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# Disentangling the Effects of Disturbance from Those of Dominant Tall Grass Features in Driving the Functional Variation of Restored Grassland in a Sub-Mediterranean Context

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**Abstract:** Land abandonment in sub-Mediterranean grasslands causes the spread of tall-grasses, affecting biodiversity and ecosystem functioning. Mowing allows the recovery of the coenological composition after invasion, but the mechanisms acting at the fine-scale are poorly investigated. Since 2010 in the Central Apennines, we fenced a grassland invaded by *Brachypodium rupestre*, divided it into two areas, half of each was mowed biyearly and half remained unmown. In 2017 we selected ten 20 × 20 cm experimental units per half-area, collecting data on species occurrences, plant traits, *B. rupestre* height and phytomass. We used generalized linear mixed-effect modelling to disentangle the role of mowing from the impact of *B. rupestre* features in driving the community functional variations. Mowing was the main driver in the recovery process, acting as an abiotic filter (enhancement of tolerance-avoidance strategies). Furthermore, the reduction of weaker competitor exclusion processes fostered the increase of functional variation between coexisting species. Both drivers acted on different plant traits (e.g., mowing on life span, vegetative propagation types and plant height, mowing and *B. rupestre* features on space occupation types, seed mass and leaf anatomy), generally enhancing the extent of functional strategies related to resource acquisition and storage, reproduction, space occupation and temporal niche exploitation.

**Keywords:** *Brachypodium rupestre* (Host) Roem. & Schult.; ecosystem functioning; weaker competitor exclusion; mowing; plant traits; abiotic filtering

## 1. Introduction

Mediterranean semi-natural grasslands, hosting a very rich flora with numerous endemic species, are considered priority habitats by the European Union (92/43/EEC Directive) and judged worthy of conservation. However, as in the rest of Europe, these ecosystems are in strong decline and are threatened by land abandonment, due to socio-economic changes that occurred after World War II and are still ongoing [1–3].

At a community level, abandonment and/or decrease in forage exploitation typically induce the spread of coarse tall-grasses with competitive stress-tolerant strategies, which trigger processes of biodiversity loss whose species identity is geographic-context dependent [4,5]. In the Italian mountain

landscapes, this group of species is well characterized by the *Brachypodium* genus. In particular, *Brachypodium rupestre* (Host) Roem. & Schult. (*Poaceae* Barnhart) dominates the low/hilly mountains up to an elevation of 1300–1400 m a.s.l., while *B. genuense* (DC.) Roem. & Schult. (a more nitrophilous, acidophilous and mesophilous species) dominates the higher mountains up to 2400 m a.s.l. The competitive behavior of perennial *Brachypodium* species is mainly related to the high tiller density and branching frequency [6], as well as to their capacity for clonal growth and clonal integration strategy [7]. These characteristics and properties, together with leaf plasticity [8], allow the rapid spread of clonal tussocks. These species are often able to form, through the coalescence of different patches, nearly mono-dominant stands [7]. This, in turn, leads to a modification of the coenological composition of pastures caused by the decrease of the grassland specialist taxa (early flowering, small-sized plants, with storage organs, etc.) and the increase of those typical of fringe communities and of nitrophilous habitats (i.e., tall herbs with late flowering strategies, species with runners and ability to form patches, etc.) [9,10], with an overall decrease in species richness and diversity [9]. Moreover, *Brachypodium* spread reduces the overall feed value of pastures [11], thus negatively affecting mountain farming economic sustainability [12]. Because of this profound impact on biodiversity and ecosystem services, restoration of pastures after tall-grass invasion (*B. rupestre* in the study case) is a paramount issue. This requires a deep understanding of the mechanisms behind the coenological recovery processes that occur after disturbance events [13,14].

It is generally assumed that a higher number of plant strategies and species are present under disturbed conditions [15] since disturbance decreases the chance of competitive exclusion of taxa with traits associated with a low competitive ability (i.e., weaker competitor exclusion) [16–18]. Generally, grazing and mowing are the principle management practices for grasslands. Grazers tend to avoid feeding on *Brachypodium* species for the presence of unpalatable leaves [19]. For this reason the feeding on this species results in harm to domestic herbivores and their welfare. This type of diet, in experimentations regarding sheep grazing, demonstrated how, feeding on this forage type, increased the rumen keratinization [12] and lowered the absorption of nutrients. For this reason, it is not feasible to use sheep grazing as a method for grassland recovery [20,21] and mowing should be the best practice in the restoration of *Brachypodium*-invaded grasslands [12]. Mowing is considered one of the most appropriate management types for ensuring the high conservation value of grasslands [22,23]. It is a non-selective disturbance [24] that, increasing light availability, promotes the survival of light-demanding seedlings, low-growth species [25,26] and germination rates of subdominant plants [27,28]. Moreover, it modifies the functional composition of plant communities by enhancing specific avoidance and tolerance strategies [29–32]. In particular, it was proven that vascular plant species richness was highest with two cuts per year, however the effect may differ in relation to the type of plant community, the timing of cutting and the biogeographic context [33]. This suggests that there is no best universal mowing frequency to promote plant species richness, however, mowing regimes need to be experimented and adapted to the regional and local environmental context.

Regarding *Brachypodium*-dominated communities, disturbance enhances plant biodiversity by reducing its abundance and preventing litter deposition [10,34]. In particular, recurrent mowing on *B. rupestre*-dominated grasslands fostered species of *Festuco-Brometea* and *Festuco-Ononidetea*, although species of *Molinio-Arrhenatheretea* partly replaced these groups after three/four years of mowing activities [35].

Notwithstanding such scientific advancement, there is still a need to understand better the effect of disturbance activities (i.e., mowing) and disentangle such effects from those related to the processes of plant-plant interaction (dominant vs subordinate species) [36]. Abiotic interactions (i.e., disturbance through mowing) could be an important driver in species coexistence at a small-scale, with different effects depending on the type and intensity of the disturbance regime, the frequency in the disturbance events [37], but also depending on the considered time scale [32]. However, biotic interactions (i.e., plant-plant interactions) are considered the major driver at a small-scale. Indeed, dominant species may remove from the community all weaker competitors (i.e., weaker competitor exclusion), acting

as a biotic filter, which leads to the coexistence of more functionally similar species. Otherwise, it is possible that in the absence of dominant species, biotic interactions may lead to coexistence of functionally dissimilar species [32,38].

It should also be considered that past research concerning the functional composition of *Brachypodium*-dominated communities arose from studies that used species abundance weighted data, while investigation with unweighted data (i.e., considering species presence/absence) were largely overlooked. The type of data used may affect the observed trait pattern, and its ecological interpretation [39] since species occurrence and their abundance may be connected to different processes [18,37]. Consequently, we used unweighted species data to investigate the dominant-subordinate plant-plant interactions and the effect of mowing, trying to disentangle their relative filtering effects on species assemblage at a fine scale.

We hypothesized that grassland restoration in a sub-Mediterranean climate context was the result of multiple assembly processes acting with different intensities. In particular, we expected that multiyear mowing, as opposed to vegetation successional processes, drove species turnover from competitive to stress-tolerant/ruderal strategies [36]. Additionally, we expected that multiyear mowing reduced the size of dominant tall grasses and fostered the shift from biotic filters (i.e., weaker competitor exclusion) to abiotic filters (i.e., tolerance and/or avoidance of disturbance) as drivers of the assembly rules. Finally, the weakening of the dominant species may change plant-plant (dominant vs. subordinate) interactions, leading to processes chiefly related to limiting the similarity among interacting individuals.

The specific research questions were: (i) do mowing and the variation of *B. rupestre*-dominance ability act on different species traits at a fine-scale? (ii) what is the relative importance of mowing, which halts the dynamic processes, and of *B. rupestre* features' changes in driving the functional variation of the plant community? (iii) how do such processes affect strategies of resource acquisition and storage, reproduction, space occupation, and temporal niche exploitation? (iv) can mowing decrease the effect that the dominant tall-grass *B. rupestre* has in shaping the functional community composition?

## 2. Materials and Methods

### 2.1. Study Area

The study area was located in the central Apennines (337,398.00 m E, 4757,200.00 m N, WGS 84 coordinate system, UTM zone 33 N) and encompassed north facing slopes, with limestone bedrock. The climate was sub-Mediterranean [40], characterized by the alternation of winter cold stress and summer drought stress. The mean annual rainfall was around 1000 mm, and the average annual temperature was 10–11 °C.

Managed grasslands belong to the *Briza mediae*-*Brometum erecti* *brizetosum mediae* Biondi, Allegrezza & Zuccarello 2005 and the 6210\* habitat [41]. It is a highly diverse, thick turf community, with aboveground productivity ranging from 170 to 200 g·m<sup>-2</sup> of dry matter [41]. Beech woods of the *Fagetalia sylvaticae* order constituted the actual potential vegetation.

The study area had 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; meadows are mown in early summer in the least steep or semi-flat slopes [41]. However, for at least the last 30 years, vast grassland areas, especially the steeper ones, have been undergrazed and are undergoing dynamic processes. Such processes foster the spread of *B. rupestre*'s clonal tussocks which form nearly mono-dominant stands by coalescence of different patches, through different modes (e.g., facilitation performed by thorny plants, accumulation of dead and senescent leaves, which protect the new shoots) [10].

The experimental site (two hectares) was established and fenced in February 2010. The site had homogeneous ecological conditions, i.e., altitude (1200–1250 m a.s.l.), aspect (west-northwest facing slope) and slope angle (20–25°), an average cover value of *B. rupestre* that exceeded 60%

and homogeneous land-use history. The fenced area had a soil (typic/lithic Haplustoll) [42] depth ranging from 30 to 40 cm and a neutral-sub-acid pH. Soil texture was characterized by sand (8–10%), silt (32–35%), and clay (50–60%). Skeleton amount ranged from 45 to 50%, while total nitrogen concentration was 6 to 7 g·kg<sup>-1</sup> [43]. The surface of the experimental sites was divided into two areas (blocks) of 1 ha (100 m × 100 m). Since 2010, within each block, half of the surface, i.e., 0.5 ha (50 × 100 m), was mown twice a year (end of June, namely, just before the *B. rupestris* flowering, and at the end of October), two cm above the soil level; hay and litter were removed after each mowing event. The other half was left unmown, without litter removal.

## 2.2. Sampling Design and Data Collection

In 2017 we randomly selected the coordinates of the lower left hand corners of 10 experimental units (20 cm × 20 cm) for each half block, for a total of 40. In each experimental unit, we recorded the list of vascular species (Table S1).

Since plant height is related to size-asymmetric competition, it is the best candidate to detect the presence of biotic filters exerted by dominant species [18,36]. Thus, we measured the *B. rupestris* plant height in each experimental unit, according to the protocol described by Pérez-Harguindeguy et al. [44], namely, the shortest distance between the upper boundary of the main photosynthetic tissues on a plant (i.e., the top of the general canopy of the plant excluding inflorescences) and the ground level. We measured the available individuals (which were always less than 25, being the experimental unit area 400 cm<sup>2</sup>) and averaged the measurements per experimental units. Finally, we clipped the aboveground phytomass (2 cm above the soil level) and separated that of *B. rupestris* from that of the other plants. We oven-dried the samples of *B. rupestris* aboveground phytomass at 70 °C and weighed them.

To investigate the functional processes behind the variation of species assemblage, for each recorded species, we gathered plant traits related to space occupation (plant height, vegetative propagation, horizontal and vertical architecture), reproductive strategies (seed mass and vegetative propagation), temporal niche exploitation (life span, leaf span) and resource storage strategies (storage organs, leaf anatomy) (Table S2). A description of each trait, with a list of the respective states and data sources, is reported in Table S3. We treated all traits as categorical variables.

## 2.3. Statistical Analysis

To assess if the management type (two level categorical variable, treated as fixed effect) exerted a significant influence on *B. rupestris* plant height and aboveground phytomass, following Bolker, et al. [45], we ran linear mixed-effects models when the response variable was normally distributed (*lmer* function of the lme4 R-package, version 1.1-21) [46], and a penalized quasi-likelihood modelling approach when it was not normally distributed and could not be normalized (*glmmPQL* function, family = gaussian, link = log, of the MASS R-package, version 7.3-51.1) [46]. We accounted for the sampling design using the block identity as a random effect. Significance values were obtained using the Type II Wald Chi-square test and the *Anova* function (car R-package, version 2.1-5) [46].

To analyze the effect of management type and *B. rupestris* aboveground traits in filtering the functional strategies displayed by subordinate species [36], we combined the “experimental unit × species (presence/absence)” matrix with the “species × trait state (presence/absence)” matrix obtaining a “experimental unit × trait state” matrix (number of species sharing the same trait state in each experimental unit). We ran a generalized linear mixed-effects model per trait state, using the Poisson distribution. Fixed effects were *B. rupestris* plant height, *B. rupestris* aboveground phytomass (both quantitative variables) and the type of management (two level categorical variable; mowed vs. unmowed). We accounted for the sampling design using block identity as a random effect. We executed these analyses using the *glmer* function and the lme4 R-package. Then, using an Akaike information criterion (AIC)-based model selection procedure applied to the full model, we selected the best fitting model for each response variable. We used the corrected AIC (AICc), since in our study the ratio between the number of observations and the number of fitted parameters was less than 40 [47]. This

model selection was performed using the *dredge* function of the MuMIn R-package (version 1.15.6) [46]. We accounted for possible within-group spatial autocorrelation of errors [48] in each reduced model, by refitting this model using the penalized quasi-likelihood GLMM (*glmmPQL* function, MASS package, version 7.3-51.1, family = Poisson) and then applying one by one the correlation structures AR1, CompSymm, Exp, Gaus, and Ratio, available in the nlme R-package library [49]. Then, for each model with a different correlation structure, we calculated the Spearman's correlation coefficient (*cor.test* function in stats package, version 3.5.3) between the model's residuals, ordered along the gradient depicted by the predictor variable(s), excluding the first residual of the series, and the residuals of the previous value along the series. Among all the fitted models, including the model without correlation structure, we selected that with the least correlated residuals (i.e., with the lowest and not statistically significant correlation coefficient).

### 3. Results

Mown and unmown experimental units differed significantly ( $p < 0.001$ ) in plant height (15.4 vs. 30.9 cm) and aboveground phytomass of *B. rupestre* (1.9 vs. 11.3 g). Descriptive statistics of *B. rupestre* aboveground phytomass and height are shown in Table 1.

**Table 1.** Descriptive statistics of aboveground phytomass and plant height of *Brachypodium rupestre* in mown and unmown experimental units.

<i>Brachypodium rupestre</i> Features	Treatment	Min.	Max.	Mean	Standard Deviation
Aboveground phytomass (g)	Unmown	5.40	20.30	11.32	4.27
	Mown	0.60	5.20	1.88	1.11
Plant height (m)	Unmown	0.22	0.47	0.31	0.06
	Mown	0.10	0.25	0.15	0.04

The variation in the three considered factors (management, *Brachypodium* aboveground phytomass and height) affected the frequency (i.e., the number of species sharing the same trait) of most of the traits considered (Table 2). In detail, the frequencies of the following trait states were the most positively influenced only by mowing: annual and perennial life span; presence and absence of vegetative propagation as well as runner and rhizome; presence of belowground storage organs, rhizome and tap root; persistent and summer green leaves; mesomorphic and scleromorphic/mesomorphic green leaves; absence of horizontal architecture and reptant species; erosulate upright forbs; plant height  $\leq 20$  and between 21–40 cm; seed mass class 0.51–1.00 and 1.01–2.00 mg (Table 2). Instead, other trait states were influenced only by the changes of *B. rupestre* features, whereby the *B. rupestre* aboveground phytomass was more important than plant height. In particular, the traits that were the most negatively influenced by *B. rupestre* aboveground phytomass were root tuber/stem tuber/root splitter; rosulate forbs; pleiocorm species; rosette and hemirosulate upright forbs; and seed mass  $\leq 20$  mg, while species with succulent leaves were negatively affected by *B. rupestre* plant height (Table 2).

Sedge growth form and spring green leaves were the only trait states positively influenced, besides mowing also by *B. rupestre* features (aboveground phytomass, the former; plant height, the latter, Table 2). Finally, some traits did not respond to any of the considered factors (Table 2).

**Table 2.** Effect of management (mowing/abandonment), *Brachypodium rupestre* plant height and aboveground phytomass (fixed effects) on the traits of species in the plant community (frequencies). A preliminary model selection was run on the full models fitted using generalized linear mixed-effect models with Poisson error distribution and block identity as the random intercept, through an Akaike Information Criterion-based (AICc) procedure. The reduced models were fitted using penalized quasi-likelihood generalized mixed-effect modelling with the same error distribution and random structure, accounting for autocorrelation of residuals. Model parameters (intercept and fixed effect estimates) were obtained after reduced models refitting using different correlation structures to account for autocorrelation, and selecting the model with the least correlated residuals. The correlation structures are indicated with a superscript. Trait states whose model residuals are in any case correlated are in italics.

Response Variable		Intercept Estimate	Fixed Effect Estimate			AICc	logLik
			Management Mown	<i>B. rupestre's</i> Phytomass	<i>B. rupestre's</i> Plant Height		
Life span	Annual <sup>a</sup>	−2.3030 ***	2.6027 ***			72.6	−33.0
	Perennial	2.0395 ***	0.6303 ***			219.1	−106.2
Vegetative propagation	Presence of vegetative propagation	1.6653 ***	0.7392 ***			203.2	−98.2
	Absence of vegetative propagation <sup>a</sup>	0.8329 **	0.6257 ***			151.4	−72.3
	<i>Bulbils</i>	−30.3026 n.s.	28.6932 n.s.			28.9	−11.1
	Root tuber/stem tuber/root splitter	0.2574 n.s.		−0.1046 **		86.5	−39.9
	Runner	1.0296 ***	0.7020 ***			160.8	−77.1
	<i>Rhizome</i>	1.5742 ***	0.6776 ***			185.4	−89.4
	Presence of belowground storage organ <sup>a</sup>	1.6771 ***	0.8840 ***			214.0	−103.7
Storage organs	Absence of belowground storage organ <sup>a</sup>	0.9272 ***				136.8	−66.8
	Rhizome	1.4400 ***	0.8507 ***			190.4	−91.9
	<i>Bulb</i>	−7.2559 n.s.	3.9508 n.s.		12.7530 n.s.	45.1	−18.0
	Root tuber/stem tuber/shoot tuber	−2.9957 ***				20.3	−8.0
Leaf persistence	Tap root	0.3498 n.s.	1.1100 ***			153.1	−73.2
	Persistent green leaves	1.3238 ***	0.6391 ***			174.2	−83.8
	Summer green leaves <sup>a</sup>	1.3863 ***	0.7419 ***			178.9	−86.1
	Spring green leaves <sup>b</sup>	−13.9086 **	8.6920 *		20.1435 *	45.2	−16.7
	<i>Overwintering green leaves</i> <sup>c</sup>	−0.3882 n.s.		0.3188 n.s.		18.4	−3.3
	Succulent leaves <sup>a</sup>	2.1662 n.s.		−2.2784 n.s.		44.5	−18.9
	<i>Succulent/hygromorphic leaves</i>	−30.3026 n.s.	28.4055 n.s.		−18.9194 *	24.0	−8.7
Leaf anatomy	Mesomorphic/hygromorphic leaves <sup>a</sup>	−1.7431 ***				45.5	−20.6
	Mesomorphic leaves <sup>a</sup>	0.7885 **	1.1062 ***			166.9	−80.1
	<i>Scleromorphic leaves</i>	0.0953 n.s.				101.4	−48.5
	Scleromorphic/mesomorphic leaves <sup>b</sup>	1.5005 ***	0.4672 ***			174.3	−83.8

Table 2. Cont.

Response Variable	Intercept Estimate	Fixed Effect Estimate			AICc	logLik
		Management Mown	<i>B. rupestris</i> 's Phytomass	<i>B. rupestris</i> 's Plant Height		
Horizontal space occupation	<i>Absence of horizontal architecture</i>	−0.7985 *	1.8101 ***		116.9	−55.1
	Caespitose <sup>a</sup>	1.6363 ***			161.8	−78.8
	<i>Pleiocorm</i> <sup>a</sup>	1.3798 ***		−0.1141 ***	143.0	−68.2
	Reptant <sup>c</sup>	0.7867 ***	0.9151 ***		149.2	−71.3
	Rosulate <sup>a</sup>	1.1130 ***		−0.1698 ***	113.6	−53.4
	Sedge	−8.6652 ***	7.5229 ***	0.3727 ***	52.3	−21.6
Vertical space occupation	Grass <sup>a</sup>	1.5265 ***			157.8	−76.7
	Rosette forb	1.0707 ***		−0.1616 ***	113.3	−53.3
	Hemirosette upright forb	1.5479 ***		−0.1051 ***	146.2	−69.7
	Erosette upright forb	0.2383 n.s.	1.1486 ***		138.9	−66.1
	Prostrate forb	−1.2138 n.s.		−0.2321 n.s.	33.9	−13.6
Plant height	≤20 cm <sup>d</sup>	0.1440 n.s.	1.5126 ***		149.7	−71.5
	21–40 cm	1.1800 ***	0.6781 ***		165.3	−79.3
	41–60 cm <sup>a</sup>	1.2025 ***			154.3	−75.0
	81–100 cm	−0.9186 *			67.4	−31.6
	≤0.20 mg	1.5283 ***		−0.2310 ***	112.0	−52.6
	0.21–0.50 mg <sup>a</sup>	0.7659 ***			124.5	−60.1
Seed mass	0.51–1.00 mg	−0.0813 n.s.	1.0986 ***		136.2	−64.8
	1.01–2.00 mg	0.9933 **	0.6457 ***		161.3	−77.3
	2.01–4.00 mg	0.2231 **			97.5	−46.6
	4.01–10.00 mg	−0.1625 n.s.			101.6	−48.7
	>10.00 mg	1.1543 n.s.		−22.0392 n.s.	23.7	−8.5

a—compound symmetry structure corresponding to a constant correlation; b—Gaussian spatial correlation; c—autoregressive process of order 1; d—exponential spatial correlation.

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

## 4. Discussion

Our results were consistent with previous findings on the negative effect of disturbance on *Brachypodium* and, as a consequence, in stopping the successional processes [34,35]. In particular, we observed a significant decrease in both aboveground phytomass and plant height. With regard to this, Canals et al. [19] stated that recurrent defoliation led to the decrease of reserves allocated to the belowground organs, which, in turn, reflected in the reduction of the aboveground phytomass [50] and cover value [35,51] of individuals. Moreover, leaf removal leads to the decrease in leaf area, leaf dry matter and lignin content, besides the increase in leaf nitrogen content, thus improving leaf palatability and enhancing the probability of leaf consumption by herbivores [12].

Regarding the variation in the functional features of the plant community at fine-scale, our results showed that, in general, disturbance and biotic interactions contributed independently to the functional changes, each affecting a specific set of trait states, overlapping only in a few cases.

### 4.1. Effects of Mowing

Consistently with previous research based on weighted abundance data [29–31], we observed that mowing chiefly affected the set of trait states linked to tolerance. In this sense, the expansion of perennial species, mainly with the ability of vegetative propagation, has proven to be fostered under management conditions [30]. These species can re-occupy the space very fast after mowing, also because they usually have belowground storage organs (tap roots, bulbs, rhizomes), which allow aboveground re-sprouting thanks to the mobilization of stored resources [36]. In addition, mowing affected traits related to avoidance strategies. In fact, we found that mowing promoted small-sized species (lower plant height classes, reptant strategy) [10,32] and fast growth strategies (i.e., annual life span) [34] or early flowering strategies, related to spring green and mesomorphic leaves, as stated by Catorci, et al. [52] for a sub-Mediterranean climate. It was argued that species with fast growth and only sexual reproduction (absence of vegetative propagation, in the study case) complete their life cycles before the growth of the dominant species [53] and the mowing events [54]. Contrariwise, the increase in species with persistent and tougher leaves (i.e., scleromorphic/mesomorphic leaves) is probably linked to the increase in light that reaches the ground level after mowing [27,55]. Finally, it is worth considering that small seed mass (0.51–2.00 mg) was affected positively by recurrent mowing in line with Kahmen, et al. [56], probably suggesting small seeds as by-products of early flowering strategies [57].

Therefore, our results confirmed the predicted shift towards avoidance and tolerance strategies due to mowing activities and a trend towards a more extensive number of strategies, particularly those linked to a temporal niche occupation. The differentiation of temporal niche occupation is a typical feature of disturbed grasslands and was proven to be related to time-specific trait patterns, driven by the interplay of the context dependent environmental conditions and the temporal fluctuation of resources [58].

### 4.2. Effects of *Brachypodium rupestre* Features

Regardless of the type of management, both the decrease in aboveground phytomass and plant height of *B. rupestre* influenced the functional composition of the plant community by reducing the number of functional features of the surrounding individuals, being aboveground phytomass (which is somehow a proxy for tussock dimension and indicates the range of horizontal space occupied by *B. rupestre* individuals) were more effective than plant height, maybe because the reduction rate of phytomass from an unmanaged to a mown condition was higher than that of plant height (−83% vs. −52%; see Table 1).

The decreasing value of *B. rupestre* aboveground phytomass also enhanced the increase of rosulate and hemirosulate upright forb species, with the main photosynthetic apparatus near the ground level. Contrariwise, sedge species, which shared a similar growth form with *B. rupestre*, showed

a positive relationship with *B. rupestre* aboveground phytomass. The weakening of competitive exclusion processes within the community seems to also be indicated by the increase in species with succulent leaves (i.e., *Sedum* species), linked to the decrease in *B. rupestre* plant height. Succulent plants have systems to store water inside leaves, so that they can grow and bloom later in the season when, in sub-Mediterranean climate, water shortage affects the systems and species with stored water can use a specific and not so crowded temporal niche for reproduction [59]. Moreover, *Sedum* species are small sized plants that can hardly compete with large and tall tussocks of *B. rupestre*. Analogously, the decreasing *B. rupestre* dominance fostered species with small seeds, which benefit from the reduced competition [60]. These results seemed to suggest that the decrease in dominance ability of *B. rupestre* promoted a shift from processes (weaker competitor exclusion) aimed at decreasing the number of functional strategies to processes (limiting similarity) aimed at increasing the number of functional strategies.

An unexpected finding was that *B. rupestre* features did not influence the height of subordinate species. Indeed, as plant height is a trait related to size-asymmetric competition for light, we would have expected a filtering effect on plant community (i.e., weaker competitor effect), reducing shorter species or enhancing the taller ones [18]. Our results, based on categorical traits data and species absolute frequencies instead of abundances, can probably mask this process.

## 5. Conclusions

We observed that recurrent mowing acted both directly and through the reduction in size of the dominant tall grass, so that the final results of the recovery processes were due both to the effect of abiotic (spread of tolerance and/or avoidance strategies) and biotic filtering (shift from weaker competitor exclusion to limiting similarity). We observed that the effect of mowing on the functional variation of the community was more effective than that related to plant-plant interactions and that different drivers mostly acted on different trait states.

Such results support the idea that in the process of plant community recovery, multiple assembly rules (abiotic and biotic filtering processes and limiting similarity) act on different trait states [37,61]. Additionally, our results suggested that one of the main effects of disturbance was the weakening of the importance of processes related to dominant species, allowing other species to coexist through the differentiation of spatial and temporal niches and by different strategies in use/acquisition of resources. This involves an increasing progressive adaptation (i.e., efficiency in resource use) of the plant community during the recovery processes to local environment features and resource fluctuation. Finally, our results strongly support previous suggestions that species success under a management regime must be evaluated with a set of different traits [30].

**Supplementary Materials:** The following are available online at <http://www.mdpi.com/1424-2818/12/1/11/s1>, Table S1: Management type, *Brachypodium rupestre* phytomass and plant height and observed species presence/absence in experimental units, Table S2: "Observed species -by- trait states" matrix, Table S3: Traits and trait states analysed in the present study, description with data sources and references.

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