Shrub Encroachment Affects the Diversity of Plants, Butterflies, and Grasshoppers on Two Swiss Subalpine Pastures

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Shrub encroachment affects the diversity of plants, butterflies, and grasshoppers on two Swiss subalpine pastures

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Abstract

The plant and insect communities of many summer pastures in the Swiss Alps are changing as they become encroached by woody plants. To understand the implications for overall biodiversity, we need to determine how different taxonomic groups respond to shrub encroachment. We investigated effects of encroachment upon species diversity of vascular plants, butterflies, and grasshoppers on two subalpine pastures (Mesocco and Guarda). On each site, we recognized a sequence of vegetation types representing a gradient of increasing shrub cover. The number of rare plant species was strongly affected by the degree of encroachment, with areas dominated by either dwarf shrubs or *Alnus viridis* having fewer species than areas of open grassland. In the Mesocco site, we also found differences in other measures of plant species richness (total species richness, number of herbaceous species) and in the number of grasshopper species. While plant richness was highest in grassland-dominated vegetation types, the species richness of grasshoppers was highest in types with a low to intermediate cover of dwarf shrubs. We found no effect of shrub cover upon butterfly species richness at either site. Biotic factors (shrub cover, grazing intensity, and also vegetation-related variables for the insect groups) explained a larger proportion of the variance in species composition of both plants and insects than did large-scale abiotic factors (altitude, aspect, and slope). Our results demonstrate that shrub encroachment is a threat to the biodiversity of subalpine grassland ecosystems. We recommend conservation actions that prevent extensive shrub encroachment but promote a mosaic of small areas at different successional stages.

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Introduction

The term *shrub encroachment* refers to the spread of indigenous woody plant species into grassland (Van Auken, 2009). Many reports suggest that encroachment is increasing in grassland and savanna ecosystems throughout the world because of changing land use and in response to climate change (Eldridge et al., 2011). The resulting transformation of grassland into woodland profoundly affects many ecosystem properties, including species diversity (Anthelme et al., 2001; Freléchoux et al., 2007), nutrient cycling (Archer et al., 2001; McKinley et al., 2008), and water balance (Huxman et al., 2005; Alewell and Bebi, 2011).

Alpine summer pastures represent a habitat type in which encroachment is now common. Although these grasslands are mainly anthropogenic, they often support a high diversity of plant and animal species (Väre et al., 2003) that have assembled over hundreds of years of extensive use (Bätzing, 2005). During the past century, however, the traditional forms of grazing management have ceased to be economically viable (MacDonald et al., 2000; Chemini and Rizzoli, 2003; Tasser et al., 2007), and many summer pastures have either been abandoned or are now used less intensively ("agricultural marginalisation": see Baldock et al., 1996). These changes have set in train successional processes that lead ultimately to closed forest (Zoller et al., 1984; Schütz et al., 2000). Indeed, forest cover in Switzerland has increased by at least one-third during the past 150 years (Brändli, 2000), with most of this occurring on summer pastures (Baur et al., 2006b; Stöcklin et al., 2007).

Above the tree line, and in certain topographic situations, dwarf shrubs form stable communities, whereas below the tree line they generally represent a successional stage from open grassland to forest (Bischof, 1984). However, even here a dense cover can prevent trees from establishing, so that dwarf shrub vegetation persists for decades or even centuries (Connell and Slatyer, 1977; Putz and Canham, 1992; Niering, 2005). In addition, the speed and course of the succession may be affected by other factors such as altitude, local climate, aspect, and slope (Schütz et al., 2000; Freléchoux et al., 2007). One of the most abundant dwarf shrubs on Swiss alpine landscapes is *Rhododendron ferrugineum*, which is frequently accompanied by *Vaccinium* species to form the *Rhododendro-Vaccinion* association. Another is *Juniperus communis* subsp. *alpina*, which together with *Arctostaphilos uva-ursi* and *Calluna vulgaris* forms the *Juniperion nanae* association (Poldini et al., 2004; Delarze and Gonseth, 2008). On more moist and nutrient rich subalpine areas, both *R. ferrugineum* and *J. communis* subsp. *alpina* also associate with *Alnus viridis* (Bischof, 1984). Although less common in the lowlands, these shrub species have little conservational value in Swiss alpine habitats (Moser et al., 2002).

In seeking to understand how land use change affects the species diversity of summer pastures, it is important to distinguish between responses due to an absence of grazing animals and those due to the spread of woody plants. In practice, however, most studies have been unable to make this distinction because they were conducted on abandoned pastures, where both processes are at work (Pykälä et al., 2005). In particular, studies have rarely examined the effects of dwarf shrubs upon biodiversity, although these shrubs

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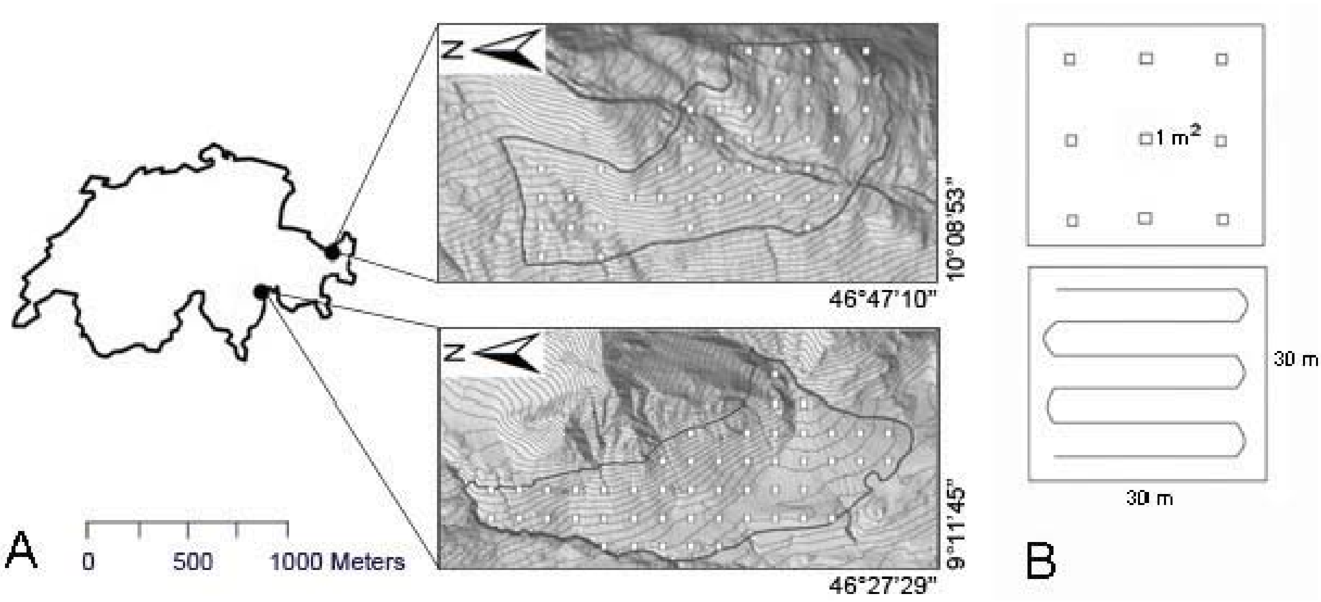

FIGURE 1. (A) The pasture areas in Guarda (top) and Mesocco (bottom) showing the boundaries and the systematically located plots. (B) The sampling design for plants (top) and insects (bottom).

may form dense stands on pastures that have been abandoned or are little used (Cavallero et al., 2007; Freléchoux et al., 2007). Another limitation of previous studies of shrub encroachment is that they have rarely included both plant and insect taxa, even though this information would be very useful for management (Wallis de Vries et al., 2002). The few studies to investigate relationships between woody cover and species diversity in alpine landscapes have reported negative or hump-shaped patterns for plants and for some invertebrate taxa, whereby species diversity is greatest at no or an intermediate amount of woody cover (Anthelme et al., 2001, 2007; Freléchoux et al., 2007; Pornaro et al., 2013).

We investigated the effects of dwarf shrub encroachment on the species richness and composition of vascular plants, butterflies, and grasshoppers on two subalpine pastures in the Swiss Alps. Aside from being important components of the biodiversity, these taxa are relatively easy to sample and identify, and react sensitively to changing environmental factors and agricultural practices (Marini et al., 2009). In our study we posed three questions: (1) How do plant assemblages on subalpine summer pastures change along a gradient of increasing encroachment? (2) How does species richness of plants, butterflies, and grasshoppers change along this gradient? (3) How important are the effects of shrub cover and other biotic factors relative to abiotic or spatial explanatory variables in shaping plant, butterfly, and grasshopper communities on encroached summer pastures?

Material and Methods

STUDY SITES AND SAMPLING DESIGN

The study sites were two subalpine pastures near the villages of Mesocco (46°23′31″N, 9°13′58″E) and Guarda (46°46′33″N, 10°08′59″E) in the Canton of Grisons in southeastern Switzerland (Fig. 1, part A). Both cattle pastures are situated in marginal locations just above the present tree line (1762–2064 m elevation in Mesocco, and 2097–2410 m in Guarda), have a south-westerly aspect, and are approximately 1.5 km^2 in area. Both have a long tradition of pastoral use between June and September (Werthemann and Imboden, 1982) but are now less used and are being encroached by dwarf shrubs (J. Barbüda and A. Toscano, personal communication).

The mean annual precipitation (years 1961–1990) measured at weather stations close to the survey sites was 1864 mm at Mesocco and 693 mm at Guarda (Schweizerische Meteorologische Anstalt, 2008). Given the underlying rocks, which are predominantly crystalline (Reinhard et al., 1962), acidic soil conditions prevail at both sites. The vegetation in both areas is a mosaic of grassland, mainly of *Nardus stricta*, and dwarf ericaceous shrubs (mainly *Arctostaphylos uva-ursi*, *Calluna vulgaris*, *Rhododendron ferrugineum*, *Vaccinium myrtillus,* and *Vaccinium gaultheroides*), and junipers (*Juniperus communis* subsp. *alpina*). Whereas these nutrient-poor *N. stricta* and shrubland vegetations dominate on steeper and remote areas of the pasture, nutrient-rich grasslands occur predominantly on flat areas and around buildings. In Mesocco there are also some areas encroached by the shrub *Alnus viridis*. A study of aerial photographs shows an increase in dwarf shrub cover by 31% in areas of the pasture at Mesocco between 1962 and 2005, despite the site never having been abandoned (Crivelli, 2011). Mismanagement and low grazing pressure of more remote and steeper areas are possible reasons for this shrub increase.

SAMPLING OF SPECIES AND ENVIRONMENTAL DATA

On each pasture, 54 plots of 30 × 30 m (900 m^2) were defined by systematic sampling (lower left corner of each plot placed at a randomly regular grid with a 155 m resolution). Plots with a slope steeper than 50° or those with more than 40% stones and rock were excluded, being unsuitable for cattle grazing. The remaining plots in the grid were all sampled, resulting in 49 plots at Mesocco and 48 plots at Guarda (Fig. 1, part A).

Data were collected between June and September 2010. To account for local heterogeneity, plants were surveyed in nine 1 m^2

quadrats arranged regularly within the 900 m^2 plot (Fig. 1, part B). The plant cover in the 1 m^2 quadrats was estimated using the Braun-Blanquet scale, and the nomenclature follows Lauber and Wagner (2001). We also recorded the presence of any additional species absent from the nine quadrats by searching the whole plot for 30 minutes. All plant species from the nine 1 m^2 quadrats and the 30 minutes' walk were pooled to calculate the total number of plant species per plot. We recorded all adult butterflies (belonging to the Rhopalocera, Hesperiidae, and Zygaenidae) and grasshoppers (Ensifera and Caelifera) by traversing the 900 m^2 plot in a serpentine transect (Fig. 1, part B; see Balmer and Erhardt, 2000). Insects of both taxa were identified visually—and grasshoppers also acoustically—between 10:00 and 17:00 on sunny days with little or no wind. The butterfly survey was repeated five times, and the grasshopper survey twice. Nomenclature of butterflies followed Bühler-Cortesi (2009) and that of grasshoppers followed Baur et al. (2006a). For both taxa, data of different sampling times were pooled at the plot level prior to data analysis.

For each 900 m^2 plot we recorded altitude, slope, aspect, and the percentage shrub cover. Moisture was disregarded in our study as an abiotic factor as the sites were relatively homogeneous in this respect. Further, both slope and aspect contribute to variation in insolation and are often used as surrogates for soil moisture spatial patterns (Tague, 2005). We also counted the cow-pats, using this number as a measure of grazing intensity.

STATISTICAL ANALYSES

To describe vegetation types of the two subalpine pastures, the plant cover data from the nine 1 m^2 quadrats were classified by means of cluster analysis. Following the suggestion of Legendre and Gallagher (2001), a Hellinger transformation was used for the plant cover data. The transformed cover data were then classified on the basis of k-means clustering using Euclidean distance.

One-way ANOVA was used to test for differences among vegetation types in various species measures: (1) total number of plant species per plot, hereafter plant species richness; (2) number of herbaceous plant species; (3) number of rare plant species, that is, species with an overall cover sum of ≤5% in the 9 × 1 m^2 quadrats; (4) number of butterfly species, hereafter butterfly species richness; and (5) number of grasshopper species, hereafter grasshopper species richness. A Bonferroni correction was used to adjust p-values to avoid type-I errors leading to a critical p-value of $p = 0.05 \div 5 = 0.01$. Tukey's honest significance tests were then carried out to identify differences between vegetation types ($p < 0.01$).

To evaluate the impact of explanatory variables on the species composition of plants, butterflies, and grasshoppers, the abundance data were analyzed by variation partitioning with a redundancy analysis (RDA) (Borcard et al., 1992). We related the data to three sets of explanatory variables: (1) biotic factors (shrub cover, its square term, grazing intensity; additionally for the insect groups: vegetation types, plant species richness); (2) abiotic factors (altitude, slope, aspect); and (3) spatial structure (characterized by principal coordinates of neighbor matrices [PCNM]). The PCNM method is based upon the orthogonal spectral decomposition of the spatial relationships among sampling sites and permits spatial patterns at different scales to be considered (Borcard and Legendre, 2002). Because PCNM assumes the analysis of data in a regular grid, separate analyses had to be performed for the two sites. To fill a gap in the regular sampling grid in Guarda, a supplementary coordinate point was added before calculating the PCNMs (Borcard and Legendre, 2002). The variables retained by the PCNM analysis were 25 for Mesocco and 26 for Guarda. A Hellinger transformation was performed on the cover data for plants and abundance data for butterflies and grasshoppers (Legendre and Gallagher, 2001). First, for each species group, forward selection using the double stopping criteria was performed on each set of variables independently to retain only significant terms (Guillaume Blanchet et al., 2008). Then, variation partitioning with RDA was used to determine how much of the variation in species assemblages was explained by pure (biotic, abiotic, spatial) and combined fractions (Borcard et al., 1992). The significance of the pure fractions was then assessed under the reduced model. Adjusted R^2 (R^2_{Adj}) values were used as input for the variation partitioning to account for the different number of terms in the sets of variables (Peres-Neto et al., 2006). Statistical analyses were performed with the packages "vegan" (Oksanen et al., 2012) and "PCNM" (Legendre et al., 2012) of the statistical program R (R Core Team, 2012).

Results

VEGETATION TYPES

The cluster analysis based upon plant species composition identified five vegetation types in Mesocco and four vegetation types in Guarda. These vegetation types can be characterized as follows (Tables 1 and 2):

Type 1 (a + b) subsumed plots in both pastures with very low shrub cover and many cow-pats (99.0 ± 20.1 and 67.0 ± 28.6 in *Types 1a* and *1b*, respectively). The vegetation can be assigned to the phytosociological association *Poion alpinae* (Delarze and Gonseth, 2008). In Mesocco (*Type 1a*) this vegetation type had a high cover of the grasses *Festuca rubra, Phleum rhaeticum,* and *Agrostis capillaris* often accompanied by *Nardus stricta*, whereas the most abundant species in Guarda (*Type 1b*) were *Deschampsia caespitosa*, *F. rubra*, *Alchemilla vulgaris,* and *N. stricta.*

Type 2b included plots in Guarda with a vegetation dominated by *N. stricta,* and which can be assigned to the *Nardion* association. The tufts of *N. stricta* were very vigorous, and few other species were present in high frequency. Similar to *Type 1*, this type was also characterized by low shrub cover and many cow-pats (109.5 ± 27.7).

Type 3 (a + b) comprised plots in both pastures with intermediate shrub cover and a mosaic of grassland and shrubs. The grassland vegetation was dominated by *N. stricta,* while the most prominent shrub was *Juniperus communis* subsp. *alpina* (hereafter *J. communis*). The *Nardion* and *Juniperion nanae* associations intermixed in these plots forming a mosaic of grassland with patchy distributed dwarf shrubs. Number of cow-pats in the vegetation *Types 3a* (34.1 ± 6.9) and *3b* (25.6 ± 3.3) was rather low compared to *Types 1* and *2*.

Type 4 (a + b) comprised plots with vegetation dominated by *J. communis*. This vegetation type is characterized by high shrub cover and can be attributed to the *Juniperion nanae* association. In Mesocco (*Type 4a*), *J. communis* was frequently accompanied by *Agrostis schraderiana*, *Rhododendron ferrugineum,* and *Alnus viridis.* In Guarda (*Type 4b*), the most frequent accompanying species were the dwarf-shrubs *Arctostaphylos uva-ursi*, *Calluna vulgaris*, *Vaccinium myrtillus,* and *Vaccinium gaultheroides*. Very few cow-pats were found in plots with vegetation *Types 4a* (3.9 ± 2.6) or *4b* (8.1 ± 3.1).

Type 5a was found only in Mesocco and was represented by plots with a complete dwarf shrub cover. No cow-pats were found in this vegetation type. The dominant species were *J. communis* and *R. ferrugineum*, but *V. gaultheroides*, *C. vulgaris,* and *V. myrtillus* were also frequent. The associations *Juniperion nanae* and *Rhododendro-Vaccinion* mixed in the plots dominated by *Type 5a* vegetation.

TABLE 1

Average (± SE) cover (%) for the most frequent plant species in the five vegetation types in Mesocco. Only species with mean percentage cover >2% in at least one type are shown in the table. Mean values >2% are shaded in gray, and those >5% are additionally highlighted in bold. Woody plant species are highlighted in bold. Biotic and abiotic factors for the vegetation types are summarized at the bottom of the table.

	Type 1a ($n = 9$)	Type 3a ($n = 12$)	Type 4a ($n = 10$)	Type 5a ($n = 12$)	Type 6a ($n = 6$)
PLANT SPECIES	*Poion alpinae*	*Nardion* and *Juniperion nanae* mosaic	*Juniperion nanae*	*Juniperion nanae* and *Rhododendro–Vaccinion* encroached areas	*Alnenion viridis*
Poa alpina	3.46 ± 1.16	1.15 ± 0.41	0.11 ± 0.08	0.02 ± 0.02	
Deschampsia caespitosa	3.64 ± 1.71	1.83 ± 0.90	1.31 ± 1.10	0.83 ± 0.83	1.25 ± 1.20
Poa chaixii	**5.90 ± 2.72**	1.77 ± 0.57	3.56 ± 1.86	0.12 ± 0.06	1.11 ± 0.74
Agrostis capillaris	**11.45 ± 4.45**	2.53 ± 0.85	0.42 ± 0.28	0.05 ± 0.05	3.80 ± 3.04
Nardus stricta	**17.16 ± 4.07**	**14.26 ± 3.38**	1.36 ± 0.56	0.58 ± 0.33	
Phleum rhaeticum	**12.14 ± 3.23**	2.28 ± 0.69	2.97 ± 0.57	0.37 ± 0.22	0.69 ± 0.29
Festuca rubra	**16.51 ± 3.21**	**5.35 ± 1.09**	2.73 ± 0.95	0.56 ± 0.26	0.46 ± 0.31
Juniperus communis	**8.21 ± 2.97**	**27.48 ± 4.14**	**25.59 ± 3.87**	**32.83 ± 5.89**	2.64 ± 1.36
Avenella flexuosa	0.03 ± 0.03	2.76 ± 0.97	4.44 ± 1.21	1.56 ± 0.71	1.34 ± 0.55
Vaccinium myrtillus	0.76 ± 0.47	**5.75 ± 1.35**	4.84 ± 1.34	**6.11 ± 1.31**	1.35 ± 0.80
Rhododendron ferrugineum	0.22 ± 0.18	3.57 ± 1.75	**6.78 ± 2.15**	**22.62 ± 4.20**	**8.34 ± 3.53**
Vaccinium gaultheroides	1.20 ± 0.75	1.79 ± 0.76	3.89 ± 1.17	**8.98 ± 2.63**	0.83 ± 0.57
Chaerophyllum villarsii	1.22 ± 0.76	1.29 ± 0.48	4.01 ± 1.87	1.65 ± 1.25	**6.21 ± 4.64**
Alnus viridis			5.97 ± 2.03	0.95 ± 0.95	**33.43 ± 6.74**
Agrostis schraderiana		0.07 ± 0.05	8.34 ± 2.38	1.09 ± 0.46	**10.00 ± 4.17**
Rubus idaeus	0.23 ± 0.22	1.00 ± 0.49	1.50 ± 0.89	3.92 ± 1.69	**8.39 ± 3.85**
Calamagrostis villosa	0.03 ± 0.03	0.05 ± 0.03	1.97 ± 0.96	**5.47 ± 2.04**	**9.26 ± 3.01**
Peucedanum ostruthium		0.02 ± 0.02	1.61 ± 0.91	0.05 ± 0.03	**7.51 ± 4.95**
Shrub cover (%)	9.8 ± 2.3	49.5 ± 5.5	62.0 ± 5.6	91.8 ± 4.4	67.8 ± 10.8
Number of cow pats	99.0 ± 20.1	34.1 ± 6.9	3.9 ± 2.6		
Slope (°)	12.8 ± 2.8	16.8 ± 2.5	27.5 ± 3.1	24.8 ± 2.9	33.0 ± 5.1
Aspect (°)[1]	25.5 ± 1.1	24.8 ± 0.9	25.4 ± 0.6	24.4 ± 0.9	25.9 ± 0.5

[1] Aspect values range from west-facing slopes (29°) to south-facing slopes (17°).

Type 6a comprised plots in Mesocco with a high cover of *Alnus viridis* and no cow-pats. This type can be assigned to the *Alnenion viridis* association. Other prominent species were *Agrostis schraderiana*, *Calamagrostis villosa*, *Rubus idaeus*, *R. ferrugineum*, *Peucedanum ostruthium,* and *Chaerophyllum villarsii*.

Types 1 to *5* occurred on rather dry sites and followed a gradient of increasing shrub encroachment, with increasing shrub cover and decreasing surface covered by grassland. In contrast to the other vegetation types, *Type 6* was only present in particularly moist sites.

The vegetation types in Guarda and Mesocco presented differences in butterfly and grasshopper compositions. Tables 3 and 4 display the most frequent species for each vegetation type.

PATTERNS OF SPECIES RICHNESS AND COMPOSITION

We recorded more species at Guarda than at Mesocco, with a total of 332 versus 318 plants, 52 versus 44 butterflies, and 14 versus 8 grasshoppers for the two sites, respectively. At both sites, we found significant variation in species richness among vegetation types, including in the number of rare plant species in Guarda, and in the numbers of vascular plants (all measures) and grasshoppers in Mesocco (one-way ANOVA; p-value < 0.01). Distinctions between the vegetation types revealed by Tukey's post hoc tests are reported in Figure 2. In general, species richness of plants (all, herbaceous, and rare species) was higher in plots with a lower shrub cover, although in Guarda, number of all plant species and herbaceous species did not vary significantly according to vegetation type. Numbers of butterfly species did not vary significantly among vegetation types in either site. However, species richness of grasshoppers was significantly higher in *Type 3a* than *Type 6a* in Mesocco, but did not vary in Guarda.

In the RDA analyses, the measured variables explained far more of the variation in species composition of plants, butterflies, and grasshoppers at Guarda than at Mesocco (38%–68.1% vs. 16.3%–33.6%; Fig. 3, Appendix A). Of this total variation, the fraction explained by

TABLE 2

Average (± SE) cover (%) for the most frequent plant species in the four vegetation types identified in Guarda. Only species with mean percentage cover > 2% in at least one type are shown in the table. Mean values >2% are shaded in grey and >5% are additionally highlighted in bold. Woody plant species are highlighted in bold. Biotic and abiotic factors for the vegetation types are summarized at the bottom of the table.

	Type 1b (*n* = 8)	Type 2b (*n* = 6)	Type 3b (*n* = 14)	Type 4b (*n* = 20)
PLANT SPECIES	*Poion alpinae*	*Nardion*	*Nardion* and *Juniperion nanae* mosaic	*Juniperion nanae*
Poa alpina	2.02 ± 0.94	0.76 ± 0.21	0.48 ± 0.13	0.04 ± 0.03
Carex ferruginea	2.05 ± 1.05			
Leontodon hispidus	2.30 ± 0.97	1.35 ± 0.99	0.07 ± 0.04	0.02 ± 0.01
Salix waldsteiniana	2.29 ± 2.25			
Agrostis capillaris	2.40 ± 1.07	1.44 ± 0.97	0.30 ± 0.10	0.31 ± 0.12
Deschampsia caespitosa	**8.69 ± 2.51**	0.10 ± 0.09	0.32 ± 0.20	
Alchemilla vulgaris	**6.05 ± 2.23**	4.49 ± 1.86	0.13 ± 0.05	
Festuca rubra	**6.53 ± 1.86**	**5.24 ± 2.24**	3.30 ± 0.86	1.26 ± 0.51
Nardus stricta	**5.17 ± 1.90**	**32.78 ± 7.37**	**25.85 ± 3.59**	3.46 ± 0.80
Geum montanum	0.21 ± 0.12	2.05 ± 0.92	1.76 ± 0.32	0.69 ± 0.13
Potentilla aurea	0.95 ± 0.24	2.34 ± 0.67	1.80 ± 0.12	0.96 ± 0.17
Gentiana punctata		3.24 ± 3.02	0.52 ± 0.22	0.34 ± 0.16
Phleum rhaeticum	1.95 ± 1.48	3.72 ± 1.28	1.14 ± 0.32	0.07 ± 0.03
Trifolium alpinum	0.14 ± 0.07	3.25 ± 1.66	**5.48 ± 0.82**	2.87 ± 0.80
Anthoxanthum odoratum	0.70 ± 0.25	1.77 ± 0.32	2.45 ± 0.58	1.30 ± 0.24
Arctostaphylos uva-ursi	1.42 ± 1.42		2.16 ± 1.08	**9.10 ± 2.39**
Vaccinium vitis-idaea	0.63 ± 0.24	0.19 ± 0.14	2.64 ± 0.47	2.43 ± 0.28
Vaccinium myrtillus	0.04 ± 0.04	1.07 ± 1.01	3.18 ± 0.99	**6.36 ± 1.17**
Carex sempervirens	1.81 ± 0.68	0.84 ± 0.67	4.90 ± 0.62	4.42 ± 0.81
Juniperus communis	0.77 ± 0.76		**21.21 ± 3.15**	**19.38 ± 3.38**
Loiseleuria procumbens			1.92 ± 1.04	2.65 ± 0.97
Vaccinium gaultheroides	0.59 ± 0.55	1.67 ± 1.67	1.73 ± 0.76	**6.14 ± 1.58**
Calluna vulgaris			0.02 ± 0.02	**6.50 ± 1.38**
Shrub cover (%)	7.5 ± 3.4	5.6 ± 3.9	32.6 ± 6.1	76.9 ± 3.6
Number of cow pats	67.0 ± 28.6	109.5 ± 27.7	25.6 ± 3.3	8.1 ± 3.1
Slope (°)	25.3 ± 4.3	18.2 ± 2.1	20.7 ± 2.1	27.9 ± 2.2
Aspect (°)[1]	26.6 ± 0.7	23.4 ± 0.9	22.6 ± 0.9	21.2 ± 1.0

[1] Aspect values range from west-facing slopes (30°) to south-facing slopes (13°).

biotic variables ranged from 10.9% to 32.1% (mean ± SE: 21.7 ± 3.1), and was significant for all groups at both sites. Abiotic variables explained between 2.7% and 19.6% (8.5 ± 2.1) of variation and showed a significant effect for all groups at Guarda, but not for plants at Mesocco. The fraction explained by spatial variables (PCNMs) was generally high, with values ranging between 10.4% and 34.4% (17.7 ± 3.2).

Discussion

The effect of shrubs on species diversity in abandoned or underused subalpine pastures has been investigated before, albeit usually focusing on plant diversity and rarely in the context of encroachment by dwarf shrubs (Anthelme et al., 2001, 2007; Freléchoux et al., 2007; Pornaro et al., 2013). In Mesocco, plant diversity, whether measured as plant species richness, number of herbaceous species, or number of rare species, was generally higher in grassland (*Poion alpinae*) and mosaic vegetation (*Nardion* with *Juniperion nanae*) than in dwarf shrub and *A. viridis* dominated stands; grasshopper diversity was highest in mosaic vegetation. In contrast, significant differences at the Guarda site were found only for the number of rare plant species, with grassland sites (*Poion alpinae*) supporting more species than sites of intermediate to high dwarf shrub cover. No significant variation in butterfly species richness was found among vegetation types. The variation in species composition of plants, butterflies, and

TABLE 3

Average (± SE) number of individuals for the most frequent butterfly and grasshopper species in the five vegetation types identified in Mesocco. Only species with mean number of individuals >1 in at least one type are shown in the table. Mean values >1 are shaded in grey and >3 for butterflies resp. >5 for grasshoppers are additionally highlighted in bold.

		Type 1a (*n* = 9)	Type 3a (*n* = 12)	Type 4a (*n* = 10)	Type 5a (*n* = 12)	Type 6a (*n* = 6)
	SPECIES	*Poion alpinae*	*Nardion* and *Juniperion nanae* mosaic	*Juniperion nanae*	*Juniperion nanae* and *Rhododendro-Vaccinion* encroached areas	*Alnenion viridis*
BUTTERFLIES	*Aglais urticae*	1.67 ± 0.44	0.75 ± 0.28	0.80 ± 0.20	0.58 ± 0.26	1.00 ± 0.37
	Erebia tyndarus	**4.00 ± 1.26**	**4.00 ± 1.47**	0.70 ±0.33	0.50 ± 0.23	0.33 ± 0.21
	Erebia melampus	**3.78 ± 1.00**	1.58 ± 0.68	1.10 ± 0.28	0.75 ± 0.30	0.67 ± 0.49
	Pieris bryoniae	2.00 ± 0.88	1.00 ± 0.44	2.50 ± 0.82	2.67 ± 0.56	**3.33 ± 0.80**
	Erebia euryale	**4.78 ± 1.63**	**11.33 ± 2.48**	**27.20 ± 4.25**	**16.67 ± 2.18**	**18.83 ± 4.50**
	Boloria euphrosyne	0.44 ± 0.24	1.25 ± 0.22	2.00 ± 0.54	1.75 ± 0.46	1.83 ± 0.79
	Coenonympha darwiniana	0.78 ± 0.36	0.83 ± 0.34	2.90 ± 0.50	0.92 ± 0.31	1.50 ± 0.67
	Erebia pharte	0.11 ± 0.11	0.67 ± 0.28	**3.30 ± 0.92**	**3.75 ± 0.82**	2.33 ± 1.12
	Erebia manto	0.78 ± 0.43				1.00 ± 1.00
GRASSHOPPERS	*Gomphocerus sibiricus*	17.11 ± 4.84	26.17 ± 12.74	6.30 ± 2.74	8.00 ± 3.40	1.17 ± 0.98
	Omocestus viridulus	32.33 ± 6.09	37.83 ± 9.99	18.70 ± 4.17	6.67 ± 2.11	4.83 ± 2.68
	Chorthippus parallelus	42.11 ± 11.29	44.83 ± 9.06	18.80 ± 3.77	6.83 ± 1.32	7.17 ± 3.38
	Podisma pedestris	10.33 ± 4.16	9.75 ± 2.06	4.20 ± 1.07	3.08 ± 1.65	0.83 ± 0.54

grasshoppers explained by biotic and spatial variable sets was generally greater than that explained by large-scale abiotic environmental variables.

VEGETATION TYPES AND SUCCESSION

The patterns of encroachment at both sites were similar and probably result from the declining use of the pastures in recent decades. However, there were also important differences in plant species composition between the sites, which presumably reflect differing climatic and topographic conditions. For example, more rainfall may explain why *R. ferrugineum* and *Alnenion viridis* vegetation was found at the Mesocco site. On the other hand, the dominance of *J. communis* at Guarda is consistent with the drier, more continental conditions at this site.

Dominant plant species in areas assigned to vegetation *Type 1 (a + b)* were mainly grasses associated with relatively nutrient-rich pastures, such as *Agrostis capillaris, Festuca rubra*, *Deschampsia caespitosa,* and *Phleum rhaeticum*. In general, *Festuca/Agrostis* vegetation depends upon high grazing intensity (Welch and Scott, 1995), which is confirmed by the high density of cow-pats in this vegetation type. The *Nardion* vegetation in Guarda also showed very low cover of shrub species and evidence of use by cattle. However, *N. stricta* is an unpalatable species that cattle tend to avoid (Welch and Scott, 1995; Jewell et al., 2005), and its presence in an underused pasture may offer an opportunity for shrub species to establish. Indeed, both pastures had extensive mosaics of *Juniperion nanae* and *Nardion* associations (*Type 3 a + b*), suggesting that dwarf shrubs are more likely to spread into vegetation with *N. stricta* than into the *Poion alpinae* association. Further, following the modeling of Schütz et al. (2000), *N. stricta* reaches a peak after *F. rubra* in the succession process, indicating that when *Nardus* is dominant, the succession is already advanced. The subsequent development of the mosaic into more dense shrub vegetation is probably driven by a positive feedback, as the shrubs are avoided by cattle while their spread is encouraged by reduced grazing (Güsewell et al., 2005; Kohler et al., 2006). Furthermore, the ability of shrubs such as *J. communis* to develop "fertility islands" (DeLuca and Zackrisson, 2007) gives them a competitive advantage in nutrient-poor pastures providing that the cattle density is not too high (Livingston, 1972).

Based upon the species overlap and the increasing cover by dwarf shrubs from open grassland vegetation types (*Poion alpinae* and *Nardion* types) via mosaic vegetation to a stage of shrub dominance, we conclude that the vegetation types at each study site represent different successional stages (excluding the *Alnenion viridis* at Mesocco). This conclusion is also in accordance with the succession model of Schütz et al. (2000). However, we found no evidence of the succession proceeding further to woodland. This is probably because the dense shrub cover inhibits the establishment of trees (Connell and Slatyer, 1977), thereby enabling this seral vegetation type to persist for decades or even centuries.

In contrast to the other vegetation types, *Type 6a,* attributed to the *Alnenion viridis* association and only present at the Mes-

TABLE 4

Average (± SE) number of individuals for the most frequent butterfly and grasshopper species in the four vegetation types identified in Guarda. Only species with mean number of individuals >1 in at least one type are shown in the table. Mean values >1 are shaded in grey and >3 for butterflies resp. >5 for grasshoppers are additionally highlighted in bold.

		Type 1b ($n = 8$)	Type 2b ($n = 6$)	Type 3b ($n = 14$)	Type 4b ($n = 20$)
	SPECIES	*Poion alpinae*	*Nardion*	*Nardion* and *Juniperion nanae* mosaic	*Juniperion nanae*
BUTTERFLIES	*Pieris bryoniae*	1.00 ± 0.73	0.17 ± 0.17		0.05 ± 0.05
	Plebeius orbitulus	1.13 ± 0.67			
	Erebia pharte	1.25 ± 0.62			
	Adscita geryon	1.63 ± 0.78	0.67 ± 0.42	0.14 ± 0.10	1.35 ± 0.55
	Aglais urticae	2.00 ± 0.53	0.50 ± 0.22	0.93 ± 0.22	0.85 ± 0.25
	Cupido minimus	**3.75 ± 1.62**	0.17 ± 0.17		
	Polyommatus semiargus	1.75 ± 0.70	1.83 ± 0.79	0.86 ± 0.23	0.55 ± 0.18
	Boloria pales	**5.00 ± 1.18**	0.83 ± 0.65	1.14 ± 0.39	0.65 ± 0.23
	Erebia melampus	2.63 ± 1.56	**7.33 ± 4.65**	1.29 ± 0.53	0.75 ± 0.55
	Erebia epiphron	1.75 ± 0.90	1.00 ± 0.45	**4.43 ± 1.04**	2.75 ± 0.69
	Coenonympha gardetta	**5.38 ± 1.69**	**8.00 ± 2.67**	**20.14 ± 2.30**	**9.25 ± 1.65**
	Erebia tyndarus	**19.63 ± 5.08**	**18.00 ± 5.90**	**22.93 ± 2.00**	**14.45 ± 1.91**
	Pyrgus serratulae	0.50 ± 0.33	1.00 ± 0.37	1.71 ± 0.35	0.85 ± 0.37
	Pyrgus malvoides	0.63 ± 0.38	1.50 ± 0.43	1.43 ± 0.56	0.40 ± 0.15
	Euphydrias aurinia	0.88 ± 0.74	2.17 ± 0.98	**3.29 ± 0.67**	1.70 ± 0.38
	Plebeius optilete		0.17 ± 0.17	0.36 ± 0.29	1.05 ± 0.43
	Boloria titania			0.36 ± 0.29	1.35 ± 0.69
GRASSHOPPERS	*Podisma pedestris*	3.13 ± 1.84	**9.67 ± 7.18**	**17.43 ± 2.35**	**20.20 ± 2.59**
	Miramella alpina	4.75 ± 1.94	2.00 ± 1.13	**8.50 ± 1.64**	4.55 ± 0.77
	Gomphocerus sibiricus	**8.00 ± 4.02**	**55.17 ± 32.38**	**80.29 ± 17.14**	**60.65 ± 12.39**
	Omocestus viridulus	**23.00 ± 4.33**	**12.50 ± 2.49**	**8.43 ± 1.97**	1.35 ± 0.58
	Chorthippus parallelus	**34.50 ± 8.97**	**33.00 ± 9.75**	**43.93 ± 8.33**	**20.65 ± 5.29**
	Metrioptera brachyptera	0.13 ± 0.13	2.67 ± 1.26	**8.00 ± 1.64**	**13.75 ± 2.67**
	Psophus stridulus			0.36 ± 0.36	1.60 ± 0.79
	Gomphocerippus rufus				1.70 ± 0.95
	Stenobothrus rubicundulus			0.07 ± 0.07	3.10 ± 1.41
	Arcyptera fusca				4.40 ± 3.38

occo site, does not appear to be part of the same successional sequence. *A. viridis* is known to indicate moister sites (Wettstein, 2001) and because of its association with nitrogen-fixing symbionts can grow very vigorously even in nutrient-poor sites (Mallik et al., 1997). The accompanying herbaceous plants (e.g., *Agrostis schraderiana*, *Calamagrostis villosa*, *Peucedanum ostruthium,* and *Chaerophyllum villarsii*) are mainly fast-growing, shade-tolerant species that thrive in the moist, nitrogen-rich soils beneath *A. viridis* (Anthelme et al., 2001; Wiedmer and Senn-Irlet, 2006). Soil moisture was not used as an abiotic factor in this study because it was assumed to be strongly related to slope and aspect, which are often used as surrogates for moisture conditions (Moore et al., 1991; Woodcock et al., 2002; Tague, 2005). The mean slope in plots with *Type 6a* vegetation is higher than for all other vegetation types. The plots colonized by *Alnenion viridis* might well be located on slide paths of snow avalanches, where this vegetation often occurs (Wiedmer and Senn-Irlet, 2006). This might explain the greater steepness and higher moisture of these sites. Nevertheless, the lack of cow-pats in plots with this vegetation type indicates an absence of grazing pressure, suggesting different plant interaction and competition patterns than for other vegetation types subjected to higher grazing intensity (Graff et al., 2007). Indeed, herbaceous plant species accompanying *A. viridis* are rather competitive.

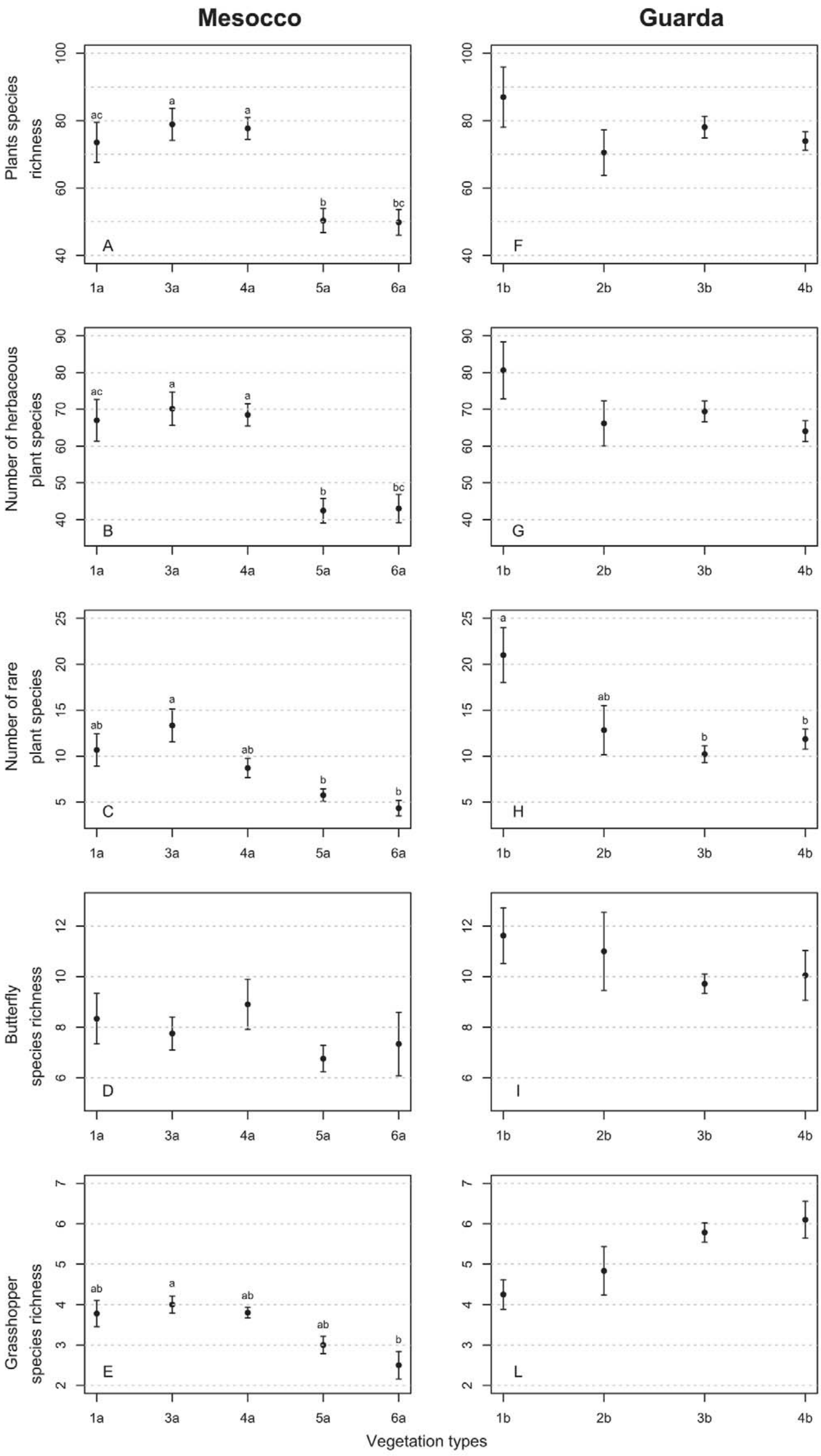

FIGURE 2. Error bar plots (mean ± SE) displaying differences between the vegetation types identified in (A–E) Mesocco and (F–L) Guarda for various plant measures (plant species richness, number of herbaceous plant species, number of rare plant species), butterfly species richness, and grasshopper species richness. Vegetation types: 1a+b: *Poion alpinae*; 2b: *Nardion*; 3a+b: mosaic of *Nardion* and *Juniperion nanae*; 4a+b: *Juniperion nanae*; 5a: encroached areas with *Juniperion nanae* and *Rhododendro-Vaccinion*; 6a: *Alnenion viridis*. Significant differences between the vegetation types detected with Tukey's post-hoc tests ($p < 0.01$) are displayed as different lowercase letters at the top of the error bars.

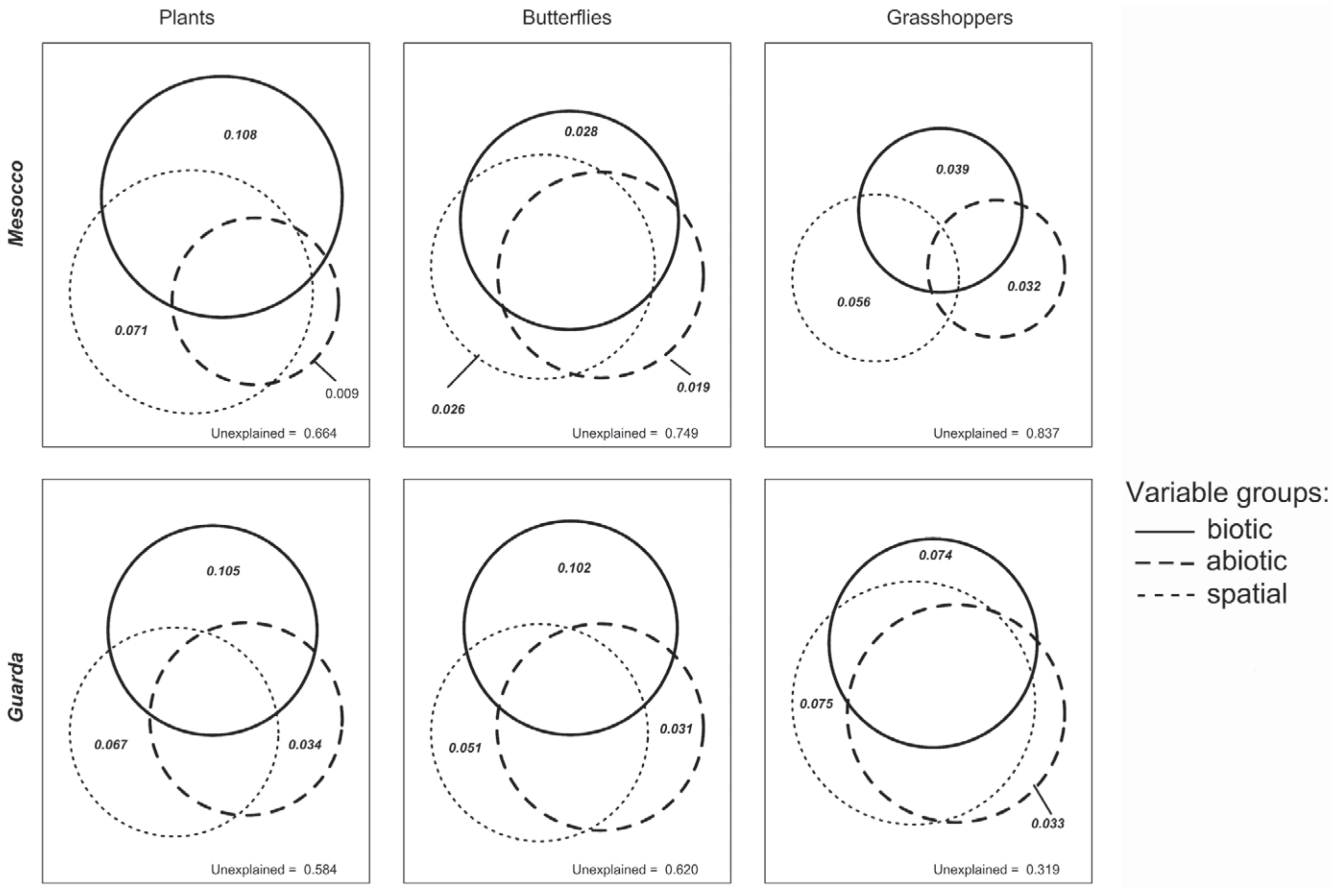

FIGURE 3. Results of variation partitioning with redundancy analysis (RDA) for the study sites Mesocco (n = 49) and Guarda (n = 48). Venn diagrams show the fractions of variance in species composition of plants, butterflies, and grasshoppers explained by pure biotic, abiotic, or spatial variables. Bold values indicate significant fractions. The unexplained variance is also reported in the single graphs. The reported fractions show adjusted R^2 to account for the different number of terms in the variable sets.

SHRUB ENCROACHMENT AND SPECIES DIVERSITY OF PLANTS, BUTTERFLIES, AND GRASSHOPPERS

The degree of shrub encroachment significantly affected the diversity of plants and grasshoppers in Mesocco, but only the number of rare plant species in Guarda. In Mesocco, the highly encroached plots (*Type 5a*) and those with *Alnus viridis* (*Type 6a*) had lower plant species richness and fewer herbaceous plant species than those with a mosaic of *Nardion* and *Juniperion nanae* (*Type 3a*) or with the *Juniperion nanae* association (*Type 4a*). Although shrub cover in plots dominated by *A. viridis* was not extremely high, plant species diversity was rather low, which is consistent with previous studies reporting *Alnenion viridis* plant communities to be particularly species-poor (Anthelme et al., 2001, 2003; Freléchoux et al., 2007). In Mesocco, encroached plots (*Type 5a*) had very low plant species richness, indicating that a high cover of dwarf shrubs has a negative effect upon plant diversity. Furthermore, herbaceous plant species occurring in highly encroached areas were mainly forest species such as *Viola biflora* and *Oxalis acetosella*, presumably because these can tolerate lower light conditions than most grassland species. In Guarda, however, where the shrub cover of the most encroached sites was lower than at Mesocco, we found no difference in plant species richness among vegetation types. These findings are in agreement with the model of Schütz et al. (2000), which shows that grassland communities dominated by *F. rubra* or *N. stricta* are particularly rich in plant species.

We found no significant differences in butterfly species richness among vegetation types at either site (Fig. 2). One possible reason for this negative result is the greater mobility of butterflies compared not only to vascular plants but also to grasshoppers, which enables them to visit less suitable patches provided that adequate resources are present in the neighbourhood (Shreeve, 1995). However, habitat size and connectivity are known to be important for less mobile butterfly species, making such species particularly sensitive to habitat loss and fragmentation (Öckinger et al., 2010). It is also possible, of course, that the scale considered was too small and/or the plots not big enough to detect differences in butterfly diversity among vegetation types. Regardless, the relatively lower number of species in vegetation types with higher shrub cover agrees with other authors that have reported that bushes and shrubs have a negative effect upon subalpine butterfly communities (Erhardt, 1985; Hohl, 2006). Another reason may be that some of the species occurring in encroached areas are either relatively undemanding in terms of habitat (Samways et al., 2012) or even require more than one type of habitat to complete their life cycle. Indeed, in a study of butterfly communities on abandoned grasslands in northeast Spain, Stefanescu et al. (2009) found that grassland specialists were replaced by common, more generalist species as succession proceeded. And in our study, at least one species, *Callophrys rubi,* needs both grassland and shrubland habitat patches, since adults feed in grassland but lay their eggs on dwarf shrubs.

In Mesocco, we found more grasshopper species in mosaic vegetation with *Nardion* and *Juniperion nanae* than in plots with *Alnenion viridis* association, while in Guarda grasshopper species richness tended to peak at intermediate shrub cover. Both findings are consistent with the study by Anthelme et al. (2001) of an *Alnus viridis* succession in the French Alps, in which orthopteran biomass was much greater when the shrub formed a mosaic with grassland than when it became more dense. Assuming that the increasing shrub cover in our plots indicates a successional sequence, our results are also consistent with studies reporting highest orthopteran species richness in grassland and coastal heathland at early to mid-successional stages (Marini et al., 2010; Schirmel et al., 2011; Fartmann et al., 2012). At the other end, the slightly lower numbers of grasshopper species in vegetation types with very low shrub cover are probably linked to the preference of species such as *Podisma pedestris* or *Metrioptera brachyptera* for habitats rich in vegetation structure, including dwarf shrubs (Szövényi, 2002; Baur et al., 2006a).

EFFECT OF BIOTIC AND ABIOTIC FACTORS ON SPECIES COMPOSITION

Overall, biotic variables (related to shrub encroachment and plant diversity for the insect groups) explained significant amounts of variance in plant, butterfly, and grasshopper species composition at both sites, while abiotic factors explained much less. This suggests that shrub encroachment plays a major role in shaping species assemblages of plants and insects on summer pastures. Similarly, Rudmann-Maurer et al. (2008) found that land use (mowing, grazing, abandonment) had a stronger impact on alpine grassland composition than abiotic factors and cultural tradition. Dullinger et al. (2003) showed that patterns of *Pinus mugo* recruitment success depended mainly on propagule pressure and invasibility of the grassland community, but only marginally on abiotic habitat conditions. However, the joint fraction of variance explained by both biotic and abiotic factors was relatively large, suggesting that interactions between these two sets of variables also play an important role in shaping spatial species distributions. Grazing patterns highly depend on pasture topography, especially slope, which is an important parameter limiting movements of grazing animals (Ganskopp and Vavra, 1987). Conversely, grazing and shrub encroachment in turn alter small-scale abiotic site conditions such as soil nutrients and moisture or shading (El-Bana et al., 2002). Given the relatively small areas surveyed, effects of microtopography upon local microclimate may be more important than larger scale environmental variables such as altitude or slope (Scherrer and Körner, 2010; Wundram et al., 2010). Thus, the scale used was potentially too small for detecting effects of the large-scale abiotic factors used in this study. Nevertheless, spatial factors at the same time accounted for a large part of the explained variance in our study, indicating that the results were influenced by factors such as nutrient availability or seed dispersal. In this regard, more research effort is needed and future investigations should also account for soil conditions and moisture in order to confirm the detected patterns. An influence of abiotic factors was found at the drier Guarda site but not in Mesocco, where mean annual precipitation is much higher. This result is consistent with previous studies suggesting an important role of water availability in shaping distribution of vegetation composition (Hodkinson et al., 1999; Michalet et al., 2002).

Conclusions

Our results suggest that shrub encroachment driven by land abandonment or underuse is a major factor affecting the diversity of plants and insects on subalpine summer pastures. However, as they are based on only two pastures, further research is needed to confirm these conclusions. Agri-environment schemes involving direct payments for ecological quality are important instruments to counteract the abandonment or underuse of marginal land that eventually leads to shrub encroachment (Strijker, 2005; Mack and Flury, 2008). In Switzerland, a scheme based upon floristic quality has been introduced to help conserve biodiversity at lower altitudes (Kampmann et al., 2012). A similar scheme for summer pastures at higher altitudes started in 2014. As vascular plants are an adequate surrogate for butterfly and grasshopper diversities in these areas (Koch et al., 2013), it can be expected that these insect groups would also benefit from such a scheme. However, given the preference of the plant and grasshopper groups for different successional stages, we recommend the maintenance of patches with different degrees of shrub encroachment. In the context of habitat fragmentation, adequate size of patches and habitat connectivity should also be ensured.

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APPENDIX

TABLE A1

Results of variance partitioning with a redundancy analysis (RDA) for plants, butterflies, and grasshoppers in Mesocco ($n = 49$) and Guarda ($n = 48$). Pure (B = biotic, A = abiotic, S = spatial), joint (∩ indicates shared variation) and unexplained fractions of variance (adjusted R^2; R^2_{Adj}), and significance values for pure fractions (p; significant values in bold) are reported.

		B		A		S		B∩A	B∩S	A∩S	B∩A∩S	Residual
Study areas	Taxon	R^2_{Adj}	p	R^2_{Adj}	p	R^2_{Adj}	p	R^2_{Adj}	R^2_{Adj}	R^2_{Adj}	R^2_{Adj}	R^2_{Adj}
Mesocco	Plants	0.108	***0.005***	0.009	*0.160*	0.071	***0.005***	0.006	0.058	0.047	0.039	0.664
	Butterflies	0.028	***0.010***	0.019	***0.047***	0.026	***0.046***	0.024	0.045	0.035	0.073	0.749
	Grasshoppers	0.039	***0.026***	0.032	***0.044***	0.056	***0.010***	0.015	<0.001	0.017	0.006	0.837
Guarda	Plants	0.105	***0.005***	0.034	***0.010***	0.067	***0.005***	0.057	0.046	0.081	0.027	0.584
	Butterflies	0.102	***0.005***	0.031	***0.015***	0.051	***0.015***	0.033	0.033	0.091	0.039	0.620
	Grasshoppers	0.074	***0.005***	0.033	***0.015***	0.075	***0.005***	0.035	0.100	0.177	0.187	0.319