover and to recurring mowing, we calculated the following indices for each sample collected every year in the experimental area, as well as for samples collected before and after six years from the start of the experiment in the unmown area: species richness (S), Shannon evenness (E_H), and Shannon index (H). We transformed H using the formula e^H (exponential Shannon or Shannon diversity number - Jost, 2006) into an effective number of elements, i.e. the number of elements in an equivalent community composed of equally common elements.

We performed the analyses using R, version 3.4.1 (R Foundation for Statistical Computing, Vienna, Austria <http://www.R-project.org>). We calculated H using the *diversity* function in the *vegan* R-package, version 2.4-4, and E_H dividing the exponential Shannon index by species richness, following Hill's formula (Hill, 1973).

To exclude that the possible modifications of grassland composition could be related to inter-annual climatic variability or other factors unrelated to the treatment, we used a BACI (Before-After Control-Impact) approach (Eberhardt, 1976; Green, 1979), where sampling is conducted at simultaneous time periods in treatment and control sites before and after treatment (Underwood 1994). The statistical approach involved the use of mixed-effects models, with the two-level categorical variables control / impact (unmown vs mown area) and before (2010) / after (2016) treatment and their interaction term as fixed effects. A significant interaction term indicates a significant effect of the treatment. As sampling units were

spatially nested in two locations and changed every year, we used the identities of samples (each sample being composed of 30 sampling units, as one different random sample was taken every year) before and after treatment nested inside the two sampled areas as random intercept. We ran the mixed-effects models for the taxonomical indices and *B. rupestre* cover using the `lme` function (*nlme* R-package). This statistical approach allows accounting for the effect of potential spatial autocorrelation (Bitomsky et al., 2019; Tordoni et al., 2019) between the sampling units of the Before-After samples nested inside the two sampled areas (Control-Impact) by improving the model fit, taking into account the structure in the residuals. To reduce the bias due to the potential effects of spatial autocorrelation, we re-fitted the models with each of the following correlation structures, available in the *nlme* library (Pinheiro et al., 2016): compound symmetry structure corresponding to a constant correlation; exponential spatial correlation; Gaussian spatial correlation; and rational quadratics spatial correlation. We selected the model with the lowest Akaike Information Criterion (AIC) value (Bitomsky et al., 2019).

Prior to the analyses, we log-transformed the Shannon evenness index to meet the model assumption of normality of the residuals and homoscedasticity.

As *S* is a count and, to our best knowledge, the only package which can fit models with the Poisson error distribution and with correlation structures, is the *MASS* R-package (v. 7.3-47), through the `glmmPQL` function (Bolker et al., 2009), we could not perform an AIC-based model selection. Thus, we compared the fitted models based on a generalized explained variance approach (Jaeger et al., 2016). We calculated the R^2 of the models without correlation structure and with each of the aforementioned correlation structures, using the `r2beta` function (*r2glmm* R-package, version 0.1.2). Then, using the `r2dt` function of the same package, we tested whether the generalized explained variances (R^2) of the models fitted with each correlation structure were significantly higher than that explained by the model fitted without correlation structure. Finally, we selected the model with the highest generalized

explained variance. Significance values were obtained using the Type II Wald Chi-square test and the Anova function (*car* R-package, version 2.1-5).

2.3.2 Variation of taxonomic diversity indices

To quantify the effect of the treatment on species richness in the different years, comparing it to species richness before treatment, we used sample-based accumulation curves, which made it possible to account for differences in sampling effort (number of sampling units) within sampling years (before treatment, and 1, 2, 4, 5, and 6 years after the beginning of the treatment). This procedure generates the expected number of species in a collection of n samples, drawn at random from the large pool of N samples (Gotelli and Colwell, 2001). The accumulation curves were produced by repeatedly re-sampling the pools of N samples without replacement, in which samples are randomly accumulated in many iterations, plotting the average number of species. For this analysis, we used the *specaccum* function of the *vegan* package, using the “random” method, which finds the mean species accumulation curve and its standard deviation adding sites from 1,000 random permutations of the data.

We ran linear mixed-effect modelling to understand how taxonomic diversity indices were affected by *B. rupestre* abundance (cover %), the number of years from the start of the treatment (i.e. recurrent mowing), and their interaction (fixed effects). We accounted for the sampling design using the sample identity as random intercept (as, every year, we randomly selected a new sample, composed of 30 different sampling units). We selected the best fitting model for exponential Shannon and Shannon evenness, based on the Akaike information criterion (AIC) (i.e. selecting the model with the lowest AIC) applied to the full model (i.e. predictors and their interactions), using the maximum likelihood (ML) method. To perform model selection, we used the dredge function of the *MuMIn* R-package (version 1.15.6). Following Bitomsky et al. (2019) and Tordoni et al. (2019), to reduce the bias due to the potential effects of spatial autocorrelation in the response variables within samples, we

repeated the model selection including different within-sample correlation structures of the data (compound symmetry structure corresponding to a constant correlation, exponential spatial correlation, Gaussian spatial correlation, and rational quadratics spatial correlation), which are available in the *nlme* library (Pinheiro et al., 2016). Among the best models (one model selected for each correlation structure, besides the model fitted without correlation structure), we chose the one with the lowest AIC (Bitomsky et al., 2019). Then, we compared the selected model with the null model (i.e. without fixed effects) to assess whether the best fitting model was statistically significant and, if so, we refitted it with the restricted maximum likelihood (REML) method to obtain more precise and unbiased parameter's estimates (Zuur et al., 2009). After the analyses, we checked the model linearity assumptions.

We used the `r.squared.GLMM` function of the *MuMIn* R-package to calculate the conditional and marginal R^2 of the final models. Conditional R^2 accounts for the explanatory power of both fixed and random effects, whereas marginal R^2 only accounts for fixed effects (Nakagawa and Schielzeth, 2013).

For the abovementioned reasons, we adopted a different approach for species richness. We calculated the R^2 of all the possible models (fitted for each combination of fixed effects and their interaction term) without correlation structure and with each of the aforementioned correlation structures, using the `r2beta` function (*r2glmm* R-package, version 0.1.2). Then, using the `r2dt` function of the same package, within each set of possible models with the same (or without) correlation structure, we selected the model whose generalized explained variance (R^2) was significantly higher than that of the other ones. Then, using the same procedure, we compared the selected models to find the one with the highest generalized explained variance.

2.3.3 Variation of functional composition

We calculated the community absolute cover value by weighting the species trait state (which in this study corresponds to 1 or 0, i.e. the presence/ absence) by the species absolute cover, excluding *B. rupestre* (Catorci et al., 2013a; Scolastrri et al., 2017).

To understand how *Brachypodium rupestre* cover and recurrent mowing and their interaction may affect the strategy related to space occupation (vegetative propagation, vertical and horizontal architecture), storage of reserves (storage organs), and reproductive strategies (flowering timing), we applied same the modelling approach used for Shannon evenness and exponential Shannon for the community absolute cover value of each trait state, accounting for spatial autocorrelation. Prior to the analyses, data of response variables were square root or cube root transformed to improve the homogeneity of variances and the normality of residuals, if necessary (Faraway, 2006).

2.3.4 Variation of pastoral value

Following Garnier et al. (2004), we calculated the community-weighted mean of the “specific index” (hereafter *PV*) for each sampling unit using the formula:

$$PV = \sum_{i=1}^n p_i S_i$$

where p_i is the relative cover of the i -th species and S_i is the presence or absence of the S_i class (that in this study correspond to 1 or 0) and n is the number of species sharing the same class. We calculated *PV* using the *functcomp* function in the *FD* package.

To understand the effect of mowing and the effect of *B. rupestre* cover on the total community pastoral value (with the presence of *Brachypodium*), we applied same the modelling approach used for Shannon evenness, exponential Shannon and absolute cover values of trait states, accounting for spatial autocorrelation.

3. Results

3.1 Variation of *Brachypodium rupestre* abundance

Brachypodium rupestre mean cover dropped from 50.7 to 9.0% in the mown area and increased from 49.6 to 75.9% in those in unmown condition, whereas litter cover decreased from 48.0 to 2.6%. Descriptive statistics regarding the variation of *B. rupestre* cover is detailed in the Appendix B (Table B) and shown in Fig. 2.

A significant effect of the treatment (i.e. significant interaction term between Before/After and Control/Impact), was detected for *B. rupestre* cover ($P < 2 \times 10^{-16}$) using the rational quadratics spatial correlation structure. The “plot x species” matrix before the start of the experiment and during the treatment time are shown in Appendix C (Table C).

3.2 Variation of taxonomic diversity indices

In the mown condition, the mean species richness progressively increased from 16.6, before the start of the experiment, to 26.8 species, recorded after the last year of treatment; the other indices showed a marked increase after one year, and then reached quite stable values by the fifth or the sixth years (Figs. 3 and 4, Appendix D - Table D). We detected a significant effect of the treatment for S ($P = 1.66 \times 10^{-5}$) fitting the model using the rational quadratics spatial correlation structure, e^H ($P = 6.07 \times 10^{-6}$) and E_H ($P = 5.4 \times 10^{-9}$), fitting the models using the exponential spatial correlation structure. We observed a clear increase in the exponential Shannon index (from 8.8 to 14.4), but a negligible increase in evenness (from 0.53 to 0.54).

The accumulation curve before the start of mowing activities showed a lower mean number of species than all the other curves and was clearly distinct from that of the last year for every number of sampling units (Fig. 5). The accumulation curve before the start of mowing activities showed a lower mean number of species than all the other curves and was clearly distinct from that of the last year for every number of sampling units (Fig. 5). The curves from two to five years after the beginning of mowing showed a similar trend up to six

cumulated sampling units, but then they began diverging, especially the curve of the first year after mowing, which became closer to that of the last year with increasing cumulated sampling units, equalling and overcoming it at the highest numbers (27-30) of sampling units (Fig. 5). The reduction of *B. rupestre* cover positively influenced all the taxonomic diversity indices; the number of years of mowing negatively affected Shannon evenness (Table 1, Fig. 4). The descriptive statistics of the indices during the treatment are shown in Appendix D (Table D); the models' AIC, AIC weight, log-likelihood value and significance value are reported in Appendix E (Table E).

3.3 Functional variation and change in pastoral value

Mixed-effects modelling revealed that the reduction of *B. rupestre* cover fostered the relative cover of species with high pabular value, as well as the absolute cover of species reproducing only sexually, rosette forbs, hemirosulate upright forbs, species with pleiocorm, and taxa with early flowering strategy (Table 2, Appendix F - Table F). Instead, it reduced the absolute cover of species with clonal growth organs, grasses, caespitose, reptant, and late-flowering species (Table 2, Table F). The number of years of treatment decreased the cover values of species with horizontally spreading clonal growth organs, grasses and caespitose species (Table 2, Table F). AIC, AIC weight, log-likelihood value and significance value are reported in Appendix G (Table G). The trends of the relations between *B. rupestre* cover and traits' weighted means over time are shown in Appendix H (Fig. H). The "species x trait states" matrix is shown in Appendix I (Table I).

4. Discussion

4.1 Variation of *Brachypodium rupestre* abundance

Our results revealed that twice-yearly mowing was effective in reducing *B. rupestre* abundance during the six-year experiment, and in maintaining it at low cover values. The very

large size of the difference in change of *B. rupestre* between the mown and the unmown areas and the increasing cover in the unmown area over the treatment period, allows us to argue that this change was caused by mowing, excluding the effect of possible confounders that might have arisen by differences among the sampling units, resulting in spontaneous vegetation processes, or by inter-annual climatic variability.

The *B. rupestre* response to mowing is consistent with previous findings (Bonanomi et al., 2006) and in line with Grime's (2001) prediction about the response of competitive stress tolerant species to disturbance. In fact, it was proven that the short-term reduction in abundance of *B. rupestre* is mostly due to the decrease in the size of individuals under disturbance regimes (Catorci et al., 2014a), as demonstrated for other dominant tall grasses (Baptist et al., 2013), which is likely a reflection of diminished tillering ability due to depletion of underground nutrient reserves (Endresz et al., 2005; Canals et al., 2017). Indeed, summer cuttings of *B. pinnatum* caused a gradual reduction in the biomass of rhizomes (Bobbink and Willems, 1991), while under traditional management, *B. rupestre* is a common component of rich grasslands, with small-sized tussocks (Catorci pers. obs.).

4.2 Variation of taxonomic diversity indices

The taxonomic diversity values were generally higher in the mown than in the unmown area, further confirming that *B. rupestre* invasion after management cessation is a major driver of change in species diversity of sub-Mediterranean grasslands, in accordance with previous findings (e.g. Catorci et al., 2011, 2012). In particular, we found an overall positive response of species richness to the decrease of the *B. rupestre* cover value during the experiment. However, the increase in species richness was anything but steady and linear (Fig. 5). The increase in species richness was particularly marked in the first year, especially at the maximum number of cumulated sampling units. The immediate response of the system could be ascribed to the strong and fast reduction of the *B. rupestre* average cover (from 50.7

to 33.3% after one year of treatment), but also to the litter removal. In fact, both modifications may promote the availability of new gaps for seedlings and the establishment of new individuals/species (e.g. Jensen and Gutkunst, 2003). This also changes the distribution pattern of species abundances, as indicated by the increase in the average values of Shannon evenness and exponential Shannon. As evidenced in other studies, this should allow for the spread of weak competitors and shade-intolerant species (Zobel, 1992; Csergo and Demeter, 2011). It is likely that, after litter removal and decrease in abundance of the dominant species, the increase in richness began with the occurrence of new species coming from the seed bank (Kalamees and Zobel, 2002) and probably from the surrounding areas (Arruda et al., 2018), in addition to those that had coexisted with *B. rupestre*, as they are able to tolerate the *B. rupestre* competition for resources and low levels of disturbance.

During the experiment, we observed not only an overall increase in species richness, but also a recovery of evenness that is, increase in species with a more even abundance distribution, reflecting in the increase in “equally-common species” (i.e. the exponential Shannon index). This is partly in accordance with the results obtained in formerly *Brachypodium pinnatum*-invaded chalk grasslands of northern France (Dutoit, 1996), where regular mowing showed a positive effect on Shannon index, but not on evenness (Muller et al., 1998). The fluctuations shown by the average values of evenness and exponential Shannon index, along with the continuous increase of mean species richness over time, suggest that there were variations in the ratio between subordinate and accidental species abundances during the experiment. The same effect of disturbance has been demonstrated in several studies, albeit with regard to different dominant tall grass species (Buckland et al., 2001; de Bello et al., 2006; Házi et al., 2011; Szentes et al., 2012). Actually, as Grime (2001) argued, the weakening of competitive species is a basic tool for grassland biodiversity conservation, following the “intermediate disturbance hypothesis” (Connell, 1978), whose general pattern has been also previously documented for systems other than grassland, such as

for tree species in managed forest systems (Wohlgemuth et al., 2002). However, the decrease of the standard deviations of the indices (Table 2), the decreasing slopes over time of the regression lines that define the relation between the indices and *B. rupestre* cover (Fig. 4), and the tendency of species accumulation curves to reach a clear plateau in the last two years of treatment (Fig. 5) are hints that the community has reduced its spatial heterogeneity and is reaching more stable conditions in terms of richness and abundance on a fine scale. Since the plant community may need very long time to reach a complete stabilization (Lepš, 2014), the monitoring of such trends is still ongoing.

4.3 Functional variations and change in pastoral value

Our results indicated that the decrease of *B. rupestre* abundance promoted two space occupation strategies: pleiocorms, with multiple stems arising from adventitious buds near the stem base, whose growth is fostered by cutting, ensuring a certain degree of horizontal spread; and rosulate / hemirosulate species. The spread of species with pleiocorms as well as of species that reproduce exclusively by seeds, may be understood as the establishment of strategies aimed at enabling fast re-occupancy of the canopy gaps after mowing, thanks to a large number of reserve buds (Klimeš and Klimešová, 2002) or through seed dispersal for faster-growing species, such as annuals (Grime, 2001).

The rosette and hemirosette growth forms are escape strategies that allow plants to survive disturbance and exploit the newly available spatial niches, taking advantage of shorter canopy height and lower competition for light (Grime et al., 2001).

Instead, caespitose and grass species were negatively influenced by the decrease of *B. rupestre* cover and the number of years of mowing. In fact, abandonment fosters their spread in sub-Mediterranean grasslands (Catorci et al., 2013b). These species have tolerance strategies, which allow tissue regrowth after defoliation in highly productive conditions, but may not ensure regeneration of shoots in the relatively unproductive conditions of the sub-

Mediterranean grasslands, where the lower resource availability does not allow regrowth of photosynthesizing tissues after repeated mowing events.

Also, clonal growth organs allowing horizontal spread and reptant growth form, were negatively influenced by the reduction of *B. rupestre* probably because they are mainly fostered by the need to find and exploit new gaps when within the community there is strong competition for resources, especially due to competitive, dominant species (Catorci et al., 2012).

With regard to temporal niche occupation, high *B. rupestre* cover was positively related with late-flowering species and negatively related to early-flowering species. In fact, Catorci et al. (2012) observed that some species are able to coexist with the competitive ones by differentiating their temporal niche, delaying their reproductive period until after the peak of flowering and phytomass production of the dominant one (Catorci et al., 2012, 2014a). Conversely, this type of strategy tends to disappear as *B. rupestre* cover decreases. The increase in abundance of the early-flowering species, related to the decrease of *B. rupestre* cover, is probably related to the higher spatial niche availability due to the decrease in abundance of the dominant species (Bergmeier and Matthäs 1996; Catorci et al., 2014b).

Our results also indicate that the reduction of *B. rupestre* cover after recurrent mowing was correlated to the increase of the relative contribution of species with high pabular value. This means that the treatment improved the overall feed value of pastures, confirming previous findings by Vitasović-Kosić et al. (2014). In addition, Catorci et al. (2014a) proved that defoliation of *B. rupestre* tussocks led to an increase in nitrogen and a decrease in lignin content of the new leaves. Analogously, recurrent mowing likely promotes the improvement of plant feed value (Faria et al., 2018), since mowing stimulates the regrowth of new tissues with higher crude protein content (Garcia et al., 2003). Overall, this result indicates that mowing has an extremely positive effect on pasture feed values, which may in turn improve

animal welfare and productivity (Lipiec et al., 2015), and thus increase the economic sustainability of mountain farming.

5 General model and conclusions

As expected, mowing was effective in reducing *B. rupestre* abundance and in enhancing the species richness, highlighting a three-step mechanism of plant community recovery. During the two years after mowing started, the decrease of the *B. rupestre* cover led to an abrupt increase of species number, probably due to the increase in the number of available niches, which are not evenly distributed within the community. In the following years, the matrix changed (*B. rupestre* individuals were confined to smaller patches) and the other species tended to be more evenly distributed; consequently, the *plateau* of accumulation curves was reached earlier. It is likely that the increase in richness began with the arrival of new species from the seed bank and the surrounding areas, in addition to those that had coexisted with *B. rupestre*, as they are able to tolerate the *B. rupestre* competition for resources and low levels of disturbance.

At the mid-point of the experiment, all the surface areas hosted a progressively increasing number of species. Furthermore, we observed changes of species abundance, reflecting the modification of functional strategies inside the community. This modification led to a rapid increase in the abundance of species recruited from the seed bank (species with exclusive sexual reproduction), re-sprouting from buds inside belowground clonal growth organs or from adventitious buds at the stem base with limited lateral spread. On the contrary, caespitose, grass species and those endowed with horizontally spreading clonal growth organs strongly decreased. Finally, repeated disturbance events led to a new arrangement of the species pool, enhancing the cover value of those best adapted to the disturbance type and intensity (mowing in the study case). This is a key step since, as demonstrated by Catorci et

al. (2014b), it allows the plant community to improve the efficiency of resource exploitation through a better temporal niche partitioning.

In fact, we can conclude that, if the goal of restoration projects in sub-Mediterranean grasslands invaded by competitive species is the recovery of species richness, short-term treatment might be sufficient, but if the objective is the recovery of taxonomic and functional aspects of plant community to re-establishing the traditional grazing, longer-term treatment is necessary. More research should be conducted on this issue, since it was argued that results of restoration experiments and related conservation recommendations depend on the temporal scale considered (Hedlund et al., 2003; Lepš, 2014; Kotas et al., 2017). However, to maintain the botanic value of these grasslands, it will be necessary to re-establish the appropriate grazing regime. This could be the basis to extend the study at least at the farm level and to explore other management options, by accessing specific public funds and involving local stakeholders in its implementation (farmers, farmers' associations, environmental management institutions, and public bodies).

Acknowledgements The research was funded by Riserva Naturale Montagna di Torricchio. The authors wish to thank Renata Gatti and Sabrina Cesaretti for their help in data collection, the “Comunanza Agraria di Fematre”, which made the land available, Mario Messini for the management of the fences, and Sheila Beatty for editing the English usage of manuscript. The authors wish to thank two anonymous reviewers for their useful comments, especially on the improvement of the statistical analyses.

Competing interests Authors declare no competing interests.

Table 1 Mixed-effect models explaining the effect of *Brachypodium rupestre* cover percentage (Br), number of years since the beginning of the treatment (Yr) and their interactions (fixed effects) on taxonomic diversity indices, with sample identity (one different sample per year) as random intercept. Intercept and slope estimates, R-package and R-function used, error distribution, marginal R^2 and conditional R^2 (in parentheses) are indicated. The models account for potential spatial autocorrelation. The correlation structures used, if any, are indicated with a superscript.

Index	Estimate				Error distribution	R-package	R-function	R^2
	Intercept	Br	Yr	Br:Yr				
S ^a	3.165***	-0.008***		0.002***	Poisson	MASS	glmmPQL	0.49 (0.49)
E _H ^b	0.751***	-0.004***	-0.032*	0.000 ^{n.s.}	Gaussian	nlme	lme	0.23 (0.25)
e ^{Hb}	15.97***	-0.109***			Gaussian	nlme	lme	0.27 (0.28)

S - Species richness, E_H - Shannon evenness, e^H - Exponential Shannon

^a Compound symmetry structure corresponding to a constant correlation; ^b Exponential spatial correlation

* $p < 0.05$; *** $p < 0.001$; n.s. not significant

Table 2 Linear mixed-effect models explaining the effect of *Brachypodium rupestre* cover percentage (Br), number of years since the beginning of treatment (Yr) and their interactions (fixed effects) on community-weighted means or community absolute values of functional traits, with sample identity (one different sample per year) as random intercept. Marginal R^2 and conditional R^2 (in parentheses) are indicated. The models account for potential spatial autocorrelation. The correlation structures used, if any, are indicated with a superscript. Only significant models are shown.

Trait	Trait state	Model's parameters	R^2
¹ Pastoral value	Relative cover of pabular species	$0.588^{***} - 0.004 \text{ Br}^{***} + 0.012 \text{ Yr}^{\text{n.s.}}$	0.49 (0.51)
	⁺ Relative cover of non-pabular species ^a	$0.591^{***} + 0.003 \text{ Br}^{***}$	0.42 (0.45)
² Vegetative propagation	⁺ Absence of vegetative propagation ^b	$4.895^{***} - 0.018 \text{ Br}^{***} + 0.050 \text{ Yr}^* + 0.003 \text{ Br:Yr}^{***}$	0.10 (0.10)
	⁺⁺ Clonal growth organs, with prevalent horizontal spread ^c	$3.365^{***} + 0.014 \text{ Br}^{***} - 0.211 \text{ Yr}^{**} + 0.004 \text{ Br:Yr}^{***}$	0.76 (0.76)
	Clonal growth organs, with prevalent vertical development and short horizontal spread ^a	$110.291^{***} + 0.330 \text{ Br}^* - 2.370 \text{ Yr}^{\text{n.s.}}$	0.13 (0.14)
² Storage organ	⁺ Presence ^c	$12.357^{***} - 0.218 \text{ Yr}^{\text{n.s.}}$	0.08 (0.08)
² Horizontal space occupation	⁺ Caespitose ^a	$8.199^{***} + 0.031 \text{ Br}^{***} - 0.413 \text{ Yr}^* + 0.006 \text{ Br:Yr}^*$	0.56 (0.59)
	⁺ Pleiocorm ^a	$6.073^{***} - 0.026 \text{ Br}^{***} + 0.170 \text{ Yr}^{\text{n.s.}}$	0.21 (0.21)
	⁺ Reptant ^a	$5.718^{***} + 0.054 \text{ Br}^{***} - 0.249 \text{ Yr}^{\text{n.s.}} + 0.004 \text{ Br:Yr}^{\text{n.s.}}$	0.62 (0.74)
	⁺ Rosulate ^a	$4.246^{***} - 0.037 \text{ Br}^{***}$	0.17 (0.17)
² Vertical space occupation	⁺ Grass ^a	$7.987^{***} + 0.032 \text{ Br}^{***} - 0.356 \text{ Yr}^* + 0.007 \text{ Br:Yr}^*$	0.57 (0.58)
	⁺ Rosette forbs ^a	$4.234^{***} - 0.037 \text{ Br}^{***}$	0.17 (0.17)
	⁺ Hemirosulate upright forbs ^a	$6.688^{***} - 0.024 \text{ Br}^* - 0.034 \text{ Yr}^{\text{n.s.}} + 0.007 \text{ Br:Yr}^{\text{n.s.}}$	0.10 (0.10)
² Flowering phenology	⁺ March-April ^c	$4.907^{***} - 0.026 \text{ Br}^{***} - 0.156 \text{ Yr}^{\text{n.s.}}$	0.06 (0.06)

⁺July-September

$$5.641^{***} + 0.052 \text{ Br}^{***} + 0.078 \text{ Yr}^{\text{n.s}}$$

0.42
(0.43)

¹ community-weighted mean; ² community absolute value

^a Rational quadratics spatial correlation; ^b Compound symmetry structure corresponding to a constant correlation; ^c Exponential spatial correlation

⁺Square root transformed, ⁺⁺Cube root transformed

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; n.s. not significant

Figures captions

Figure 1. Location of the study area (indicated with a small circle in the map in the upper-right-hand corner) and of the site chosen for the study, composed of two contiguous 100 m x 100 m fenced areas (indicated the dotted rectangle), in each of which a sample of 30 sampling units (0.5 m × 0.5 m) was randomly selected every year.

Figure 2. Box-plots showing the variation of (a) *Brachypodium rupestre* cover (%) and (b) litter cover (%), before and during the treatment. The baseline year (2010) is referred to as “year 0” (mown area, before the start of the treatment); years 1, 2, 4, 5, and 6 correspond to 2011, 2012, 2014, 2015, and 2016.

Figure 3. Variation of species richness (a), Shannon evenness (b), and exponential Shannon index (c) during the treatment. The baseline year (2010) is referred to as “year 0” (mown area, before the start of the treatment); years 1, 2, 4, 5, and 6 correspond to 2011, 2012, 2014, 2015, and 2016.

Figure 4. Effect of *Brachypodium rupestre* cover percentage and number of years since the beginning of treatment on species richness (a), Shannon evenness (b), and exponential Shannon index (c).

Figure 5. Accumulation curves indicating the contribution to community species richness (mean values), 1, 2, 4, 5, and 6 years after the start of the experiment, compared with the contribution before the start of the experiment. Error bars represent $\pm 2SD$.

Figure 1

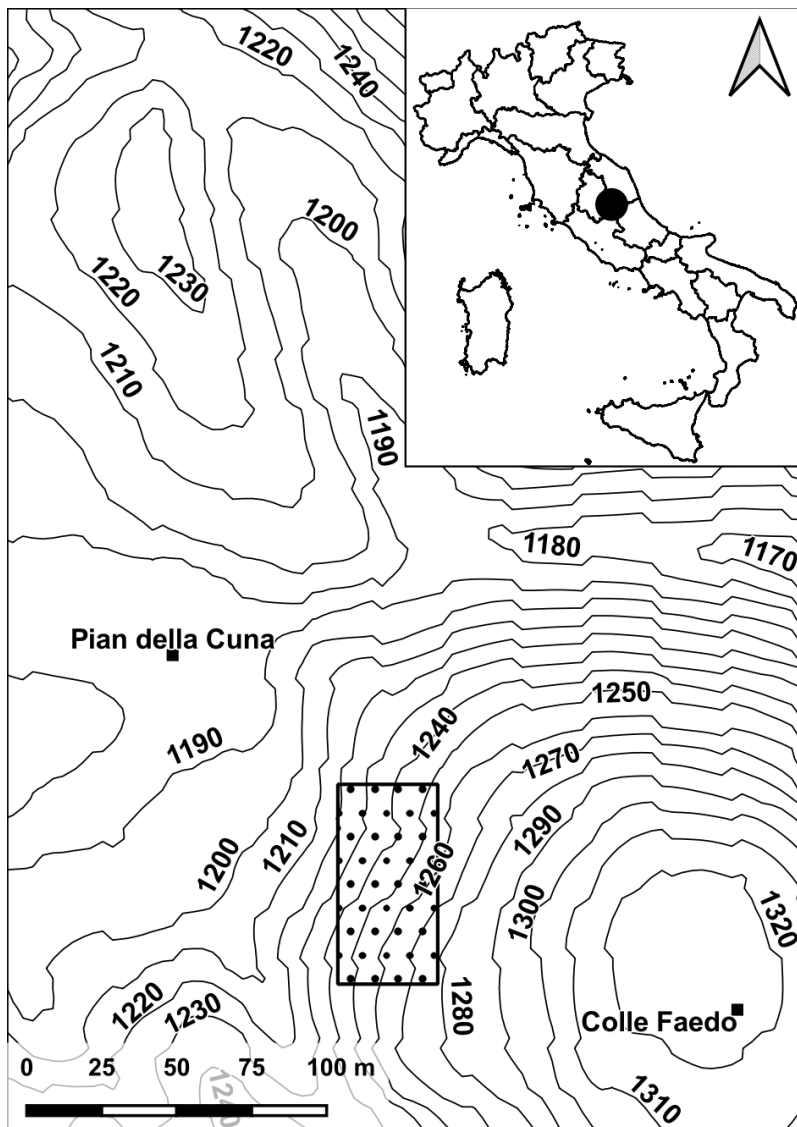


Figure 2

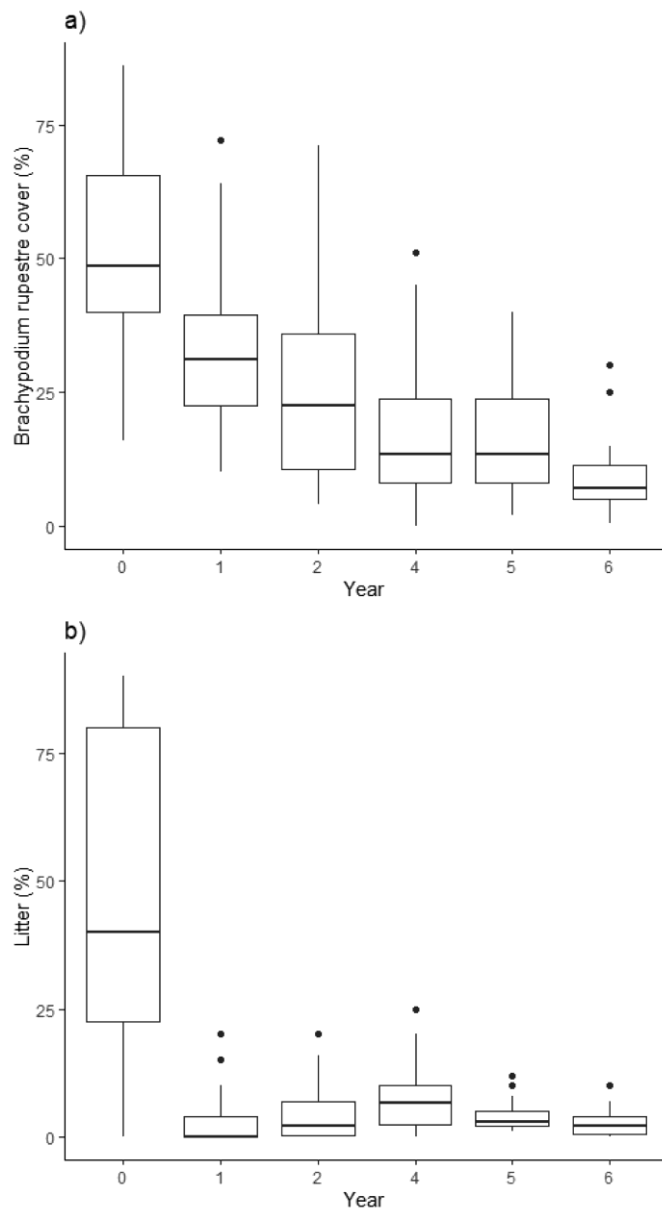


Figure 3

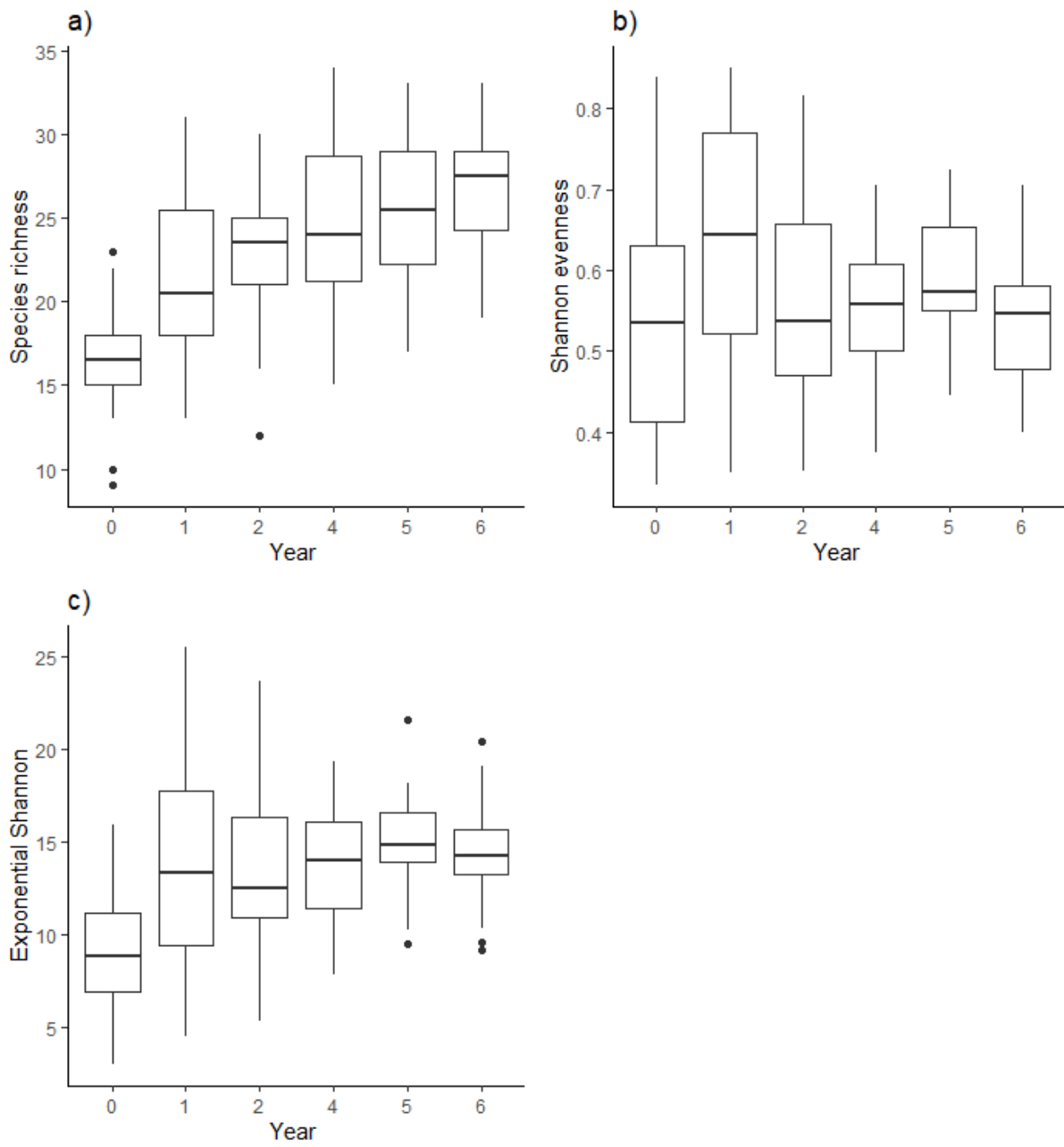


Figure 4

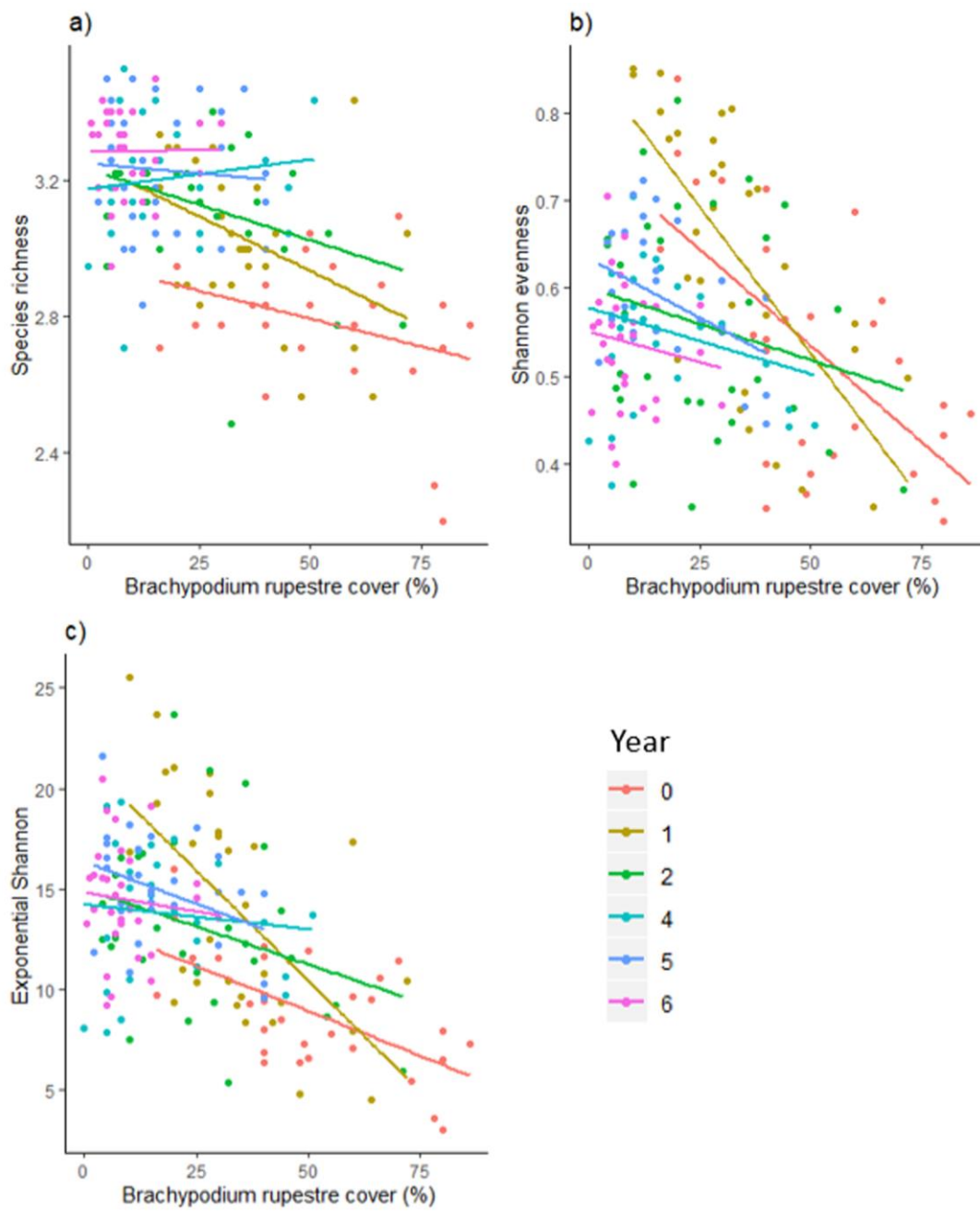
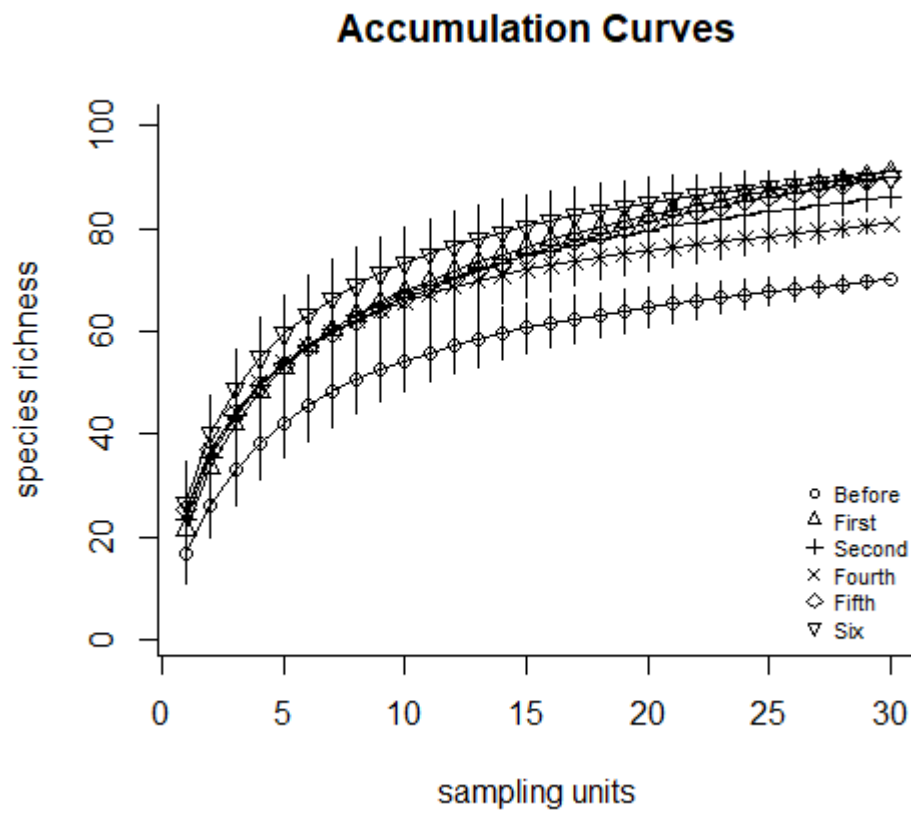


Figure 5



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