

Rewilding With Large Herbivores Helped Increase Plant Species Richness in Dry Grasslands.

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Abstract

Rewilding is a form of environmental conservation and ecological restoration that has the potential to enhance biodiversity and create self-sustainable natural environments. The key approach is reintroducing lost keystone animal species, e.g. large herbivores and predators. One of the few places in all Central Europe where such efforts can be seen in practice is located in Milovice, Czech Republic, where European bison, Exmoor pony, and Tauros cattle have been introduced in 2015-2016 to a former military training area, now NATURA 2000 site and National nature monument Milovice-Mlada. The prevailing vegetation type is a forest-steppe with *Bromus erectus* dominated dry grasslands mixed with deciduous shrubs and trees. After the cessation of military use, the area was mostly left unmanaged during 1989-2010 which led to successional changes and increased dominance of tall grasses, and bush encroachment. We monitored grassland vegetation in 2017–2019 in 30 randomly distributed plots (2×2 m) inside the grazed area and in ungrazed control plots. Natural grazing increased species richness and the cover of forbs, while the proportion of grasses and legumes remained little affected. Grazing promoted small-statured species while ungrazed plots harboured taller ones. Large herbivores thus made the grassland shorter and richer both in overall species and flowering forbs. We can conclude that the introduction of large herbivores has had a beneficial effect on species richness and helped in restoring forest-steppe vegetation of better quality and conservational value.

Introduction

Rewilding is a powerful new term in conservation (Soulé and Noss 1998), presenting a form of environmental conservation and ecological restoration that has far-reaching potential to enhance biodiversity, make self-sustainable environments and alleviate impacts of climate change. Key efforts in rewilding aim at reintroducing lost animal species to natural environments, restoring natural processes and wilderness areas, and providing connectivity between such areas (Schepers and Jepson 2016). Most rewilding approaches fit the concept of trophic rewilding, defined as “an ecological restoration strategy that uses species introductions to restore top-down trophic interactions and associated trophic cascades to promote self-regulating biodiverse ecosystems” (Bakker and Svenning 2018). Importantly, rewilding has received increasing consideration among the public and policymakers as a conservation tool for the 21st century (Jepson 2016; Svenning et al. 2016; Pettorelli et al. 2018; Root-Bernstein et al. 2018).

Herbivory by large ungulates shapes the structure, diversity, and functioning of most terrestrial ecosystems. In Europe, however, like in other parts of the world, large grazers have been either extinct for centuries (wild horses, aurochs – wild cattle), or survived in captivity only (wisent – European bison) (Németh et al. 2017). With large grazers absent, forest and grassland ecosystems lack an essential link in the trophic chain, and, perhaps more importantly, keystone species capable of ecosystem engineering, a power strong enough to create and maintain particular habitats (Feurdean et al. 2018). Therefore, contemporary endeavours in the management of nature reserves, grassland ecosystems in particular, have to adopt costly means of preventing succession towards the closed forest, something which had been secured by large grazing mammals and elements (e.g. fire) in the past. Accordingly, the intent of

reintroducing megaherbivores to maintain diverse plant and animal communities is financially rational from a long-term perspective. Last decades in Europe have seen attempts to (re)introduce large grazers to areas intended for rewilding, with a well-known pilot project in the nature reserve of Oostvaardersplassen in the Netherlands (e.g. Lorimer and Driessen 2014). Activities of aurochs, horses, and wisents include selective grazing and browsing (bark peeling, twig removal), trampling, wallowing, and dung and urine deposition. These processes affect grassland composition and structure (Cromsigt et al. 2017; Zielke et al. 2019), growth of shrubs and trees (Garrido et al. 2020; Guyton et al. 2020), and nutrient distribution (e.g. van Klink et al. 2020), which in turn strongly influence not only rare or endangered plants but also populations of other organisms, e.g. arthropods (van Klink et al. 2016; Garrido et al. 2019). Although rewilding projects are apparently on increase globally, manipulative experiments in this field remain scarce. Thus, conservative policymakers lack simple hard data on the suitability of this still unusual and novel practice of nature conservation, hindering its implementation.

Plants evolved multiple strategies how to avoid, tolerate, or resist grazing, which supports a broad variety of small species, often forbs and legumes at the expense of tall grasses (Garrido et al. 2019). Species with enhanced capacity of lateral spread and clonal reproduction may profit under disturbed grazed conditions (Klimešová and Herben 2016). Species with high specific leaf area (SLA hereinafter), capable of fast compensation of lost biomass, can also increase (Gilhaus et al. 2017; Garrido et al. 2019). Small seeded species better survive in animal entrails and are better dispersed via endozoochory, while large-seeded species should get an advantage in ungrazed areas with dense vegetation with deteriorated light conditions for seedlings (Albert et al. 2015).

Here we report on the first rewilding project in the Czech Republic, Central Europe, established in 2015 in Milovice, and focus on one elementary question: How does the introduction of large grazers affect vegetation in a forest-steppe ecosystem? We expect a change in species composition, directed towards more forb and legume dominated grassland (Hypothesis H1). We expect a rise in species richness because trampling and grazing have the potential to disrupt the dominance of competitively strong species (e.g. *Bromus erectus*) and create microhabitats for colonization (H2). We expect a shift in species strategies reflected by traits towards species with low stature, high capacity for clonal growth, small seeds, and high SLA under the grazed conditions (H3). We also evaluated the potential of grazed vegetation for the conservation of rare or endangered plants.

Methods

Study site

The Milovice military training area was established in 1904 on 34.6 km² and gradually expanded its area to 50 km². Following the cessation of military use in 1989 and departure of Soviet army in 1991, parts of the open training fields were subjected to public development, while three large areas were proclaimed a Site of European Community Importance (SCI) Milovice-Mladá, and eventually a National nature

monument Milovice-Mlada. It remained unmanaged, except for occasional/local disturbance by armoured/offroad vehicles since 2009-2010.

The natural setting is the gently rolling Středočeská Tabule Plain formed by Mesozoic carbonate-rich sandstones, siltstones, and claystone, and covered by brown soils, rendzinas, and carbonate-rich sands. The locality elevation spans between 200–250 m a.s.l., with mean annual temperature 8–9 °C and annual precipitation 500–600 mm. Woodlands dominated by *Quercus petraea*, *Pinus sylvestris*, and *Betula pendula* are interspersed by finely grained mosaics of shrublands, grasslands, and early successional stages of vegetation (Čížek et al. 2013). Much of the locality had suffered succession-driven homogenization of the once diverse vegetation mosaic by competitively strong grasses, mainly *Calamagrostis epigejos*, *Bromus erectus*, and *Arrhenatherum elatius*, ruderal forbs, and shrubs, mainly *Crataegus* sp., *Prunus cerasifera*, *Prunus spinosa* and *Rosa canina*.

There are two separate pastures maintained by large ungulates, Southern (Milovice) and Northern (Traviny). The Southern locality (Milovice, 40 ha; 106 ha since 2018; 50.2373122N, 14.8878125E) has been grazed since spring 2015 by ca. 35 Exmoor ponies and ca. 20 Tauros cattle. The Northern locality (Traviny, 125 ha; 50.2821017N, 14.8740686E) has been grazed since winter 2015/2016 by ca. 35 Exmoor ponies and ca. 20 wisents. Both localities are thus year-round grazed by horses and big bovids. During the period 2017-2019, the Southern and Northern area was grazed by a combined density of 1.0-0.6 animal ha⁻¹ and 0.2-0.4 animal ha⁻¹, respectively (numbers of animal density are given in chronological not numerical order and exclude young-of-the-year).

To provide variable management regimes, both temporally and permanently ungrazed plots of various sizes (units to tens of hectares) are present both within and outside the grazing reserves at any given time. The animals receive no supplementary feeding and no medication, except for strictly individual cases, e.g. translocations. Predators and small to mid-sized wild animal species, e.g. roe- and fallow deer, may (and do) enter the pastures either freely (electric wire-fenced Southern area) or using designated wildlife passes (mesh wire-fenced Northern area) (Jirků et al. 2018). To control grazing intensity, social stress and facilitate gene-flow, two to three-year-old surplus animals are transferred to similar projects in the Czech Republic and abroad.

Vegetation sampling

In 2017, we established 30 monitoring sites inside both grazed areas, each containing two plots (2×2 m), one grazed and one ungrazed (control), located in a wooden enclosure (4×4 m). However, most fenced enclosures (controls) were damaged, so that we monitored only nine plots that were clearly without grazing impact in 2017. In 2018, even these nine control plots were damaged and at least partly grazed. We, therefore, established seven additional control plots outside the grazed area, within the same vegetation type in close vicinity. In all the plots we visually estimated cover of vascular plants at the peak of vegetation season in June/July 2017–2019. The grazing had been underway for two years already at the time when we set up the plots in the Southern area, and for one year in the case of the Northern area.

Therefore, the grazed plots have been different from the ungrazed ones from the beginning of our monitoring.

Plant functional traits and functional groups

To characterize the main species strategies (see e.g. Klimešová and Herben 2016), we excerpted 6 plant functional traits from available databases. Specific leaf area (SLA), canopy height, and seed mass (SM) were taken from the LEDA database as the mean value of multiple entries in the database (Kleyer et al. 2008). Clonal growth characteristics, i.e. persistence of the clonal connection, multiplication rate, and lateral spread, were taken from the CloPla database (Klimešová et al. 2017). We also characterized species as grasses (*Poaceae*), legumes (nitrogen fixing dicots, *Fabaceae*), and forbs (other dicots).

Statistical analyses

Effect of grazing and the difference between the years in species composition of the plant community was analyzed by Canonical Correspondence Analysis (CCA) using the Canoco 5 software (ter Braak and Šmilauer 2012). At first, we tested the effect the grazing and year together, i.e. using these factors as explanatory variables. Then we tested the effect of grazing (with the effect of the year as a covariate, i.e. removing its effect from the analysis) and effect of the year (with the effect of grazing as covariate) separately. Significance was tested by Monte-Carlo permutation test with 999 permutations (Šmilauer and Lepš 2014). As the species CCA score from analysis which tested the effect of grazing indicates whether plant species prefer grazed or ungrazed conditions, we used this score to identify species traits important for response to grazing (Šmilauer and Lepš 2014). The species CCA score was explained by traits using the conditional interference tree, which is a method of non-parametric regression. It displays a binary tree built through a process of recursive partitioning. The hierarchical splitting of the data was based on selecting the trait best distinguishing species response and dividing samples into two groups (according to the splitting value of the trait). The analyses were performed using the R Party package (Hothorn et al. 2006). Other univariate variables, i.e. number of species, Simpson diversity index, and the cover of functional groups, we tested with two-way analysis of variance, where the effect of grazing and year were used as explanatory variables. If the effect of grazing was significant, we tested its effect within each year separately using a t-test. All univariate analyses were conducted in the R software version 3.5.1. (R Core Team 2018).

Results

Overall, we recorded 157 species, out of which 7 species appeared on the red list (Grulich 2012) (*Carlina biebersteinii*, *Centaureum erythraea*, *Cirsium acaulon*, *Dorycnium herbaceum*, *Gentiana cruciata*, *Potentilla recta*, *Lotus maritimus*). No species was in the category of critically endangered. The composition of the vegetation was significantly affected by grazing and differed between years (Figure 1, Table 1). Grazing increased species with lower canopy height. No other trait significantly discriminated CCA score of species in the conditional interference tree analysis (Figure 2).

Grazed plots contained significantly more species than ungrazed plots during all three years ($F= 29.4, P < 10^{-3}$; Figure 3). Species number per plot did not differ between the years ($F= 2.8, P= 0.065$). Simpson diversity was significantly higher in grazed plots only in the first year ($F= 20.8, P < 10^{-3}$; Figure 3) and did not differ between the years ($F= 0.7, P= 0.484$). No interaction of grazing and year was significant.

Cover of grasses was not significantly affected by grazing ($F= 2.7, P= 0.102$), but differed between the years ($F= 5.8, P= 0.004$; Figure 4). Cover of forbs was higher in grazed plots in all three years ($F= 14.0, P < 10^{-3}$). Over the years, the cover of forbs increased ($F= 9.5, P < 10^{-3}$). Legumes were affected neither by grazing ($F= 2.4, P= 0.128$) nor by year ($F= 1.2, P= 0.296$). No interaction of grazing and year was significant.

Discussion

The number of rewilding projects in Europe has been on a steady increase and their perspectives in vegetation and wildlife recovery are vividly discussed (Svenning et al. 2016). Nevertheless, empirical evidence has been inadequate and direct experiments rare so far. Here we summarize the effects of grazing on dry grassland vegetation and its functional composition following the introduction of large ungulates in Milovice, Czech Republic, in 2015.

As an immediate effect of the year-round wild ungulates presence in the two areas, visible at first sight even by a non-trained eye, we observed a distinct reduction of tall coarse grasses and an increase in the exposed barren ground (cf. Henning et al. 2017), and browsing influence on shrubs and trees. Vegetation changes, as captured by our small-scale monitoring, were partly expectable (Henning et al. 2017; Chodkiewicz 2020). Grazing affected vegetation composition and promoted species with lower canopy height. Regarding species richness, grazed plots were more diverse and getting richer in forbs over the years. The same direction of vegetation changes following the introduction of large grazers, towards swards of lower canopy height richer in flowering forbs, was also reported from grasslands in Sweden (Garrido et al. 2019) and sandy grasslands and heathlands in Germany (Henning et al. 2017). Such an outcome is in line with experimental herbivore exclusion undertaken in Oostvaardersplassen, the Netherlands, which after three years led to a strong decline in plant species richness in established pastureland (van Klink et al. 2016). In their exceptional 3-year-long experiment with horse grazing, Garrido et al. (2019) concluded not only rising plant diversity and activity of pollinators in grazed areas, but also established a link between plant species richness and the number of pollinators.

The analysis of functional composition revealed no changes in SLA, contrary to the expected increase noticed elsewhere (Garrido et al. 2019). High SLA is a trait associated with fast growth, e.g. in ruderal communities, or under intense grazing pressure and subsequent quick biomass recovery in plants with grazing-tolerance strategy. It probably takes longer than three years for such a change to manifest at the community level, going along with still more pronounced change in species composition. Seed mass and the three clonal growth traits remained also unsupported, again likely needing more than three seasons of grazing to cause a fundamental change to the community structure.

We were thus able to validate two of our six hypotheses. Changes in species richness and canopy height occurred rapidly over three years and can be related to the fast reduction of dominant tall grasses and the creation of gaps by trampling. Such release in cover offered better conditions for species with lower canopy height already present in the plots, and also provided space for the establishment of seedlings or vegetative colonization; gap colonization is considered an underlying source of grassland community change (Bullock et al. 1995).

The tricky part of the experiment was keeping the animals out of enclosures, i.e. enclosures containing the control plots. Despite massive efforts, all enclosures were gradually damaged with signs of grazing or resting inside. It is a quite well-known fact from agricultural practice, that such enclosures located in pastures attract animals because they contain ungrazed vegetation and provide excellent scratching opportunities. Therefore, it is advisable to equip the enclosure with accessory fencing in a form of electric fence or barb wire, the latter prohibited by law in the Czech republic, to discourage scratching and penetration of animals. However, the enclosure electric-wiring requires either close proximity of border electric fence, or excess costs for individual energy supply for each enclosure, thus hampering random distribution and/or sustainability of underfinanced projects, respectively. Another option is to locate the control plots outside the grazed areas; such an approach is, however, feasible only when there is vegetation of similar qualities in close vicinity. Needless to say that if the control plots remained unaffected by animals, the difference we found between grazed and ungrazed vegetation would likely be more pronounced.

We conclude that three years of large grazers' presence in the two areas substantially modified the vegetation, helped increase plant species richness as well as the proportion of flowering forbs. Vegetation changes caused by grazing will undoubtedly continue and much will depend on its intensity. Having in mind the welfare of other important taxonomic groups, e.g. arthropods, it is the low-to-intermediate level of grazing pressure that is desirable. The density of large herbivores in our study area is appropriate in this respect (below 0.5 livestock units ha⁻¹ since 2020) and should be adequate for creating and maintaining a mosaic of short and tall vegetation of various successional stages, beneficial to the diversity of plants and arthropods.

Declarations

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Conflicts of interest/Competing interests

The authors have no conflicts of interest to declare that are relevant to the content of this article.

Availability of data and material

Data will be available via Dryad repository.

Code availability

Not applicable.

Authors' contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Ondřej Mudrák and Miroslav Dvorský. The first draft of the manuscript was written by Miroslav Dvorský and Ondřej Mudrák and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Ethics approval

Not applicable.

Consent to participate

Not applicable.

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Tables

Table 1 Summary of the CCA testing the effect of grazing and year on the species composition of plant community.

Explanatory variable	Covariate	Explained variability	pseudo-F	P
Grazing, Year	None	5.85%	2.2	0.001
Grazing	Year	2.59%	2.8	0.001
Year	Grazing	3.33%	1.8	0.001

Figures

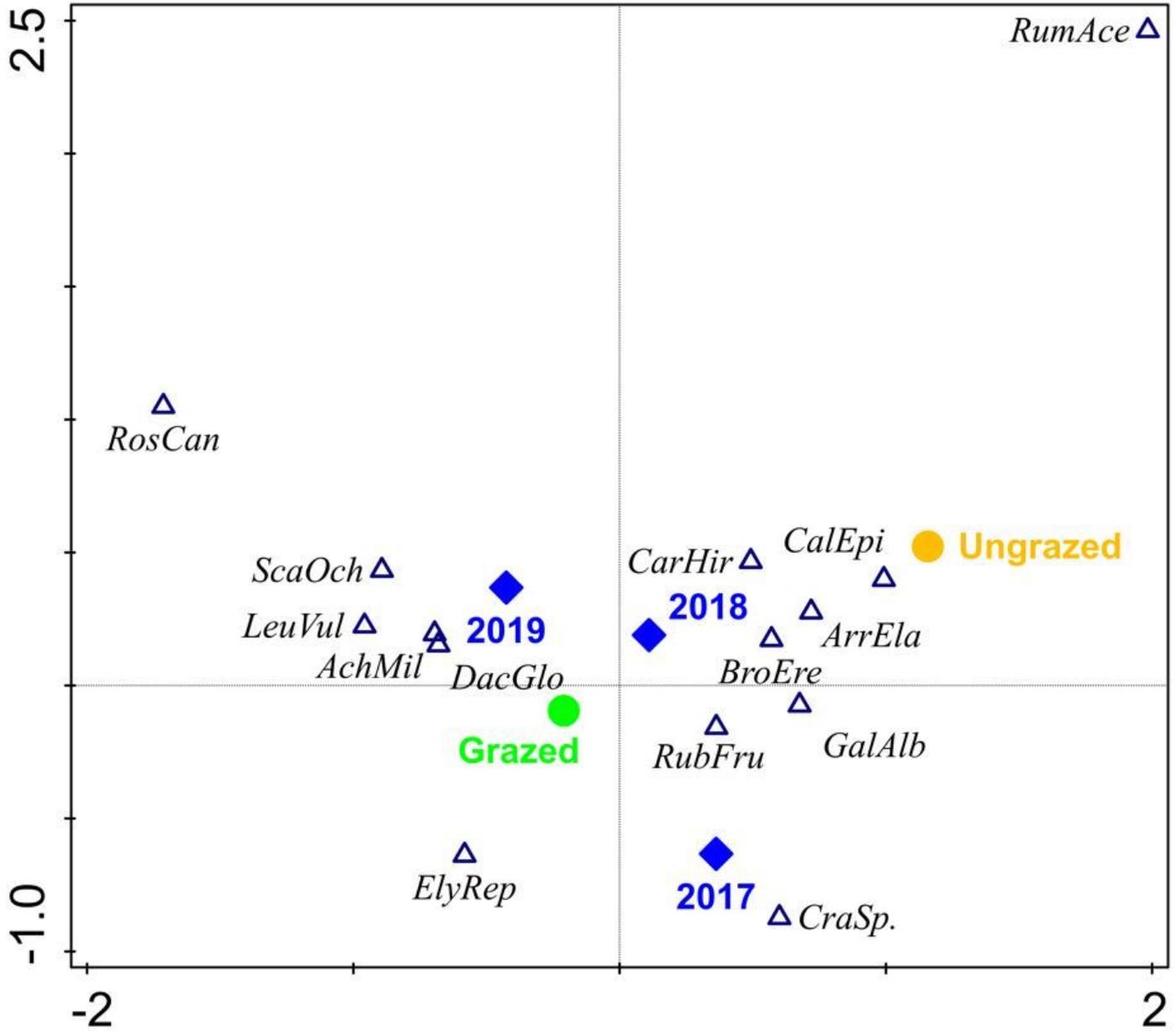


Figure 1

Results of the CCA analyzing the effect of grazing and year on the species composition of the vegetation. For significance, see Table 1. Species abbreviations: AchMil – Achillea millefolium agg., ArrEla – Arrhenatherum elatius, BroEre – Bromus erectus, CalEpi – Calamagrostis epigejos, CarHir – Carex hirta, CraSp. – Crataegus sp., DacGlo – Dactylis glomerata, ElyRep – Elymus repens, GalAlb – Galium album, LeuVul – Leucanthemum vulgare, RosCan – Rosa canina agg., RubFru – Rubus fruticosus agg., RumAce – Rumex acetosa, ScaOch – Scabiosa ochroleuca.

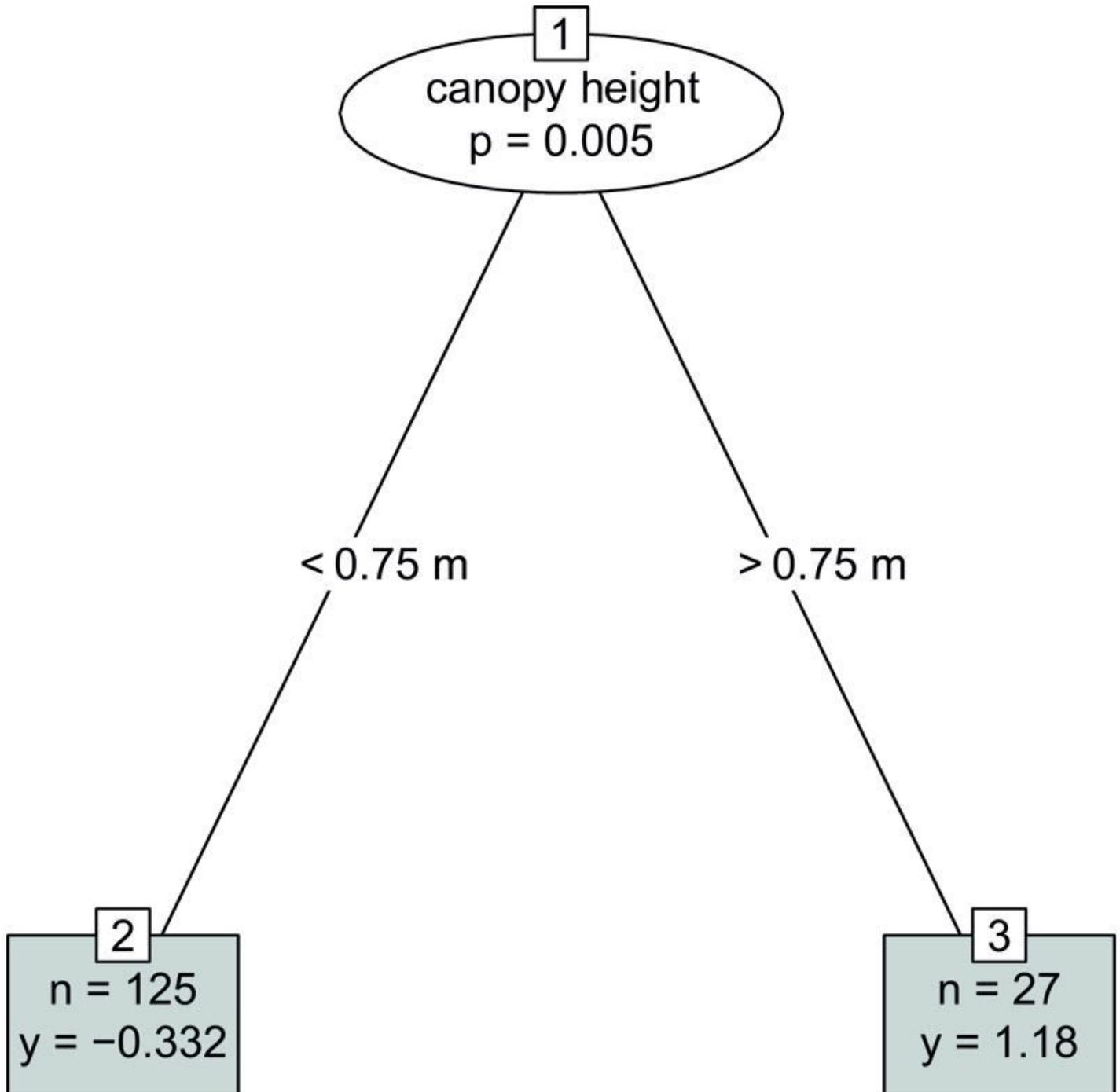


Figure 2

Conditional interference tree of the species CCA score (y). A negative value of y indicates species preference for grazing while a positive value indicates species preference for ungrazed plots. "n" shows the number of species within the category.

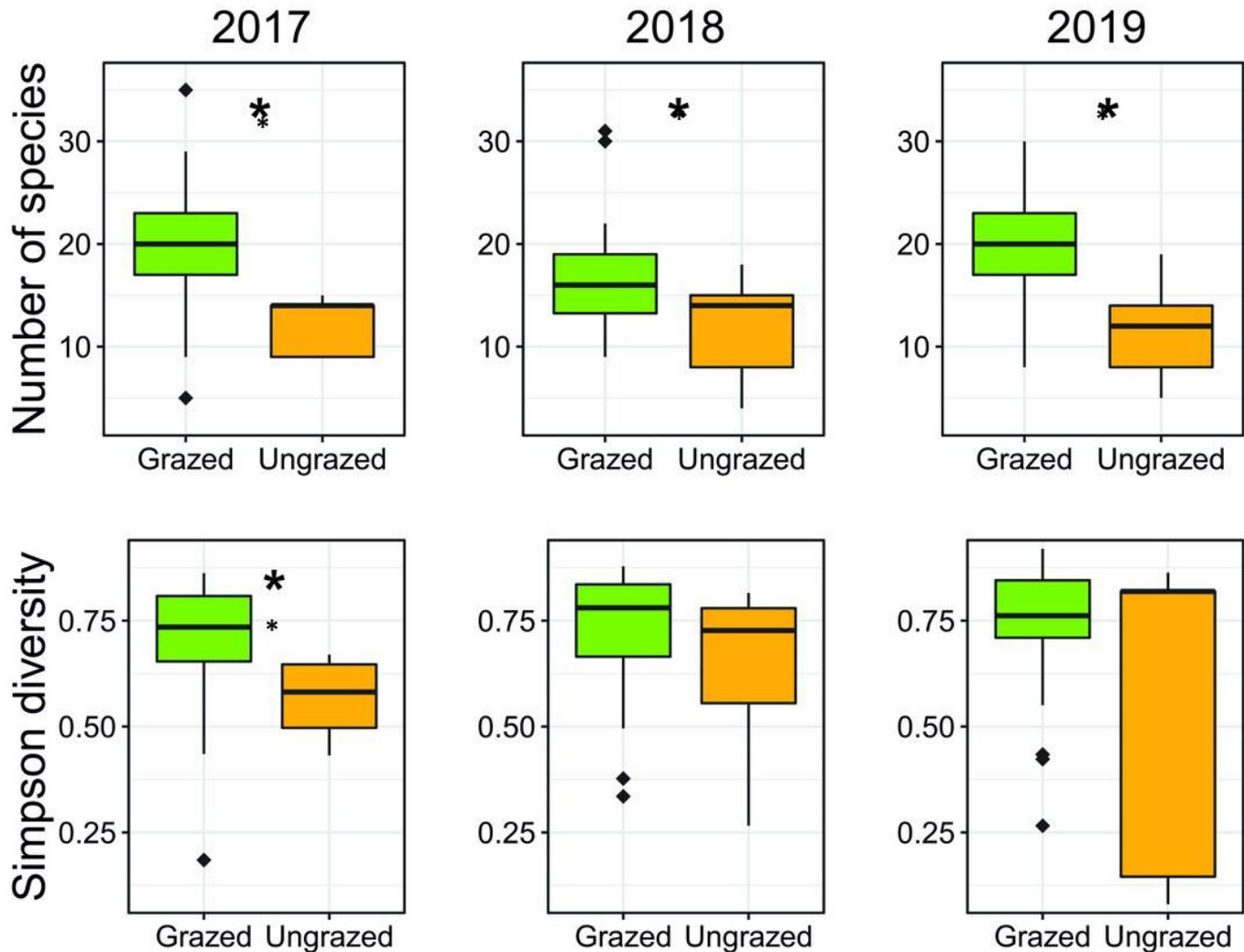


Figure 3

Species number and Simpson diversity index in grazed and ungrazed plots in individual years. Asterisk signs the significant difference ($P < 0.05$) between grazed and ungrazed plots indicated by t-test. Shown are median, inter-quartile range, and span of the values. Outliers are displayed as diamonds.

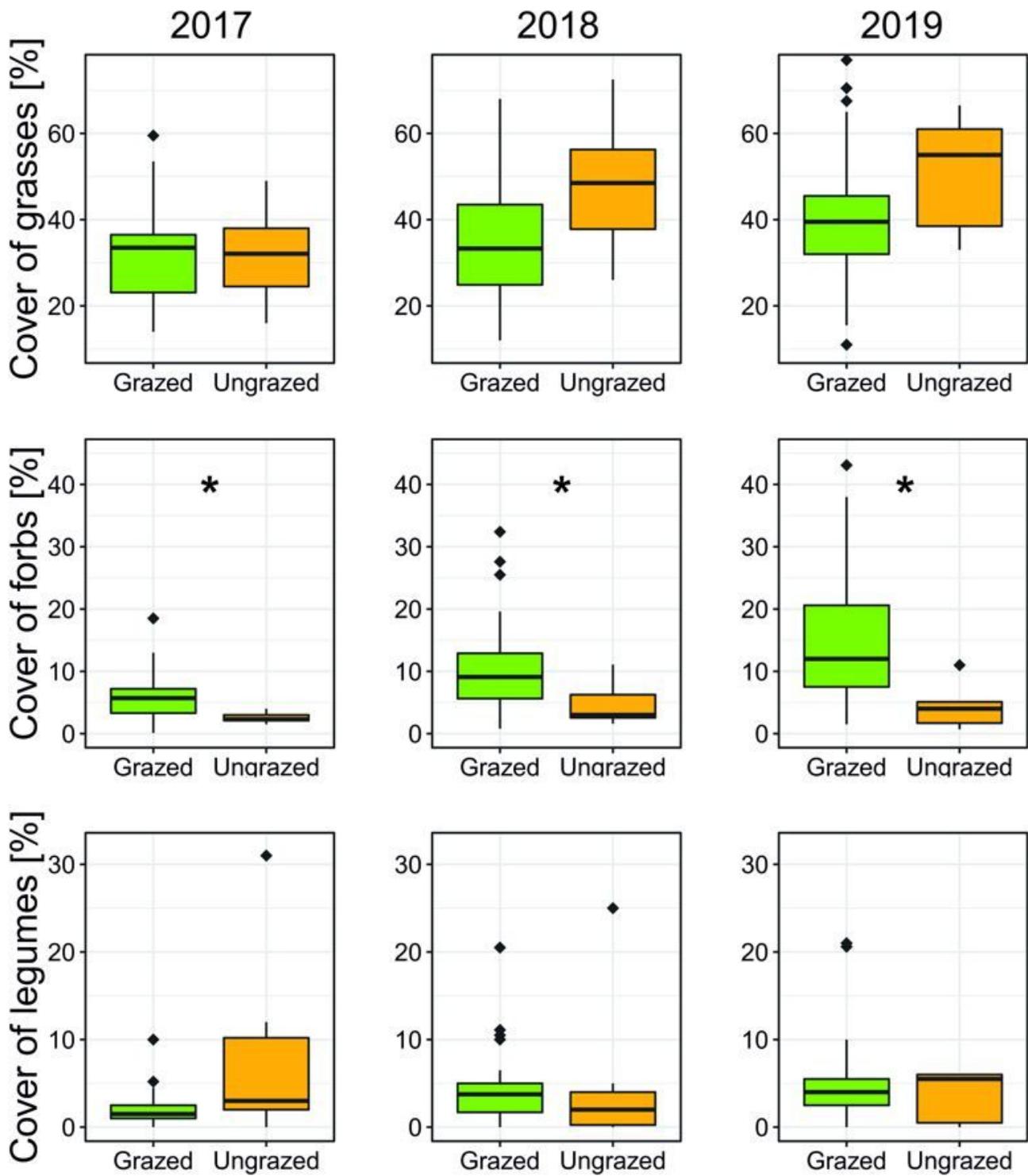


Figure 4

Cover of functional groups in grazed and ungrazed plots in individual years. Asterisk signs the significant difference ($P < 0.05$) between grazed and ungrazed plots indicated by t-test. Shown are median, interquartile range, and span of the values. Outliers are displayed as diamonds.