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Influences of mowing and grazing on plant species composition in calcareous grassland

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Abstract

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In the Jura mountains extensive management created some of the species-richest plant communities of central Europe: calcareous grasslands of the Teucrio-Mesobrometum type. Here we summarize evidence about the influence of contrasting management on species diversity and species abundance in these grasslands. Based on phyto-sociological relevés (each ca. 0.1 ha) of 72 sites, 46 of which were regularly grazed by cattle and 26 were mowed, it is shown that pastures tend to be richer in species (on average 59 versus 46 species in meadows). 90% of all 137 species recorded occurred in both types of grassland. The higher species diversity in pastures is explained by greater spatial heterogeneity due to micropatterns of grazing, trampling and dung deposition. We conclude that only a minor set of species can be considered to be management-specific while the majority of species is equally abundant in both types of grassland. Hence, responses of the vegetation to a change in management are likely to cause only small alterations in community structure, at least for periods of several years to a few decades.

Key words: Biodiversity, conservation, land use, pasture, management, Mesobrometum, Swiss Jura Mountains.

Introduction

In southern Central Europe, calcareous grasslands are among the most species-rich plant communities. Up to 70 species per 100 m^2 have regularly been found (Zoller 1954, Moor 1962) and as much as 40 species may inhabit one square meter (Gigon and Leutert 1996). These man-made grasslands of unknown age are certainly older than 100 years, but some may be older than 1000 years and substitute former beech forests (Studer-Ehrensberger 1995; see also Bush and Flenley 1987, Bush 1993). Potential reasons for their species richness are manyfold, but microhabitat diversity (regeneration niches; Grubb 1977) and diverse plant life strategies (Grime 1990) certainly add to the overall effect of great age. Both natural (e.g. voles; Gigon and Leutert 1996) and anthropogenic disturbances – the topic of this paper – create high microscale dynamics which contribute to the coexistence of so many species at such small scales (Herben et al. 1993, Ryser et al. 1995, Gigon and Leutert 1996).

A large fraction of these grasslands has disappeared within the last 30 years (Zoller et al. 1986). Reasons are changes in land use like reforestation, more intense management, including fertilizer application, conversion to arable land, settlement and road construction. Some of the remaining sites are now protected and the agricultural use is restricted in order to maintain the biological diversity and to conserve a number of rare species typically found in such grasslands.

A good understanding of management consequences is imperativ for conservation. Mowing, for instance, could lead to the loss of species on former pasture land, and grazing on previously mown areas could have similar effects. Here we ask the question whether and how species composition and species richness change as a consequence of a conversion of pastures to heyfields, the predominant direction of change during the last century.

The analysis presented here was conducted as part of a multi-disciplinary long-term research project, aiming at an understanding of the causes and functional links of biological diversity and ecosystem function (Körner 1995, Matthies et al. 1995, Weber et al. 1995). Calcareous grassland was chosen for this purpose as a model system for species rich ecosystems. Experimental installations (e.g. for CO_2 enrichment) partly required replacement of grazing by mowing. Hence, besides their significance for conservation, the results of the present analysis will also serve as a reference for the likely implications of management changes imposed as part of this project.

Study area and methods

The survey considers grassland sites scattered over an area of 650 km^2 in the northern part of the Jura mountains in north-western Switzerland, mostly between 350 and 700 m of altitude. Although precipitation varies between 800 and 1000 mm a^{-1} in this region (with a peak in summer), shallow soils cause these grasslands to experience regular soil drought (Gigon 1968, Kuhn 1984). The mowing period falls between the end of May and early June. Extensive cattle grazing is controlled by fencing and normally lasts from mid-May to September/October.

Between 1982 and 1989, students of H. Zoller collected species lists of all species-rich and nutrient-poor calcareous grasslands in northern Switzerland (Frey 1983, Wagner 1984, Möckli 1987, Fiechter 1989), using the Braun-Blanquet system (Braun-Blanquet 1964). The total number of sites (i.e. relevés for ca. 0.1 ha plots) is 72, all belonging to the same association, the Teucrio-Mesobrometum, i.e. the most abundant type of Mesobrometum in this area and altitude (Zoller 1947). 46 of the sites had been used as pastures for cattle and 26 were regularly mown. All species occurring on less than 5 sites were omitted, leaving a total of 137 species which could be used for this analysis. Out of the available relevés, all sites on nutrient-poor rendzina soils with southern (SE to SW) exposure were analysed for cover, species diversity and abundance. In the interpretation of the results we also considered the Swiss Red List of highly endangered species (Landoldt 1991). In a first step, species richness in pastures and hayfields were compared. Then, a direct gradient analysis of vegetation-environment relationships by canonical correspondence analysis (ter Braak 1987) was applied. In addition to the hayfield-pasture axis, exposure, elevation above sea level and inclination of slope were also ordinated and tested for significant eigenvalues. Significance of the results was tested with a Monte Carlo permutation test which links randomly the environmental data to the species data. Statistically significant differences refer to $p<0.05$, non-significant ones are anoted as n.s. Variance is given as ± standard deviation throughout the text.

Results

Species diversity in pastures and in hayfields

The mean number of species in pasture relevés is 59.1±2.1 species and 46.3±1.4 species in hayfields (difference sign., Tabs. 1 and 2). Exclusively in pastures occurred *Senecio jacobaea, Centaurium erythrea, Lolium perenne, Echium vulgare, Taraxacum laevigatum, Hypochoeris radicata, Arenaria serpyllifolia, Trifolium ochroleucon, Agrostis tenuis* and *Juniperus communis,* exclusively in hayfields *Onobrychis vicifolia, Vicia cracca* and *Orchis militaris.* The other 90% of the 137 ordinated species are found in both types of grassland. The mean number of typical Mesobromion species (species with no symbol in Tabs. 1 and 2) tends to be slightly higher in pastures (22±5.7) than in hayfields (16±4; Fig. 1), but the relative con-

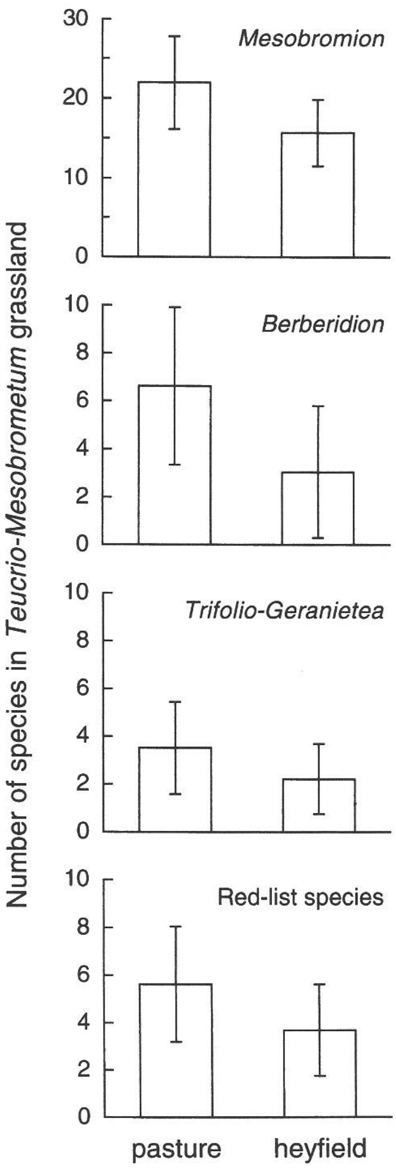

Fig. 1. The mean number (±s.d.) of species typically associated with three different plant associations (see Tabs. 1 and 2), but found growing together in the Teucrio-Mesobrometum investigated here, plus the frequence of endangered, socalled 'red list' species. Note that typical Mesobromion elements are slightly more frequent in the grazed than in the mown sites.

Tab. 1. Plants with positive relative importance values along the pasture-axis.

Species	Relative importance value		Red-list status	Record no.	
				G	M
Juniperus communis	2.73	+	U	6	0
Senecio jacobaea	2.70		U	9	0
Centaurium erythraea	2.64	*	U	13	0
Succisia pratensis	2.52		U	11	1
Crataegus laevigata	2.48	+	U	6	1
Lolium perenne	2.36		U	6	0
Echium vulgare	2.35		U	8	0
Hypochoeris radicata	2.22		U	8	0
Taraxacum laevigatum	2.21	*	U	5	1
Orchis morio	2.14	*	E	6	0
Tetragonolobus maritimus	2.07	*	U	5	0
Arenaria serpyllifolia	2.05		U	8	0
Vincetoxium hirundinaria	1.87	°	U	16	2
Chamaespartium sagittale	1.85	*	U	27	2
Campanula rotundifolia	1.85		U	27	2
Agrostis tenuis	1.84		U	7	1
Potentilla erecta	1.80		U	18	3
Globularia punctata	1.80	*	U	17	3
Trifolium ochroleucon	1.79	*	V	21	3
Inula salicina	1.74	°	U	6	1
Sedum album	1.74		U	5	1
Stachys recta	1.74	*	U	24	5
Bupleurum falcatum	1.73	°	U	9	1
Rosa spec.	1.72	+	U	17	2
Carlina acaulis	1.72	*	V	26	4
Cynosurus cristatus	1.67		U	21	2
Danthonia decumbens	1.61		U	10	1
Betonica officinalis	1.60		U	16	3
Peucedanum cervaria	1.55	°	U	14	2
Polygala amarella	1.52	*	U	13	3
Prunus spinosa	1.49	+	U	27	5
Pyrus communis	1.47	+	U	4	2
Quercus petraea	1.38	+	U	11	2
Ligustrum vulgare	1.38	+	U	5	1
Gentiana cruciata	1.36	*	E	5	1
Fagus sylvatica	1.36	+	U	5	1
Malus sylvestris	1.34	+	U	5	1
Koeleria pyramidata	1.34	*	U	44	8
Teucrium chamaedrys	1.31		U	39	9
Sedum sexangulare	1.28		U	5	1
Crataegus monogyna	1.28	+	U	26	2
Ophrys holosericea	1.27	*	E	5	5
Trifolium repens	1.25		U	18	3
Campanula glomerata	1.24	*	V	28	4
Berberis vulgaris	1.12	+	U	8	1
Anthericum ramosum	1.12	°	U	16	3
Cirsium acaule	1.04	*	V	35	7
Hypercium perforatum	1.03	°	U	28	9

Tab. 1. (continued).

Species	Relative importance value		Red-list status	Record no. G	Record no. M
Veronica prostrata	1.01	*	V	5	2
Carlina vulgaris	1.01	*	U	4	2
Veronica teucrium	0.95	°	E	11	2
Trifolium medium	0.93	°	U	11	6
Teucrium montanum	0.92	*	U	20	2
Asperula cynanchica	0.88	*	U	29	6
Carpinus betulus	0.85	+	U	14	2
Pinus sylvestris	0.82	+	U	17	5
Galium verum	0.79	*	U	28	5
Potentilla neumanniana	0.78	*	U	27	5
Hieracium pilosella	0.75		U	40	15
Prunella grandiflora	0.74	*	U	43	15
Thymus pulegioides	0.71		U	34	16
Helianthemum nummularium	0.69	*	U	41	5
Taraxacum officinale	0.65		U	12	3
Platanthera chlorantha	0.61	*	V	8	4
Cerastium fontanum	0.59		U	5	2
Arabis hirsuta	0.57		U	9	2
Origanum vulgare	0.56	°	U	24	10
Carex caryophyllea	0.55		U	35	16
Euphorbia cyparissias	0.53		U	39	12
Festuca ovina	0.44		U	42	19
Trifolium montanum	0.44	*	V	35	10
Genista tinctoria	0.35	*	V	14	5
Senecio erucifolius	0.34		U	9	4
Festuca rubra	0.32		U	6	2
Centaurea scabiosa	0.32		U	6	10
Rhinanthus minor	0.26	*	U	16	4
Bellis perennis	0.26		U	7	5
Ononis repens	0.12	*	U	25	10
Achillea millefolium	0.10		U	30	14
Viola hirta	0.03		U	29	14
Briza media	0.03	*	U	40	20
Linum catharticum	0.01	*	U	35	21
Sanguisorba minor	0.01		U	27	23

* species with main distribution in the Mesobromion; ° species with main distribution in the Trifolio-Geranietea; + Berberidion species. Record numbers refer to the number of relevés (sites) in which the species was recorded. G = grazed sites, M = mowed sites.

tribution of these species to total species richness is similar in the two types of grassland (40±7% Mesobromion species in pastures versus 39±9% Mesobromion species in hayfields, n.s.). Berberidion species, typical for the shrubby variant of such grasslands, are more common in pastures (6.7±3.2) than in hayfields (3.1±2.9; sign.). Also the species of the more fertile Trifolio-Geranietea are more frequent in pastures than in mowed grassland (3.5±1.9 versus 2.3±1.5; sign.). The mean percentage of ground cover by vegetation is similar in

Tab. 2. Plants with negative relative importance values along the pasture-axis. Their abundances are therefore higher in mowed grasslands (symbols as in Tab. 1).

Species	Relative importance value		Red-list status	Record no.	
				G	M
Onobrychis viciifolia	–4.04	*	U	0	15
Trisetum flavescens	–3.88		U	3	10
Arrhenaterum elatius	–3.77		U	1	12
Vicia cracca	–3.63		U	0	10
Orchis militaris	–3.52	*	E	1	5
Buphthalmum salicifolium	–3.49	*	R	4	11
Picris hieracioides	–3.21		U	2	7
Rhinanthus alectorolophus	–2.91		U	2	4
Ophrys apifera	–2.87	*	E	2	5
Anacamptis pyramidalis	–2.27	*	E	7	12
Salvia pratensis	–2.41	*	U	21	21
Holcus lanatus	–2.14		U	8	7
Centaurea jacea	–2.09		U	24	19
Galium album	–2.00		U	12	14
Vicia sativa	–1.95		U	4	3
Lathyrus pratensis	–1.84		U	12	12
Rumex acetosa	–1.82		U	7	6
Coronilla varia	–1.75		U	6	5
Festuca pratensis	–1.73		U	5	3
Leucanthemum vulgare	–1.64		U	32	23
Anthyllis vulneraria	–1.25	*	U	30	21
Gymnadenia conopsea	–1.25	*	U	6	8
Knautia arvensis	–1.18		U	33	20
Daucus carota	–0.92		U	33	22
Lotus corniculatus	–0.92		U	45	23
Agrimonia eupatoria	–0.90	*	U	15	11
Euphorbia verrucosa	–0.89	*	U	16	10
Prunella vulgaris	–0.89		U	15	10
Aster amellus	–0.84	°	U	11	4
Leontodon hispidus	–0.76		U	31	16
Thlaspi perfoliatum	–0.76	*	U	4	2
Inula coniza	–0.69	°	U	4	2
Poa pratensis	–0.64		U	24	14
Hippocrepis comosa	–0.60	*	U	40	20
Anthoxanthum odoratum	–0.58		U	20	11
Medicago lupulina	–0.58		U	33	19
Dactylis glomerata	–0.57		U	27	18
Brachypodium pinnatum	–0.51	°	U	27	16
Pimpinella saxifraga	–0.47	*	U	25	10
Primula veris	–0.47	*	U	37	16
Trifolium campestre	–0.46	*	U	12	3
Thymus forelichianus	–0.43	*	U	4	3
Ajuga reptans	–0.43		U	4	2
Euphrasia rostkoviana	–0.41	*	U	4	2
Polygala comosa	–0.26	*	V	21	15
Bromus erectus	–0.25	*	U	46	26
Plantago media	–0.25	*	U	43	23

Tab. 2. (continued).

Species	Relative importance value		Red-list status	Record no. G	Record no. M
Plantago lanceolata	–0.25		U	44	18
Carex montana	–0.22		U	36	18
Gallium pumilum	–0.21		U	9	5
Thesium pyrenaicum	–0.20	*	E	4	2
Luzula campestris	–0.17		U	6	4
Carex flacca	–0.10		U	43	22
Ranunculus bulbosus	–0.09		U	36	19
Scabiosa columbaria	–0.09	*	V	35	15
Trifolium pratense	–0.09		U	37	14

mowed sites and in pastures (94.0±0.8% versus 92.6±1.1%). The mean number of endangered species (as specified in the Swiss 'red list') is significantly higher in pastures (5.7±2.4 versus 3.7±1.9).

Canonical correspondence analysis

Elevation, exposure and inclination of slope at the different sites had no significant influences on species composition of communities (eigenvalues of 0.059, 0.045 and 0.033 respectively). Sites can therefore be assumed to be very similar, thus permitting unbiased treatment (i.e. management) comparisons. Canonical correspondence analysis revealed a significant ordination of the species which are present in more than five sites along the pasture-hayfield ordination axis. Out of 137 ordinated species, 80 showed positive ordination values on the pasture-axis (Tab. 1). 57 showed negative ordination values on the pasture-axis and therefore appear to do better in hayfields (Tab. 2). The eigenvalue is 0.148 (i.e. relatively low), indicating that the species are not separated into distinct groups related to management. This corresponds with the observation that most of the species are present in both types of grassland.

Among the species with positive ordination values to the pasture-axis are species with woody stems (13 species) and species with defense structures, such as spines (10 species). Furthermore, 67% (22 species) of all plants which are poisonous or non-palatable for cattle, and 73% (8 species) of the plants with leaf rosettes show a pasture preference. The family Poaceae, responsible for 70% of total aboveground biomass in this type of calcareous grassland (Huovinen-Hufschmid and Körner, this issue), showed the following preferences: tall species do better in hayfields, small species are favoured on pastures. Some of the most abundant species like *Bromus erectus, Festuca ovina, Carex caryophyllea* and *Trifolium pratense,* possess relatively low ordination values, and thus react indifferently to the two types of land use.

Discussion

The change from grazing to mowing seems to have surprisingly little influence on the community structure of south-facing, oligotrophic calcareous grasslands in north-western

Switzerland. The slightly higher species richness per relevès on pastures can be explained by the greater heterogeneity of microhabitats (Begon et al. 1990) as compared with hayfields. The spatial heterogeneity on such pastures is largely the result of cattle trampling and associated gap dynamics (3 to 9% of the surface area according to Marti 1994), which may lead to higher species richness (Whittaker and Levin 1977; see also references in Mooney and Godron 1983). In addition, deposition of cattle dung is random over the pasture area (Marsh and Campling 1970). Dung deposition sites are avoided by cattle for some time (Edwards and Hollis 1982), leading to mosaics of ungrazed but fertilized patches. In pastures stocked below capacity, a significant fraction of the vegetation remains ungrazed but may be trampled. At a small scale, this creates areas with contrasting leaf area indices, wind influence and moisture gradients in the vegetation. On slopes, cattle trampling leads to step-like structures with several distinct microhabitats.

Grazing pressure may further prevent vigorous "tasty" species from outcompeting other species. Zoller (1954) stated that tufts of *Bromus erectus* on mowed grasslands often reach 20 cm or more in diameter, while they hardly reach 10 cm on pastures. As the ordination data show, smaller species and plants with rosettes are favoured on pastures. They benefit from the fact that cattle is mostly not grazing below 5 cm above ground. Shrubby, woody plants which do better on pastures, provide shelter for shade-tolerant or grazing-intolerant species. "Mowing pressure" as imposed by higher mowing frequency (e.g. annually or biannually instead of every fifth year) also tends to enhance species richness in calcareous grassland (Ryser et al. 1995).

Hence, there are many reasons why pastures can become species richer than meadows and gap creation *per se* may not always be so important. While Reader (1993) found a significant (largely negative) influence of a dense vegetation cover on seedling recruitment Ryser (1993) found no evidence that seedlings (in general) do require gaps for establishing in such grassland swards, and Thompson et al. (1996) suggest that calcareous pasture species are "strategically" relatively uniform, so microhabitat differentiation may not be all that important. Accordingly, Van der Maarel and Sykes (1993) suggest that grazed species can reach and recruit at virtually all microsites in such swards. They question the usefulness of the niche concept for explaining species richness and co-existence in calcareous grassland. The data presented here suggest that at scales of <0.1 ha and over periods of at least several decades the reduced disturbance in meadows as compared to pastures tends to diminish species richness (the number of realized niches). However, this may not reflect the number of potential niches which might be filled over periods of heyfield management even longer than the ones covered by this survey.

Baker (1937) investigated grasslands near Oxford (England) which had been pastures for 900 years, and compared them with adjacent areas, which have been mown for a very long time. He found that only 32% of the 95 species present occurred in both pastures and hayfields, whereas in our study 90% of species were found in both pastures and hayfields. Perhaps this is related to the more recent conversion from pastures to meadows in our case. Zoller (1954) concluded that most of the currently mown sites were pastures until the 19th century. He observed hardly any differences between mown and grazed sites at the end of the 1940es, a situation that appears not to have changed until now, supporting the theory that the phytosociological pasture-hayfield differentiation (if there is one) takes a very long time on these sites. Krüsi (1981) arrived at a similar conclusion, although his 3-year phenological observations during contrasting experimental management revealed some species-specific responses (for instance in flowering). In line with the results of our analysis, Milberg and Hansson (1993) found no difference in seedbank composition of grazed and ungrazed calcareous grassland in southern Sweden after 17 years of contrasting land use.

Besides successional stage, the difference in response to management between the English and the Swiss calcareous grassland studied here, may also have to do with differences in grazing pressure. Grazing pressure excerts great influences on species composition of pastures. The higher the pressure, the more grazing-resistant species will become abundant. There are examples from Germany, where *Bromus erectus* became extinct on heavily grazed areas, and re-established after grazing pressure was diminished (Kuhn 1937, Lohmeyer 1953). Obviously, the impact of sheep (England) is different from the one by cattle. Sheep tend to graze very closely to the ground, and therefore favour prostrate and rosette species (Körner 1980, Ellenberg 1996). Also the weight of cattle is of importance. Locally, severe soil erosion is found on steep slopes in the Jura mountains grazed with heavier, modern breeds of cattle.

The survey presented here aimed at a broad picture. A more detailed analysis might reveal a number of conservationally important, but perhaps more variable or only locally important aspects of the pasture-meadow distinction. For instance, some species yielded ordination values deviating from what might be expected from longterm field experience (H. Zoller, personal observation): The two species *Plantago media* and *Prunella vulgaris* emerge as typical meadow elements, but in reality may often appear as rather characteristic species on moist pastures. *Orchis morio* and *Tetragonolobus maritimus* also occur quite often on mown grassland, although here, they reach high relative importance values on pastures. Species of the *Genitanaceae,* which are not included in our study because of their rarity and irregular distribution, often show high affinities to pastures. Longterm field observations at the famous "Blauenweide" near the village of Blauen clearly indicate that *Blackstonia perfoliata* expands its abundance under pasture management.

In conclusion, species spectra in pastures and meadows in this area are surprisingly similar and seem to be quite resilient to changes in the management, provided no fertilizer is employed, an aspect not considered here. However, a small set of differential species does exist and, as a general trend, pastures appear to be richer in species than mown areas at the scale considered here (ca. 0.1 ha). The change from grazing to mowing can thus be expected to lead to the gradual loss of some species. Most sensitive candidates are *Senecio jacobaea, Blackstonia perfoliata* and *Centaurium erythraea.* On the other hand, it is important to maintain mowing on some of these oligotrophic calcareous grasslands, because several endangered species (e.g. Orchids) are more abundant on meadows (H. Zoller, personal observation).

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Zusammenfassung

Der Einfluß von Mahd und Beweidung auf die Artengarnitur von Kalkmagerrasen

Extensiv genutzte Kalkmagerrasen des Theucrio-Mesobrometum-Typs im Jura stellen eine der artenreichsten Pflanzengemeinschaften Mitteleuropas dar. Hier präsentieren wir eine Zusammenfassung über die Folgen unterschiedlicher Landnutzung auf das pflanzliche Artenspektrum und die Artenhäufigkeit. Auf der Basis von pflanzensoziologischen Aufnahmen für 72 Standorte, von denen 46 regelmäßig beweidet und 26 gemäht wurden, wird aufgezeigt, daß Weiden eher artenreicher sind (im Mittel 59 gegenüber 46 Arten). 90% aller 137 Arten wurden aber in beiden Graslandtypen gefunden. Die größere Artenzahl auf

Weiden wird mit größerer mikrostandörtlicher Variabilität, bedingt durch Fraß, Tritt und Düngerdeposition, erklärt. Nur ein kleiner Teil der Artengarnitur ist nutzungsspezifisch – die meisten Arten sind auf Weiden und Mähdern gleich häufig. Auf eine Umstellung des Managements sollten daher – zumindest im Zeitraum von mehreren Jahren bis Jahrzehnten – nur geringe Veränderungen in der Artengarnitur dieses Vegetationstyps auftreten.

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