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ORIGINAL PAPER

Omnipresence of leaf herbivory by invertebrates and leaf infection by fungal pathogens in agriculturally used grasslands of the Swiss Alps, but low plant damage

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Abstract Agriculturally used grasslands in the Alps are characterised by a trade-off between high fodder production in some and high plant species richness in others. In contrast to plant species richness and production, however, little is known on the relevance of biological interactions between plants, invertebrate herbivores, and fungal pathogens for grasslands in the Alps. At the time when the vegetation was fully developed, but prior to agricultural use, we examined whether leaf damage by herbivory and fungal pathogen infection, and their diversity, are affected by plant functional group, land use, and altitude. Moreover, we studied whether extent and diversity of leaf damage are related to each other, to plant species richness, and to standing crop. We recorded the leaf area damaged by ten types of herbivory and five types of fungal pathogen infection on 12,054 plant leaves of legumes, other forbs, and graminoids collected in 215 grassland parcels in 12 valleys in the Swiss Alps. With 83 % of all leaves infested, herbivory and fungal pathogen infection were omnipresent. However, only 2.7 % leaf area was damaged by herbivory and 1.2 % by fungal pathogens. Damage by herbivory was highest on legumes, and damage by fungal pathogens was highest on graminoids. More leaf damage by herbivory occurred in

traditionally mown sites and at lower altitudes, while damage by fungal pathogen infection was independent of land use and altitude. Most types of herbivory were found on legumes and on leaves from fertilised sites, whereas the number of fungal pathogen types was highest on graminoids and in unfertilised sites. Larger standing crop was associated with higher leaf damage and diversity of herbivory types per leaf. Neither damage by herbivory nor by fungal pathogens was correlated with plant species diversity. In more plant species rich parcels, the number of herbivory types was lower at the leaf level, but tended to be higher at the parcel level. Our results highlight the omnipresence of plant–herbivore and plant–pathogen interactions. They suggest that current land use changes from mowing to grazing or to abandonment decrease the diversity of herbivory, and that fertilisation decreases pathogen diversity. As our results did not reveal conservation conflicts between diversities of plants, herbivores, and fungal pathogens, and as the damage from herbivory and pathogens is generally low, we conclude that for protecting the high diversity of plant–herbivore and plant–pathogen interactions a diverse low-intensity land use should be maintained.

Keywords Agricultural land use · Biodiversity · Biological interactions · Conservation · Forbs · Fungi · Grasses · Invertebrate herbivores · Legumes · Plant functional groups

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Introduction

Meadows and pastures are an important element of the cultural landscape of the Alps and are well-known for their characteristic and diverse flora and fauna (Ellenberg 1996). The various landscapes of the Alps have been shaped by

humans and their cattle over thousands of years (Ellenberg 1996) and they are among the European areas richest in plant species (Väre et al. 2003). Different cultural traditions (Germanic, Romanic, and Walser) with their specific farming practices have contributed to the high diversity of the alpine landscapes (Bätzing 2003). In the Alps, land use is undergoing major changes (Bätzing 2003) where both abandonment and intensification of land use are reducing the plant species diversity of many grasslands (Olsson et al. 2000; Fischer and Wipf 2002; Tasser and Tappeiner 2002; Maurer et al. 2006; Niedrist et al. 2009, Fischer et al. 2008). In addition to land use, biodiversity is also affected by geological, topographic, and climatic conditions (Kikvidze et al. 2011). In the Alps, the altitudinal gradient is particularly important (Rahbek 1995; Theurillat et al. 2003; Sergio and Pedrini 2007; Stöcklin et al. 2009; Fischer et al. 2011). Clearly, comprehensive ecological understanding should be based on the knowledge of biodiversity at all levels and spatial scales (Fischer et al. 2010). However, while local plant species richness is comparatively well studied for many grasslands in the Alps, information about the local importance and diversity of herbivores and plant pathogens is very scarce.

In addition to its ecological interest, grassland diversity also matters from the points of view of agriculture and conservation. Conservation conflicts arise if high diversity of herbivores or plant pathogens is associated with low diversity of the other group, or of plants. Moreover, if high diversity of herbivores and pathogens would be associated with substantial plant biomass losses, their conservation would conflict with the agricultural goal of high biomass production. Currently, the relationships between plant species richness, diversity of herbivory and fungal pathogen infection, and standing crop are not known for mountain grassland.

Several studies with herbivores and pathogens in colline and montane grassland suggest that degree and diversity of herbivory and pathogen infection are affected by land use (Wettstein and Schmid 1999; Kruess and Tschardtke 2002), site productivity (Siemann 1998; Haddad et al. 2000; Mulder et al. 2002), and plant species diversity (Knops et al. 1999; Mitchell et al. 2002; Scherber et al. 2006; Haddad et al. 2009; Woodcock and Pywell 2010). Moreover, altitudinal effects on the extent of herbivory have been reported (Scheidel and Bruelheide 2001). In grasslands in foothills of the Alps, the diversity and abundance of grasshoppers and butterflies were negatively affected by management and declined with altitude (Wettstein and Schmid 1999). However, a comprehensive study of degree and diversity of herbivory and pathogen infection is missing for grassland at subalpine and alpine altitudes.

Different plant functional groups are likely to be differently affected by herbivores and pathogens (Symstad et al.

2000). Due to their high nitrogen contents, legumes are likely to be preferred by herbivores (Mattson 1980). Pathogens are more likely and more abundant in larger host populations (Mitchell et al. 2002). Therefore, due to their usually high abundances, graminoids may be more likely to be infected by fungal pathogens than forbs or legumes are.

We measured leaf damage by herbivory and by fungal pathogen infection at three altitudinal levels around each of the 12 villages across the Swiss Alps as an indicator for the intensity of plant–herbivore and plant–pathogen interactions in mountain grassland. We measured leaf damage once, whenever possible at the time of maximum standing crop, just prior to agricultural land use. We classified leaf damage according to different types of herbivory and fungal pathogen infection. For scoring leaf damage by different herbivory types we followed Crawley (1983) who classified leaf damage by herbivores according to feeding habit. Because single damage types can be caused by several taxa, it is not possible to identify the species that caused a particular damage type. Nevertheless, Crawley's classification of damage types of herbivores allowed us to assess the diversity of herbivory types. As there is no classification of leaf damage by different types of fungal pathogens, we used broad taxonomic categories that could be distinguished with a binocular microscope for assessing fungal pathogen diversity.

We studied the degree of damage by different types of herbivory and fungal pathogen infection of leaves of 215 grassland parcels of different land uses at different altitudes in the Swiss Alps. To account for potential regional and cultural differences, these grassland parcels represented four villages of each of the three main cultural traditions in the Swiss Alps, Romanic, Germanic, and Walser (Fischer et al. 2008; 2011). Our main questions were (1) How large is the damage of plant leaves by herbivory and fungal pathogen infection, and does the extent of leaf damage depend on plant functional group, land use, and altitude? (2) Which, and how many, different types of herbivory and fungal pathogen infection are present on leaves of different origin, and do number and composition of types depend on plant functional group, land use, and altitude? (3) How are leaf damage and the diversity of types of herbivory and fungal pathogen infection related to each other, to plant species richness, and to the amount of standing crop per grassland parcel? We discuss our findings considering ecological, agricultural and conservation perspectives.

Materials and methods

Study sites

We studied grassland in 12 villages in the Swiss Alps, four of each of the three cultural traditions Romanic, Germanic, and

Table 1 Ten types of leaf damage by herbivory and five types of leaf damage by fungal pathogens and their characteristics scored on 12,054 leaves of plants from 215 grassland parcels in the Swiss Alps

Category	Characteristics
Herbivory	
Clipping	Damage of leaf margins; usually sharp edges
Holing	Damage within leaf; continuous hole in the leaf
Windowing	Damage within leaf, but with remaining single cell layer
Rasping	Removal of single cell layers from surface; often white short dashes
Mining	Continuous mine in the leaf, visible from both sides
Skeletonising	Damage by continuous hole along the leaf veins
Spinning	Cocoons or cocoon-like structures
Puncturing	Fine punctured stitch-like pattern
Eggs	Mostly accumulated, but also single ones
Larvae/pupae	Mostly single
Fungal pathogens	
Rust fungus	Greyish sporangia with brown rusty spores, crumb-like on leaf surface or veins
Hyphomycetes	Small, black, cloud-like structures on leaf surface
Powdery mildew	Patches of fine white mycelium, mostly on upper leaf surface
Ascomycetes	Patches with pustule-like structure in the centre
Unknown Fungi	Undefined damage (patches with parchment-like inner part, holes with red margin, mine visible from only one side, other concentric coloured patches with light centre/dark margin)

Walser (Maurer et al. 2006; Fischer et al. 2008; Rudmann-Maurer et al. 2008). Each village belongs to a separate alpine valley, and the 12 villages are located along an East–West gradient of about 170 km (see Fig. 1; Table 1 in Maurer et al. 2006). We selected villages whose agriculture has only changed modestly during the last 50 years, that have not undergone major changes due to tourism, and that have fewer than 1,500 inhabitants.

At three altitudinal levels per village (valley at about 1,000 m asl, intermediate altitudes about 1,500 m asl, and Alp at about 2,000 m asl), we selected parcels of land representing up to 12 different land use combinations (Maurer et al. 2006; Fischer et al. 2008; Rudmann-Maurer et al. 2008). Parcels were fertilised or unfertilised, had traditionally been mown or grazed, and were currently mown, grazed, or abandoned. In total, we selected 215 grassland parcels, ranging from 12 to 24 per village.

Leaf sampling

We had taken vegetation records in two 5 m × 5 m plots separated by about 5 m in each grassland parcel in summer 2002 (69 parcels) and summer 2003 (147 parcels) to assess

plant species composition and diversity (Maurer et al. 2006; Rudmann-Maurer et al. 2008). Although the summer of 2003 was much drier than that of 2002, this was not apparent at our study sites at the time of taking vegetation records. As close as logistically possible, we did this when the vegetation was best developed, shortly before managed parcels were mown or grazed. At this time, leaf damage is not only most relevant from the point of view of agriculture, but also from the ones of ecology and conservation, simply because subsequent mowing and grazing remove large parts of the host plants and pathogens. In addition to taking vegetation records, in each plot we harvested biomass 4 cm above ground in a randomly selected area of 0.5 m × 0.5 m to assess standing crop (Redjadj et al. 2012). At the same time, in the 215 parcels we collected one leaf of each of ten plants of the three functional plant groups graminoids (Poaceae, *Carex*, and *Luzula*), legumes, and non-legume forbs (except for thistles and orchids). In each plot, we collected leaves of plants closest to positions defined by a walking grid. This procedure resulted in a sample of 30 randomly selected leaves per plot, i.e. 60 leaves per parcel, except for parcels without or with only few legume plants. Sampling a certain number of leaves using a walking grid gives more weight to more abundant species, while sampling leaves of a pre-defined set of species would not. We transported the leaves in plastic bags, pressed them in plant presses for up to 5 days, and dried them in a drying oven at 40 °C for at least 2 days.

Scoring of herbivory and fungal pathogen infection

In winter 2003/2004, we visually screened all 12,054 leaves for damage by herbivory and fungal pathogen infection with a binocular microscope. To classify different types of leaf damage, we distinguished ten categories of infestation by herbivory and five categories of infestation by fungal pathogen infection (Table 1). For herbivory, we distinguished between clipping, holing, rasping, mining, skeletonising, and spinning according to Crawley (1983). Additionally, we considered the categories windowing, puncturing, eggs, and larvae/pupae. We considered eggs and larvae/pupae after realising their frequent presence and large numbers on the leaves. We are aware that scored eggs and larvae/pupae would have developed into one of the other categories. Nevertheless, introducing the classes of eggs and larvae/pupae was not only due to practicability, because the simultaneous occurrence of different stages of development also constitutes diversity.

We scored fungal pathogen infection according to taxonomical categories and distinguished between rust fungi, powdery mildew, hyphomycetes, and ascomycetes. Because it was not possible to unambiguously classify all infestations by fungal pathogens, we also introduced the category of

unknown fungi, which may, however, to some degree include infection by the groups mentioned above. Finally, we classified any leaf damage as unknown, which could not be ascribed to any of these categories. We did not include such unknown damage in the analyses.

For each leaf, we estimated the leaf area damaged by herbivory and fungal pathogen infection separately in percent. Then, we recorded the presence and absence of all categories of leaf damage. Additionally, we noted the category that caused the largest area of leaf damage, both for herbivory and fungal pathogen infection. To estimate the proportion of damage per leaf we compared the leaves with leaf templates with known proportions of damaged area. For damage amounting to less than one percent, we used the value 0.5 for the calculations. Although our estimates are less accurate than direct measures of damage, we consider them sufficiently accurate for our purpose because of the large number of >12,000 leaves. Moreover, only this method enabled us to study leaves from >200 grasslands.

Data analysis

We included all 12,054 leaves and assessed damage by herbivory and by fungal pathogen infection per leaf, per functional group and parcel, and per parcel. We analysed the effects of land use and altitude on damaged leaf area and diversity of types of herbivory and fungal pathogen infection with analyses of variance (ANOVA) using a hierarchical mixed model including the factors culture, village, altitude, fertilisation, abandonment, current land use, traditional land use, parcel and all interactions (Appendix). Villages were nested within cultures, and current land use was nested within abandonment, because in our study current land use is meant to refer to currently mown and grazed grassland parcels. To analyse differences between functional groups, we added the factor functional group and all its interactions to the model. In all analyses, we treated village and parcel as random factors.

Aspect and slope of a parcel, and yearly differences could affect herbivores and fungal pathogens. However, including aspect, slope, and year of leaf harvest as covariates did not change levels of significance. Therefore, we present results of the model without covariates. We point out all significant results in the results section.

To analyse differences in the composition of damage types between parcels, first, we conducted a principal component analysis (PCA) of the occurrence of different categories of herbivory and fungal pathogen infection per leaf. Then, to test for effects of altitude and land use on the composition of herbivory and fungal pathogen diversity we did an ANOVA of the four principal components with the same model as mentioned above.

Results

Leaf damage by herbivory and fungal pathogen infection

82.8 % of the 12,054 leaves were damaged by at least one category of herbivory or fungal pathogen infection. The most frequent categories of herbivory were, in declining order, clipping, holing, rasping, and windowing (Table 2). Moreover, eggs were present on 49 % of all leaves and dominant on 25.1 % of them, indicating that damage by number of occurring herbivory types would presumably increase after egg development. For fungal pathogen infection, the most frequent categories, in declining order, were rust fungi (18.91 %), hyphomycetes (3.5 %), powdery mildew (2.1 %), and ascomycetes (1.2 %). Compared with these numbers the proportion of 0.4 % of leaves with unknown fungi was small (Table 2). 58.7 % of the leaves were infested by herbivory only, 6.0 % by fungal pathogens only, and 18.0 % by both.

We recorded 2.7 ± 0.13 % (mean \pm SE) leaf damage by herbivory, and 1.2 ± 0.09 % by fungal pathogen infection. Parcels with higher damage of leaf area by herbivory also had higher damage by fungal pathogen infection ($N = 215$, $R = 0.18$, $p < 0.01$, Fig. 1a). Herbivory was most pronounced on legumes (4.5 ± 0.3 % damage per leaf), followed by non-legume forbs (2.6 ± 0.1 %), and graminoids (1.3 ± 0.1 %, Fig. 2a). In contrast, fungal pathogen infection was most pronounced on graminoids (1.5 ± 0.1 %), followed by non-legume forbs (1.2 ± 0.1 %), and legumes (0.7 ± 0.1 %, Fig. 2a).

The lower the altitude, the more leaf area was damaged by herbivory (valley 3.3 ± 0.2 %, intermediate altitudes 2.6 ± 0.2 %, alp 2.0 ± 0.2 %; $N = 215$, $F_{1,98} = 34.1$, $p < 0.001$). The damaged leaf area of legumes was higher in the valley than at intermediate altitudes, where it was higher than at the alp level ($N = 638$, $F_{2,199} = 14.1$, $p < 0.001$, Fig. 3a). On graminoids, damage was also higher in the valley grassland, but did not differ between grassland at intermediate altitudes and at the alp level. Leaf damage of forbs was independent of altitude. Moreover, altitude did not affect damage by fungal pathogen infection.

In traditionally mown grasslands, more leaf area was damaged by herbivory on legumes and forbs than in those that had always been grazed, whereas there was no such effect for graminoids ($N = 638$, $F_{2,199} = 5.6$, $p < 0.01$, Fig. 3b). Moreover, land use did not affect leaf damage by fungal pathogens.

None of the studied variables differed between villages of the three different cultural (i.e. Romanic, Germanic and Walser) traditions. Therefore, we do not mention cultural tradition in the subsequent results sections.

Table 2 Percentage of leaves of legumes, non-legume forbs, and graminoids damaged by 10 different herbivory types, by five different fungal pathogen types, and by unknown causes in 215 grassland parcels in the Swiss Alps. Also included are the percentage of each damage category present per parcel, and the percentage of leaves for which the particular category was the dominant cause of damage

Type of leaf damage	Present (%)					Parcels	Dominant in leaves (%)
	Leaves of legumes	Leaves of non-legume forbs	Leaves of graminoids	Leaves of all groups			
Herbivory							
Clipping	38.29	23.12	8.09	22.43	100.0	16.9	
Holing	38.23	20.84	4.15	20.24	99.5	10.0	
Windowing	28.34	15.59	8.97	17.11	99.5	7.5	
Rasping	27.45	12.63	20.56	19.86	94.9	14.3	
Puncturing	2.51	2.56	0.24	1.73	45.6	0.4	
Skeletonising	2.32	0.19	0.47	0.93	28.8	0.3	
Mining	0.94	0.52	1.12	0.85	29.8	0.4	
Spinning	0.52	1.00	0.14	0.56	16.3	0.2	
Eggs	54.74	53.10	39.95	49.00	100.0	25.1	
Larvae/pupae	2.48	5.91	1.83	3.45	74.4	1.5	
Fungal pathogens							
Rust fungi	14.44	19.23	22.43	18.91	65.1	3.1	
Hyphomycetes	4.05	2.49	4.11	3.53	43.7	1.1	
Powdery mildew	2.34	1.38	2.52	2.07	23.3	1.1	
Ascomycetes	1.71	1.33	0.57	1.18	16.7	0.4	
Unknown Fungi	0.69	0.52	0.14	0.44	97.7	18.3	
Unknown	8.3	9.2	5.7	23.3	100.0	–	

Number of types of herbivory

Per leaf, we recorded 1.36 ± 0.01 of the ten types of herbivory. Per parcel, we recorded 6.89 ± 0.07 types of herbivory. The number of herbivory types per leaf was higher in parcels with higher average leaf damage by herbivory ($N = 215$, $R = 0.40$, $p < 0.001$, Fig. 1c).

More herbivory types occurred on legumes (1.90 ± 0.05 types per leaf) than on non-legume forbs (1.35 ± 0.03), and graminoids (0.86 ± 0.03). The lower the altitude, the more types of herbivory occurred per leaf (valley 1.53 ± 0.05 types per leaf, intermediate altitudes 1.40 ± 0.04 , alp 1.01 ± 0.04 ; $N = 215$, $F_{1,98} = 137.8$, $p < 0.001$). This was more pronounced for legumes than it was for graminoids and non-legume forbs (functional group by altitude interaction; $N = 638$, $F_{2,199} = 3.2$, $p < 0.05$, Fig. 4a).

More types of herbivory occurred in traditionally mown grassland parcels (1.45 ± 0.04 types per leaf) than in grazed ones (1.20 ± 0.04 , $N = 215$, $F_{1,98} = 18.3$, $p < 0.001$, Fig. 4b). Moreover, more types of herbivory occurred in fertilised (1.62 types per leaf ± 0.03) than in unfertilised grassland (1.18 ± 0.05 , $N = 215$, $F_{1,98} = 42.4$, $p < 0.001$, Fig. 4c). The differences in the numbers of types of herbivory per leaf, which were highest on legumes, intermediate on non-legume forbs, and lowest on graminoids, were more pronounced in traditionally mown grassland parcels than in traditionally grazed ones (functional group by traditional land use interaction, $N = 638$, $F_{2,199} = 8.8$, $p < 0.001$, Fig. 4b).

Number of types of fungal pathogen infection

Per leaf, we recorded 0.26 ± 0.004 of the five types of fungal pathogen infection, and per parcel, we recorded 2.47 ± 0.07 . The number of types of fungal pathogen infection per leaf was higher in parcels with higher average leaf damage by fungal pathogen infection ($N = 215$, $R = 0.675$, $p < 0.001$, Fig. 1d). Fungal pathogen diversity was highest for graminoids (0.30 ± 0.01 types per leaf), followed by forbs (0.25 ± 0.01) and legumes (0.22 ± 0.01).

While the number of fungal pathogen types did not differ among altitudes, it was affected by land use. On graminoids in unfertilised sites, we found more types of fungal pathogen infection (0.34 ± 0.02 per leaf) than in fertilised ones (0.23 ± 0.03 ; functional group by fertilisation interaction, $N = 638$, $F_{2,199} = 13.1$, $p < 0.001$). Moreover, we recorded more types of fungal pathogen infection on graminoids in abandoned sites (0.45 ± 0.05) than in managed ones (0.27 ± 0.01 ; functional group by abandonment interaction, $N = 638$, $F_{2,199} = 11.8$, $p = 0.078$).

Composition of types of damage by herbivory and fungal pathogen infection

Analysis of variance of the principal components of types of damage by herbivory demonstrated significant effects of altitude (PC1, $N = 215$, $F_{1,101} = 99.0$, $p < 0.001$) and traditional land use (PC1, $N = 215$, $F_{1,101} = 18.5$, $p < 0.001$) on the composition of these types. This reflects the higher

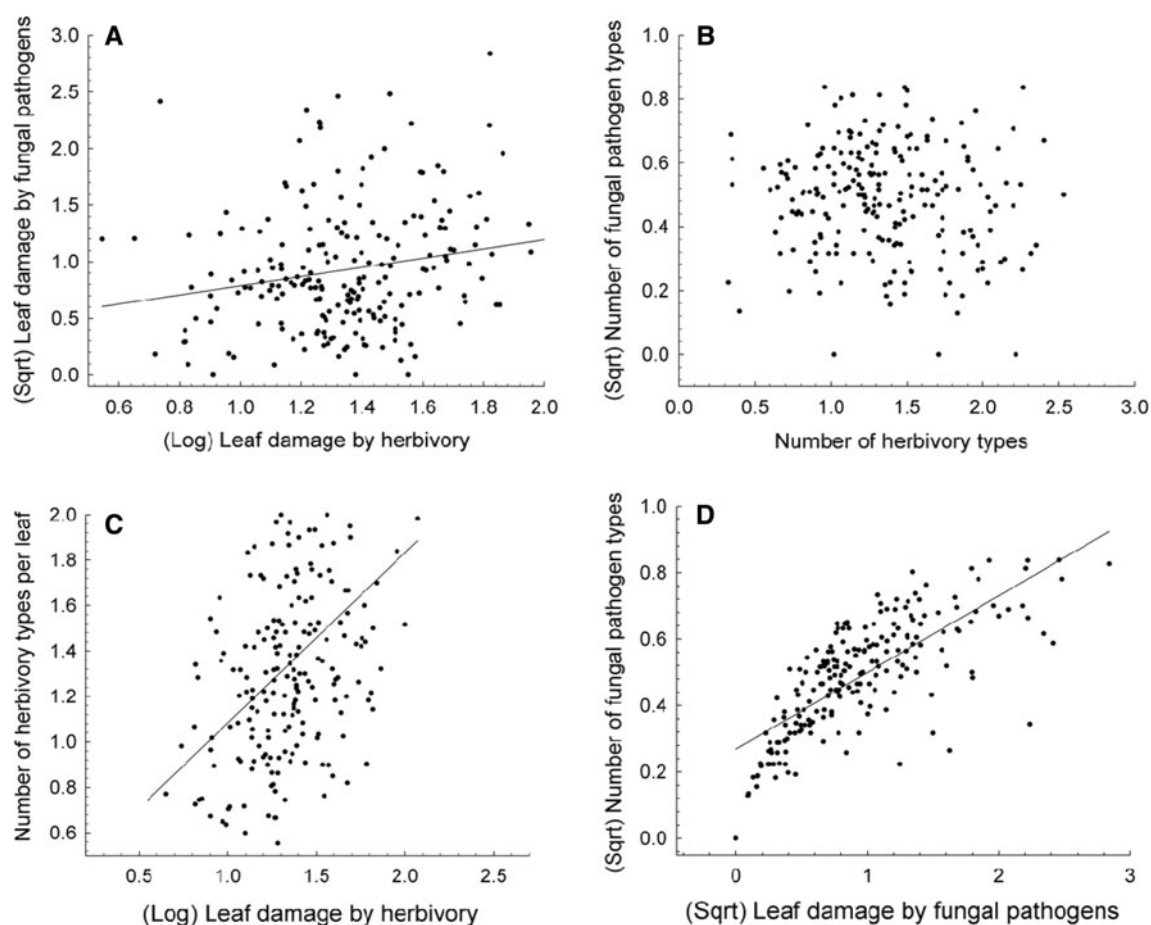


Fig. 1 Relationships between **a** leaf damage by herbivory and by fungal pathogen infection, **b** number of types of herbivory and fungal pathogen infection, **c** leaf damage and number of types of herbivory and **d** leaf damage and number of types of fungal pathogen infection,

on leaves from 215 grassland parcels in the Swiss Alps. *Sqrt* square root transformation, *log* logarithm to the base of ten, *trend lines* are given for significant relationships

number of eggs on leaves from valleys and intermediate altitudes than from high altitudes ($N = 215$, $F_{2,212} = 13.8$, $p < 0.001$), and the larger damage by clipping ($N = 215$, $F_{1,213} = 16.8$, $p < 0.001$), holing ($N = 214$, $F_{1,212} = 7.8$, $p < 0.01$), and windowing ($N = 214$, $F_{1,212} = 13.6$, $p < 0.001$) in traditionally mown than in grazed parcels. In contrast to herbivory, the composition of types of fungal pathogen infection was independent of altitude and land use.

Relationships of herbivory and fungal pathogen infection with standing crop and plant species diversity

Standing crop per parcel was positively correlated with the leaf area damaged by herbivory ($N = 209$, $R = 0.184$, $p < 0.001$, Fig. 5a), the number of herbivory types per leaf ($N = 209$, $R = 0.174$, $p < 0.05$, Fig. 5c), the leaf area damaged by fungal pathogen infection ($N = 209$, $R = 0.277$, $p < 0.001$, Fig. 5e), and the number of fungal pathogen infection types per leaf ($N = 209$, $R = 0.433$, $p < 0.001$, Fig. 5g). With the increasing number of plant

species per parcel the number of herbivory types per leaf decreased ($N = 215$, $R = -0.288$, $p < 0.001$, Fig. 5d).

Discussion

Leaf damage by herbivory and fungal pathogen infection

The infestation of 83 % of all sampled leaves demonstrates the omnipresence of plant–herbivore and plant–pathogen interactions in mountain grassland. According to the visibly damaged leaf area, herbivory is more important than fungal pathogens. However, the low extent of damage by herbivores and fungal pathogens indicates that biomass losses are not substantial. The 2.7 % average leaf damage by herbivores is in line with other results showing that leaf damage in 10 herbaceous species in early successional habitats rarely exceeded 3 % (Carson and Root 1999). Such low amounts of leaf damage due to herbivory seem to be quite common (Landsberg and Ohmart 1989, Scherber et al. 2006). The

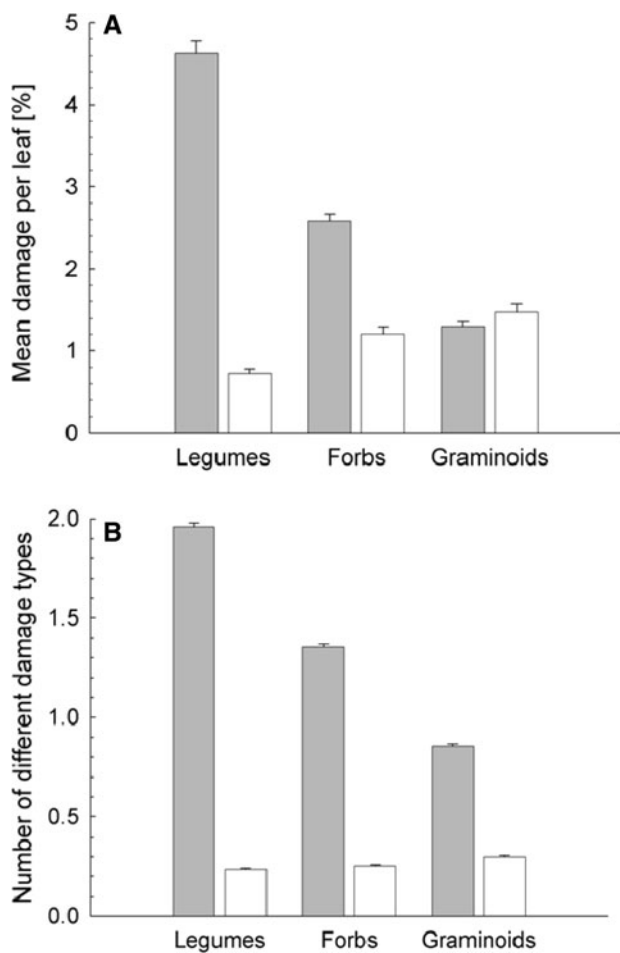


Fig. 2 **a** Mean damage per leaf by herbivory (*shaded*) and fungal pathogen infection (*open*), and **b** mean number of different damage types by herbivory (*shaded*) and fungal pathogen infection (*open*) recorded on leaves of the three functional groups (legumes, non-legume forbs, graminoids) from 215 grassland parcels in the Swiss Alps. *Error bars* denote 1 standard error

observed percentage of leaf damage by fungal pathogens of 1.2 % is much higher than the 0.05 % damaged leaf area recorded in two tree species (Siemann and Rogers 2003). However, for pathogens comparable data for grassland are lacking. The low community leaf damage by herbivory in our semi-natural grassland sites was not related to plant species diversity, corresponding to the findings of an experimental grassland study by Scherber et al. (2006). In our study damage by fungal pathogens was also not related to plant species diversity and we conclude that among diverse mountain grasslands plant species diversity is hardly relevant for the extent of damage by herbivores or fungal pathogens.

The relatively high leaf damage by herbivory on legumes is in line with the idea that legumes are an important source of nutrient supply for herbivores, and that nitrogen is a limiting nutrient for herbivores (Mattson 1980). The

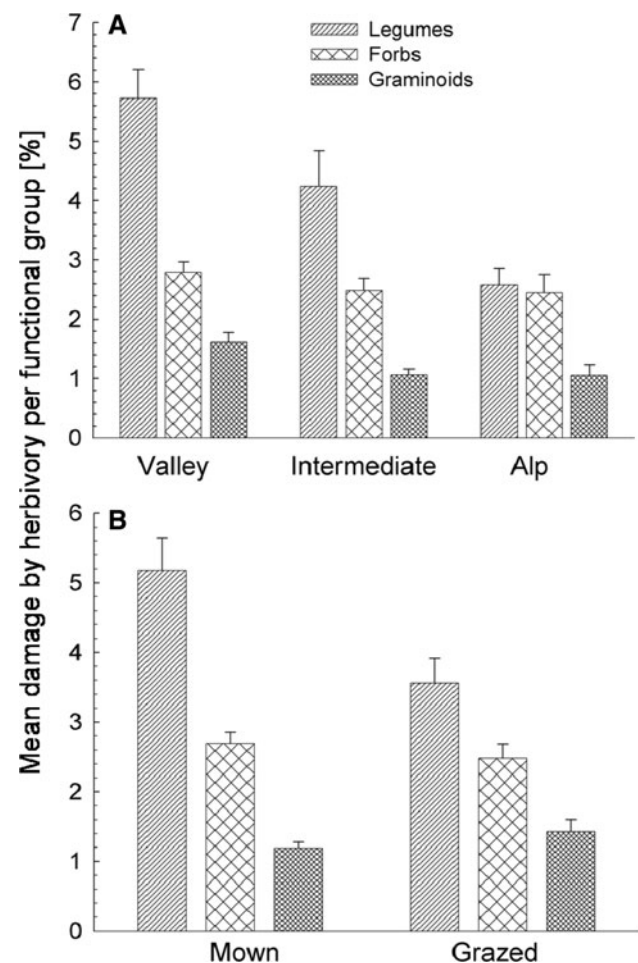


Fig. 3 The relationship between mean leaf damage by herbivory per functional group (legumes, non-legume forbs, graminoids) in 215 grassland parcels in the Swiss Alps and **a** the altitudinal belt where the parcel is situated, and **b** traditional land use. *Error bars* denote 1 standard error

dominant leaf damage of fungal pathogens on graminoids suggests that factors other than nitrogen affect the preference of fungal pathogens. Possibly, fungal pathogens are dominant on graminoids, because these are more abundant in grassland. Correspondingly, rust species, the most frequent fungal pathogens in our study, are common on pasture grass species (Braverman 1986).

The positive correlation of leaf damage by herbivory and leaf damage by fungal pathogen infection suggests that herbivore damage favours fungal pathogen infection. Insect herbivores can serve as vectors for plant pathogens (Kluth et al. 2002). It was suggested that herbivores affect plants more as vectors of disease than as biomass consumers (Ohnesorge 1976). However, in our study leaf damage by fungal pathogens was even lower than the one by herbivores. Alternatively, although many pathogens infest undamaged plants, the positive correlation of leaf damage by herbivory and by fungal pathogen infection may also reflect that leaf

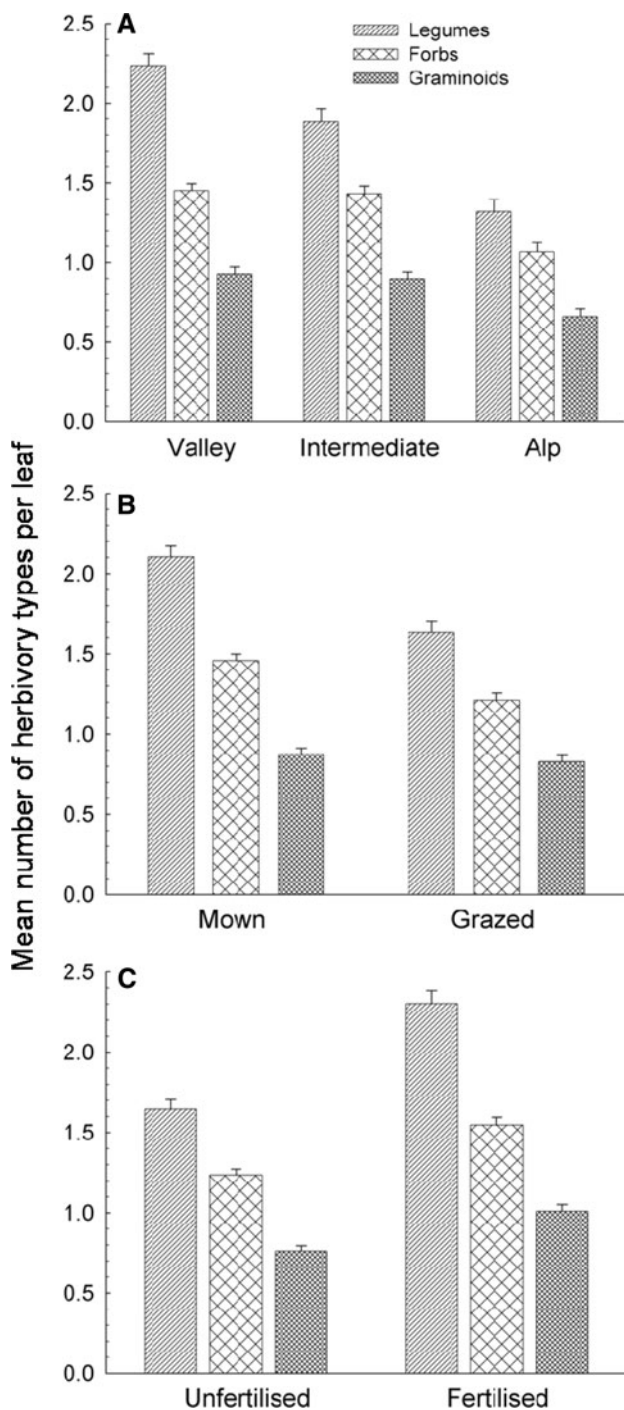


Fig. 4 The relationship between number of herbivory types per leaf and functional group (legumes, non-legume forbs, graminoids) in 215 grassland parcels in the Swiss Alps and **a** the altitudinal belt where the parcel is situated, **b** traditional land use, and **c** fertilisation. Error bars denote 1 standard error

damage by herbivores can facilitate certain pathogen infections (Hatcher 1995). Whereas the leaf damage by both groups was positively correlated, the number of types of herbivory and fungal pathogen infection were independent

of each other. This indicates no conflict between a high diversity of herbivores and a high diversity of fungal pathogens, at least for our coarse measures of diversity based on damage type. Apparently, both groups contribute independently to biodiversity of mountain grassland.

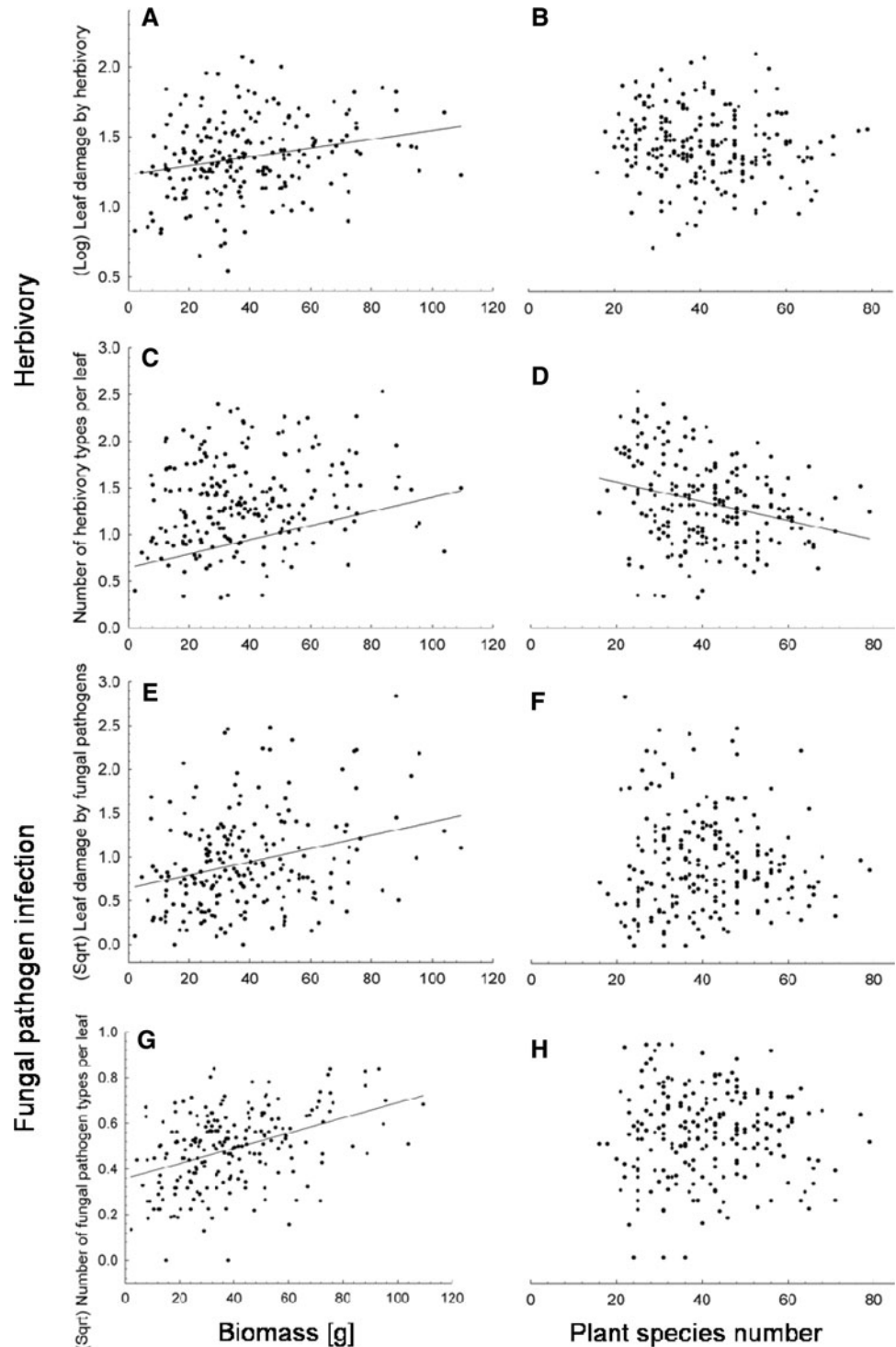
At higher altitudes herbivory damage decreased, while damage by fungal pathogens was not affected by altitude. Lower temperature and shorter season seem to restrict herbivores more than they restrict fungal pathogens. More pronounced herbivory at lower altitudes was also found for grasshoppers (Wettstein and Schmid 1999) and molluscs (Baur and Raboud 1988; Scheidel and Bruelheide 2001). Moreover, in our study especially legume leaves were more damaged by herbivory at lower altitudes, emphasising the importance of this functional group as food supply for herbivores.

The observed higher herbivory damage in traditionally used meadows indicates a preference of herbivores for mown sites, most likely due to frequent disturbances of pastures by trampling by cattle. Accordingly, disturbances in grazed sites were found to negatively influence the presence and establishment of herbivores (Kerley et al. 1993), and intensive grazing was reported to disturb plant–insect interactions (Kruess and Tschamtkke 2002). Thus, in cases where formerly mown grasslands now have to be grazed to reduce labour, the number of cattle and the duration of grazing need to be limited. As differences in biomass production were quite small between mown and grazed grasslands of our study (Maurer et al. 2006), they are unlikely to have caused differences in herbivory between pastures and meadows. Microclimatic conditions could also play a role for herbivores, but there were probably not much differences between pastures and meadows as this would most likely have affected the level of fungal pathogen infections, which did not differ between pastures and meadows. Finally, as far as damage was caused by flower-visiting insects or their larvae, in the Alps herbivores may prefer mown over grazed grassland, because here mown grassland parcels are usually more flower-rich than grazed ones are (Fischer and Wipf 2002).

Diversity and composition of types of herbivory and fungal pathogen infection

More types of herbivory on legume leaves, more fungal pathogen types on grass leaves, and more types of herbivory at lower altitudes correspond with the results on leaf damage, and with the positive correlation of the number of types of both herbivory and fungal pathogen infection with leaf damage. Possibly, this indicates a simple mass effect, where a higher number of plant–parasite interactions is associated both with more severe leaf damage and a higher likelihood that a higher number of different herbivore and fungal pathogen groups is involved. Alternatively, it could indicate a direct relationship

Fig. 5 Relationships between leaf damage by herbivory and **a** standing crop, **b** plant species number; between number of herbivory types per leaf and **c** standing crop, **d** plant species number; between leaf damage by fungal pathogen infection and **e** standing crop, **f** plant species number; between number of types of fungal pathogens per leaf and **g** standing crop and **h** plant species number, in 215 grassland parcels in the Swiss Alps. *Sqrt* square root transformation, log denotes logarithm to the base of ten



between higher diversity of interactions and more severe leaf damage. In any case, the damage by single types of herbivory or fungal pathogen infection remained small. Therefore, we conclude that in mountain grassland herbivores and fungal pathogens do not develop the disease-like character described for crop monocultures (Oerke et al. 1994).

The higher number of types of herbivory at low altitudes is in line with the higher amount of leaf damage there. Most

likely it is due to climatic conditions, which may also explain the altitudinal effect on the composition of herbivory types. The above-average number of eggs on leaves from low altitudes reflects the higher reproduction rates of insects under more advantageous climatic conditions (Virtanen and Neuvonen 1999).

Herbivory was more diverse in mown than in grazed parcels, and the categories with the highest overall

frequencies, clipping, holing, and windowing, were also more frequent on mown sites. We conclude that herbivores with these feeding habits prefer mown over grazed grassland. However, the preference of herbivores to specific land use regimes may differ between taxonomic groups. For example, a more diverse grasshopper community was reported from grazed wetland sites in the pre-Alps, whereas in mown sites the diversity of butterflies was higher (Wettstein and Schmid 1999). Jeanneret et al. (2003) suggested that there are no general rules relating species diversity to habitat and landscape features, because such relationships strongly depend on the specific organism and study region. Nevertheless, in the Alps mown grassland may be likely to be preferred by herbivores, because meadows are often richer in attractive flowers than pastures (Fischer and Wipf 2002) and many insect herbivores are flower visitors.

Increased herbivore diversity may be related to increased productivity of plants via an increase of overall herbivore abundance (Siemann 1998). Moreover, leaves are generally of higher quality and palatability after nitrogen fertilisation (Davidson and Potter 1995). Accordingly, we found more different types of herbivory per leaf in fertilised than in unfertilised parcels. In contrast, per parcel the number of types of herbivory did not differ between fertilised and unfertilised parcels. Most likely in fertilised parcels the higher diversity of herbivory per leaf was counterbalanced by a lower diversity of herbivory between species, because fertilised parcels are less rich in plant species. Accordingly, in experimental and agricultural grassland the diversity of herbivores increased with the number of weed species (Dyer and Stireman 2003). As biomass production was higher in the studied fertilised grasslands than in the unfertilised ones (Maurer et al. 2006), while the number of herbivory types did not differ between mown and grazed parcels, biomass production is unlikely to underlie this pattern.

The higher diversity of types of fungal pathogen infection on graminoids in unfertilised grassland, both per leaf and per parcel, most likely is due to an indirect effect of plant species abundance, as in unfertilised sites overall plant species richness is high whereas grass abundance is low. As species specificity restricts the majority of fungal pathogens to one or few closely related host-species (Brandenburger 1985; Burdon 1994), we suggest that this specificity might play a greater role for the diversity of fungal pathogen infection than fertilisation does.

Relationship between herbivory, fungal pathogen infection, and standing crop

The positive correlation between standing crop per parcel and leaf damage by, and diversity of types of, herbivory might reflect differences in leaf quality or leaf quality variation between sites. In alpine grassland dominated by a single

sedge two specialized and very abundant grasshopper species caused heavy biomass losses (Blumer and Diemer 1996). If, however, plant and herbivore communities are highly diverse, effects of herbivory are found to be dispersed across plant structures and species (Hunter and Price 1992; Tilman 1982) and little biomass is consumed. In our grassland parcels, biomass losses, as indicated by levels of leaf damage, remained low even in the fertilised and more productive sites. Possibly, this is due to the still relatively high plant species diversity of these grasslands in the Alps, where the specificity of many herbivores does not allow for large biomass losses. Alternatively, it might reflect positive effects of herbivory on plant growth, as reported for herbivory by insects (McNaughton 1983) and mammals (Paige 1992).

Standing crop was positively correlated with the amount of leaf damage by fungal pathogen infection and the diversity of different types per leaf. Possibly, differently productive sites also differed in leaf quality or in leaf quality variation. Moreover, higher standing crop could promote fungal pathogens because it is associated with higher levels of moisture (Kochy and Wilson 2004). Furthermore, as higher standing crop was associated with lower plant species diversity and therefore higher abundance per plant species, higher pathogen damage per leaf could also have been due to higher host plant abundance.

At the parcel level, we found no significant relationships between the diversity of different types of herbivory and the biomass of standing crop, and between the diversity of fungal pathogen infection and this biomass. This indicates no conflicts between the agricultural goal of high biomass production and high diversities of fungal pathogens and herbivores.

Relationship between herbivory, fungal pathogen infection, and plant species diversity

At first glance, more types of herbivory per leaf in plant species poor parcels appear to suggest a conservation conflict between plant species diversity and herbivore diversity. However, this relationship disappeared when the diversity of types was considered at the parcel level. Pathogen diversity was also independent of plant species diversity. Moreover, leaf damage by herbivory or fungal pathogens was also not related to plant species diversity. We suggest promoting low-intensity land use as this would allow high plant, herbivore, and pathogen diversity to contribute to high overall community biodiversity while biomass losses by herbivores and pathogens would be low.

Conclusions

Our comprehensive study across 12 villages from several regions in the Swiss Alps demonstrates the omnipresence of

herbivores and fungal pathogens in mountain grassland and indicates that plant–herbivore and plant–fungal pathogen interactions contribute largely to community diversity. At the same time, leaf damage by herbivores and fungal pathogens was very moderate, even in the case of legumes and at lower altitudes where leaf damage was highest. Therefore, conserving the diversity of plant–herbivore and plant–pathogen interactions will not be at the expense of dramatic plant biomass losses, which would have compromised agricultural goals.

Our indirect approach of measuring biological interactions allowed us to distinguish between eight categories of leaf damage by herbivores and four frequent taxonomical categories of fungal pathogen infection. This approach enabled us to assess herbivore and fungal pathogen diversity for a large number of field sites in a large area within a sufficiently short period of time. This worked especially well for plant–herbivore interactions. Because some damage by fungal pathogens could not be classified, the method should be improved for the indirect assessment of plant–pathogen interactions.

Currently, much grassland in the Alps is undergoing land use changes. An increasing proportion of grassland is fertilised and formerly mown grasslands are grazed or abandoned. We found low altitude and traditional mowing to promote plant–herbivore interactions, while fertilisation negatively affected fungal pathogens. This implies that the current land use changes in the Alps from mowing to grazing or to abandonment decrease the diversity of plant–herbivore interactions, and fertilisation decreases pathogen diversity. As our results did not reveal conservation conflicts between plants, herbivores, and fungal pathogens, our study suggests that for conserving and maintaining a great diversity of plant–herbivore and plant–pathogen interactions a diverse low-intensity land use should be maintained.

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Appendix

ANOVA model of leaf damage by, and number of types of herbivory and fungal pathogen infection on 12,054 leaves of plants from 215 grassland parcels from different altitude and land use in 12 villages of 3 different cultural traditions in the Swiss Alps.

Source of variation	Mean Squares	Variance ratios (<i>F</i> values)
Culture	ms _{cult}	ms _{cult} /ms _{vill}
Village	ms _{vill}	ms _{vill} /ms _{residual}
Altitude	ms _{alt}	ms _{alt} /ms _{residual}
Fertilisation	ms _{fert}	ms _{fert} /ms _{residual}
Traditional land use	ms _{trad}	ms _{trad} /ms _{residual}
Abandonment	ms _{aband}	ms _{aband} /ms _{curr}
Current land use	ms _{curr}	ms _{curr} /ms _{residual}
Traditional land use × Fertilisation	ms _{trad} × fert	ms _{trad} × fert/ms _{residual}
Abandonment × Fertilisation	ms _{aband} × fert	ms _{aband} × fert/ ms _{curr} × fert
Current land use × Fertilisation	ms _{curr} × fert	ms _{curr} × fert/ms _{residual}
Abandonment × Traditional land use	ms _{aband} × trad	ms _{aband} × trad/ ms _{residual}
Culture × Altitude	ms _{cult} × alt	ms _{cult} × alt/ms _{vill} × alt
Village × Altitude	ms _{vill} × alt	ms _{vill} × alt/ms _{residual}
Culture × Fertilisation	ms _{cult} × fert	ms _{cult} × fert/ ms _{vill} × fert
Culture × Traditional land use	ms _{cult} × trad	ms _{cult} × trad/ ms _{vill} × trad
Culture × Abandonment	ms _{cult} × aband	ms _{cult} × aband/ ms _{vill} × aband
Culture × Current land use	ms _{cult} × curr	ms _{cult} × curr/ ms _{vill} × curr
Village × Fertilisation	ms _{vill} × fert	ms _{vill} × fert/ms _{residual}
Village × Traditional land use	ms _{vill} × trad	ms _{vill} × trad/ms _{residual}
Village × Abandonment	ms _{vill} × aband	ms _{vill} × aband/ ms _{residual}
Village × Current land use	ms _{vill} × curr	ms _{vill} × curr/ms _{residual}
Fertilisation × Altitude	ms _{fert} × alt	ms _{fert} × alt/ms _{residual}
Traditional land use × Altitude	ms _{trad} × alt	ms _{trad} × alt/ms _{residual}
Abandonment × Altitude	ms _{aband} × alt	ms _{aband} × alt/ ms _{curr} × alt
Current land use × Altitude	ms _{curr} × alt	ms _{curr} × alt/ms _{residual}
Culture × Altitude × Fertilisation	ms _{cult} × alt × fert	ms _{cult} × alt fert/ ms _{vill} × alt × fert
Culture × Altitude × Traditional land use	ms _{cult} × alt × trad	ms _{cult} × alt × trad/ ms _{vill} × alt × trad
Culture × Altitude × Abandonment	ms _{cult} × alt × aband	ms _{cult} × alt × aband/ ms _{vill} × alt × aband
Culture × Altitude × Current land use	ms _{cult} × alt × curr	ms _{cult} × alt × curr/ ms _{vill} × alt × curr
Village × Altitude × Fertilisation	ms _{vill} × alt × fert	ms _{vill} × alt × fert/ ms _{residual}
Village × Altitude × Traditional land use	ms _{vill} × alt × trad	ms _{vill} × alt × trad/ ms _{residual}
Village × Altitude × Abandonment	ms _{vill} × alt × aband	ms _{vill} × alt × aband/ ms _{residual}
Village × Altitude × Current land use	ms _{vill} × alt × curr	ms _{vill} × alt × curr/ ms _{residual}
Residual	ms _{residual}	

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