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Quantifying edge influence on plant community structure and composition in semi-natural dry grasslands

Rocco Labadessa , Audrey Alignier, Stefania Cassano, Luigi Forte & Paola Mairota

Keywords

Alta Murgia; Boundary attribute; Depth of edge influence; Edge dynamic; Edge effect; Grassland conservation; Habitat fragmentation; Magnitude of edge influence

Abbreviations

DEI = Depth of edge influence; EIV = Ellenberg–Pignatti indicator values; MEI = Magnitude of edge Influence.

Nomenclature

Conti et al. (2005) for vascular plants, Mucina et al. (2016) for plant communities

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Introduction

Semi-natural grasslands of the Western Palearctic region are considered among the most species-rich habitats in the world (Dengler et al. 2012), where biodiversity had

incrementally increased during millennia of extensive land-use and management practices, including grazing and deliberate burning regimes (Willems 1990; Turbé et al. 2010; Dengler et al. 2014). Vascular plant diversity of certain European grasslands even exceeds that of

Abstract

Aims: We investigated the influence of anthropogenic boundaries on semi-natural grassland plant communities in terms of: (1) depth and magnitude of edge influence and (2) changes in plant community composition associated with boundary attributes.

Location: Alta Murgia, Puglia, southeast Italy.

Methods: Sampling sites were selected taking into account three boundary attributes thought to be most important in the study area, i.e. adjacent land use, presence/absence of stone wall at the patch boundary and occurrence of slope. Plant communities were surveyed along 40-m transects perpendicular to the patch boundary. Each transect was divided in six plots at given distances from patch boundary. Data were collected related to a set of plant community descriptors referring to structure, composition, life history traits and ecological attributes. A novel methodology that relies on the definition of inner plots as relative interior habitat was introduced for assessment of the depth and magnitude of edge influence. DCA was then used to characterize edge communities.

Results: Significant edge influence on grassland plant communities was limited to the adjacent boundary (<2.5 m). For the majority of descriptors, magnitude of edge influence was higher in grasslands adjacent to crops rather than to roads, in sloping rather than flat edges, and in wall-bounded rather than unbounded patches. Plant assemblages dominated by either ruderal species or xerothermic grassland species were, in all cases, associated with unbounded edges, while distinct assemblages were observed in wall-bounded plots according to their different morphology. Wall-bounded sloping edges were characterized by woodland species, whereas their non-sloping analogues were associated with calcareous grassland species.

Conclusions: Our findings provide new insights into the influence of anthropogenic boundaries on semi-natural dry grassland by assessing the depth and magnitude of edge influence, as well as the changes in composition of edge plant communities as a function of the combination of boundary attributes. While the method implemented enabled us to address many of the issues experienced in quantification of edge influence in herbaceous communities, it also allowed us to demonstrate the major role of boundary attributes in modulation of edge community patterns.

tropical rain forests (Wilson et al. 2012), traditionally thought to be the most diverse ecosystems on Earth. Today, many of these semi-natural grassland ecosystems of high conservation value are threatened by dramatic land-use changes associated with the current socio-economic and political context in Europe (Cousins & Eriksson 2008). Land-use change is one of the main factors responsible for the loss, modification and fragmentation of habitats (Wiens 1992; Forman 1995).

As a direct consequence of fragmentation, the increasing extent of patch boundaries leads to a series of specific habitat modifications, the so-called edge influence, which may have strong consequences on habitat and community structure and on their dynamics (Saunders et al. 1991; Forman 1995; Laurance et al. 2002; Cadenasso et al. 2003). When compared with interior habitat, communities at the boundary zone (edge; cf Forman 1995) commonly show significant variation in species richness and diversity (Risser 1995; Ries et al. 2004), becoming richer in generalist and invasive species (Brothers & Spingarn 1992; Cadenasso & Pickett 2001) but also representing invaluable refugia for rare or edge-specialist organisms (MacArthur & MacArthur 1961; Berg & Part 1994; Ries & Sisk 2010).

These effects on biodiversity, as well as many other edge-related patterns, are further modulated by boundary attributes, e.g. related to morphology and origin (Forman 1995). Adjoining land-use type and slope, as much as the presence/absence of barriers are key features in modulating edge ecological patterns (e.g. Saunders et al. 1991; Harper et al. 2005; Jansson 2009). For example, being adjacent crops leads to an increase in nutrient inputs at the edge, which may favour the growth and dispersal of nitrophilous plant species (Pocewicz et al. 2007), while roadside edges are likely to be colonized by non-native plant species (Forman & Alexander 1998; Hansen & Cleverger 2005). Changes in water, light and nutrient availability along sloping edges act as direct drivers of plant growth and vegetation dynamics (Beatty 1984; Matlack 1993; Fox et al. 1997). The occurrence of abiotic barriers to migration and/or seed dispersal, such as walls or ditches, is also crucial in modulating exchanges among ecosystems (Mader et al. 1990; Higgins et al. 2003). Therefore, a thorough understanding of edge patterns in relation to the role of boundary attributes is required for the assessment of conservation strategies for fragmented semi-natural habitats.

Despite increasing efforts for the conservation of European semi-natural grassland ecosystems, current theories and methods for investigation of edge-related patterns mostly rely on studies from forest edges (e.g. Ranney et al. 1981; Chen et al. 1992; Harper & Macdonald 2001), where grasslands only play a minor role when considering the forest–grassland interface (e.g. Camarero et al. 2000;

Breshears 2006; Alignier & Deconchat 2013). Approaches traditionally taken to assess the depth and magnitude of forest edge influence may show significant limitations when applied to different types of vegetation. Most approaches require the pre-definition of independent reference sites representing the homogeneous interior habitat (Chen et al. 1992; Didham & Lawton 1999; Harper & Macdonald 2001). However, such pre-definition of interior habitat is not always straightforward in mosaic herbaceous communities, for example in many rocky and stony semi-natural grasslands. While many vegetation types may show rather constant structural and functional community patterns across different sites and scales, this is not the case for many forms of herbaceous vegetation that are known to be naturally heterogeneous and variable in spatial and species arrangement (Giladi et al. 2011; Dengler et al. 2014; Turtureanu et al. 2014).

In this context, our aim was to investigate the influence of anthropogenic boundaries on the structure and composition of grassland plant communities of Alta Murgia (southeast Italy) in order to provide new insights for assessment of conservation strategies for protected semi-natural grasslands. More specifically, we used a comparative approach to assess (1) the depth and magnitude of edge influence and (2) changes in plant community composition associated with boundary attributes.

Methods

Study area

This study was carried out in the central portion of Alta Murgia (40.985°–40.885° N, 16.470°–16.570° E), a calcareous plateau in southeast Italy and partly included within the Natura 2000 site “Murgia Alta” and the National Park “Alta Murgia”. Ranging from 300 to 700 m a.s.l., this area is primarily characterized by its compact platform of Cretaceous limestone, with very shallow and rocky soils and total lack of surface water courses. The climate is typically sub-mediterranean, with annual temperatures from 7 °C in Jan to 25 °C in Jul/Aug, and rainfall mostly in autumn–winter, of 570 and 700 mm·yr⁻¹ with occasional snowfall above 500 m a.s.l. The phytoclimate is semi-continental, with meso-mediterranean thermo-type, ombro-type, from dry to sub-humid, and growing season bound by both winter temperature and summer drought (Forte et al. 2005).

With the exception of residual patches of downy oak (*Quercus pubescens* s.l.) woodland and Aleppo pine (*Pinus halepensis*) plantations, the upper part of the plateau is mainly covered with semi-natural dry grasslands. Substantial losses of this ecosystem occurred between 1990 and 2000, mainly due to the increase in durum wheat production (Boccaccio et al. 2013). To date, grasslands cover

~29 800 ha and represent what remains of the ~80 000 ha existing at the beginning of the 20th century (Mairota et al. 2013).

Among the most interesting grassland plant communities occurring in this area, those belonging to the endemic alliance *Hippocrepido glaucae-Stipion austroitalicae* (class *Festuco-Brometea*, order *Scorzoneretalia villosae*) are listed in Habitat Directive 92/43/EEC (Natura 2000 code: 62A0). These grasslands are primarily characterized by the endemic feather-grass *Stipa austroitalica* (Annex II Habitat Directive), and host a remarkable set of species of biogeographic concern, e.g. the endemic taxa *Thymus spinulosus*, *Helianthemum jonium*, *Centaurea deusta* subsp. *deusta*, *Carduus micropterus* subsp. *perspinosus*, *Dianthus garganicus* and *Iris pseudopumila* (Forte et al. 2005).

Sampling design

We collected plant data during Apr–May 2013 within 16 grassland sites (mean patch size = 248.6 ± 136.9 ha; see also Appendix S1). These sites had all been similarly subjected to grazing and periodic light summer burning and are still actively managed through extensive sheep grazing. They were selected considering a range of boundary conditions representative of the study area. We considered two alternatives for the three boundary attributes thought to be the most important in the study area: adjacent land use (annual crop or road), presence/absence of stone wall at the patch boundary, and inclination of the grassland towards the boundary on a slope $>25^\circ$ (steep or flat boundary). We selected two sites for each combination of attributes, so that each option was represented in 50% of the sites.

Within each of the 16 sites we surveyed plant communities from six non-adjacent plots (2.5 m \times 0.5 m) along a 40-m transect perpendicular to the patch boundary. The six plots were laid at given distances from the patch boundary (0–40 m) with their longer side parallel to the patch boundary and according to a geometric sequence (ratio 2): A = 0 m, B = 2.5 m, C = 5.0 m, D = 10.0 m, E = 20.0 m and F = 40.0 m (Fig. 1).

A set of plant community descriptors, i.e. referring to structure, composition, life history traits and ecological attributes, was then used for the subsequent analyses. Cover values of vascular plant species (%) were recorded

in each plot and used to compute species richness (S), Shannon index (H') and Simpson index (λ). Mean height of the grass layer (cm) was also noted in the field. Species were classified according to nine life-form categories based on Raunkiaer's (1934) classification: phanerophytes (Phan), chamaephytes (Cham), perennial grasses (H grass), perennial forbs (H forb), biennials (H bien), annual grasses (T grass), annual forbs (T forb), bulbous geophytes (G bulb), rhizomatous geophytes (G rhiz). Ellenberg–Pignatti indicator values (EIV; Pignatti et al. 2005), weighted by plant species cover, were also computed for plots. EIVs are based on ecological requirements and specific plant traits of adaptation to light (L), temperature (T), continentality (C), moisture (H), soil pH (R) and nutrients (N).

Statistical analysis

A methodological modification was introduced to the conceptual framework presented by Harper & Macdonald (2001) for quantification of the depth and magnitude of edge influence because the heterogeneous spatial and species arrangement of the studied herbaceous communities hindered pre-definition of interior habitat, which is usually needed for assessment of edge influence. In particular, the novelty of the method consists in the comparison of each vegetation plot with the set of inner plots relative to it, therefore representing a comparative, rather than an absolute reference for interior habitat.

For each community descriptor we first computed the mean value among plots surveyed at the same distance. Then we used ANOVA (using SPSS 16.0; SPSS, Chicago, IL, US) to compare the plot mean with the mean of subsequent inner plots, which represents its relative interior habitat. For instance, the mean of A plots was compared with the mean of all plots from B to F, then the mean of B plots was compared with the mean of plots between C and F, etc. Least square difference (LSD) post-hoc test was used to identify pair-wise significant differences between means. Significance threshold was selected at $P < 0.05$. When evaluating edge influence we considered only consecutive significant variations, moving from boundary to interior. Conversely, the significant values that are discontinuous along the gradient were not regarded as directly influenced by the boundary.

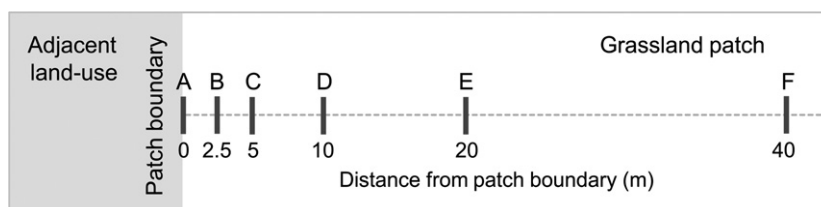


Fig. 1. Scheme of plots distribution along the gradient of distance from patch boundary.

The series of consecutive plots (distances) showing a significant difference from their relative interior habitats allowed estimation of the depth (distance) of the edge influence (DEI; Chen et al. 1992; Forman 1995; Cancino 2005; Harper et al. 2005; Ewers & Didham 2006). For each variable, the magnitude of edge influence (MEI) was defined as the maximum difference between plots and their relative interior habitat (Chen et al. 1992; Burton 2002; Harper et al. 2005; Ewers & Didham 2006). As the effect of the boundary may determine an increase or a decrease of the value of each descriptor, we also noted the sign (+/−) of the difference between plots and their relative interior habitat. In order to evaluate variations associated with a particular boundary attribute rather than associated with the edge itself, we used ANOVA followed by LSD *post-hoc* test separately on each of the half-data sets (eight plots) based on the alternative options occurring for each boundary attribute (land use, wall, slope).

In order to define plant assemblages associated with edge attributes, we applied DCA for the ordination of species occurring at patch boundaries (A plots). Both species presence/absence data and the 16 plots were simultaneously ordered. To derive information for the interpretation of ordination axes, Kruskal–Wallis Chi-squared test (χ^2) was then performed between species scores along the two DCA first axes and species EIV. DCA and χ^2 tests were performed using R 3.2.3 (R Foundation for Statistical Computing, Vienna, AT).

Results

In total, 291 vascular plant species were recorded, mostly belonging to the Poaceae (39 species), Asteraceae (37 species) and Fabaceae (31 species). Mean species richness (\pm SD) was 103.70 ± 13.50 for sampled sites and 41.42 ± 11.17 for plots. Life-form assortment was largely dominated by therophytes (50.4%) with a high proportion of hemicryptophytes (19.5%) and geophytes (15.7%).

Changes in the mean of descriptor values were found along the gradient of distance from the grassland boundary. For instance, Fig. 2 shows the variation of mean grass height, light value and annual forb cover at increasing distance from the grassland boundary as examples of grassland structure, EIV and life form (see also Appendix S2).

Depth and magnitude of edge influence

The comparison between the mean of descriptor values per plot and the mean of subsequent inner plots resulted in significant changes among plant communities located within the shortest distances from the grassland boundary ($0 \text{ m} < \text{DEI} < 2.5 \text{ m}$). For most parameters, MEI was generally higher in grasslands adjacent to crops rather than to

roads, in sloping rather than flat edges, and in wall-bounded rather than unbounded patches (Fig. 3).

With regard to the overall data set, a significant increase in grass height, humidity, phanerophytes, perennial forbs and annuals was found in plots nearest to the boundary, whereas values for light and rhizomatous geophytes increased significantly in innermost plots. In general, no significant change in species richness and diversity, or the EIV for temperature, continentality, pH and nutrients, or in chamaephyte and bulbous geophyte cover was found along the gradient (Fig. 3).

When considering the adjacent land use, we found significant changes in annuals and rhizomatous geophytes at boundaries bordering arable crops, while the perennial forbs value was seemingly influenced by proximity to a road (Fig. 3). The occurrence of a stone wall was associated with a larger increase in grass height and higher cover of biennials. There was a significant change in EIV for soil moisture and cover value of grasses and rhizomatous geophytes in unbounded patches. Phanerophyte cover increased at patch boundaries if protected by a wall, but decreased when the wall was absent (Fig. 3). A significant increase in perennial forb cover was observed along sloping boundaries, while higher cover values of phanerophytes, annual grasses and rhizomatous geophytes were found along flat boundaries (Fig. 3).

Edge plant community composition

The ordination of plant species occurring immediately adjacent to patch boundaries (plots A, distance = 0 m) enabled us to obtain distinct relationships between boundary attributes and plant assemblages. The two-first DCA components were considered as they accounted for 63.08% of the variance. The primary component reveals a gradient of increasing EIV for nutrients and decreasing for light and continentality (Table 1). The second component seems to be effective in segregating unbounded edges from those bounded by a stone wall. Plant assemblages dominated by either ruderal species (e.g. *Malva multiflora*, *M. sylvestris*, *Erodium malacoides*, *Sisymbrium officinale*, *Bromus diandrus*) or xerothermic grassland species (e.g. *Cachrys ferulacea*, *Sedum rupestre*, *Rostraria cristata*, *Petrorhagia saxifraga*) were associated with all cases of unbounded edges (Fig. 4).

Moreover, there were distinctive assemblages in wall-bounded plots according to their different morphology. Wall-bounded sloping edges were characterized by woodland species (e.g. *Q. pubescens*, *Rosa sempervirens*, *Osyris alba*), whereas their non-sloping analogues were associated with calcareous grassland species (e.g. *Festuca circum-mediterranea*, *Stipa austroitalica*, *Crupina crupinastrum*, *Charybdis pancratium*; Fig. 4).

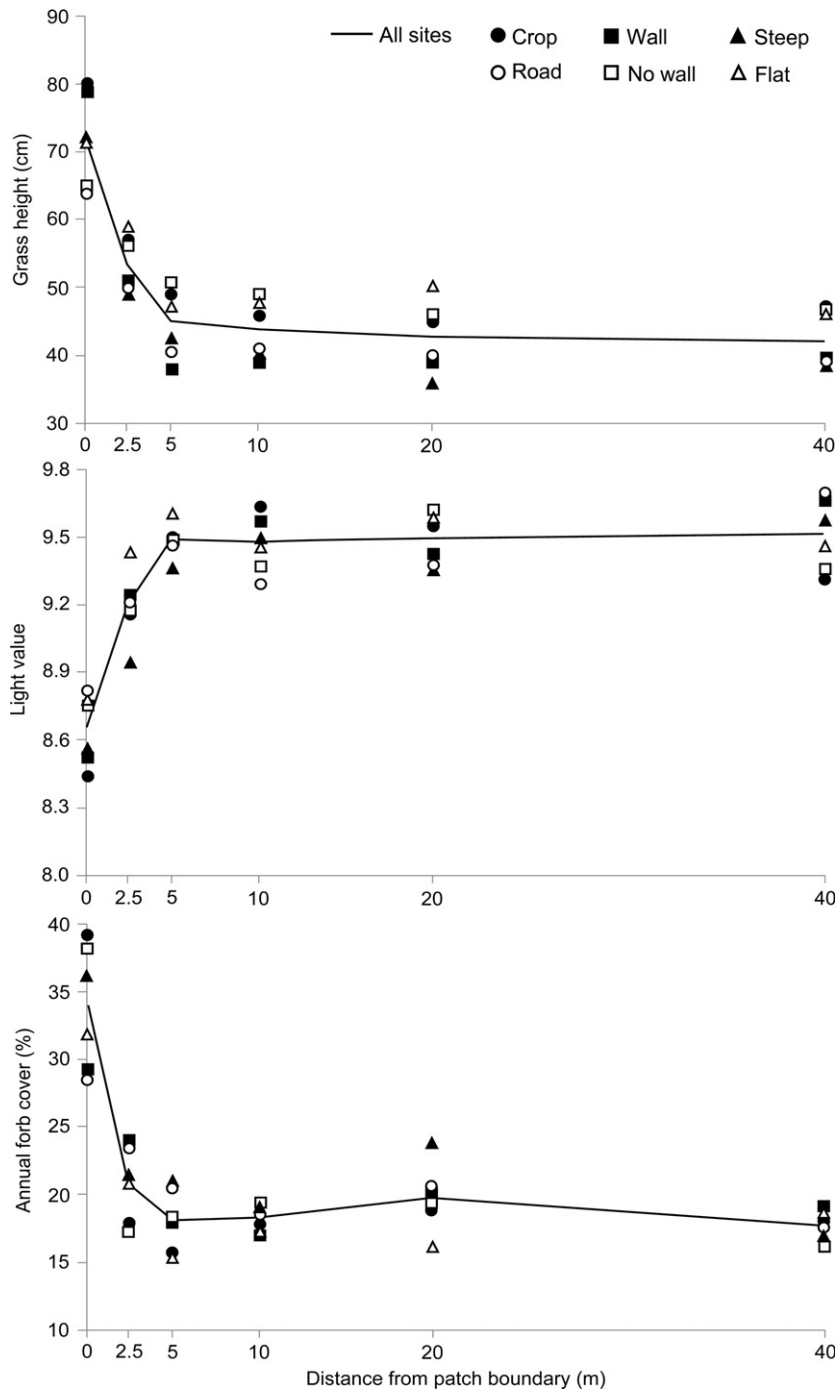


Fig. 2. Mean values of grass height, EIV for light and annual forb cover at increasing distance from patch boundary. Means are reported for all sites (line) and for selected boundary attributes (symbols).

Discussion

Depth and magnitude of edge influence

In this study we analysed changes in plant assemblages along a gradient of distance from anthropogenic

boundaries in protected semi-natural dry grasslands. The methodological modification adopted (i.e. comparison of each plot with its relative interior) represents an original grassland-specific development of methods currently adopted for investigation of edge-related vegetation

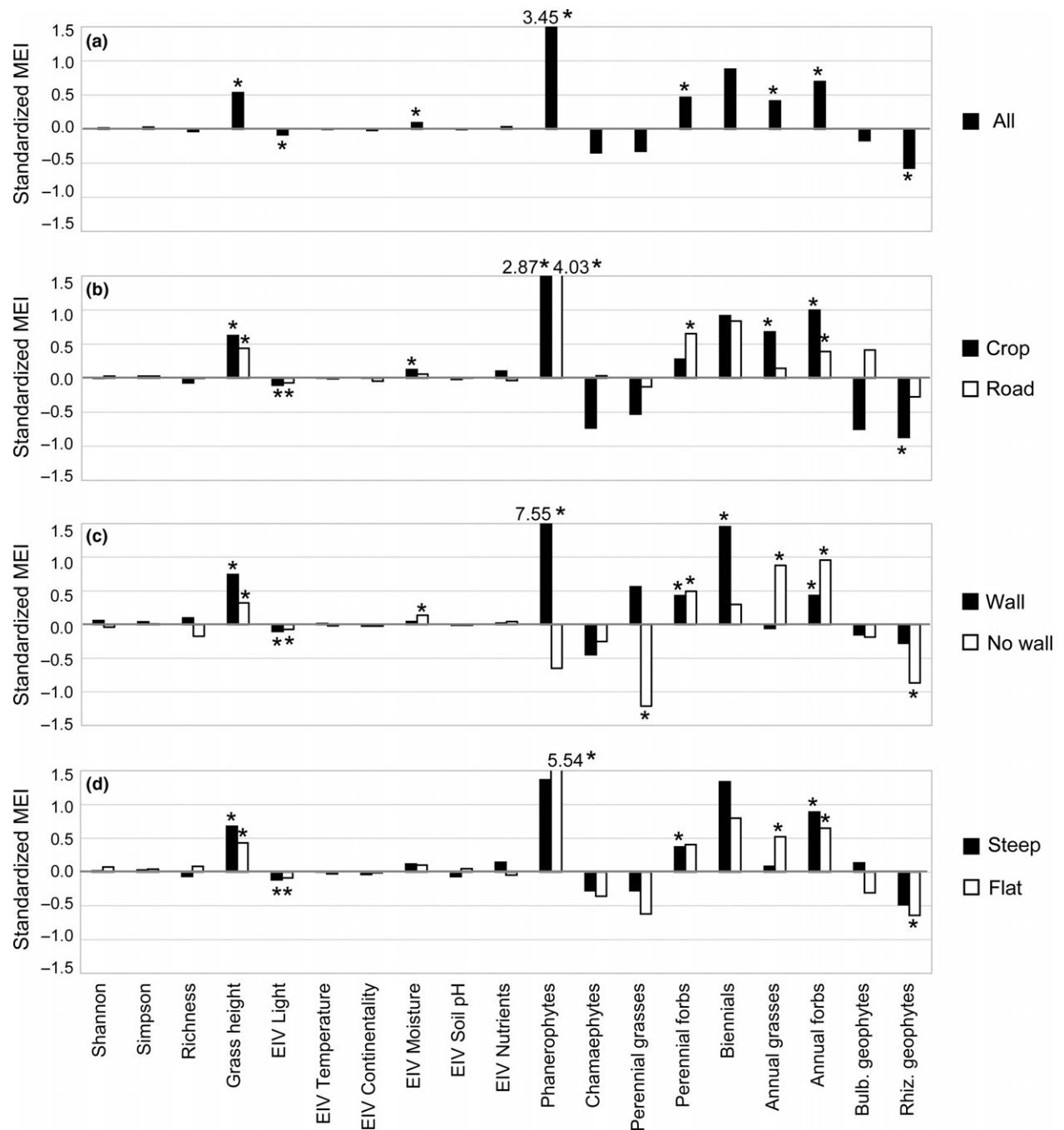


Fig. 3. Standardized Magnitude of Edge Influence (MEI) on selected community descriptors in the tested sites, according to all edges (a), adjacent land-use (b), presence of stone wall (c) and slope (d). Values out of range are reported as numbers above the column. Significant values are marked with an asterisk.

patterns. It allowed us to assess the importance (in terms of depth and magnitude) of edge influence on vegetation patterns in grassland plant communities.

Our approach does not require any *a priori* definition of a reference interior habitat, as such pre-definition can be problematic when considering mosaic herbaceous communities such as those occurring in many semi-natural dry

grasslands (Giladi et al. 2011; Turtureanu et al. 2014). Therefore, this approach appears effective in overcoming some of the main issues regarding quantification of edge influence in grassland communities by rethinking the concept of reference interior habitat; here considered as the relative inner portion along the distance gradient. In fact, the definition of an arbitrary fixed reference distance

Table 1. Kruskal–Wallis Chi-squared tests between species scores of DCA components and EIV.

EIV	DCA 1st Component			DCA 2nd Component		
	χ^2	df	P	χ^2	df	P
Light	13.259*	6	0.039	4.0615	6	0.668
Temperature	9.107	8	0.333	4.322	8	0.827
Continentality	11.291*	5	0.046	3.347	5	0.646
Moisture	10.717	5	0.057	1.859	5	0.868
Soil pH	5.419	8	0.713	6.705	8	0.568
Nutrients	20.739*	9	0.014	7.885	9	0.545

*Significant values ($P < 0.005$).

(Chen et al. 1992; Brand & George 2001; Hylander 2005) and identification of reference sites outside the studied gradient (Didham & Lawton 1999; Harper & Macdonald 2001) could thus be avoided.

Overall, we showed that the boundary itself had a significant influence on plant communities, although this effect was restricted to the shortest distance from the grassland boundary ($0 \text{ m} < \text{DEI} < 2.5 \text{ m}$). DEI is much smaller than that shown in the majority of studies on natural or anthropogenic forest edges (e.g. Ranney et al. 1981; Chen et al. 1992; Hibbs & Giordano 1996; Harper & Macdonald 2001), underlining the importance of scale-dependent factors when determining edge effects (Keitt et al. 1997; Turner et al. 2001). Moreover, our findings provide evidence of the fine-scale effects of habitat fragmentation within the

framework of its context-dependent effects on the quality of individual habitat patch at larger scales (Mairota et al. 2015; Wilson et al. 2016).

No distinct increase in overall plant species richness and diversity was detected at the grassland edge (edge effect *sensu stricto*), which is apparently in contrast to previous work on the interface between different ecosystems (Lovejoy et al. 1986; Risser 1995). These results may correspond to Van der Maarel's (1990) definition of ecotones, where no increase in species richness may occur due to important variations in environmental factors in the transition zone (Buisson & Dutoit 2004; Dutoit et al. 2007). This pattern may also be explained in terms of a balance between positive and negative responses of single species, thus resulting in an overall neutral response at the edge (Ries et al. 2004). Moreover, boundary proximity may act as a driver of species competitive exclusion (Hardin 1960) rather than species addition dynamics. Indeed, when compared with forest undergrowth, denser and/or richer grassland communities can strongly reduce resource availability for incoming herbaceous species (Grime 1973; Davis et al. 2000).

However, boundary proximity was found to be associated with a general increase in herb height, forb proportion and humidity, as well as with a decrease in light value and cover of rhizomatous geophytes. These patterns indicate that the occurrence of encroachment by generalist and

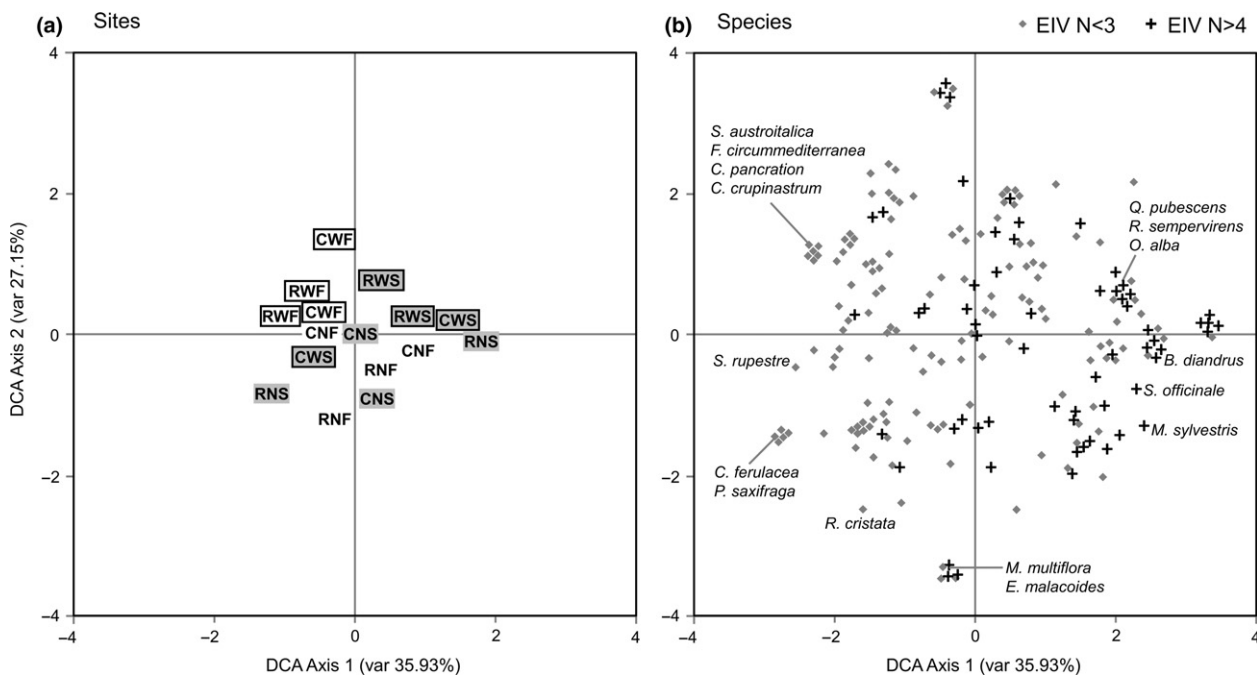


Fig. 4. Biplot of the DCA ordination of sites (a) and species (b). Sites are marked according to the combination of edge attributes: adjacent land-use type (C: crop; R: road); stonewall (W: wall; N: no wall); slope (S: steep; F: flat). Site boxes are highlighted in case of wall (outline) or steep slope (grey shade). Species are marked according to EIV N value (EIV N < 3 in grey and EIV N > 4 indicated by '+'). Names are only reported for the plant species cited in the text.

taller forb species at the boundary is detrimental to those species that are well adapted to dry oligotrophic pastures. This finding is in line with the assumption that anthropogenic margins tend to be richer in eurieious and invasive species (Forman 1995; Cadenasso & Pickett 2001).

Important results were further achieved on the role of boundary attributes in modulating the strength (MEI) of descriptor variations, in accordance to previous work (Ries et al. 2004; Harper et al. 2005; Jansson 2009). For the majority of parameters, we found higher MEI in grasslands bordering crops rather than roads, in sloping rather than flat boundaries, and in wall-bounded rather than unbounded patches.

With regard to the vicinity of arable crops, we found a larger increase in annual forbs in both bounded and unbounded edges, which could indicate either direct encroachment of non-native annual species (across unbounded edges) or input of nutrients from cultivated areas (bypassing wall barriers; Pocewicz et al. 2007).

Edge plant community composition

The occurrence of stone walls was associated with contrasting vegetation patterns. In the case of sloping conditions, wall-bounded edges were richer in forest edge species, confirming that downstream stone walls may also act as a resource hub for more edaphically demanding species (MacArthur & MacArthur 1961; Berg & Part 1994; Ries & Sisk 2010). As further evidence, phanerophytes increased at boundaries protected by walls, but decreased when walls were absent. These findings will be of interest for the evaluation and management of woody encroachment, which is considered an important issue for the conservation of grassland in the study area (Mairota et al. 2014) and in several other dry ecosystems (Chopping et al. 2008). In the case of flat morphology, edges were mostly characterized by typical grassland species (e.g. the protected feather-grass *S. austroitalica*), suggesting that stone walls may have a protective role in the plant communities studied. Therefore, when assessing the impact of human structures on grassland conservation status, stone wall barriers should be taken into account as either detrimental or protective elements, depending on the soil morphology.

With regard to unbounded edges, the lack of change in species assemblages was clearly explained by adjoining land-use type or slope, and plant communities of this type or boundary are characterized by a considerable number of species typical of over-grazed pastures. This finding suggests that coupled effects of boundary attributes and grazing intensity (including its variability through time) may occur. These need to be further investigated when assessing plant community changes associated with edge

configuration, especially when considering extensive grazing management in fragmented landscapes (Dureau & Bonnefon 1998; Buisson & Dutoit 2004).

Conclusions

This work provides new insights on the influence of man-made boundaries on the structure and composition of semi-natural dry grassland of conservation concern. First, the depth and the magnitude of edge influence were quantified using a comparative approach, which enabled us to address many of the issues experienced in the quantification of edge influence in herbaceous communities. Second, changes in the composition of edge plant communities were assessed as a function of a combination of boundary attributes. The relevance of boundary attributes, with regard to their major role in the definition of multiple and contrasting community dynamics, should be taken into account together with other factors (e.g. grazing distribution and intensity) when planning land modifications and local management actions. Finally, all this information is needed for the assessment of conservation strategies aimed at dealing with the consequences of global loss and fragmentation of semi-natural habitats.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Location map of the study sites.

Appendix S2. Descriptor means per plot (A–F).