Human impact on the vegetation of limestone cliffs in the northern Swiss Jura mountains

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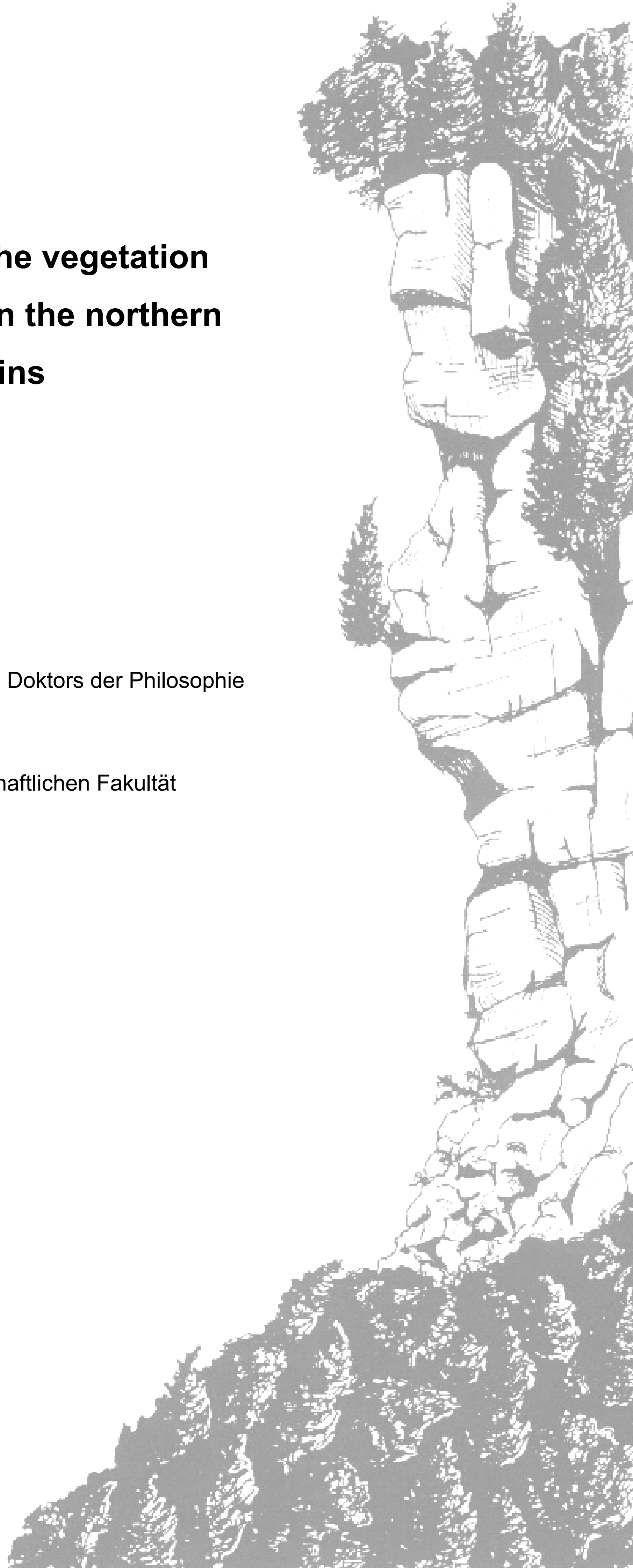

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Table of contents

Summary

Cliffs provide unique habitats for many specialised organisms, including chamaephytes and slowly growing trees. Drought, high temperature amplitude, scarcity of nutrients and high insolation are general characteristics of exposed limestone cliff faces. The vegetation of limestone cliffs in the Swiss Jura mountains consists of plants of arctic-alpine, continental and Mediterranean origin. Several populations exhibit relicts from post- or interglacial warm or cold climatic periods. Grazing goats and timber harvesting influenced the forests surrounding the limestone cliffs in northern Switzerland for many centuries. During the twentieth century, however, these traditional forms of forest use were abandoned.

In recent years, rock climbing enjoys increasing popularity in mountain areas at low elevation, where this sport can be performed during the whole year. The limestone cliffs of the Jura mountains provide unique opportunities for sport climbers. As a consequence, more than 2000 climbing routes with fixed protection bolts have been installed on 48 rock cliffs in the region of Basel, Switzerland.

Overgrowing forest, due to the abandonment of forestry and damages due to recreational activities including rock climbing reduce the quality and size of the cliff habitats. In my dissertation, I examined quantitative, spatial and temporal patterns of human impacts on the cliff flora and on the genetic population structure of two plant species on isolated cliffs in the Jura mountains of northern Switzerland.

The assessment of plant cover and species density at various distances from frequently used climbing routes in the region showed that plant cover was significantly reduced at the base of climbing routes. Furthermore, species density (number of species per m^2) at the cliff base as well as plant cover and species density on the cliff face tended to increase with distance from the route.

The comparison of the vegetation at the cliff base and on the cliff face of five frequently climbed cliffs with that of seven unclimbed cliffs indicated that rock climbing significantly altered the plant composition. Specialised rock species occurred less frequently on climbed cliffs than on unclimbed cliffs.

At the Gerstelflue, a popular recreational climbing site with rock climbing activities since more than 40 years, plant cover and species density (number of species per m^2) were reduced in climbed areas. Rock climbing also reduced the density (number of individuals per m^2) of forbs and shrubs, whereas the density of ferns tended to increase in climbed areas. In addition, rock climbing caused a significant shift in plant species composition and altered the proportions of different plant life forms.

Species diversity and cover of lichens, and possible associations between lichens and lichen-feeding land snails were assessed in climbed and unclimbed areas of 10 isolated cliffs. Total lichen species density was not correlated with the complexity of the rock surface, climbing frequency and age of the climbing route. The species density of epilithic lichens was lower along climbing routes than in unclimbed areas, whereas no difference in species density of endolithic lichens was found between climbed and unclimbed areas. Furthermore, climbed and unclimbed areas did not differ in total lichen cover. The dissimilarity of the lichen communities between climbed and unclimbed areas increased with increasing climbing intensity on the focal route in climbed areas, but not with the age of the climbing route. Within cliffs, plots along climbing routes harboured fewer snail species and individuals than plots in unclimbed areas.

The effects of forestry practices on the species richness and abundance of vascular plants on the face, at the base and on the talus have been investigated by comparing two different forestry practices (clear-cutting and shelter tree cutting) with forest reserve (i.e. no management in the past 80 years)) on three cliffs. Plant species density and vegetation cover was higher in the shelter-cut areas than in the forest reserves on the talus as well as at the cliff base. Clear-cut areas showed a higher vegetation cover than forest reserves on the talus. Shelter-cut areas harboured a larger proportion of plants with high light demands and plant indicator species showed a higher mean light score than in clear-cut areas and forest reserves.

The analysis of time-series of air photographs taken between 1951 and 2000 at six cliffs revealed an increase in tree cover from 60% to 85% between 1951 and 1964 after which the increase levelled off. The increase in tree cover showed a distinct spatial pattern. It was significant in the talus and on the cliff face, but not on the plateau (at the top of the cliffs).

Possible effects of isolation and the presumed colonisation history of cliffs as well as of anthropogenic activities on the genetic population structure of two plant species with different life-histories were assessed using RAPD-polymorphisms. Fourteen populations of *Draba aizoides* L. and 12 populations of *Melica ciliata* L. living on isolated limestone cliffs were examined. Analysis of molecular variance revealed a high among-population variation of each 27% in the gene pools of both species. A clear isolation-by-distance pattern and a separation of populations from the Jura mountains and the Alps were found in *D. aizoides*. This provides evidence for glacial relict endemism in this species, resulting from nunatak survival in the Jura mountains. In *M. ciliata*, UPGMA-analysis showed clusters of plant populations growing on cliffs with castles with shared historical incidents, indicating zoochorical dispersal related to human settlements.

The various studies emphasise the uniqueness and vulnerability of the limestone cliff ecosystem of northern Switzerland. Protection measures in several fields of activity are needed to preserve the unique relict vascular plant, lichen and animal communities. Adequate management actions should be developed and implemented. Actions should particularly be directed to cliffs with numerous arctic-alpine plant species to protect them from mechanic disturbances by sport climbing and hiking. The prohibition of sport climbing on cliffs with a high number of specialised plant or animal species and the establishment of climbing-free protection zones in popular areas are the most effective and adequate measures in this context. However, any management plan should include a comprehensive information campaign to show the potential impact of intensive sport climbing on the specialised flora and fauna and to increase the compliance of these measures by the climbers. Forestry practices that keep the supply of light on a high level at the lower parts of the cliffs are required to preserve the relict plant species. Selective thinning on the talus results in relatively large plots with good light conditions and therefore promotes the rare, relict plant species with high light demands. Selfevidentely, forestry actions and climbing prohibitions should be executed in coordination. Another measure to manage the lower parts of cliffs could be to use them as temporal pastures for goats. Finally, the preservation of mediaeval sites also connotes the conservation of plant species introduced into the area during the time of human activities.

General Introduction

Characteristics of the limestone cliffs of northern Switzerland

The limestone cliffs of northern Switzerland are of particular peculiarity due to the extraordinary environmental conditions and their history, affected by glacier advancements and different human use forms.

Dryness, high temperature amplitude, scarcity of nutrients and high insolation are general characteristics of exposed limestone cliff faces. The combined effects of drought and low nutrient availability, light and gravity limit plant growth in these extreme habitats (Coates and Kirkpatrick 1992). The structural complexity of cliff faces causes microclimatic and edaphic differences on a very small scale. Exposed patches are generally hotter and drier than protected ones, fractures are colder and wetter than ledges, and overhangs shadow deeper situated parts (Ashton and Webb 1977).

The taluses of limestone cliffs provide dynamic, relatively unstable habitats, which are characterized by the displacement of the debris and by mircoclimatic differences due to cold air drainage and different exposure to sun. On the plateaus of limestone cliffs, the insolation is less extreme, but the porousness of the calcareous rock and the exposure to winds lead to dry conditions comparable to those of floodplains or ruderal plains. All these effects lead to a highly diverse mosaic of microhabitats, which allow the existence of specialised chamaephytes and slowly growing trees (Escudero 1996, Larson et al. 2000).

In northern Switzerland, compact coral-chalks from the late Jura Age ("Rauracien") formed numerous rock cliffs which belong to the Jura mountains

(Bitterli-Brunner 1987). In contrast to large rocky areas of the Alps and other high-elevation mountains, the cliffs of the Jura Mountains are small and frequently isolated, and in most cases surrounded by forest, which has been partly cleared and subsequently used as pasture for some centuries.

Limestone cliff vegetation

Lichens, ferns and mosses constitute the main components of the cliff face vegetation (Oberdorfer 1992). The vascular plant vegetation consists of plants of arctic-alpine, continental and Mediterranean origin (Zoller 1989, Wassmer 1998). For several alpine and arctic plant species, the cliffs served as peripheral refugia which formed a periglacial steppe together with continental plants during the Pleistocene glacier advancements from the Alps and the Black Forest (Walter and Straka 1986). The arctic-alpine plant species and the xerothermic oak forest species (*Quercetalia pubescenti-petraeae*) colonised the south-exposed taluses and the plateaus of the Jura Mountains during postglacial warm periods (Ellenberg 1986). Due to the establishment of beech-forests under more temperate climate conditions, they were displaced towards the wood-free cliff sites. On the plateaus, these plant communities intersperse with beech and pine communities adapted to the arid conditions (*Molinio-Pinetum, Carici-Fagetum*; Ellenberg 1986).

Rock climbing on the limestone cliffs

Rock climbing enjoys increasing popularity in mountain areas at low elevation, where this sport can be performed during the whole year (Hanemann 2000). More than 2000 climbing routes with fixed protection bolts have been installed on 48 rock cliffs in the region of Basel, Switzerland (Andrey et al. 1997). Approximately 70% of these climbing routes were opened between 1985 and 1999. The enormous throng, however, leads to serious local environmental disturbances. In adjacent Southern Germany, climbing has been restricted at many sites due to conflicts between climbing activity and nature conservation. As a result, a further increase in climbing activities has been observed in the Jura mountains of North-western Switzerland.

Damage to the vegetation due to rock climbing were recorded on limestone cliffs in the upper Danube valley (Herter 1993). Damages included a reduction of vegetation cover and the extinction of species sensitive to disturbance and of specialists adapted to these extreme habitats. In addition, the clearing of soil from crevices and the erosion of the cliff edge and face were recorded. Furthermore, the species richness of ruderal plants increased. Rock climbing also led to skewed size and age distributions both in *Solidago sciaphila* in North-western Illinois (Nuzzo 1995) and *Thuja occidentalis* on the Niagara Escarpment in Canada (Kelly & Larson 1997). On exposed dolomitic cliffs in North-western Illinois, climbing reduced the cover and species richness of lichens by 50% (Nuzzo 1996). Despite the potential damage, relatively few studies have addressed the impact of rock climbing on cliff flora or fauna (Larson et al. 2000).

Nuzzo (1996) pointed out that environmental and physical variables were the primary determinants of the cliff flora. Any identification of causal links between human disturbance and vegetation structure requires a careful assessment of the geological and environmental factors that strongly influence both human use and vegetation dynamics (Nuzzo 1996, Farris 1998).

Forestry around the limestone cliffs

Grazing goats and timber harvesting influenced the forests surrounding the limestone cliffs in northern Switzerland for many centuries. During the middle ages and until the 19th century, the steep slopes at the cliff bases were predominantly managed as coppice forests for the production of firewood, charcoal, bedding and raw materials for craftsmen and as temporal pasture (Burnand and Hasspacher 1999). As a result of these human activities, the canopy of the forest sourrounding limestone cliffs was open providing good light and temperature conditions for the relict plant species.

Because of the excessive exploitation of the forests, governamental decrees prohibited pasturing and bedding at the end of the 19th century (Suter 1971, Blöchlinger 1995, Stuber and Bürgi 2002a, Stuber and Bürgi 2002b). Additionally, the demand for firewood decreased dramatically after 1950. Nowadays, the cliff bases are exclusively used as timber forests, usually under a shelterwood system (Hendry 1998). As a result of the less intensive forestry, the forests became older and denser (Schiess and Schiess-Bühler 1997, Wohlgemuth et al. 2002). The enhanced shadowing reduces the quality and size of the habitats for light-demanding species. This is particularly true for relict plants on limestone cliffs and at their base (Wassmer 1998) and for reptiles (Jäggi and Baur 1999).

There is empirical evidence for negative effects of the overgrowing forests on relict plant species on the taluses of limestone cliffs (Schiess and Schiess-Bühler 1997, Ewald 2000, Fachstelle Naturschutz Kanton Zürich 2004). Overgrowing forests lead to a decrease in the abundance of cliff plants with a high light demand and are therefore in some cases the main factor for the local extinction of threatened or rare species like *Dianthus gratianopolitanus, Daphne cneorum* or *Kernera saxatilis* (Wassmer 1998, Käsermann 1999).

Aims of the thesis

In the first part of the thesis, I investigate the impact of rock climbing on the vegetation on limestone cliffs in the Northern Swiss Jura mountains. So far, little was known about the spatial pattern of the impact of rock climbing within a cliff. In **chapter 1**, I examined plant cover, species density and composition at varying distances from frequently used climbing routes. Existing studies on the impact of rock climbing focused on single cliffs (Herter 1993, 1996) or rock formations (Nuzzo 1996, McMillan & Larson 2002). None of the studies compared climbed and unclimbed cliffs over an entire mountain range. I surveyed the vegetation of five climbed and seven unclimbed cliffs in the Northern Swiss Jura mountains to assess possible effects of rock climbing on a regional scale.

To complement this approach, **Chapter 2** focuses on the impact of rock climbing on a single cliff region. As an example, I considered the Gerstelfluh near Waldenburg. In Chapter II, differences in plant cover and species composition between climbed and unclimbed areas and between different heights at the cliff faces are presented.

Besides the impact on vascular plants, I also investigated the impact of climbing on the highly diverse lichen communities of the cliffs (Clerc 2004). In **chapter 3**, I present a comparison of diversity patterns of calcicolous lichens in climbed and unclimbed areas of 10 cliffs. We also considered the relationships between lichen species richness and cover and the intensity of sport climbing, the microstructure of the rock surface and the presence/absence and abundance of lichen-feeding gastropods.

The impact of forestry at the cliff base and in the talus of cliffs is analysed in **chapter 4**. I examined the effects of two different forestry practices on the composition of the ground vegetation on the face, at the base and on the talus of limestone cliffs and compared them with forest reserves (no forestry). I also assessed the temperature regime (and therefore indirectly the light regime) in areas with different forestry practices both in the talus and on the face of cliffs. With this study, I intended to provide basic information for an optimisation of forestry practices with respect to the preservation of relict and endangered plant species.

A prerequisite for future improvements concerning forestry in cliff areas is the knowledge of the spatial and temporal pattern of changes, in particularly with respect to overgrowing forest. Therefore, I quantified the extent of overgrowing forest and examined the spatial and temporal patterns of overgrowing forest on six limestone cliffs by analysing time series of aerial photographs in **chapter 5**.

Another prerequisite for an efficient protection and also for the assessment of the conservation value of the cliff ecosystems is the knowledge of the genetic structure of the plant populations on cliffs. In **chapter 6**, I examine the genetic structure of two relict plant species with different breeding and dispersal modes, *Draba aizoides* and *Melica ciliata* (L.) on isolated cliffs.

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Chapter 1

Rock climbing alters the vegetation of limestone cliffs in the northern Swiss Jura mountains

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Rock climbing alters the vegetation of limestone cliffs in the northern Swiss Jura Mountains

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Abstract: Exposed cliffs in the northern Swiss Jura Mountains harbour a highly diverse flora with numerous endangered and relic plant species. On these cliffs, sport climbing is enjoying increasing popularity. We examined the ecological effects of sport climbing on vascular plants at the cliff base and on the cliff face by assessing plant cover and species density at various distances from frequently used climbing routes. Plant cover was significantly reduced at the base of climbing routes. Furthermore, species density (number of species per square metre) at the cliff base, as well as plant cover and species density at the cliff face, tended to increase with distance from the route. We also compared the vegetation of five frequently climbed cliffs with that of seven unclimbed cliffs. Climbing significantly altered the plant composition. Specialized rock species occurred less frequently on climbed cliffs than on unclimbed cliffs. Management plans and conservation actions are needed to preserve the threatened plant species on frequently climbed cliffs. Such plans should include the establishment of climbing-free protection areas on cliffs with a high number of specialized, relic plants and the protection of entire cliffs that are not yet climbed.

Key words: disturbance, vegetation, Jura Mountains, rock climbing, limestone cliff.

Résumé : Les falaises escarpées des montagnes du nord du Jura Suisse comportent une flore très diversifiée comprenant de nombreuses espèces menacées ainsi que des espèces de plantes reliques. Sur ces falaises, l'escalade sportive connaît une popularité croissante. Les auteurs ont examiné les effets écologique de l'escalade sportive sur les plantes vasculaires à la base de la falaise aussi bien que sur sa face, en évaluant le couvert végétal et la densité des espèces, à diverses distances de routes d'escalades fréquemment utilisées. La couverture végétale est significativement réduite à la base des routes d'escalades. De plus, la densité des espèces (nombre d'espèces par mètre carré) à la base des falaises, ainsi que la couverture végétale et la densité des espèces sur la face des falaises, tendent à augmenter avec la distance des routes d'escalade. Les auteurs ont aussi comparé la végétation de cinq falaises fréquemment escaladées avec sept autres non-escaladées. L'escalade altère significativement la composition végétale. Les espèces rupicoles spécialisées sont moins fréquentes sur les falaises escaladées que sur celles qui ne le sont pas. Des plans d'aménagement et des activités de conservation sont nécessaires pour conserver les espèces végétales menacées sur les falaises fréquemment escaladées. Ces plans devraient inclure la mise en place d'aires protégées sans escalade sur les falaises comportant un grand nombre d'espèces spécialisées, de plantes reliques, ainsi que la protection totale des falaises qui n'ont jamais été escaladées.

Mots clés : perturbation, végétation, montagnes du Jura, escalade, falaise calcaire.

[Traduit par la Rédaction]

Introduction

Cliffs and their bases provide unique habitats for many specialized organisms. Dryness, high-temperature amplitude, scarcity of nutrients, and high insolation are general characteristics of exposed cliff faces and bases. The combined effects of lack of moisture and low nutrient availability, light, and gravity are limiting to plant growth in these extreme habitats (Coates and Kirkpatrick 1992). Nevertheless, specialized plants are able to colonize pockets, fractures, and ledges in rock cliffs (Ursic et al. 1997). The structural complexity of cliff faces causes microclimatic and edaphic differences on a very small scale. Exposed patches are generally hotter and drier than protected ones, fractures are colder and wetter than ledges, and overhangs shadow deeper situated parts (Ashton and Webb 1977). All these effects lead to a highly diverse mosaic of microhabitats, which allow the existence of specialized chamaephytes and slowly growing trees (Escudero 1996; Larson et al. 2000*a*).

In the Jura Mountains of northern Switzerland, compact coral chalks from the late Jura Age ("Rauracien") formed numerous rock cliffs (Bitterli-Brunner 1987), which harbour a unique flora with many rare species (Zoller 1989). Lichens, ferns, and mosses constitute the main components of the cliff-face vegetation (Oberdorfer 1992). Vascular plants with low edaphic and water demands such as *Kernera saxatilis* (L.) Rchb. or *Draba aizoides* L. occur in minute soil patches on the cliffs (Wilmanns 1993). In contrast with large rocky areas of the Alps and other high-elevation mountains, the cliffs of the Jura Mountains are small and isolated and mostly surrounded by forest, which has been partly cleared and subsequently used as pasture for some centuries.

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In this landscape, the rocky habitats represent islands of special environmental conditions (Wilmanns 1993). A variety of plants growing on these cliffs are inter- or post-glacial relics with a recent mediterranean or arctic–alpine distribution (Walter and Straka 1970). Similarly, the vegetation at the base of the cliffs contains relics from postglacial warm periods. The south-exposed slopes of the Jura Mountains are covered by xerothermic oak forests (*Quercetalia pubescenti-petraeae*), which colonized the region from refuges in southern France and the Balkans (Ellenberg 1986), and by slowly growing beech forests with translucent canopies and a highly diverse ground vegetation (Moor 1972). The high species richness and large number of rare species, the rarity of the habitat type, and the historical pecularity give the rock cliffs a high conservation value (Wassmer 1998; Knecht 1999[2]).

Rock climbing is enjoying increasing popularity in mountain areas at low elevation where this sport can be performed during the whole year (Hanemann 2000). More than 2000 climbing routes with fixed protection bolts have been installed on 48 rock cliffs in the region of Basel, Switzerland (Andrey et al. 1997). Approximately 70% of these climbing routes were opened between 1985 and 1999. The enormous throng, however, leads to serious local environmental disturbances. In adjacent southern Germany, climbing has been restricted at many sites because of conflicts between climbing activity and nature conservation. As a result, a further increase in climbing activities has been observed in the Jura Mountains of northwestern Switzerland.

Damage to the vegetation due to rock climbing was recorded on limestone cliffs in the Upper Danube Valley (Herter 1993). Damages included a reduction of vegetation cover and the extinction of species sensitive to disturbance and of specialists adapted to these extreme habitats. In addition, the clearing of soil from crevices and the erosion of the cliff edge and face were recorded. Furthermore, the species richness of ruderal plants increased. Rock climbing also led to skewed size and age distributions both in *Solidago sciaphila* in northwestern Illinois (Nuzzo 1995) and in *Thuja occidentalis* on the Niagara Escarpment in Canada (Kelly and Larson 1997). On exposed dolomitic cliffs in northwestern Illinois, climbing reduced the cover and species richness of lichens by 50% (Nuzzo 1996). Despite the potential damage, relatively few studies have addressed the impact of rock climbing on cliff flora or fauna (Larson et al. 2000*b*).

Nuzzo (1996) pointed out that environmental and physical variables were the primary determinants of the cliff flora. Any identification of causal links between human disturbance and vegetation structure requires a careful assessment of the geological and environmental factors that strongly influence both human use and vegetation dynamics (Nuzzo 1996; Farris 1998).

The aim of the present study was to examine the impact of rock climbing on the vegetation on limestone cliffs in the northern Swiss Jura Mountains. We investigated vegetation cover and plant species density and composition in climbed and unclimbed areas in relation to other environmental factors. The impact of climbing is not equally distributed over an entire cliff, because climbing routes are exclusively installed in rock walls suitable for climbing. So far, little is known about the spatial pattern of the impact of climbing within a cliff. We therefore examined plant cover, species density, and composition at varying distances from frequently used climbing routes.

Existing studies on the impact of rock climbing focused on single cliffs (Herter 1993, 1996) or rock formations (Nuzzo 1996; McMillan and Larson 2002). None of the studies compared climbed and unclimbed cliffs over a whole mountain range. Therefore, we also examined the vegetation of five climbed and seven unclimbed cliffs in the northern Swiss Jura Mountains to assess possible effects of rock climbing on a regional scale. In particular, we addressed the following questions: (1) To what distances on either side of frequently used routes are effects of sport climbing on plant cover and species density detectable? (2) Do climbed and unclimbed cliffs differ in plant composition and proportion of specialized plant species? (3) Do plant species occurring on climbed cliffs have other environmental demands compared with species on unclimbed cliffs?

Materials and methods

Study sites

The present study was carried out at the base and in the lower part of limestone cliffs in the northern Swiss Jura Mountains (cantons of Solothurn and Basel–Landschaft) in an area of 30 km × 30 km (Fig. 1). The cliffs are located at elevations ranging from 480 to 820 m above sea level (Table 1). They mainly consist of Jurassic coral chalks (Bitterli-Brunner 1987). The characteristic plant community of the predominantly south-facing cliffs belongs to the Potentillo–Hieracietum association (Richard 1972). The cliff bases are covered by different stands of deciduous forests belonging to Fagetum and Tilietum associations (Burnand and Hasspacher 1999).

Small-scale disturbance

We examined the spatial pattern of climbing impact in six frequently visited areas (cliffs 1–6 in Table 1) by recording the abundances of plant species in plots at varying distances from popular climbing routes and in control plots in an undisturbed part of the same cliff. We chose cliffs of similar exposure, insolation, and climbing intensity. Plots of 1 m^2 were marked in the centre of selected climbing routes (indicated by fixed protection bolts) and at horizontal distances of 2 and 5 m from the climbing route both at the cliff base (adjacent to the cliff face) and at a height of 0.5–1.5 m on the cliff face. At each cliff, three frequently climbed routes were chosen. In some instances, a neighbouring climbing route was within 10 m of the focal route. In these cases, the plots at the 5 m distance were not considered. Similarly, the plots at the 2 m distance were not considered if the neighbouring climbing route was within 4 m of the focal route. Previous observations indicated that direct climbing effects to the cliff vegetation rarely exceeded a distance of 3 m. However, at the bases of frequently visited cliffs, larger areas might be affected by climbing activities, for instance, by securing the climbing partner, observing the climbing route,

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[2] D. Knecht. 1999. Felsinventar Basler Jura und Schutzkonzept. Unpublished report. Basel, Switzerland. [In German.]

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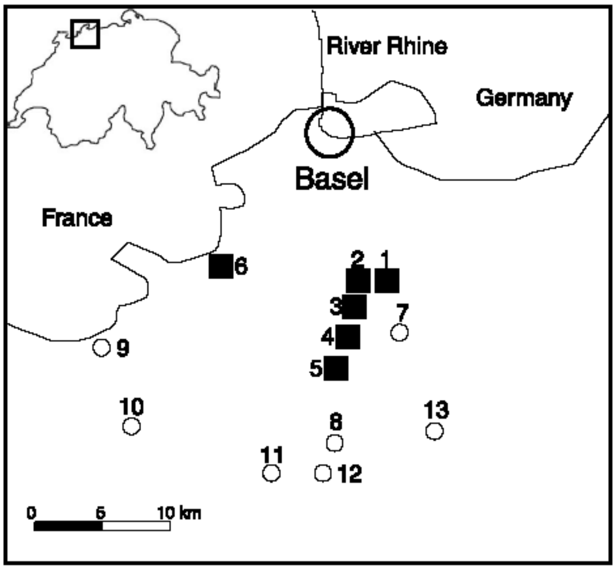
Table 1. Description of cliffs investigated in the northern Swiss Jura Mountains.

Cliff	Cliff number (Fig. 1)	Occurrence of sport climbing	Number of installed climbing routes[a]	Elevation (m a.s.l.)[b]	Exposure
Schartenflue	1	Yes	124	700	SW
Ingelsteinflue	2	Yes	48	510	SW
Tüfleten	3	Yes	78	480	S–SW
Falkenflue	4	Yes	246	550	SWNW
Pelzmühletal	5	Yes	254	490	SW
Hofstetter Chöpfli	6	Yes	68	500	SW–W
Bürenflue	7	No	0	660	SE–S
Portiflue	8	No	0	820	S–SW
Blauenstein	9	No	0	550	S
Roti Flue	10	No	0	690	S–SW
Titterten	11	No	0	530	SW–NW
Ryfenstein	12	No	0	590	SW
Fäldmenegg	13	No	0	790	S

[a] Obtained from Andrey et al. (1997).

[b] At cliff base.

Fig. 1. Map of the examined cliffs in the northern Jura Mountains of Switzerland. Full squares indicate climbed cliffs and open circles are unclimbed cliffs. For a description of the cliffs, see Table 1.



and depositing climbing materials. We chose frequently used routes (Andrey et al. 1997, and personal communications of climbers) that allowed us to set up plots at the distances mentioned. The undisturbed control plots at the cliff bases were chosen using the following criteria: (1) the control plot has the same exposure as the area at the base of the climbing route, (2) control plot and area at the base of the climbing route were situated within 10–50 m of each other, and (3) both receive the same insolation. At the cliff faces, we used the plots at a distance of 5 m as control plots, because an influence of climbing activities can be excluded at this distance.

In each sampling plot, the number of individuals and the cover of each plant species were recorded three times between May and September 2001. We also estimated the percentage of total plant cover and that of rock cover in each sampling plot using the Domin-Krajina scale (Müller-Dombois and Ellenberg 1974). The exposure of each plot was measured, and the extent of shadowing of the rock surface was estimated using a scale ranging from 1, no shadow, to 10, total shadowing. Fracturing of the rock surface was estimated using a scale ranging from 1, smooth rock with no fracture, to 5, numerous, large fractures.

Analyses of variance (ANOVA) were used to examine the impact of sport climbing and abiotic factors on the plant cover and species density (number of species per square metre). For the data collected at the cliff base, a four-way ANOVA was performed with the factors cliff, distance to the nearest situated climbing route, shadowing, and exposure as a covariable. For the data collected on the cliff face, we used a five-way ANOVA with the additional factor fracturing. Data on vegetation cover were arcsin transformed. Post hoc differences among plots at different distances to the climbing route were examined using Tukey's test. Statistical analyses were conducted using SAS version 8.02.

Regional survey

Any observed small-scale disturbances of the vegetation close to the climbing routes could be due to the climbers' preference to establish routes on cliff sections with no or only sparse vegetation. A comparison of the vegetation of climbed and unclimbed cliffs allows the assessment of this explanation.

We compared the vegetation of five very popular climbing cliffs (cliffs 1, 3, 4, 5, and 6 in Fig. 1) with seven cliffs that have never been subjected to any climbing activities (cliffs 7–13 in Fig. 1). All investigated areas were similar in terms of topography and exposure (Table 1). No significant differences were found in degree of fracturing and elevation between climbed and unclimbed cliffs (Mann Whitney *U* test; in both cases, $P > 0.07$). We used horizontal transects of 100 m in length to examine any possible impact of rock climbing on the vegetation of the cliffs. On each transect, six

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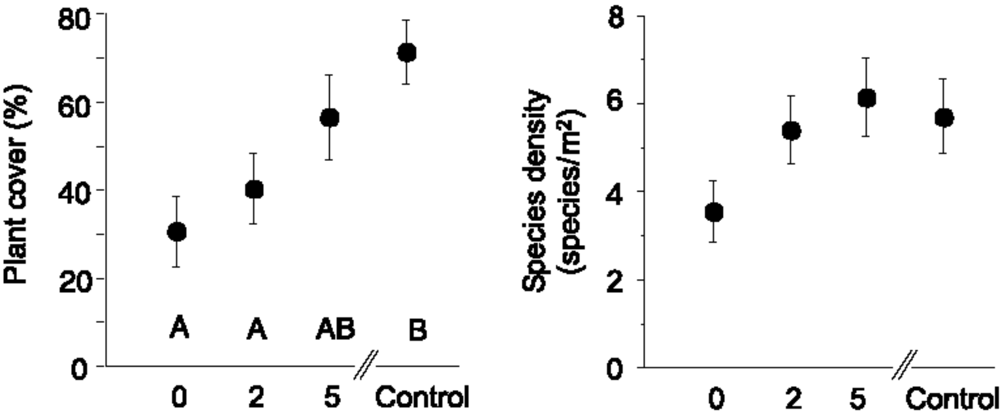
Fig. 2. Plant cover and species density (number of species per square metre) at the cliff base in relation to distance to the climbing route. Mean values ± SE of 18 routes (six cliffs with three routes each) are shown. Different letters indicate significant differences between distances (Tukey's test; $P < 0.05$).



sampling plots of 1 m^2 were established at regular distances of 20 m at the cliff base and at a height of 0.5–1.5 m at the cliff face. The starting point of the transect was randomly chosen within a sector that allowed us to install all six plots. Plant cover, species density, and environmental parameters were recorded as described previously. Thus, the survey consisted of two treatments (climbed vs. unclimbed) with five and seven replicates, each of them based on mean values of six plots.

According to the degree of dependency on rocky habitat, each plant species was assigned to one of the following groups (Wassmer 1998): (1) specialized rock species (species exclusively growing on rocky habitat), (2) species with a moderate association to rocky habitat, and (3) species with no association to rocky habitat. To relate plant communities to abiotic environmental factors, we used the indicator scores of Landolt (1977): light (scale ranging from 1, species in deep shade, to 5, plants in full sun), temperature (scale ranging from 1, indicator for cold conditions found only in alpine zones, to 5, thermophilous species), soil humidity (1, arid land plants, to 5, wetland plants), humus (1, plants of raw soil, to 5, plants of humus-rich soil), and soil nutrients (1, species with low soil nitrogen requirements, to 5, species with high soil nitrogen requirements). Comparisons of Landolt scores were Bonferroni-corrected following Rice (1989). Nomenclature of plants follows Binz and Heitz (1990).

Detrended correspondence analysis (DCA) was used to examine whether climbing affects the structure of the plant community on different cliffs (Hill and Gauch 1980). Prior to ordination, the data were log transformed. Species found on only one cliff were removed from the analysis, and species that were less frequent than the median frequency were down-weighted in proportion to their frequencies (Eilertsen et al. 1990). Statistical analyses were conducted using the software package StatView (version 5, SAS Institute Inc. 1998). The multivariate analysis (DCA) was performed using CAP version 1.3 (PISCES Conservation Ltd. 1999).

Results

Small-scale effects at the cliff base

Climbing activity caused small-scale disturbances on the vegetation at the cliff base and on the cliff face. Plant cover and species density (number of species per square metre) at the cliff base increased with distance from the starting point of the climbing routes (Fig. 2). Tukey tests revealed that plant cover was significantly higher in control plots than in plots at the starting point of the climbing route and in those 2 m from the route. Compared with the control plots at the cliff base, the vegetation cover of the plots at a distance of 5 m from the nearest climbing route was reduced by 19%. The plots at a distance of 2 m showed a reduction of 43%, and those at the starting point of a climbing route 57%. Species density at the starting point of the route was significantly lower than species density at distances of 2 or 5 m from the climbing route and in control plots (distance 0 compared with pooled data from distance 2, 5, and control plots; Mann–Whitney U test: $z = 2.32$, $N = 65$, $P = 0.0209$; Fig. 2). The result of the ANOVA showed that vegetation cover at the cliff base was affected by the distance to the climbing route, the locality (cliff), the extent of shadow, and exposure (Table 2). The locality (cliff) affected species density at the cliff base, whereas the distance to the climbing route was only marginally significant in influencing species density ($p = 0.0523$). The extent of shadow and exposure did not influence species density at the cliff base.

A significant decrease in abundance with increasing distance from the starting point of climbing routes was found in *Laserpitium siler* L. and *Thlaspi montanum* L., both obligate rock species that occur exclusively on limestone cliffs. By contrast, *Melica nutans* L., a species with no association to rocky habitat, and trampling-tolerant species such as *Plantago major* L. and *Taraxacum officinale* G.H. Weber ex Wiggers aggr., were found in plots at the base of climbing routes, but not in undisturbed control plots.

Small-scale effects at the cliff face

As at the cliff base, plant cover and species density on the cliff face increased with increasing distance from the climbing route (Fig. 3). The ANOVA revealed that the distance to the climbing route was only marginally significant in influencing the vegetation cover on the cliff face ($P = 0.0523$; Table 3). Vegetation cover was also influenced by the locality (cliff), extent of insolation (shadowing), and fracturing of the rock surface (Table 3). Species density on the cliff face

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Table 2. Results of the four-way ANOVA of factors influencing the vegetation cover and species density (number of species per square metre) at the base of six limestone cliffs.

Factor	df	SS	MS	*F*	*P*
Vegetation cover					
Distance to climbing route	3	2.283	0.761	4.52	0.0071
Cliff	5	5.827	1.165	6.92	<0.0001
Shadowing	7	2.708	0.387	2.30	0.0419
Exposure	1	1.942	1.942	11.54	0.0014
Error	48	8.079	0.168		
Species density					
Distance to climbing route	3	61.263	20.42	2.76	0.0523
Cliff	5	167.022	33.404	4.51	0.0019
Shadowing	7	48.082	6.869	0.09	0.4935
Exposure	1	2.731	2.731	0.04	0.5464
Error	48	355.169	7.399		

Fig. 3. Plant cover and species density (number of species per square metre) on the cliff face in relation to distance to the climbing route. Mean values ± SE of 18 routes (six cliffs with three routes each) are shown. Plots 5 m from the climbing route can be considered as controls.

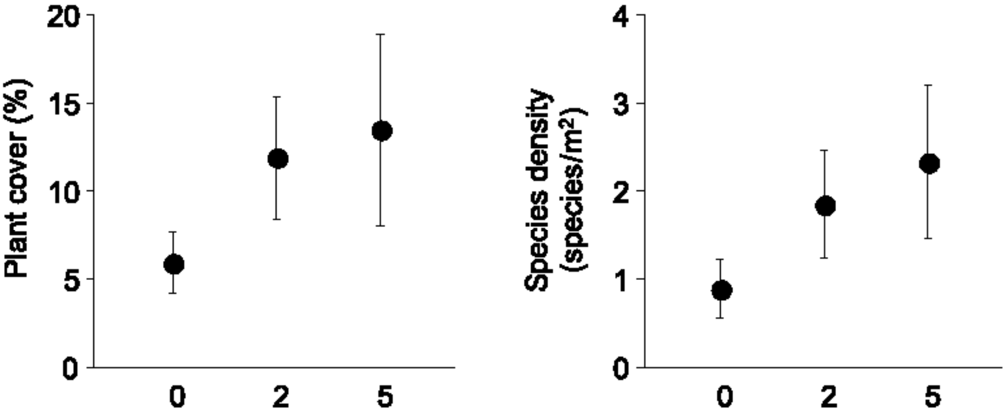

Table 3. Results of the five-way ANOVA of factors influencing the vegetation cover and species density (number of species per square metre) on the face of six limestone cliffs.

Factor	df	SS	MS	*F*	*P*
Vegetation cover					
Distance to climbing route	2	0.050	0.025	3.26	0.0523
Cliff	5	0.136	0.027	3.54	0.0123
Shadowing	8	0.230	0.029	3.76	0.0037
Fracturing of rock surface	4	0.429	0.107	14.03	<0.0001
Exposition	1	0.002	0.002	0.032	0.5732
Error	30	0.230	0.008		
Species density					
Distance to climbing route	2	25.280	12.640	5.10	0.0124
Cliff	5	22.324	4.465	1.80	0.1425
Shadowing	8	52.801	6.600	2.66	0.0244
Fracturing of rock surface	4	69.718	17.430	7.04	0.0004
Exposition	1	1.227	1.227	0.50	0.4870
Error	30	74.303	2.477		

was affected by the distance to the climbing route, the extent of insolation, and the degree of fracturing of the rock surface (Table 3).

Regional survey

At the cliff bases, a total of 43 plant species were recorded in the five climbed areas and 65 plant species in the

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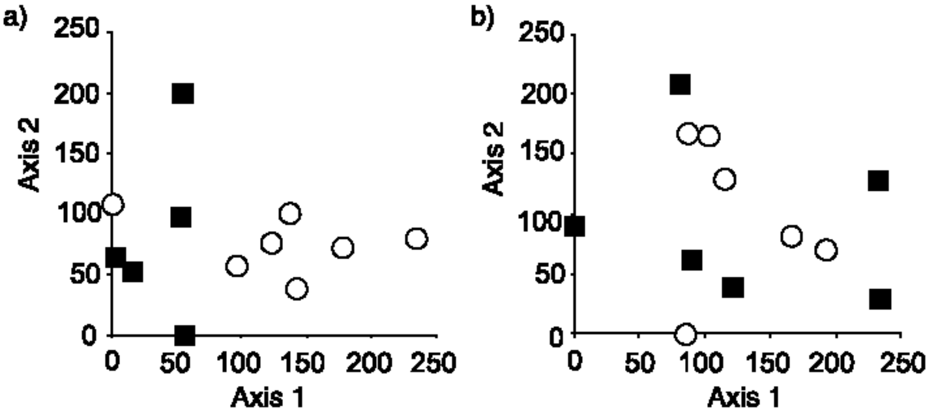
Fig. 4. Ordination diagram produced by detrended correspondence analysis of the vascular plant species on climbed cliffs (full squares) and unclimbed cliffs (open circles) in the northern Swiss Jura Mountains. (*a*) Vegetation at the base of cliffs and (*b*) on the face of cliffs.



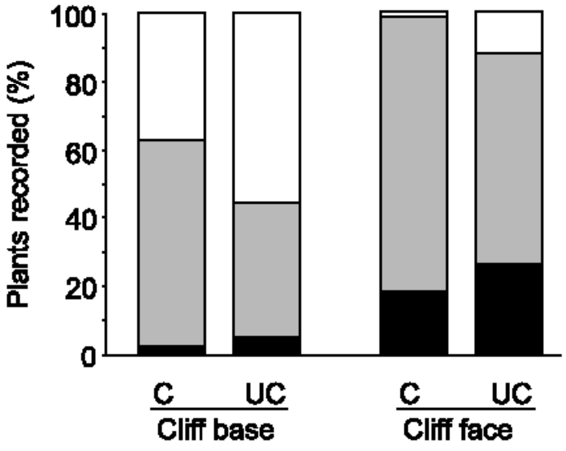
seven unclimbed areas. A total of 30 species (38.5% of the total 78 species) were found in both climbed and unclimbed areas, 35 species (44.9%) were found exclusively in unclimbed areas, and 13 species (16.7%) only in climbed areas. Mann Whitney *U* tests of exposure (quantified as degrees deviating from north), degree of shadowing, and fracturing of the rock surface revealed no differences between climbed and unclimbed cliffs ($P > 0.05$ for all parameters).

The DCA ordination revealed a separation of climbed and unclimbed areas on the basis of their plant composition (Fig. 4). The first axis (Eigenvalue = 0.352) showed a significant difference between climbed and unclimbed cliffs (Mann–Whitney *U* test: $z = 2.03$, df = 1, $P = 0.042$). Climbing activities resulted in a change in plant composition, indicated by the proportion of plants with different dependencies on rocky habitat (Fig. 5). Highly specialized rock species occurred less frequently at the base of climbed cliffs than at the base of unclimbed cliffs. Similarly, nonspecialized plant species were found less frequently on climbed cliffs than on unclimbed cliffs. In contrast, plant species with a moderate association to rocky habitats occurred more frequently at the base of climbed cliffs than at that of unclimbed cliffs ($\chi^2 = 11.94$, df = 2, $P = 0.0026$).

Light scores of plants (Landolt indicator values) at the base of climbed cliffs were higher than at the base of unclimbed cliffs (unpaired Student's *t* test: $t = 3.20$, df = 64, $P = 0.0021$, Bonferroni-corrected $P = 0.0105$). The shade-tolerant wood herbs *Lamiastrum galeobdolon* (L.) Ehrend. & Polatschek and *Mercurialis perennis* L. were not recorded at the base of climbed cliffs, but were frequently found at the base of unclimbed cliffs. Furthermore, temperature scores ($t = 2.49$, df = 64, $P = 0.0154$, Bonferroni-corrected $P = 0.0616$) and humus scores ($t = 2.14$, df = 64, $P = 0.0359$, Bonferroni-corrected $P = 0.1077$) tended to be higher at the base of climbed cliffs than at the base of unclimbed cliffs.

Vegetation cover was positively correlated with degree of shading at the base of climbed cliffs ($r = 0.90$, $n = 5$, $P = 0.0376$). At the base of unclimbed cliffs, no correlation was found between vegetation cover and degree of shade ($r = -0.55$, $n = 7$, $P = 0.22$). At the base of unclimbed cliffs, species density increased with decreasing degree of shade ($r = -0.98$, $n = 7$, $p < 0.001$; Fig. 6). At the base of climbed cliffs, however, species diversity decreased with decreasing degree of shade ($r = 0.92$, $n = 5$, $P = 0.0263$).

Fig. 5. Proportion of plants with different dependency on rocky habitat recorded at the base and on the face of five climbed (C) and seven unclimbed (UC) cliffs (classes following Wassmer 1998). Percentages are based on cumulative data. True rock plant species (■), species with a moderate association to rocky habitat (▨), species with no association to rocky habitat (□). Cliff base: $\chi^2 = 11.94$, df = 2, $P = 0.0026$; cliff face: $\chi^2 = 7.28$, df = 2, $P = 0.0263$.



On the cliff faces, a total of 22 plant species were recorded in the five climbed areas and 41 species in the seven unclimbed areas. A total of 15 species (31.5% of the total 48 species) were found in both climbed and unclimbed areas, 26 species (54.2%) were found exclusively in unclimbed areas, and 7 species (14.7%) only in climbed areas.

In contrast to the cliff bases, the community structure on the cliff faces did not differ between climbed and unclimbed areas (Fig. 4). Nevertheless, the proportions of plants with different dependencies on rocky habitat differed between climbed and unclimbed areas (Fig. 5; $\chi^2 = 7.28$, df = 2, $P = 0.0263$). As at the cliff base, true rock species and nonspecialized plant species occurred less frequently on the face of climbed cliffs than on that of unclimbed cliffs. Plant species with a moderate association to rocky habitat occurred more frequently on the face of climbed cliffs than on un-

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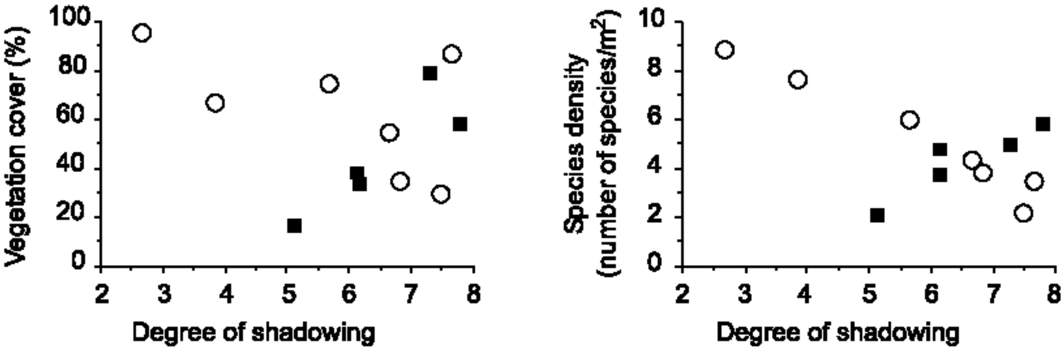
Fig. 6. Correlations between degree of shading and plant cover and species density at the cliff bases. Full squares indicate climbed cliffs and open circles unclimbed cliffs.



climbed cliffs. Plant indicator values did not differ between climbed and unclimbed cliffs ($P > 0.1$ in all scores). However, on the cliff faces the fracturing of the rock surface was positively correlated with both plant cover ($r = 0.42$, $n = 72$, $P < 0.001$) and species number ($r = 0.41$, $n = 72$, $P < 0.001$).

Discussion

The present study shows a significant impact of rock climbing on the vegetation of limestone cliffs in the northern Swiss Jura Mountains. Climbing decreased plant cover and species density in climbing routes and changed species composition.

The distance between two neighbouring climbing routes is frequently less than 2 m at several cliffs in the northern Swiss Jura Mountains (Andrey et al. 1997). Cliff bases with numerous routes are therefore highly disturbed habitats. Specialized rock species occur at the base of undisturbed limestone cliffs. The reduction in plant species density, the lack of true rock species, and the occurrence of trampling-tolerant species in the starting area of climbing routes indicated a high degree of disturbance at these sites. This may prevent any successful colonization of true rock plant species.

Exposure and degree of shading strongly influenced the vegetation cover at the cliff bases (Table 2). South-facing cliff bases with full sun exposure showed the highest plant cover. Relic plant species with high light demands are restricted to these sites (Richard 1972; Oberdorfer 1992). Southeast to southwest facing cliffs are also the preferred climbing areas in the northern Jura Mountains (data from Andrey et al. 1997). On these cliffs, climbers install routes by selecting locations where the cliff face is high enough and allows routes with challenging motion sequences. Due to the favourable exposure, climbing can take place throughout the year and even shortly after periods of rain. Thus, the cliffs with the highest conservation value are also the most preferred areas of climbers. Consequently, relic plant species are most exposed to the impact of rock climbing activities.

Our study also showed a negative impact of rock climbing on plant cover and species density on the cliff face. Characteristic species of the limestone cliffs in central Europe are typically perennial rosette plants with a short-range dispersal and a high reproductive effort (Frey et al. 1995). Frequently used climbing routes may divide populations of these specialized plants. Due to the limited dispersal of their seeds, the plants might not be able to cross these human-made gaps. Moreover, the life-history strategy of *Draba aizoides*, *Saxifraga paniculata*, *Kernera saxatilis*, and numerous other rock plant species with heavy propagules is not adapted for a fast recolonization of the rocky habitat after disturbance (Wilmanns and Rupp 1966). Therefore, these species will be replaced by other species, even though the disturbed area measures only a few square metres.

The fracturing of the rock surface determined plant cover and species density on the cliff face (Table 3). Fractured cliffs contain more soil and exhibit a higher microclimatic diversity than smooth cliffs and therefore harbour greater densities and higher plant species richness. On cliff systems in Minnesota, cracks were more common on climbed cliffs than on unclimbed cliffs, whereas ledges were less common (Farris 1998). Climbers use the small cracks as holds for hand and feet. Using small brushes they frequently clean the holds from any dust, soil particles, and stone debris. In this way, a microhabitat for highly specialized plant species is destroyed. Shading, which decreases microclimatic differences between the exposed cliff surface and the protected zones within fractures and on ledges, was the other significant factor for vegetation cover and species density on the cliff face.

In contrast to other studies, which focused on a single cliff system (e.g., Nuzzo 1996; McMillan and Larson 2002; Rusterholz et al. 2004), the present study examined the impact of sport climbing on the vegetation in a region with several isolated (independent) rock cliffs. Previous studies showed reductions in plant cover and species number on climbed cliffs. In our study we tried to keep environmental differences between climbed and unclimbed cliffs as minimal as possible. All unclimbed cliffs examined were potential climbing sites. The absence of climbing on these cliffs cannot be attributed to unsuitable rock faces, but might rather be due to their remote location (large distance to nearest town) or lack of infrastructure (no car parking area, no access by public road). Some of these cliffs were not climbed, most probably because they are not high enough for the establishment of interesting climbing routes. As environmental and physical factors are the primary determinants of the cliff flora (Nuzzo 1996), differences in plant cover, species number, and species composition could also be a result of differences in exposure, degree of shading, or fracturing of the rock surface. In the present study, however, climbed and unclimbed areas did not differ in any of these factors. Therefore, the separation of climbed and unclimbed cliffs in the DCA for the vegetation on the cliff base was not due to different environmental conditions, but rather was the result of trampling by climbers.

Differences in species composition revealed by the DCA were confirmed by changes of Landolt's indicator values. Light scores of plants were higher on climbed than on unclimbed cliffs. Furthermore, the correlations between the degree of shading, vegetation cover, and species density at the cliff base were negative on unclimbed but positive on climbed cliffs (Fig. 6). Both the increase in light scores and the correlation of vegetation cover and the degree of shading indicate that trampling is influencing the ecosystem.

On the cliff face, the DCA revealed a similar pattern. Plant cover and species number were correlated with the fracturing of the rock surface, but not with other factors such as degree of shading or exposure. The correlations suggest that the fracturing of the rock surface was the primary determinant for the species composition of the cliff face. Similar findings have been reported for sandstone cliffs in Tasmania (Coates and Kirkpatrick 1992), granite outcrops in Victoria (Ashton and Webb 1977), and dolomitic cliffs in Illinois (Nuzzo 1996).

Despite the strong influence of environmental factors, a decrease in the abundance of specialist species and an increase in plant species moderately adapted to rocky habitats were recorded on climbed cliffs. The decrease of specialized plants both at the base and on the face of climbed cliffs supports the hypothesis of Grime (1979) and Larson et al. (1989) that cliff plant communities are composed of species tolerant to environmental variability but intolerant to disturbance. Plants with a moderate dependency on rocky habitats are disturbance-tolerant species, e.g., graminoids such as *Sesleria albicans* or annual plants such as *Geranium robertianum*. In contrast to the specialized, true rock species, these plants may benefit from disturbances caused by climbing.

Management implications

Our study showed that specialized plants, which include many relic species from the last glaciations and the present that are restricted to limestone cliffs of the Swiss Jura Mountains, are negatively affected by climbing activities. Therefore, management plans and actions have to be developed and implemented. These actions should consider the vulnerability of the disturbance-sensitive plant populations. The prohibition of sport climbing on cliffs with a high number of specialized, relic plants and the establishment of climbing-free protection zones in popular areas are the most effective and adequate measures. As Camp and Knight (1998) pointed out, the compliance of these measures will be increased when recreationizts realize how their activities may alter the native biological diversity of a region. Therefore, all management plans should include comprehensive information campaigns regarding these topics. Accordingly, measures can be based on the conscience of every single climber rather than the artificial authority of restrictions.

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Chapter 2

Effects of rock climbing on the plant communities on exposed limestone cliffs of the Gerstelflue in the northern Swiss Jura mountains

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Effects of rock climbing on plant communities on exposed limestone cliffs in the Swiss Jura mountains

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Abstract. Exposed cliffs of the Swiss Jura mountains harbour a highly diverse flora with many rare and endangered plant species. Many cliffs are frequently visited by rock climbers. We examined the impact of rock climbing on vascular plants in the lower part of four cliffs of the Gerstelflue (NW Switzerland) by comparing the vegetation of climbed and unclimbed areas. In climbed areas plant cover and species density were reduced. Similarly, the density of forbs and shrubs decreased, whereas the density of ferns tended to increase. In addition, rock climbing caused a significant shift in plant species composition and altered the proportions of different plant life forms. Rock climbing can be a threat to sensitive plants of the limestone cliff community.

Keywords: Disturbance; Switzerland; Vascular plants.

Nomenclature: Binz & Heitz (1990).

Introduction

The cliffs of the Jura mountains in NW Switzerland support unique and diverse plant communities (Zoller 1989). Vascular plants with low edaphic and water demands such as *Draba aizoides* and *Sedum acre* occur in minute soil patches in ledges and cracks on the cliffs (Wilmanns 1993). Lichens, ferns and mosses constitute a main component of the rock face vegetation (Oberdorfer 1992). In contrast to the large rocky areas of the Alps, the cliffs of the Jura mountains are small and isolated and mostly surrounded by forest. A variety of plants growing on these cliffs are inter- or postglacial relics currently with a mediterranean or arctic-alpine distribution (Walter & Straka 1970). Similarly, the vegetation at the base of the cliffs contains relics such as *Ilex aquifolium* from postglacial warm periods. The south exposed slopes of the Jura mountains are covered by xerothermic *Quercetalia pubescenti-petraeae* (oak wood), which colonized the region from refuges in S France and the Balkans (Ellenberg 1986) and by slow growing *Fagus* (beech) wood with translucent canopies and highly diverse ground vegetation (Moor 1972). The high species richness and large number of rare plant species, the rarity of the habitat type and the historical peculiarity give the rock cliffs a high conservation value (Keller & Hartmann 1986; Egloff 1991; Wassmer 1998; Knecht unpubl.).

Rock climbing enjoys increasingly popularity, particularly in mountain areas at low altitudes, where the sport can be performed all year round (Hanemann 2000). More than 2000 climbing routes with fixed protection bolts have been installed on 48 rock cliffs in the Basel region (Andrey et al. 1997). Ca. 70% of these climbing routes were opened between 1985 and 1999. The large impact of climbers, however, locally leads to serious environmental disturbance. In adjacent southern Germany, climbing has been restricted at many sites due to severe conflicts with nature conservation. As a result a further increase in climbing activities has been observed in the Jura mountains of northwestern Switzerland.

Effects of recreational activities on plant communities are attracting more and more attention (Liddle 1997). However, little information is available about the impact of rock climbing on cliff plant communities. In the upper Danube valley in Germany severe disturbance of vegetation on limestone cliffs due to climbing has been recorded (Herter 1993, 1996). Damage included (1) reduction of plant cover; (2) extinction of species sensitive to disturbance and of specialists adapted to these extreme habitats; (3) clearing of soil from crevices; (4) erosion of the cliff edge and face; (5) increase in ruderal species. Rock climbing also led to skewed size and age distributions of *Solidago sciaphila* (Nuzzo 1995) and *Thuja occidentalis* (Kelly & Larson 1997). On exposed dolomitic cliffs in NW Illinois, climbing reduced lichen cover and species richness by 50% (Nuzzo 1996). Other studies showing reduced plant diversity and altered community structure include Farris (1998), Camp & Knight (1998), Larson et al. (2000) and McMillan & Larson 2002). The removal of plants and soil may also alter the abiotic conditions for the remaining plants on the cliff.

The aim of this study was to examine the impact of rock climbing on plant cover, diversity and composition on limestone cliffs of the Gerstelflue in the northern Swiss Jura mountains.

Material and Methods

Study site

The present study was carried out in the lower part of cliffs of the Gerstelflue near Waldenburg (canton Basel-Landschaft) in the northern Swiss Jura mountains (30 km SE of Basel). The cliffs of the Gerstelflue mainly consist of Jurassic coral chalk (Bitterli-Brunner 1987). The plant community investigated on the cliffs is the *Potentillo-Hieracietum* association (Richard 1972).

The Gerstelflue is a popular recreational climbing area. Rock climbing has occurred in the area for ca. 40 yr (Andrey et al. 1997). At present, there are 67 graded routes distributed over 12 cliffs (Andrey et al. 1997). The climbing routes are situated within a horizontal distance of 650 m at altitudes of 775-1018 m a.s.l. Over the past five years, a moderate number of climbers have used the routes mainly for exercising alpine climbing techniques (P. Müller pers. comm.).

Methods

We examined the impact of rock climbing on the vegetation in the lower part of four different cliffs of the Gerstelflue (referred to as A-D). The cliffs were situated 150 - 320 m apart, partly interspaced by forest. At each cliff, we chose a site with established climbing routes (climbed area) and an unclimbed area (undisturbed control area) in its close neighbourhood on the basis of following criteria: (1) the climbed and unclimbed areas have the same exposure (southeast) and are situated within a horizontal distance of 10 - 50 m; (2) the climbed and the unclimbed area receive the same insolation; (3) the areas do not differ in type and structure of the rock surface and (4) the control areas show no obvious sign (fixed protection bolts) of recent climbing activity.

The plant survey was conducted using horizontal transects at three different heights on the lower part of the cliff faces (at 0 - 1.0 m, 1.1 - 2.0 m and 2.1 - 3.0 m measured from the cliff base). On each transect, 3 - 5 sampling plots of 1 m^2 were established. Table 1 presents number of sampling plots for each transect and their length. Transect length (7.5 m - 15 m) was determined by the homogeneity and structure of the rock face. The horizontal distance between single sampling plots ranged from 2 to 6 m. A total of 44 sampling plots in climbed areas and of 48 sampling plots in unclimbed areas were examined. The abundance of each plant species was recorded in each sampling plot at three occasions (in May, July and September 2001). Plant cover was visually estimated using the Domin-Kraijina scale (Mueller-Dombois & Ellenberg 1974). We also visually estimated the proportion of area covered by litter and rock in each sampling plot.

Table 1. Number of 1-m^2 sampling plots at different heights in the lower part of climbed (cl) and unclimbed (uncl) areas on four limestone cliffs (A-D) of the Gerstelflue. Figures in brackets indicate the length of the horizontal transects (m).

	Height of the transect					
	0 - 1.0 m		1.1 - 2.0 m		2.1 - 3.0 m	
Cliff	Cl	Uncl	Cl	Uncl	Cl	Uncl
A	5 (15)	5 (15)	4 (8)	5 (15)	3 (8)	5 (15)
B	3 (8)	3 (7.5)	4 (10)	4 (10)	4 (10)	4 (7.5)
C	4 (8)	4 (10)	4 (10)	4 (10)	4 (10)	4 (8)
D	3 (8)	3 (8)	3 (10)	3 (8)	3 (10)	4 (10)

To relate the plants of the investigated areas to abiotic environmental factors, we used the indicator scores of Landolt (1977) including light, temperature, humus, soil nutrients and soil moisture. Mean indicator values were calculated both on the basis of presence/absence data and on the abundance of individual plant species for each sampling plot (Jongman et al. 1995). Plant species were assigned to different functional types using the criteria of Grime (1979).

Species lists and data on number of plants recorded in climbed and unclimbed areas at different heights on the four limestone cliffs of the Gerstelfluh are available at http://www.unibas.ch/dib/nlu/res/cliffs/gerstel.pdf

Data analysis

ANOVAs were used to examine the impact of rock climbing on the cover of plants, litter and rocks and on species richness (number of plant species) and diversity (Shannon-Wiener diversity index) as well as on species density (m^{-2}) of ferns, graminoids, forbs, shrubs and trees and the mean indicator values of Landolt (1977). Prior to the analyses all data were log or square root-transformed. The ANOVA model included the factors cliff, treatment (climbed vs unclimbed) and height at the cliff face. First an overall comparison between climbed and unclimbed areas was made using a two-way ANOVA (factors treatment and cliff). According to the design, 'cliff' was used as fixed factor and treatment was nested within cliff. In a second step, the effect of rock climbing on various parameters of the vegetation was analysed separately for each cliff face height.

To examine whether species richness differs independently of the number of individuals recorded, we used ANCOVA with treatment and cliff as factors and number of individuals as covariate. The influence of rock climbing on changes in the abundance of different plant life forms was evaluated using contingency analysis separately for each cliff face height.

Detrended Correspondence Analysis (DCA) was used to examine whether the composition of plant species

Table 2. Effect of rock climbing on various variables of the plant community in the lower part of four limestone cliffs of the Gerstelflue. Mean values ± S.E. are shown; *n* indicates the total number of 1-m^2 sampling plots.

Variable	Climbed area (n = 44)	Unclimbed area (n = 48)	ANOVA $F_{1,3}$	P
Plant cover (%)	16.3 ± 1.8	21.8 ± 2.0	36.19	0.009
Litter cover (%)	6.0 ± 1.1	3.3 ± 0.7	13.03	0.037
Rock cover (%)	78.0 ± 2.5	74.6 ± 2.4	12.91	0.036
Species density	6.4 ± 0.5	12.3 ± 0.6	18.05	0.024
Species diversity (*H*')	1.3 ± 0.1	1.8 ± 0.1	8.18	0.064
Number of specimens of different life forms/m^2				
Ferns	0.6 ± 0.2	0.2 ± 0.1	0.86	0.422
Graminoids	27.8 ± 3.7	39.6 ± 4.0	2.49	0.221
Forbs	8.3 ± 1.2	24.2 ± 1.7	29.15	0.012
Shrubs	11.1 ± 2.5	18.8 ± 2.0	12.43	0.039
Trees	0.7 ± 0.3	2.1 ± 0.8	2.59	0.210
Landolt indicator values (abundance-based)				
Light (L)	3.95 ± 0.02	4.07 ± 0.01	4.87	0.114
Temperature (T)	3.15 ± 0.02	3.17 ± 0.02	0.03	0.822
Humus (H)	2.81 ± 0.01	2.78 ± 0.01	0.48	0.537
Soil nutrients (N)	2.02 ± 0.01	2.03 ± 0.02	0.80	0.438
Soil humidity (F)	1.72 ± 0.04	1.71 ± 0.03	0.30	0.624

differed between climbed and unclimbed areas (Hill & Gauch 1980). Prior to ordination, species that were less frequent than the median frequency were down-weighted in relation to their frequencies (Eilertsen et al. 1990). Statistical analyses were conducted using SAS version 8.02. The multivariate analysis (DCA) was performed using CAP version 1.3 (PISCES Conservation LTD).

Results

In total 6091 individual plants of 44 species were recorded in the 92 sampling plots (1921 individuals from 32 species in the four climbed areas and 4170 individuals from 44 species in the unclimbed areas). The results of the ANOVA yielded to reduced plant cover, but increased cover by litter and rock in climbed compared to unclimbed areas (Table 2). Furthermore, in climbed areas species density and species diversity were reduced by 50% and 30%, respectively. The density of forbs and shrubs were reduced by 66% and 41%, respectively, in climbed areas (Table 2). In contrast, the density of ferns tended to increase in climbed areas (Table 2). However, climbed and unclimbed areas did not differ in any of Landolt's (1977) indicator values, corroborating that both areas provided similar conditions (Table 2). Results of three-way ANOVAs showed significant among-cliff effects on plant cover ($F_{3,80} = 7.01$; $p = 0.001$) and diversity ($F_{3,80} = 2.74$; $p = 0.048$) and a marginally non-significant effect on species density ($F_{3,80} = 2.69$; $p = 0.052$).

The composition of different functional types of plants – *sensu* Grime (1979) – did not differ between climbed and unclimbed areas (contingency test; $\chi^2 = 0.32$; $df = 2$; $p = 0.86$).

Plant species richness was lower at heights of 1.1 - 3 m in climbed than in unclimbed areas (Table 3).

In general, plant cover in climbed areas was lower than in unclimbed areas. This finding is mainly a result of a significantly reduced plant cover in climbed areas at heights of 1.1-3 m from the cliff base (Fig. 1a). At heights of 0-1 m, plant cover did not differ significantly between climbed and unclimbed areas. In unclimbed areas compared to climbed areas, species density was higher at all three heights (Fig. 1b) and species diversity (*H*') was higher at heights of 1.1-3 m (Fig. 1c).

The proportions of different plant life forms differed between climbed and unclimbed areas at all heights examined (all *p*-values < 0.001; Fig. 2). The response of different plant life forms to rock climbing varied among heights of the cliff face (Fig. 2).

For a given number of plant individuals species richness was significantly lower in climbed than in unclimbed areas, as indicated by the different intercepts of the regression (ANCOVA; $F_{1,82} = 14.14$; $p = 0.001$; Fig. 3). Furthermore, no significant interactions between number of plant individuals and treatment (climbed vs unclimbed area; $F_{1,82} = 0.30$; $p = 0.58$) and between number of plant individuals and cliffs ($F_{3,82} = 0.89$; $p = 0.45$) were found.

Table 3. Number of plant species recorded at different heights in climbed and unclimbed areas at the base of four limestone cliffs of the Gerstelflue. Number of plants are given in parentheses and number of sampling plots in brackets.

Height of transect (m)	Climbed area	Unclimbed area	ANOVA $F_{1,3}$	P
0.0 - 1.0	30 (950) [15]	39 (1366) [15]	6.97	0.077
1.1 - 2.0	25 (428) [15]	43 (1508) [16]	49.23	0.005
2.1 - 3.0	23 (518) [14]	40 (1284) [17]	21.96	0.019
Total	32 (1896) [44]	44 (4170) [48]	28.19	0.013

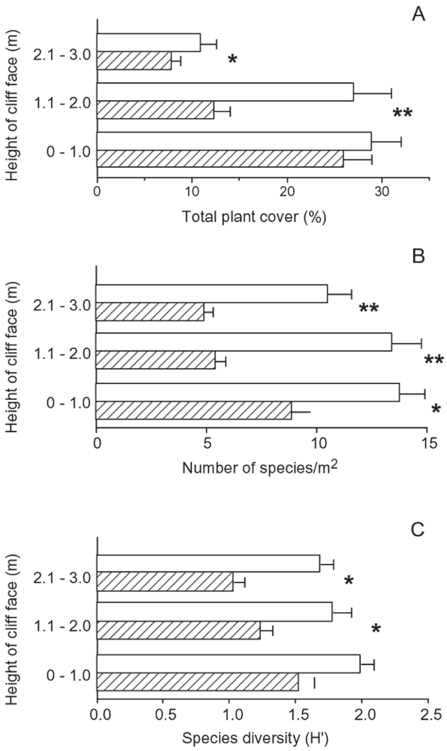

Fig. 1. A. Plant cover (%); **B**. Species density (m^{-2}); **C**. Shannon-Wiener index, *H'*, at different heights of climbed (hatched bars) and unclimbed areas (open bars) of four limestone cliffs of the Gerstelflue. Mean values ± S.E. are shown. The number of sampling plots in climbed/unclimbed areas were 15/15 (0 - 1.0 m); 15/16 (1.1 - 2.0 m); 14/17 (2.1 - 3.0 m). $* = p < 0.05$; $** = p < 0.01$.

The DCA resulted in a separation by plant species composition of climbed and unclimbed areas (Fig. 4). The eigenvalue of axis 1 (0.229) showed a significant separation of climbed and unclimbed areas ($\chi^2 = 5.33$; $df = 1$; $p = 0.021$).

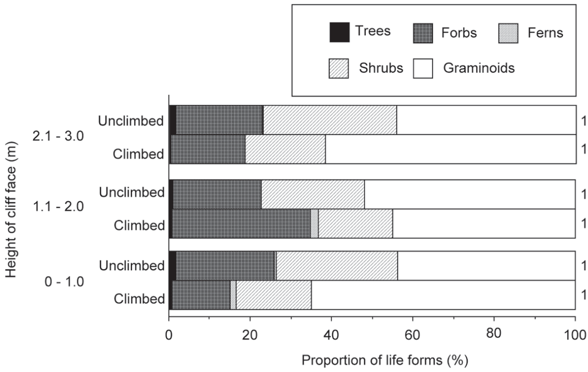

Fig. 2. Proportions (%) of different plant life forms occurring at different heights in climbed and unclimbed areas on four limestone cliffs of the Gerstelflue. Figures indicate the number of 1-m^2 sampling plots.

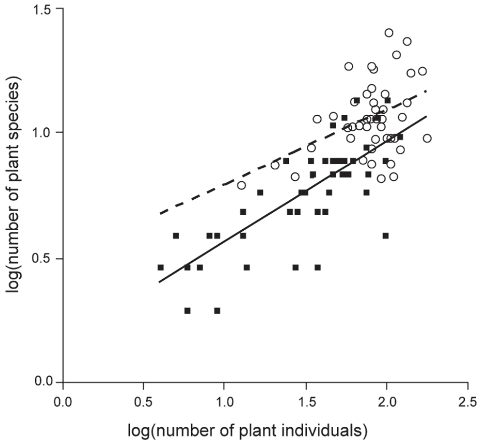

Fig. 3. Relationship between number of plant individuals and number of plant species (both log-transformed) in climbed (■ : 44 1-m^2 plots) and unclimbed (○ : 48 1-m^2 plots) areas on four limestone cliffs of the Gerstelflue. For a given number of plant individuals species richness was lower in climbed than in unclimbed areas. Solid line illustrates regression line for climbed areas and dashed line represents unclimbed areas.

Discussion

The present study shows that rock climbing affected the cliff plant community at the Gerstelflue in the Swiss Jura mountains. A significant decrease in plant cover and species density and a shift in the community structure were recorded in climbed areas. Similar climbing related changes in vegetation have been reported in other studies (Herter 1993, 1996; Nuzzo 1995; Camp & Knight 1998; Farris 1998; Kelly & Larson 1997; McMillan & Larson 2002).

In our study, the impact of rock climbing on plants was differently pronounced at different heights of the cliff face. In the 1-m wide horizontal strip at the cliff

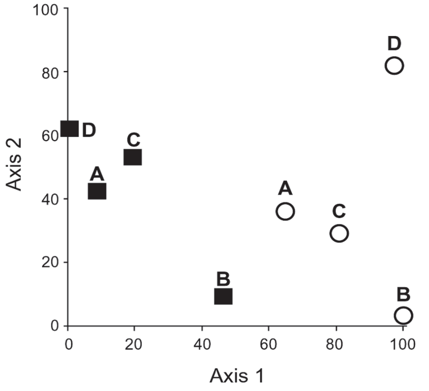

Fig. 4. DCA diagram showing the plant species composition in climbed (■) and unclimbed areas (○) in the lower part of four limestone cliffs (A-D) of the Gerstelflue. Axis 1 separates by $P = 0.02$; eigenvalue is 0.229.

base, plant cover was not significantly affected by climbing. However, the reduced plant species richness in the climbed areas also indicate human disturbance at this height.

In contrast to the cliff base, plant cover and species diversity were significantly reduced in climbed areas at a cliff height of 1.1 - 3.0 m. This could partly be explained by the fact that during the installation of a climbing route part of the vegetation is removed to create additional hand and foot holds (Nuzzo 1995; Kelly & Larson 1997). Furthermore, the frequent use of the same climbing route may damage the remaining plants growing in crevices and cracks. The larger proportion of bare rock in climbed areas might also be a result of frequent climbing activities. Herter (1996) reported that handholds including crevices and cracks contained significantly fewer plant species in cliffs with frequent rock climbing than in corresponding control areas.

Contrasting results concerning changes in the abundances of grasses have been reported. Farris (1998) and McMillan & Larson (2002) found an increase in grass abundance, while Nuzzo (1995) and Camp & Knight (1998) reported a decrease in grass abundance due to climbing activities. Available evidence suggests that the abundance of grasses increases at low climbing intensity, but decreases at very high climbing intensity. Species-specific differences in the sensitivity to human disturbance might be the main reason for the observed shift in species composition. Plant species which are tolerant to human disturbance can successfully survive and reproduce irrespective of climbing whereas sensitive species, including many forbs, show a reduced fitness or even disappear from cliffs (Parikesit et al. 1995). The lack of trampling-tolerant species, such as *Poa annua* and *Plantago major*, as well as the relatively slight decrease in plant cover at the cliff base of climbed areas indicate that the extent of rock climbing at the particular height at the investigated cliffs of the Gerstelflue is less pronounced than reported from cliffs in the Danube valley (Herter 1993, 1996), the Niagara Escarpment (McMillan & Larson 2002) and other limestone cliffs in the northern Jura mountains (e.g. Schartenflue, Tüfleten, Pelzmühlital; S. Müller unpubl.).

Grime (1979) and Larson et al. (1989) hypothesized that cliff plant communities are composed of a few species tolerant to environmental variability but intolerant to disturbance. The reaction of plant species to human disturbance is often related to life form (Cole 1995a, b). In the present study, however, the changes in species composition due to disturbances cannot be attributed to differences in plant life forms. Plant species with identical life form differed in their response to rock climbing. For example, the frequency of the dwarf shrub *Teucrium chamaedrys* increased in climbed areas, whereas the frequency of the dwarf shrub *T. montanum* decreased. Further examples include the perennial rosette plants *Campanula rotundifolia* and *Hieracium humile*, which both occurred at higher abundance in climbed areas, whereas the abundance of *Leucanthemum adustum* was reduced in climbed areas. A possible explanation for these contrasting findings could be species-specific differences in the vulnerability of the reproductive phase. In addition, the finding that climbed and unclimbed areas did not differ in the composition of plant functional types is not surprising as the majority of rock dwelling plants are stress-tolerant (*sensu* Grime 1979).

Cliff vegetation can also be affected by natural disturbances. In some areas, natural defoliation can have a significant impact on the amount of plant cover (Ursic et al. 1997). Dougan & Associates (1995) reported that defoliation, erosion and soil loss at the cliff faces are primarily a result of natural disturbances. Shading by trees is another influence on the species composition of cliff plant communities. However, we found that the mean indicator values of Landolt (1977) for light, temperature and soil nutrients did not differ between climbed and unclimbed areas, indicating that plants were exposed to similar environmental conditions in both types of area. Alternatively, these environmental variables are not the key factors for the existence of cliff plants.

The cliff-top vegetation can be considered as a source of propagules which is essential for the (re-) establishment of cliff vegetation. Changes in the cliff-top vegetation due to human trampling can modify the amount and composition of propagules and, therefore, indirectly influence the composition of the cliff face vegetation. In the present study, traces of human activity were found on the top of three of the four cliffs examined. However, species composition of the cliff top vegetation did not differ among the cliffs (H.-P. Rusterholz unpubl.).

Our results support other studies on changes in plant populations and communities due to climbing activities (Nuzzo 1996; Farris 1998; Herter 1996; Camp & Knight 1998; McMillan & Larson 2002). To preserve the threatened cliff plant communities in the Swiss Jura mountains, management plans need to be developed and implemented. Closure or controlled access to frequently climbed areas would stop additional species loss and changes in cliff plant communities. This aim could be reached by closing parking lots or parts of the trail systems because the majority of climbing activities usually occur in their close neighbourhoods. However, closure of areas with heavy recreational use is not the best solution, because visitors tend to respond to such closure by moving into undisturbed habitats.

A monitoring program of the population size of selected indicator plants in climbed and unclimbed cliffs could provide a basis for future management plans.

Furthermore, user-friendly information on the potential impact of recreational activities on the local biodiversity should be provided. Recreationists accept management plans when they are aware of ecological reasons behind the restrictions.

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Chapter 3

Effect of rock climbing on the calcicolous lichen community of limestone cliffs in the northern Swiss Jura mountains

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Effect of rock climbing on the calcicolous lichen community of limestone cliffs in the northern Swiss Jura Mountains

by

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Abstract: Exposed limestone cliffs in the Swiss Jura Mountains harbour a diverse lichen community with some rare species. Sport climbing has recently increased in popularity on these cliffs. We examined the effect of sport climbing on calcicolous lichens by assessing species diversity and cover of lichens in climbed and unclimbed areas of 10 isolated cliffs in the northern Swiss Jura Mountains. We also investigated possible associations between lichens and lichen-feeding land snails on these cliffs. A total of 38 calcicolous lichen species, three bryophytes and one alga were found on the rock faces of 10 cliffs. Twenty lichen species (52.6%) were epilithic, 16(42.1%) endolithic and two (5.3%) foliose. Overall, the epilithic lichen species covered 8.3% of the rock surface, endolithic species 10.2%, and foliose species 0.03%. Climbed and unclimbed rock areas did not differ in total number of lichen species, species density (number of species per 100 cm^2) or total lichen cover. However, the frequency of occurrence of epilithic lichens was lower along climbing routes than in unclimbed areas. A multi-response permutation test showed that the lichen community composition of climbed areas differed from that of unclimbed areas. The dissimilarity of lichen communities between climbed and unclimbed areas increased with increasing climbing intensity on the focal route in climbed areas, but not with the age of the climbing route. Five of the 11 snail species recorded on the cliff faces were specialized lichen feeders. Plots along climbing routes harboured fewer snail species than plots in unclimbed areas. Total snail abundance was positively correlated with lichen species richness, but no correlation between snail species richness and lichen species richness was found. Our results indicate that frequent rock climbing can change the lichen community and reduce the snail community of limestone cliffs. A climbing-related reduction of snail abundance may also alter the lichen-herbivore interaction and indirectly change competitive interactions among lichen species.

Keywords: Disturbance, Jura Mountains, lichen, gastropod, rock climbing, limestone cliff.

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Introduction

The limestone cliffs in the northern Jura Mountains in Switzerland support unique plant, bryophyte and lichen communities (Zoller 1989; Oberdorfer 1992; Clerc 2004). In contrast to large rocky areas of the Alps and other high-elevation mountains, the cliffs of the Jura Mountains are small and isolated, and mostly surrounded by beech forests or xerothermic oak forests, which have been partly cleared and subsequently used as pasture for some centuries (Moor 1972). In this landscape, the rocky habitats represent islands of special environmental conditions (Wilmanns 1993). A variety of plants growing on these cliffs are inter- or post-glacial relics with a recent mediterranean or arctic-alpine distribution (Walter & Straka 1970). The high species richness, large number of rare species, rarity of the habitat type, and the area's historical peculiarity give the limestone cliffs a high conservation value (Wassmer 1998; Baur 2003; Baur et al. 2005).

Rock climbing is increasingly popular in these mountain areas at low elevation, where this sport can be performed during the whole year (Hanemann 2000). More than 2000 sport climbing routes with fixed protection bolts have been installed on 48 rock cliffs in the region of Basel, Switzerland (Andrey et al. 1997). Approximately 70% of these sport climbing routes were opened between 1985 and 1999 (Andrey et al. 1997). The enormous throng, however, leads to serious local environmental disturbances. Damage to vascular plant vegetation due to rock climbing was recorded on limestone cliffs of the Jura Mountains (Müller et al. 2004; Rusterholz et al. 2004), and on other rocky cliffs in Germany (Herter 1993, 1996) and North America (Nuzzo 1995, 1996; Kelly & Larson 1997; Camp & Knight 1998; Farris 1998; McMillan & Larson 2002). Damage includes a reduction of vegetation cover, alterations in the plant community and extinction of species sensitive to disturbance and specialists adapted to these extreme habitats. In addition, clearing of soil from crevices and erosion of the cliff edge and face were recorded.

Climbing-related effects on lichen communities have received less attention. On exposed dolomitic cliffs in north-western Illinois, climbing reduced the cover and species richness of lichens by 50% (Nuzzo 1996). Similarly, Schöller (1994) found a significant reduction of lichen cover as a result of intensive rock climbing on the cliff of Buchstein, Germany. On cliffs of the Niagara escarpment in southern Ontario, Canada, lichen species richness was significantly lower in climbed areas and community composition was altered, but the frequency of lichens did not differ between climbed and unclimbed areas (McMillan & Larson 2002). Farris (1998) found lichen cover and frequency to decrease with climbing activity at some sites but to be unaffected or even to increase at other sites on cliffs in Minnesota.

Lichen species composition and the abundance of single species can also be affected by interspecific competition and herbivory by snails (Pfeiderer & Winkler 1991; Baur et al. 1995). Limestone cliffs support high levels of gastropod diversity. Some of these snail species are specialized lichen feeders. Laboratory experiments revealed that snails from different species fed on 67-100% of the lichen species offered (Baur et al. 1994). Experiments also demonstrated species-specific lichen preferences and that both intra- and interspecific competition for lichens occur in rock-dwelling snail species (Baur 1988; Baur & Baur 1990; Fröberg et al. 1993; Baur et al. 1995). Rock climbing may negatively affect snail communities. For example, on cliffs of the Niagara escarpment, snail density and diversity were lower along climbing routes than in unclimbed areas, and community composition differed between climbed and unclimbed samples (McMillan et al. 2003). This suggests that rock climbing could indirectly reduce the grazing pressure on lichens growing on cliff faces. A reduced grazing pressure in turn could change competitive interactions among lichen species resulting in altered species abundances.

In this study, we compared community patterns of calcicolous lichens in climbed and unclimbed areas of 10 rock cliffs in the northern Swiss Jura Mountains. We also examined possible relationships between lichen species richness and cover and the intensity of sport climbing, the microstructure of the rock surface and the presence/absence of lichen-feeding gastropods. In particular, we addressed the following questions: (1) Are species richness and cover of calcicolous lichens affected by sport climbing? (2) Are epilithic, endolithic and foliose lichens differently affected by sport climbing? And (3) Do the microstructure of rock surface and presence of lichen-feeding gastropods influence calcicolous lichen communities?

Materials and methods

Study sites

The present study was carried out in the lower part of 10 isolated limestone cliffs in the northern Swiss Jura Mountains (cantons of Solothurn and Basel-Landschaft) 10-15 km S of Basel (47°35'N, 7°35'E). The cliffs are situated at elevations ranging from 440 to 720 m above sea level and are 1-9 km apart from each other (Table 1). They mainly consist of Jurassic coral chalks (Bitterli-Brunner 1987). The cliff bases are covered by different stands of deciduous forests belonging to Fagetum and Tilietum associations (Burnand & Hasspacher 1999).

Field survey

We recorded species richness and cover of calcicolous lichens and bryophytes on sport climbed cliff faces and on undisturbed rock faces (control areas) on the same cliffs. We placed six 10 cm × 10 cm plots in a vertical line with an interplot distance of 10 cm in selected sport climbing routes (indicated by fixed protection bolts) at a height of 1-2 m. At a horizontal distance of 1.5 m from each focal climbing route we placed another six sampling plots (three on either side) in vertical line. With the same spatial arrangement we placed twelve 10 cm × 10 cm control plots in an unclimbed part of the same cliff face. The following criteria were used to select the unclimbed control areas: (1) both control and climbed area have the same exposure, (2) both areas are situated within 10-30 m, (3) both receive the same insolation, and (4) the control area and climbed area are similar in rock surface complexity (see below). Lichens were examined in a total of 240 sampling plots in July 2001 and April 2002. In each sampling plot, we recorded the number of lichen and bryophyte species and the cover of each species. We used a 1-cm^2-grid to assess the area covered by each species (to the nearest 0.5 cm^2). The person (L.F.) who monitored the lichens and bryophytes was not aware of the climbing intensity of a particular route. Lichen nomenclature follows Clerc (2004) and Santesson et al. (2004). We also recorded two species of vascular plants: *Asplenium trichomanes* L. covering 4 cm^2 in two plots and *Campanula rotundiflora* L. covering 1 cm^2 in one plot. The low frequency of vascular plant occurrence did not allow any data analysis.

In the same climbing routes and control areas we also recorded the species richness and species abundance of rock-dwelling gastropods. For this purpose we placed three 50 cm × 50 cm plots in a vertical line along each focal climbing route and in each control area at a height of 0.5 to 2 m. We carefully examined the rock surface, fissures and pockets for attached gastropods using a magnifying

Table 1. Description of cliffs and climbing routes investigated in the northern Jura Mountains, Switzerland.

			Characteristics of the climbing routes examined					
Cliff (Abbreviation)	Elevation (m a.s.l.)	No. of climbing routes[1]	Exposure	Year of first ascent (reconstruction)[1]	Difficulty grade[1,2]	Frequency of climbing[3]	Width of bare ground at the cliff base (m)	Complexity of rock surface[4]
Falkenflue (Fa)	550	254	WNW-NW	1988	8b	4	6	4
Hofstetter Chöpfli (Hc)	510	70	WSW	1983 (1994)	6a	3	3	14
Pelzmühletal (Pe)	510	252	SSW	1982 (1994)	7a	4	4	5
Schartenflue (Sf)	720	120	WSW-W	1983 (1994)	7b	5	1.5	6
Tüfleten (Tu)	440	78	SSW-W	1991	6c	4	2.5	9
Bärenfels (Ba)	480	68	SSW-SW	before 1987	6c	2	0	10
Tannenflue (Ta)	635	60	SSE-SSW	1992	6b	2	2.5	16
Wolfenried (Wo)	650	18	ESE-SE	before 1980	4	1	0.5	3
Schauenburg (Sb)	625	90	ESE-SE	1985 (1996)	6b	4	2	9
Chaltbrunnental (Cb)	490	35	SSW	1997	6b	2	0	6

[1] Following Andrey et al. (1997)
[2] French scale of difficulty grade
[3] Information obtained from local climbers: scale from 1, rarely to 5, very frequently
[4] Cumulative scores of three plots: scale from 0 (no structure in the rock surface) to 18 (highly structured rock surface); see methods

glass (3×). We surveyed plots only under dry weather conditions. We considered exclusively living snails resting attached to the rock surface. After species determination we released the snails at the spot where they were found. Gastropod identification and nomenclature follows Kerney et al. (1983). We used a compass to assess the exposure of the cliff face (in degrees from north) at the study sites. The elevation of the study sites was extracted from topographical maps. Information on the year of first ascent, year of reconstruction and difficulty grade for climbing (French scale) of the routes was found in Andrey et al. (1997). Estimates of the frequency of climbing on the routes examined were obtained from local climbers (scale from 1, rarely to 5, very frequently). The ground vegetation on the talus of cliffs is often reduced or completely vanished at the base of frequently climbed routes. As a further estimate of climbing frequency we measured the width of bare ground perpendicular to the focal climbing route or control area. The width of bare ground at the base of the rock area examined was positively correlated with the climbing frequency estimated by climbers (Spearman rank correlation, $r_s = 0.85$, $N = 20$, $P = 0.0002$).

To assess the complexity of the rock surface we determined the number of fissures (narrow linear crevices or cracks extending into the rock surface), the number of ledges (any features extending out horizontally from the rock surface), and pockets (solution pockets consisting of circular or ovoid features extending into the rock surface) in each of the three 50 cm × 50 cm plots (see gastropod survey). To express rock surface complexity we used a semi-quantitative scale of cumulative scores assessed in each plot. The scores considered fissures: (0) no fissures present, (1) total fissure length = 30 cm, (2) total fissure length > 30 cm; ledges: (0) no ledges present, (1) total ledge length = 30 cm, (2) total ledge length > 30 cm, and pockets: (0) no pockets present, (1) total pocket diameter = 10 cm, (2) total pocket diameter > 10 cm. Thus, plots received scores ranging from 0 (no structure in the rock surface) to 6 (highly structured rock surface). To characterize the rock surface of the focal climbing route (or control area) we added the scores of the three plots, resulting in total scores ranging from 0 to 18. Our measure of rock surface complexity relates only to the lower part of the cliff (height 0-2 m), namely to the area in which the lichens, bryophytes and gastropods were examined. In contrast, the difficulty grade for climbing relates to the entire climbing route (length 12-30 m). The climbed and control areas examined did not differ in the complexity of the rock surface (paired sign test, $P = 0.73$). Furthermore, they did not differ in exposure ($t_9 = 0.33$, $P = 0.75$).

Statistical analyses

Means ± 1 SE are given unless stated otherwise. We applied paired t-tests to examine whether species richness, species density and cover of lichens were affected by sport climbing (climbed vs. unclimbed areas in all 10 cliffs). Data which did not fit normal distributions were $\log_{10}$- or arcsin-transformed. In previous analyses we tested whether the position of the sampling plots had any influence on species richness and cover of lichens. However, in no case any significant effect of sampling plot position on species richness and cover of lichens was found (analyses not shown).

We assessed differences in species composition of the lichen and snail communities between climbed and unclimbed plots using the permutation procedure of PERMANOVA (Anderson 2001; McArdle & Anderson 2001). Analyses were based on Euclidean distances of log-transformed values of species cover (lichens) or abundance (snails) and were performed with 999 permutations. Within cliffs, post-hoc comparisons of climbed and unclimbed plots were based on 999 permutations. We also used detrended correspondence analysis (DCA) to examine differences in lichen and gastropod communities between climbed and unclimbed areas (Hill & Gauch 1980). DCA was performed separately for both groups of organisms, based on log-transformed data on species cover (lichens) and abundance (snails). Species found on only one cliff were excluded from the analysis. Species that were less frequent than the median frequency were down-weighted in proportion to their frequencies (Eilertsen et al. 1990). DCA was performed using CANOCO version 4.5 (ter Braak & Smilauer 2002). The dissimilarity in the lichen or gastropod community between climbed and unclimbed areas was represented by the pairwise distance between these two areas depicted in the ordination diagram of the DCA. We used Cartesian coordinates to calculate this distance for each cliff in the ordination diagram. We applied Spearman rank correlations to analyze associations between the extent of dissimilarity and climbing intensity and age of the climbing route. Spearman rank correlations were used to examine possible associations between species richness and cover/abundance of lichens and gastropods with climbing intensity, age of the climbing route, complexity of the rock surface and width of bare ground at the base of the rock area studied. We applied Pearson correlations to examine possible associations between lichen and gastropod communities (log-transformed values).

Results

Species richness and species density of lichens

A total of 38 calcicolous lichen species, three bryophytes (*Tortella tortuosa* (Hedw.) Limpr., *Homalothecium* sp., *Schistidium* sp.) and one alga (*Trentepohlia* sp.) were recorded in the 240 sampling plots (Table 2). Twenty lichen species (52.6%) were epilithic, 16 (42.1%) endolithic and two (5.3%) foliose (Table 2). Total lichen species richness of single cliffs ranged from 9 to 17 species. However, climbed and unclimbed cliff areas did not differ in total number of lichen species recorded (Table 3). Climbed and unclimbed areas did not differ in lichen species density (Table 3). Furthermore, species density of calcicolous lichens was not correlated with the complexity of the rock surface, the climbing intensity and the age of the climbing route (Spearman rank correlation, in all cases $P > 0.23$).

Frequency of occurrence

Of the 38 lichen species recorded, only 13 occurred with a frequency of > 5% (common species, i.e. they were found in more than 12 sampling plots; Table 2). Two species (*Caloplaca cirrochroa* and *Verrucaria* cf. *muralis*) were found on all ten cliffs and further three species (*Caloplaca flavescens*, *Catillaria lenticularis* and *Verrucaria baldensis*) on nine of the ten cliffs (Table 2). In contrast, seven lichen species were recorded only in a single plot. Considering all species, the frequency of lichen occurrence was slightly, but not significantly lower along climbing routes than in unclimbed areas (337 vs. 362 or 48.2% vs. 51.8%; binomial test, $P = 0.18$). However, the frequency of occurrence of epilithic lichens was lower along climbing routes than in unclimbed areas (183 vs. 225 or 44.9% vs. 55.1%; binomial test, $P = 0.021$). In contrast, the frequency of occurrence of endolithic lichens was slightly, but not significantly higher along climbing routes than in unclimbed areas (151 vs. 135 or 52.8% vs. 47.2%; binomial test, $P = 0.16$). We also recorded two foliose lichen species (*Collema fuscovirens* and *Leptogium plicatile*) in five (2.1%) of the 240 sampling plots (three plots along climbing routes and two plots in unclimbed areas) distributed over four cliffs (Table 2). Considering the 13 common species, the two epilithic lichens *Caloplaca chrysodeta* and *Verrucaria nigrescens* occurred less frequently along climbing routes than in unclimbed areas (binomial test, in both cases $P < 0.0001$), and a further epilithic species (*Caloplaca flavescens*) tended to occur less frequently along climbing routes ($P = 0.095$; Table 2). In contrast, the endolithic lichen *Caloplaca ochracea* occurred more frequently along climbing routes than in unclimbed areas ($P < 0.0001$), and the epilithic lichen *Dirina massiliensis* tended to occur more frequently along climbing routes ($P = 0.064$). The remaining eight common species did not differ in frequency of occurrence between climbed and unclimbed areas.

Table 2. Frequency of occurrence of calcicolous lichen taxa in climbing routes and control areas of ten cliffs in the northern Jura Mountains, Switzerland. Number of samplings plots with lichen species occurrence in climbed area/ corresponding figure in control area. Lichen type: D = endolithic, P = epilithic, F = foliose. For abbreviations of cliffs see Table 1.

Taxa	Lichen type	Cliff										Total climbed/ unclimbed
		Fa	Hc	Pe	Sf	Tu	Ba	Ta	Wo	Sb	Cb	
Acrocordia conoidea (Fr.) Körb.	D	2/12	0/2	0/8	-	-	-	0/1	8/7	-	10/0	20/30
Caloplaca chrysodeta (Räsänen) Dombr.	P	-	-	0/6	-	-	-	-	0/3	-	1/12	1/21
Caloplaca cirrochroa (Ach.) Th.Fr.	P	12/0	9/11	4/1	3/9	3/10	12/12	12/12	12/4	4/10	6/0	77/69
Caloplaca citrina (Hoffm.) Th.Fr. s. lat.	P	1/1	0/2	-	3/0	1/1	3/9	4/0	2/0	1/0	-	15/13
Caloplaca dolomiticola (Hue) Zahlbr.	P	-	-	-	-	-	-	1/0	-	-	-	1/0
Caloplaca flavescens (Huds.) J.R.Laundon	P	-	0/8	0/2	2/3	0/3	2/6	7/8	6/7	10/4	2/0	29/41
Caloplaca holocarpa (Ach.) A.E.Wade s. lat.	D	-	-	-	-	-	-	2/0	-	-	-	2/0
Caloplaca ochracea (Schaerer) Flagey	D	-	-	-	-	-	2/1	-	5/0	9/0	-	16/1
Caloplaca saxicola (Hoffm.) Nordin	P	2/0	-	-	7/0	-	-	-	-	-	-	9/0
Caloplaca xantholyta (Nyl.) Jatta	P	-	-	-	-	0/1	-	-	-	-	-	0/1
Catillaria chalybeia (Borrer) A.Massal.	D	-	-	-	2/0	-	-	-	0/1	-	-	2/1
Catillaria lenticularis (Ach.) Th.Fr.	D	0/1	10/8	12/0	0/1	0/7	1/0	1/0	2/1	5/3	-	31/21
Catillaria minuta (A.Massal.) Lettau	D	-	-	-	-	-	-	-	-	-	0/1	0/1
Clauzadea metzleri (Körb.) D.Hawksw.	D	0/1	-	-	0/1	-	-	-	-	-	1/0	1/2
Collema fuscovirens (With.) J.R.Laundon	F	-	0/2	1/0	-	-	-	-	-	-	1/0	2/2
Diplotomma alboatrum (Hoffm.) Flot.	P	-	-	-	1/0	-	-	-	-	-	-	1/0
Dirina massiliensis Durieu & Mont.	P	7/2	-	-	10/0	7/9	1/0	1/0	1/0	0/5	-	27/16
Gyalecta jenensis (Batsch) Zahlbr.	D	-	-	-	0/1	-	-	-	-	-	0/1	0/2
Lecania rabenhorstii (Hepp) Arnold	P	-	0/1	-	-	-	-	-	-	-	1/0	1/1
Lecanora crenulata Hook.	D	3/0	-	-	2/0	-	-	-	-	-	-	5/0
Lepraria cf. *eburnea* J.R.Laundon	P	-	-	-	-	-	-	-	-	-	0/5	0/5
Lepraria lobificans Nyl.	P	-	-	-	-	-	-	-	-	-	0/8	0/8

Taxa	Lichen type	Cliff										Total climbed/ unclimbed
		Fa	Hc	Pe	Sf	Tu	Ba	Ta	Wo	Sb	Cb	
Lepraria sp.	P	-	-	0/2	-	-	-	-	-	-	-	0/2
Leptogium plicatile (Ach.) Leight.	F	-	-	-	-	-	-	-	1/0	-	-	1/0
Mycobilimbia lurida (Ach.) Hafellner & Türk	P	-	-	-	-	-	-	-	-	1/0	-	1/0
Opegrapha cf. *dolomitica* (Arn.) Clauzade & C.Roux	D	0/2	-	2/0	0/2	-	-	-	-	-	-	2/4
Petractis hypoleuca (Ach.) Vezda	P	-	-	-	-	-	-	-	-	-	4/0	4/0
Protoblastenia rupestris (Scop.) J.Steiner	P	-	0/2	-	0/4	-	-	-	-	-	-	0/6
Pseudosagedia linearis (Leight.) Hafellner & Kalb	D	-	1/4	0/1	-	0/1	-	1/0	-	-	-	2/6
Rinodina dubyana (Hepp) J.Steiner	D	2/0	-	-	-	1/0	7/6	12/1	0/4	2/8	1/0	25/19
Staurothele caesia (Arnold) Arnold	D	-	0/2	-	-	-	-	-	-	-	3/0	3/2
Thelidium decipiens (Nyl.) Kremp.	D	0/3	-	-	-	-	-	0/1	-	1/0	-	1/4
Verrucaria baldensis A.Massal.	D	0/1	1/6	4/1	0/4	-	1/0	0/2	7/5	4/2	4/2	21/23
Verrucaria caerulea DC.	P	-	-	-	-	-	-	-	-	5/0	-	5/0
Verrucaria glaucina auct., non Ach.	P	-	0/1	-	-	-	-	-	-	-	-	0/1
Verrucaria macrostoma DC.	P	-	-	-	1/0	-	0/3	1/0	1/4	-	4/5	7/12
Verrucaria cf. *muralis* Ach.	D	0/1	7/4	2/0	0/3	0/2	1/1	1/2	1/3	8/0	0/3	20/19
Verrucaria nigrescens Pers.	P	0/3	0/5	-	1/12	-	1/3	0/5	-	3/1	-	5/29
Number of (climbed/unclimbed) plots with lichen species		29/27	28/58	25/21	32/40	12/34	31/41	43/32	46/39	53/33	38/37	337/362
Number of species (climbed/unclimbed)		7/10	5/14	6/7	10/10	4/8	10/8	11/8	11/10	12/7	12/8	30/29
Total number of species		14	14	11	17	9	11	15	14	13	17	38

Table 3. Species richness and species density of lichens and snails and lichen cover in climbed and unclimbed areas of ten cliffs in the northern Jura Mountains, Switzerland. Mean values ± 1 SE are given.

	Cliff area		Paired *t*-test	
	Climbed	Unclimbed	t_9	P
Lichen species richness	8.9 ± 1.0	9.1 ± 0.7	0.38	0.71
Lichen species density (# species per 100 cm^2)	2.8 ± 0.3	3.0 ± 0.3	0.52	0.62
Total lichen cover (%)	20.2 ± 3.1	17.0 ± 3.6	0.52	0.61
Cover of epilithic lichens (%)	9.1 ± 3.4	7.6 ± 1.7	0.42	0.69
Cover of endolithic lichens (%)	11.1 ± 2.7	9.4 ± 4.2	0.29	0.78
Snail species density (# species per 0.25 m^2)	1.2 ± 0.2	2.6 ± 0.2	2.80	0.021
Snail abundance (# individuals per 0.25 m^2)	7.8 ± 3.1	16.6 ± 7.0	1.02	0.34

Lichen cover

The overall cover of calcicolous lichens averaged 18.6% on the cliffs examined. On average, epilithic lichen species covered 8.3% of the rock surface, endolithic species 10.2%, and foliose species 0.03%. Climbed and unclimbed areas differed neither in epilithic nor in endolithic lichen cover (Table 3). Total lichen cover was not correlated with climbing intensity, age of the climbing route or complexity of the rock surface (in all cases $P > 0.49$). The cover of epilithic lichens, however, was positively correlated with the species richness of epilithic lichens ($r = 0.71$, $N = 20$, $P = 0.0003$) and the cover of endolithic lichens was positively correlated with the species richness of endolithic lichens ($r = 0.78$, $N = 20$, $P < 0.0001$). Furthermore, the cover of endolithic lichens was negatively correlated with the cover of epilithic lichens ($r = -0.61$, $N = 20$, $P < 0.0038$). However, total lichen species richness was not correlated with total lichen cover ($r = 0.37$, $N = 20$, $P = 0.11$).

Considering single species, *Acrocordia conoidea* was the most abundant species in unclimbed areas, covering an average of 5.3% of the rock surface, followed by *Dirina massiliensis* (1.9%), *Caloplaca chrysodeta* (1.7%), *Verrucaria baldensis* (1.5%), and *Caloplaca flavescens* (1.3%). Thus, in unclimbed areas, the five most abundant lichen species covered together 11.7% of the rock surface, whereas the remaining species covered only 5.3%. In climbed areas, *D. massiliensis* was the most abundant species (4.8%), followed by *A. conoidea* (2.7%), *Catillaria lenticularis* (2.4%), *C. chrysodeta* (2.0%), and *V. baldensis* (1.7%). In climbed areas, these five most abundant lichens covered together 13.7% of the rock surface examined, the remaining species 6.1%.

Differences in the lichen communities

PERMANOVA analysis revealed a significant effect of climbing on the lichen communities ($F_{9,220} = 8.14$, $P < 0.001$). Pair-wise post-hoc comparisons showed significant differences ($P < 0.05$) between climbed and unclimbed plots in eight out of the 10 cliffs. The cliffs whose lichen communities did not differ between climbed and unclimbed areas (Bärenfels and Wolfenried) have low climbing frequencies (Table 1).

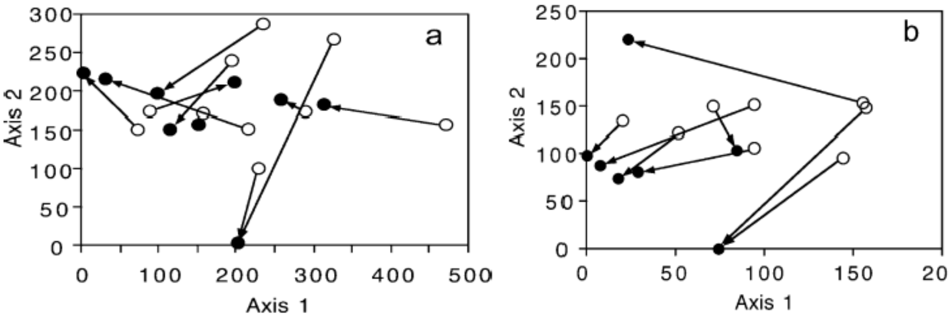

Fig. 1. Ordination diagrams based on detrended correspondence analysis of (a) calcicolous lichens and (b) rock-dwelling land snails in unclimbed (dots) and climbed (open circles) areas of 10 cliffs in the northern Swiss Jura Mountains, displaying the major variation in species composition. Arrows indicate the within-cliff dissimilarity between the communities of unclimbed and climbed areas. The extent of dissimilarity is proportional to the length of the arrow.

In the DCA ordination the first axis (Eigenvalue = 0.832) explained 17.3% of the variance in lichen species data (together with the second axis 26.9%). In the ordination diagram the distance between the two points representing the climbed and unclimbed area of a cliff indicates the dissimilarity between the two lichen communities (Fig. 1a). The lichen community dissimilarity between climbed and unclimbed areas increased with increasing climbing intensity on the focal route in the climbed area ($r_s = 0.73$, $N = 10$, $P = 0.0288$). However, the dissimilarity between the lichen communities of climbed and unclimbed areas was not correlated with the age of the climbing route ($r_s = 0.02$, $N = 10$, $P = 0.95$).

Bryophyte and alga occurrence and cover

Three bryophyte species were found in 11(4.6%) of the 240 sampling plots distributed over three cliffs (in 8 sampling plots at Hofstetter Chöpfli, 2 at Chaltbrunnental and 1 at Tannenflue). In these 100-cm^2-plots bryophyte cover ranged from 1 to 30 cm^2 (5.1 ± 2.6 cm^2, $N = 11$). Climbed and unclimbed areas did not differ in bryophyte cover (Mann-Whitney U-test, $P = 0.57$). Considering all sampling plots, bryophytes covered 0.23% of the rock surface examined. The low frequency of bryophyte occurrence did not allow any further data analyses. We also found one alga (*Trentepohlia* sp.) covering parts of the rock surface in 27(11.3%) of the 240 sampling plots. Twelve of these sampling plots occurred in climbed areas, 15 in control areas. Alga cover ranged from 1 to 50 cm^2 (5.7 ± 2.0 cm^2, $N = 27$). Considering all sampling plots, *Trentepohlia* sp. covered 0.65% of the rock surface examined.

Gastropod community

Eleven snail species were recorded attached to the cliff faces examined. Five of them (*Chondrina avenacea* Bruguière, *Abida secale* Drap., *Clausilia parvula* Férussac, *Neostyriaca corynodes* Held and *Pyramidula rupestris* Drap.) are specialized lichen feeders. Plots along climbing routes harboured fewer snail species than plots in unclimbed areas

(Table 3). Snail species richness was negatively correlated with the climbing intensity ($r_s = -0.67$, $N = 20$, $P = 0.0033$). However, snail species richness was neither correlated with the age of the climbing route nor with the rock surface complexity (in both cases $P > 0.42$). Most (93.4%) of the snail individuals recorded belonged to the five lichen-feeding species. Plots in climbed areas contained slightly fewer individuals than those in unclimbed areas (Table 3). However, this difference was statistically not significant. As for the lichen data, PERMANOVA analysis revealed a significant effect of climbing on the gastropod communities ($F_{9,40} = 6.59$, $P < 0.001$). Pair-wise post-hoc comparisons showed significant differences ($P < 0.05$) between climbed and unclimbed plots in five of 10 cliffs. Similarly, DCA ordination revealed that the snail community composition differed between climbed and unclimbed cliff areas (Fig. 1b). The two groups, however, showed a large overlap. The first axis (Eigenvalue = 0.338) explained 25.5% of the variance in snail species data (together with the second axis 45.6%). The extent of dissimilarity between the snail communities from climbed and unclimbed areas (indicated by arrows in Fig. 1b) was neither correlated with the climbing intensity on the focal route nor with the age of the climbing route (in both cases $P > 0.23$).

Correlations between lichens and gastropods

Lichen species richness was positively correlated with total snail abundance ($r = 0.46$, $N = 20$, $P = 0.0399$) but not with snail species richness ($r = 0.34$, $N = 20$, $P = 0.15$). Furthermore, we found no correlations between total lichen cover and either snail species richness ($r = 0.04$, $N = 20$, $P = 0.88$) nor snail abundance ($r = 0.03$, $N = 20$, $P = 0.92$). Considering different lichen groups, snail species richness was positively correlated with the cover of endolithic lichens ($r = 0.54$, $N = 20$, $P = 0.0135$), but not with epilithic lichen cover ($r = 0.19$, $N = 20$, $P = 0.42$).

Discussion

This study shows that frequent rock climbing can change the lichen community of limestone cliffs. Although there was no detectable difference in lichen cover between climbed and unclimbed plots, species density of epilithic lichens was lower along climbing routes than in unclimbed areas. The lichen community composition differed between climbed and unclimbed areas and the dissimilarity of the communities increased with climbing intensity. These results confirm findings of earlier studies on other cliffs. McMillan & Larson (2002) examined cliffs of the Niagara escarpment and found no differences in lichen cover between climbed and unclimbed plots, but there were fewer lichen species in climbed plots than in unclimbed ones. In terms of lichen community composition, the ordination diagram of the canonical correspondence analysis showed a separation of climbed from unclimbed plots (McMillan & Larson 2002). Farris (1998) found lichen cover and frequency to decrease with climbing activity at some sites but to be unaffected or even to increase at other sites on cliffs in Minnesota. Nuzzo (1996) examined dolomitic outcrops above the Mississippi River in Illinois and found that lichen cover decreased significantly in climbed areas. Compared to vascular plants, climbing-related damage to lichens appears to be more subtle and differs among lichen type.

The community structure and spatial distribution of lichens, bryophytes and vascular plants are influenced by the slope, exposure and microtopography of a cliff (e.g. Farris 1998; Larson et al. 2000). We used a sampling design with pairs of climbed and unclimbed (control) areas that did not differ in slope, exposure and complexity of the rock surface and examined replicates of this set-up on 10 different cliffs. The lichen communities vary among cliffs. However, it is rather unlikely that differences in species richness and cover of lichens or abundance of snails reflect differences in microsite characteristic between climbed and unclimbed areas within a cliff.

The sensitivity of an organism to climbing disturbance may be related to its growth form. Among lichens, we expected foliose lichens to be most sensitive to disturbance, followed by epilithic lichens and finally endolithic lichens being most resistant to disturbance. A previous work has demonstrated that the mycobiont layer of endolithic lichen species as found in this study reaches a depth of 0.25-3 mm in the rock of the vertical cliffs, while their photobiont layer occurs at a depth of 0.15-0.25 mm (Pinna et al. 1998). Therefore, endolithic lichen species should be better protected against trampling and abrasion than foliose and epilithic species. Accordingly, we found that species density of epilithic lichens was reduced along climbing routes and the two epilithic lichens *Caloplaca chrysodeta* and *Verrucaria nigrescens* occurred less frequently in climbed areas than in unclimbed ones. *Acrocordia conoidea*, an endolithic lichen, was the most abundant species in unclimbed areas (5.3% cover) in our study. In climbed areas *A. conoidea* covered only 2.7%. Interestingly, this species showed the same pattern in unclimbed plots on cliffs of the Niagara escarpment (McMillan & Larson 2002). Furthermore, McMillan & Larson (2002) recorded other epilithic species of the genus *Lepraria* most often in unclimbed plots. We also found *Lepraria* spp. exclusively in unclimbed areas. These coinciding results from studies in two continents confirm the species-specific sensitivity of lichens to disturbance. Among colonizing species, some were only found along climbing routes (e.g. *Caloplaca holocarpa*, *C. saxicola* and *Lecanora crenulata*), while *C. citrina* was also recorded on unclimbed surfaces. It is possible that intensive rock climbing causes exposed areas, where colonisers can easily establish.

Our study also demonstrates a relatively high species richness of calcicolous lichens on vertical cliffs of the Jura Mountains. Twenty-six of the 38 species found in the present study were recorded for the first time in the canton Solothurn and three species for the first time in the canton Basel-Landschaft (cf. Clerc 2004). This reflects the different stage of knowledge on lichen distribution in neighbouring geographical regions in Switzerland. Unfortunately, the Red List of Switzerland considers only epiphytic and terricolous lichens (Scheidegger & Clerc 2002). The proportion of threatened epiphytic species was 37% and that of terricolous 24%. Most probably the proportion of threatened calcicolous lichen species is within this range. It also showed that climbed areas harboured fewer snail species and individuals than unclimbed areas. McMillan et al. (2003) examined living snails and empty shells in soil samples from climbed and unclimbed sections of cliffs at the cliff edge, cliff face and talus of the Niagara escarpment. The authors did not distinguish between different groups of snails, but found that total snail species richness and density were lower along climbing routes than in unclimbed areas, and community composition differed between climbed and unclimbed samples.

Limestone cliffs provide a variety of different microhabitats for snails, including xerothermic vegetation at the cliff edge and on ledges, accumulated rock and debris partly covered with vascular plants, bryophytes and decaying leaf litter at the talus, fissures, solution caves and shallow crevice caves in the rock face, and unstructured rock surface (Larson et al. 2000). Most snail species exhibit particular habitat requirements and thus occur only in certain microhabitats on rocky cliffs. Among them, a highly specialized group of snails (i.e., rock-dwelling species) exists exclusively on rock faces. These snails are very resistant to drought and their specialized radula enable them to graze epi- and endolithic lichens and cyanobacteria growing on rock faces (Baur et al. 2000; Fröberg et al. 2001, 2006). The snails are active during periods of high air humidity, otherwise they rest attached to the exposed rock surface or in small fissures (Baur & Baur 1991). When feeding on lichens, the snails sequester lichen compounds, which in turn may be utilized for their own chemical defense against predators such as birds (Hesbacher et al. 1995). These small-sized animals (adult shell width or height ranging from 2 to 10 mm) show a limited mobility. For example, displacements per year ranged from 1.4 to 2.4 m in *Chondrina avenacea* living on vertical cliffs (Baur & Baur 1994). Attached to the rock surface, these snails are exposed to the risk of being crushed by climbers, which may result in a reduced snail density in climbed areas. Such reduced snail populations could indirectly decrease grazing pressure on lichens growing on cliff faces. A reduced grazing pressure, in turn, could change competitive interactions among lichen species resulting in altered species abundances. The hypothesis that rock climbing indirectly affects the lichen community through a reduction of the density of lichen-feeding snails should be experimentally tested.

Management implications

Our study showed that calcicolous lichen communities can be changed by intensive climbing activities. So far vascular plants have been frequently used as an indicator group for assessing the impact of recreational activities on natural habitats, including rock cliffs (e.g., Herter 1993; Farris 1998; Larson et al. 2000; Rusterholz et al. 2004; Müller et al. 2004). Our findings indicate that impact assessments in rocky habitats should be complemented by other groups of organisms. Lichens and snails coexist on vertical rock faces with simple surface structure, including places where no or very few vascular plants can be found. Furthermore, the growth rate of lichens is generally low, especially in endolithic species. Our study also indicated that some lichen and snail species are disturbance-sensitive. Therefore, future management plans and actions ought to consider these groups of organisms as well. The prohibition of sport climbing on cliffs or cliff areas with a high number of specialized plant or animal species and the establishment of climbing-free protection zones in popular areas are the most effective and adequate measures. However, any management plan should include a comprehensive information campaign to show the potential impact of intensive sport climbing on the specialized flora and fauna and to increase the compliance of these measures by the climbers.

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Chapter 4

Effects of forestry practices on relict plant species on limestone cliffs in the northern Swiss Jura mountains

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Effects of forestry practices on relict plant species on limestone cliffs in the northern Swiss Jura mountains

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Abstract

Limestone cliffs in the forests of the Swiss Jura mountains harbour a highly diverse plant community including glacial relict species. This unique cliff vegetation is increasingly threatened by overgrowing forest and recreational activities (sport climbing and picnicking). Management objectives of the surrounding forest focus on the conservation of the cliff vegetation. The most suitable forestry practice to achieve this goal is, however, still unknown. We examined the effects of two different forestry practices (clear-cutting and shelter tree cutting) on the species richness and abundance of vascular plants on the face, at the base and on the talus of three cliffs. As controls we considered areas with no management in the past 80 years (forest reserves) at the same cliffs. Plant species density (number of species/m^2) and vegetation cover were higher in shelter cut areas than in the forest reserves both on the talus and at the cliff base. Clear-cut areas had a higher vegetation cover than forest reserves on the talus. Shelter cut areas showed a larger proportion of plants with high light demand and a higher mean light score of plants than clear-cut areas and forest reserves. We conclude that selective cutting of trees (shelter tree cutting) is the best forestry practice for the conservation of a high biodiversity and a multitude of relict plant species on limestone cliffs in the Jura mountains. However, this forestry practice is time-consuming and thus expensive. To preserve the specialised cliff flora, sponsorship for this forestry practice is needed from governmental and non-governmental organisations.

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Keywords: Cliff ecology; Light-conditions; Beech-forests; Plant conservation

1. Introduction

Maintenance of biodiversity has been recognized as an important component of sustainable development (UNEP, 1992; O'Riordan, 2002). The protection of native forests is a major means of biodiversity conservation (UN, 1992; Fearnside, 2005). In most forests, however, biodiversity is not equally distributed over their entire landscape. For example, in the forests of the northern Jura mountains, Switzerland, isolated limestone cliffs harbour unique assemblages of plants and invertebrates and are therefore considered as local biodiversity hotspots (Zoller, 1989).

The vegetation of limestone cliffs in the Jura mountains consists of plants of arctic-alpine, continental and Mediterranean origin (Wassmer, 1998). For several alpine and arctic plant species, these cliffs serve as peripheral refugia which formed a periglacial steppe together with continental plants during the Pleistocene glacier advancements from the Alps and the Black Forest (Walter, 1986). During postglacial warm periods, xerothermic oak forest species (*Quercetalia pubescenti-petraeae*) colonised the south-exposed slopes of the Jura Mountains (Ellenberg, 1986). Due to the establishment of beech-forests under the recent, temperate climate conditions, both the arctic-alpine as well as the xerothermic plant species were displaced towards the wood-free cliff sites.

Human activities have influenced the forests surrounding the limestone cliffs of northern Switzerland for many centuries. During the middle ages, the steep slopes at the cliff bases were predominantly managed as coppice forests for the production of firewood, charcoal, bedding and raw materials for craftsmen and as temporal pasture, mainly for goats (Burnand and Hasspacher, 1999). These forms of forest use disappeared gradually in the past 120 years (Suter, 1971; Blöchlinger, 1995; Stuber and Bürgi, 2002). After 1950, the

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demand for firewood decreased dramatically. As a result, the forests became older and denser (Schiess and Schiess-Bühler, 1997; Wohlgemuth et al., 2002). The enhanced shadowing of the increasingly denser forests reduces the quality and size of the habitats for light-demanding species. This is particularly true for relict plants on limestone cliffs and at their base (Wassmer, 1998). In the past decade, disturbances by recreational activities such as sport climbing, hiking and mountain biking increasingly threatened the sensitive cliff vegetation (Müller et al., 2004; Rusterholz et al., 2004).

Nowadays, the cliff bases are extensively used as timber forests, usually under a shelterwood system (Hendry, 1998). To preserve the species-rich flora and fauna in the northern Swiss Jura mountains, two different management strategies are pursued: the establishment of forest reserves with no further exploitation or specific silvicultural interventions to promote light-demanding species including relict plants. The latter selectively reduces the shadowing by dominant trees at rocky sites. However, this forestry practice is very time-consuming and expensive because of the topography and inaccessibility of the cliffs. Therefore, knowledge about the physical and biological processes after applying different forest practices is highly relevant for an optimal use of the available funds.

In the present study, we examined the effects of two different forestry practices and of a non-forestry practice as control on the composition of the ground vegetation on the face, at the base and on the talus of limestone cliffs in the northern Swiss Jura mountains. We also assessed the temperature conditions (and therefore indirectly the light regime) in areas with different forestry practices and in unexploited control areas both on the talus and face of cliffs. Our findings provide basic information to optimize forestry practices with respect to the preservation of relict and endangered plant species.

2. Materials and methods

2.1. Study sites and experimental design

The present study was carried out at three limestone cliffs (Ingelstein, Titterten and Santel) in the northern Swiss Jura mountains from April to August 2002 and from April to August 2003 (Fig. 1; Table 1). The cliffs mainly consist of Jurassic coral chalk (Bitterli-Brunner, 1987) and are located at altitudes ranging from 500 to 800 m a.s.l. The cliff bases investigated consist of rendzic leptosol and are covered by different stands of deciduous forests belonging to Fagetum and Tilietum associations (Burnand and Hasspacher, 1999). On the talus and the base of each of the selected cliffs, three differently managed forest areas of 30 m × 60–100 m could be distinguished: (1) recent clear-cutting (in the winter 2001/2002), (2) shelter tree cutting approximately 10 years ago (with a tree cover of approximately 50%), and (3) unexploited forest (forest reserve, no management in the past 80 years). For simplicity, these forestry practices are hereafter referred to as recent clear-cutting (RCC), shelter tree cutting (STC), and unexploited forest (UF = control).

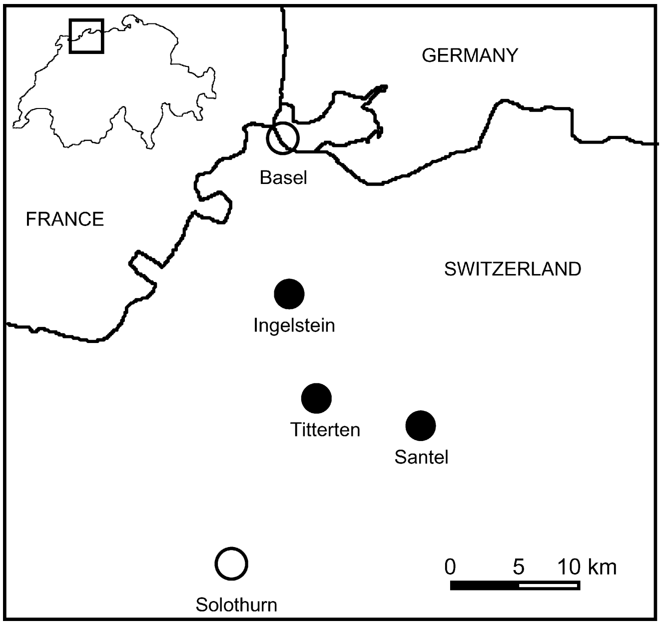

Fig. 1. Location of the three limestone cliffs examined in the northern Jura mountains, Switzerland.

To examine species richness and abundance of plants of the ground vegetation, we established six permanent plots of 1 m^2 at distances of 10 m each on the lower part of the cliff face (at a height of 1–2 m from the cliff base), at the cliff base and on the talus (10 m away from the cliff base). Thus, 54 sampling plots (3 cliffs × 3 forestry practices × 6 plots) were examined each on the cliff face, at the cliff base and on the talus. The investigation plots were placed in the center of the areas of different forestry practices, so that the distance from the edge could be maximized and edge effects could be avoided.

2.2. Field survey

In each sampling plot, the number of individuals and the cover of each plant species were recorded on six occasions

Table 1
Description of the cliffs investigated in the northern Swiss Jura mountains

Cliff	Elevation cliff base (m a.s.l.)	Exposure	Maximum height (m)	Vegetation of cliff base (Beratungsgemeinschaft für Umweltfragen, 1983)
Ingelstein	500–550	SSE	30	*Tilio-Fagetum*, *Aceri-Fagetum*, *Dentario-Fagetum*
Santel	670–800	SW	30	*Dentario-Fagetum*
Titterten	500–650	WSW–WNW	70	*Tilio-Fagetum*

(three times between April and September 2002 and three times between April and September 2003). We also estimated the percentage of total plant cover and that of rock cover in each sampling plot using the Domin–Krijina scale (Mueller-Dombois and Ellenberg, 1974). The exposure of each plot was measured using a compass, and the extent of shadowing of the rock or talus surface was estimated using a scale ranging from 1, no shadow to 10, total shadowing.

To relate plant communities to abiotic environmental factors, we used the indicator scores of Ellenberg et al. (1991) for light (scale ranging from 1, species of deep shade, to 9, plants of full sun) and temperature (scale ranging from 1, indicator for cold conditions found only in alpine zones, to 9, thermophilous species). Furthermore, we assigned the plant species recorded to different ecological groups according to the Red list of Switzerland (Moser et al., 2002).

In the two areas with different forestry practices and in the control area at each cliff, we simultaneously measured air temperature 2 cm above ground on the cliff face and on the talus during each three days in spring, summer, autumn and winter 2002. Two temperature loggers (Tiny Talks, Gemini Data Loggers Inc., Chichester, UK) were placed in two neighbouring sampling plots on the talus and in one sampling plot on the cliff face in areas with the two forestry practices and in the unexploited forest at each cliff (totally 27 loggers). Data loggers were programmed to measure temperature every 5 min and discrete values were merged to average values per hour. To cover the entire area of an investigation site and to minimize variation due to spatial heterogeneity, we transferred the two data loggers to the remaining sampling plots after 24 and 48 h.

2.3. Statistical analyses

Statistical analyses are based on mean values of two years, because data collected in both years did not differ from each other (repeated measures ANOVA $P > 0.05$ for the factor year; data not shown). We used five-way ANCOVAs (general linear model, procedure glm, SAS Version 8.02) to examine the effects of forestry practice, cliff (nested in factor forestry practice), plot (nested in factor cliff), exposure and shadowing (as a covariate) on plant cover and species density (number of plant species/m^2). Data were $\log(x + 1)$-transformed, those on species density were additionally arcsin-transformed. As exposure and shadowing neither influence plant cover nor species density (see Section 3), we dropped these factors and performed a three-way ANOVA (factors: forestry practice, cliff and plot). We evaluated differences between forest practices using Tukey's post hoc test.

We compared mean indicator scores pairwise in areas with different forestry practices using unpaired *t*-tests (if data were normally distributed) and with Mann–Whitney *U*-tests (if data were not normally distributed). We compared the abundance weighted proportions of plants of different ecological groups with χ^2-tests using JMP Version 3.2.2.

3. Results

A list of the plant species recorded is given in Appendix A.

The results of the ANOVAs showed that the different forestry practices had a significant effect on species density on the cliff face, at the cliff base and on the talus (Table 2). Furthermore, the different forestry practices had a significant effect on vegetation cover both at the cliff base and on the talus (Table 2). They also tended to affect species density on the cliff face ($P = 0.07$). The factor cliff had a significant effect on species density and vegetation cover at the cliff base and on species density on the talus. However, the location of the plots within cliff sector had no effect. The five-way ANCOVA revealed that shadowing and exposure had no significant effects (in all cases $P > 0.05$), except that shadowing tended to influence species density at the cliff base ($F_{1,53} = 3.36$, $P = 0.08$) and vegetation cover on the cliff face ($F_{1,53} = 3.98$, $P = 0.06$; data not shown).

Pairwise comparisons of forestry practices indicate that on the cliff face, plant species density (number of species/m^2) did not differ among the forestry practices considered (Fig. 2a). At

Table 2

Effects of forestry practice, cliff and plot location on species density (number of species/m^2) and vegetation cover on the face, at the base and on the talus of cliffs

	Cliff face		Cliff base		Talus	
	Species density	Vegetation cover	Species density	Vegetation cover	Species density	Vegetation cover
Forestry practice						
d.f.	2	2	2	2	2	2
F	2.88	2.15	5.33	7.51	4.06	9.4
P	0.07	0.13	0.0104	0.0023	0.0276	0.0007
Cliff (forestry practice)						
d.f.	4	4	4	4	4	4
F	0.96	1.18	12.99	18.77	3.16	0.77
P	0.44	0.34	<0.0001	<0.0001	0.0278	0.56
Plot (cliff)						
d.f.	15	15	15	15	15	15
F	0.77	0.35	0.95	1.02	1.21	0.44
P	0.70	0.98	0.52	0.47	0.32	0.95

The results of three-way ANOVAs are presented.

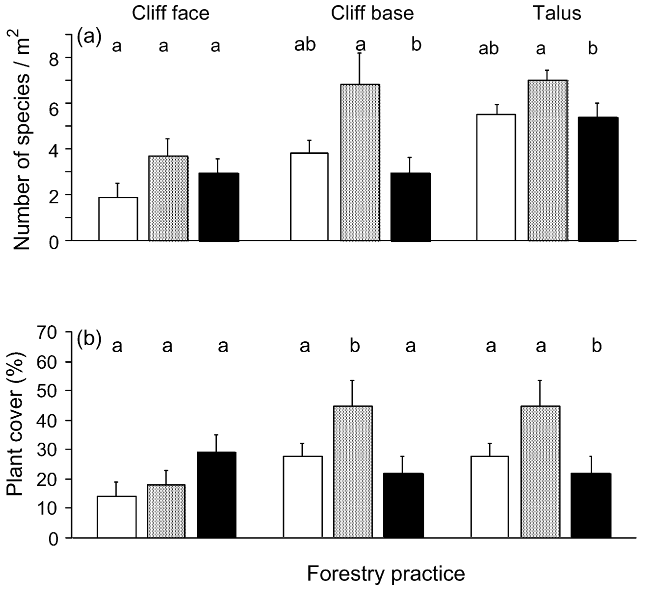

Fig. 2. Plant species density (number of species/m^2) (a) and vegetation cover (b) in areas with different forestry practices (□, recent clear-cutting; ▨, shelter tree cutting; ■, unexploited forest) on the face, at the base and on the talus of cliffs. Means ± 1S.E. are shown. Different letters indicate significant differences between forestry practices (Tukey's post hoc test; $P < 0.05$).

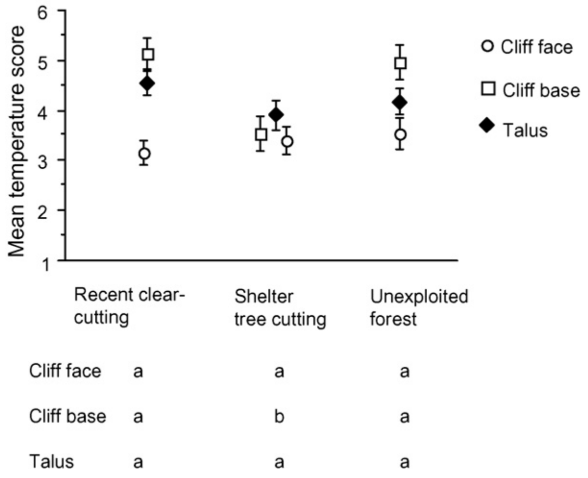

Fig. 3. Temperature scores (means ± 1S.E.) in areas with different forestry practices on the face, at the base and on the talus of limestone cliffs. Different letters indicate significant differences between forestry practices (Mann–Whitney U-test; $P < 0.05$).

the cliff base and on the talus, however, species density was lower in the unexploited forest than in areas with shelter cutting (Fig. 2a). Similarly, plant cover on the cliff face did not differ in areas with different forestry practices (Fig. 2b). At the cliff base, plant cover was higher in clear-cut areas than in areas with shelter-cutting and in unexploited forest (Fig. 2b). On the talus, plant cover was higher in areas with shelter cutting and clear-cutting than in unexploited forest (Fig. 2b).

At the cliff base, the mean temperature score of plants was lower in shelter-cut areas than in areas with other forestry practices (Fig. 3). On the talus, mean temperature scores tended to be lower in shelter-cut areas than in clear-cut areas, but this difference was not significant (Mann–Whitney U-test, $n = 36$, $P = 0.088$). The mean light score of plants on the talus was lowest in the clear-cut areas and highest in the shelter-cut areas (Fig. 4). On the cliff face, the mean light score of plants was higher in shelter cut than in unexploited areas.

The proportions of plants belonging to different ecological groups differed with respect to forest practice both on the cliff face ($\chi^2 = 57.6$, d.f. = 8, $P < 0.0001$, Fig. 5a) and at the cliff base ($\chi^2 = 24.8$, d.f. = 12, $P = 0.016$, Fig. 5b), more strongly on the cliff face. After clear-cutting, the proportion of plants without any association to rocky habitats (wood plants) decreased both on the cliff face and at the cliff base in relation to the unexploited forest (control area). On the cliff face, mountain plants tended to increase in abundance. At the cliff base, plants of nutrient-poor grassland mainly benefited from shelter cutting. On the talus, wood plants were dominant in the three differently managed areas. More than 75% of the plants found had no association to rocky habitats.

Large diurnal air temperature amplitudes were recorded both on the cliff face and the talus in spring and summer (Fig. 6). Pairwise comparisons of temperature ranges (difference between daily minimum and maximum temperature per logger) showed significant differences between clear-cut areas and unexploited forest on the talus in spring (unpaired t-test: $t = 3.75$, d.f. = 10, $P = 0.004$) and on the cliff face in summer (unpaired t-test: $t = 7.32$, d.f. = 4, $P = 0.002$). Due to cloudy weather conditions, daily temperature amplitudes were less pronounced in autumn and winter (data not shown) than in spring and summer.

4. Discussion

Our results confirm a high impact of forestry practice on the relict plant vegetation of the investigated cliffs in the northern Jura mountains. In this mountain area, the relict species include mountain plants, pioneer plants at low elevation and plants of nutrient-poor grassland (Wassmer, 1998). Plants of these three

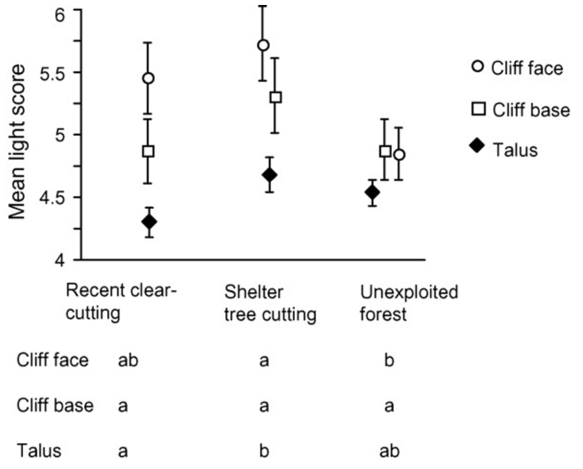

Fig. 4. Light scores (means ± 1S.E.) in areas with different forestry practices on the face, at the base and on the talus of limestone cliffs. Different letters indicate significant differences between forestry practices (Mann–Whitney U-test; $P < 0.05$).

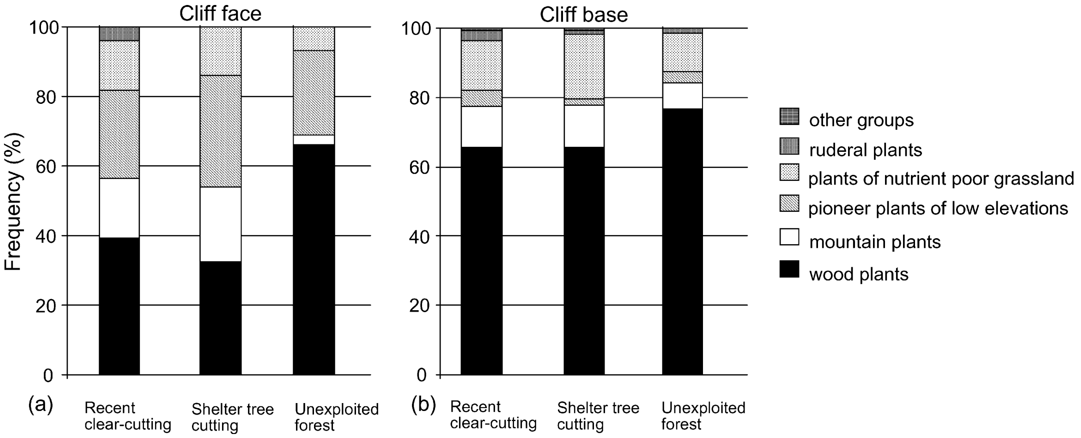

Fig. 5. Percentage of plant species belonging to different ecological groups (weighted by their abundance) on the cliff face (a) and at the cliff base (b). Data from three cliffs were pooled.

categories increased in abundance both after shelter-cutting and clear-cutting (Fig. 5). The maximum species density found in areas managed by shelter cut is consistent with the intermediate disturbance hypothesis (Grime, 1973; Connell, 1978) and supports the assumption that the severity of ecological change decreases from clear-cutting to shelter wood (Marshall, 2000). Atauri et al. (2005) found a similar peak in biodiversity at intermediate disturbance levels in deciduous forests in northern Spain. Disturbance provides the driving force for forest dynamics and regeneration through structural change, the initiation of secondary succession and creation of habitat diversity (Quine et al., 1999). Disturbances of intermediate severity are a major diversifying force in forest ecosystems (Petraitis et al., 1989), and random periodic disturbances are known to maintain high species richness and productivity and limit competitive exclusion (Huston, 1979). Apparently, biodiversity in temperate forests responds to disturbances in a similar way as in other ecosystems, e.g. grasslands (Gibson et al., 1978), pasture-woodland (Kirby et al., 1995) and coral reefs (Connell, 1978).

Two findings of our study indicate that the demand of light is a key factor determining the plant composition on limestone cliff faces and their talus. First, light indicator scores at the cliff face were higher in shelter cut and clear-cut areas than in unexploited forests. Second, plants with high light demand, e.g. the mountainous plants on the cliff face, were more abundant in shelter cut and clear-cut areas than in unexploited forests. Thus, the lack of forest management leads to overgrowing forests, which in turn decreases the abundance of cliff plants with a high light demand. In some cases, this can result in the local extinction of threatened or rare species like *Dianthus gratianopolitanus*, *Daphne cneorum* or *Kernera saxatilis* (Wassmer, 1998; Käsermann, 1999). Similarly, overgrowing forest reduces the number and quality of basking sites for the

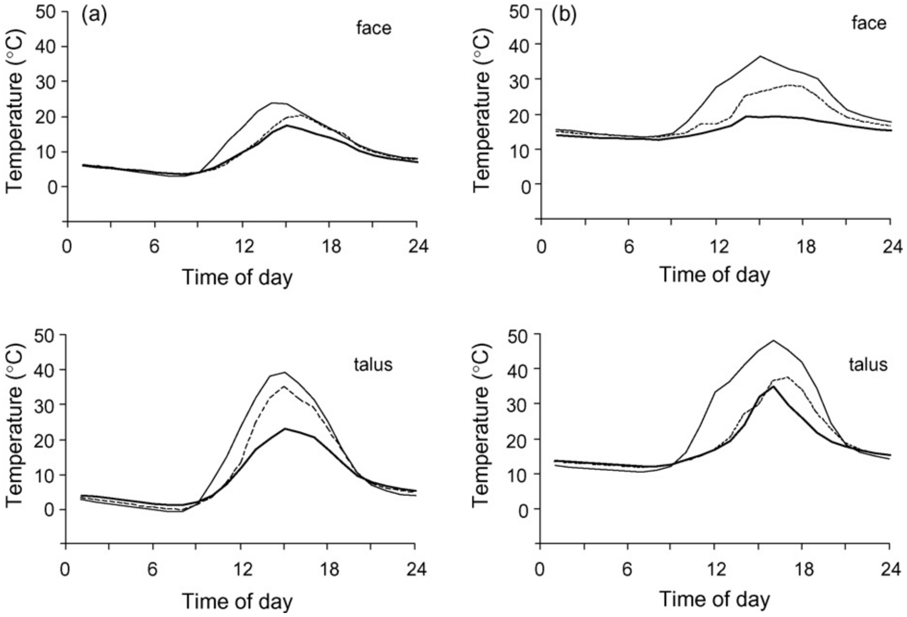

Fig. 6. Daily cycle of air temperature measured 2 cm above ground (a) in spring, and (b) in summer 2002 on the cliff face (top) and on the talus (bottom). Mean values of three days per season are indicated. Solid line: recent clear-cut, dotted line: shelter tree cutting, bold line: unexploited forest.

Asp viper (*Vipera aspis*), which results in the local extinction of this threatened snake in the northern Swiss Jura mountains (Jäggi and Baur, 1999).

The temperature patterns recorded illustrate the special conditions on vertical cliff faces and both the direct and indirect influences of the vegetation on the microclimatic conditions on the talus and at the cliff base. The talus (with an inclination of approximately 45°) receives a higher irradiance than a vertical cliff face of the same aspect (Garnier and Ohmura, 1968; Larson et al., 2000). Therefore, the air temperature measured on the talus shows higher diurnal and seasonal amplitudes than that on cliff faces. The effects of radiation on the microclimate are amplified by the high albedo of the bright limestone (Rejmanek, 1971). In the unexploited parts of the forests, the shadowing by growing trees diminishes the extreme radiation and temperature amplitude on cliff faces in summer. This may lead to an increase in the abundance of non-specialised, woody plants. Thus, selective cutting of shadowing trees is essential to reverse the proceeding change of the plant community from the specialised cliff flora (with high light-demands) into a common forest community (with low light-demands). Several studies documented a decrease in species richness after the abandonment of any forestry practices in Northern Switzerland and confirmed the importance of light for the preservation of specialized plant species in these forests (Keller and Hartmann, 1986; Egloff, 1991; Schiess and Schiess-Bühler, 1997).

To maintain the typical species richness at the base of limestone cliffs in the northern Swiss Jura mountains, forestry practices should mimic an environment of intermediate disturbance. This contrasts the general goal of nature conservation-oriented silviculture in Central Europe, which is to guide the forest stand development towards the potential, original forest cover (Parviainen, 1999). In Switzerland, close to nature silviculture in that sense is practised by removing single trees (“Plentering”) or small groups of trees (“Femelschlag”). With this forestry practice, a constant timber wood state has been reached. As Schütz (1999) supposed, single-tree selection is not the appropriate way to ensure regeneration of light-demanding species. The forestry practice applied in our shelterwood treatment was a much more intensive, selective thinning. This thinning results in relatively large plots with good light conditions and promotes the rare, relict plant species with high light demands. Our results indicate that this forestry practice is the most favourable for the conservation of a high biodiversity and a multitude of relict plant species in the cliff areas of the Jura mountains. This finding is consistent with other studies investigating forests under selective thinning (Götmark et al., 2005). However, this forestry practice is not profitable, because it is extremely time-consuming and delivers only a marginal timber harvest due to the unfavourable edaphic conditions. Therefore, sponsorship for special action plans is needed from governmental and non-governmental organisations to preserve the specialised cliff flora.

Acknowledgements

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Appendix A

List of species recorded on the three cliffs examined. Figures indicate the number of plots in which a particular plant species was recorded (maximum = 6). RCC: recent clear-cutting; STC: shelter tree cutting; UF: unexploited forest. Nomenclature of plant species following Lauber and Wagner (1996). EG: ecological group according to Moser et al. (2002): 1 = wood plants; 2 = mountain plants; 3 = pioneer plants of low elevation; 4 = plants of nutrient-poor grassland; 5 = ruderal plants; 6 = other groups.

Cliff (forestry practice)	EG	Ingelstein RCC	Ingelstein STC	Ingelstein UF	Santel RCC	Santel STC	Santel UF	Titterten RCC	Titterten STC	Titterten UF
Talus										
Abies alba	1						1			
Acer campestre	1				1					1
Acer pseudoplatanus	1		4	1	5	5	1	2	4	3
Arabis alpina	2							1	1	
Arabis turrita	1					1				
Asarum europaeum	1		4					6	1	3
Brachypodium sylvaticum	1				1	1		1	2	
Bupleurum falcatum	4							1		
Calystegia sepium	5			1						
Campanula trachelium	1						1			
Campanula rotundifolia	4		1					2		
Cardamine heptaphylla	1	5	6	4	2	3				
Carex alba	1							3		
Carex digitata	1					1				
Carex ornithopoda	1						1		3	
Carex sylvatica	1							2		

Appendix A (*Continued*)

Cliff (forestry practice)	EG	Ingelstein RCC	Ingelstein STC	Ingelstein UF	Santel RCC	Santel STC	Santel UF	Titterten RCC	Titterten STC	Titterten UF
Clematis vitalba	1	1								
Coronilla coronata	1								1	
Convallaria majalis	1		1	2			1			
Cornus sanguinea	1								1	
Corylus avellana	1		1				1	1		
Dryopteris filix-mas	1			1					1	
Euonymus europaeus	1						1			
Eupatorium cannabinum	6	1	1		3	1				
Fagus sylvatica	1		2	1	5	1	5	2	4	1
Fragaria vesca	1					1				
Galium mollugo aggregate	1				3			1		
Galium odoratum	1			2	2	1	1		2	
Galium pumilum	4	4		2	1	6	3		1	
Geranium robertianum	5	4	2	2					1	
Hedera helix	1	3	5	4	2			3	3	2
Helleborus foetidus	1		3	2				2		1
Hieracium humile	3			1			1		1	
Hieracium murorum	1					1	4			
Hippocrepis emerus	1				1	2	1			
Hypericum montanum	1					1		1		
Ilex aquifolium	1					1				
Lamium galeobdolon	1	6	4	1				5	4	1
Lamium maculatum	5						2			
Laserpitium latifolium	2						1			
Laserpitium siler	2									
Lathyrus vernus	1		5	3		1				
Lonicera xylosteum	1					1			1	
Melica nutans	1		1	1		1	2	1		
Melitis melissophyllum	1		2				2			
Mercurialis perennis	1	6	6	5	5	3	2	6	5	4
Mycelis muralis	1		1	2	3		1	1	1	
Origanum vulgare	4		1			1				
Phyteuma spicatum	1		1				1			
Picea abies	1			1			1			
Polygonatum odoratum	4		1				1			
Prenanthes purpurea	1					1	4			
Quercus petrea	1			2						
Rhamnus alpinus	2					1	4			
Rubus idaeus	1				4	6				
Rubus montanum	1				1	1				
Sambucus racemosa	1					4				
Sesleria caerulea	2					1		1	1	
Sorbus aria	1									1
Sorbus aucuparia	1			3				2	6	5
Taraxacum officinale	6	1								
Taxus baccata	1						3			3
Teucrium scorodonia	1	1				1				
Thlaspi montanum	3							2	3	
Ulmus glabra	1			1						
Vincetoxicum hirudinaria	1						1			

Cliff (forestry practice)	EG	Ingelstein RCC	Ingelstein STC	Ingelstein control	Santel RCC	Santel STC	Santel control	Titterten RCC	Titterten STC	Titterten control
Cliff base										
Acer pseudoplatanus	1		4	2		6		1		
Amelanchier ovalis	3		1				1			
Arabis alpina	2		1		1	2		1		
Arabis hirsute	4		1		1					
Arabis turrita	1				2					
Arum maculatum	1		1					1		
Asarum europaeum	1		3		1	1		1		
Brachypodium sylvaticum	1		2	1		1				

Appendix A (*Continued*)

Cliff (forestry practice)	EG	Ingelstein RCC	Ingelstein STC	Ingelstein control	Santel RCC	Santel STC	Santel control	Titterten RCC	Titterten STC	Titterten control
Bromus species	5				1					
Bupleurum falcatum	4		1	2				1		
Campanula rotundifolia	4		5	3	1			2		
Cardamine heptaphylla	1	1		2						
Carduus defloratus s.l.	2		3	1	3	2		1		
Carduus nutans s.l.	5									
Carex alba	1			1				2		
Carex ornithopoda	1		2							
Centaurea scabiosa s.l.	4		1							
Clematis vitalba	1		1							
Convallaria majalis	1		1	1						
Cornus sanguinea	1		1					1		
Coronilla coronata	1			1						
Corylus avellana	1		2					2		1
Draba aizoides	2		1							
Dryopteris filix-mas	1								1	
Eupatorium cannabinum	6				1					
Euphorbia amygdaloides	1	1	1	1						
Euphorbia cyparissias	4									
Fagus sylvatica	1		1	1			1	1		1
Galium odoratum	1		1		2					
Galium pumilum	4	2	2	2	1	6		2		
Geranium robertianum	5		1					1		
Hedera helix	1		2	2				1		
Helleborus foetidus	1	1	2	2	1	2		3		
Hieracium humile	3			1	2	1				
Hieracium murorum	1		3	3	2	1	1			
Hippocrepis comosa	4					2				
Hippocrepis emerus	1		3	4	5	2	2	2		
Hypericum montanum	1							1		
Ilex aquifolium	1		1	1			1			
Impatiens glandulifera	5			1						
Kernera saxatilis	2					1				
Lamium galeobdolon	1	4	6					4	1	1
Laserpitium siler	2		3							
Lathyrus vernus	1		1			2				
Lonicera xylosteum	1									1
Melica ciliata	4				1					
Melica nutans	1		4	1						
Melitis melissophyllum	1		1							
Mercurialis perennis	1	5	4	2			1	6	2	4
Moehringia muscosa	1					1				
Mycelis muralis	1	1	2	1	1					1
Origanum vulgare	4		1	1						
Orobanche caryophyllacea	4				1					
Phyteuma spicatum	1		2							
Picea abies	1		1			1	1			
Poa nemoralis	1		1							
Polygonatum odoratum	4		2							
Prenanthes purpurea	1						1			
Pyrus pyraster	1		1							
Quercus petraea	1									1
Rhamnus alpinus	2			1	3	1	1			
Rosa species	–		2							
Rubus idaeus	1			1	1	5				
Rubus montanus	1				1					
Sambucus racemosa	1				2	2				
Senecio jacobaea	4			1					1	
Sesleria caerulea	2		1	2	1	3		2		
Sonchus asper	5				1					
Sorbus aria	1		3							
Sorbus aucuparia	1		1							1

Appendix A (*Continued*)

Cliff (forestry practice)	EG	Ingelstein RCC	Ingelstein STC	Ingelstein control	Santel RCC	Santel STC	Santel control	Titterten RCC	Titterten STC	Titterten control
Sorbus mougeotii	1						1			
Stachys alpina	2		1							
Stachys recta s.l.	4							2		
Taraxacum officinale	6		1							
Taxus baccata	1									
Teucrium chamaedrys	4					2				
Teucrium scorodonia	1					2				
Thlaspi montanum	3							3		1
Vincetoxicum hirudinaria	1		3	1				1		
Cliff face										
Acer pseudoplatanus	1									1
Arabis alpina s.l.	2		1		1	2			1	
Arabis hirsuta aggregate	4							1	1	
Arabis turrita	1									1
Asarum europaeum	1									3
Asplenium ruta-muraria	3		3			2			3	2
Asplenium trichomanes	3	1	4	5	1	3	1	4	4	5
Asplenium viride	3						1			
Brachypodium sylvaticum	1			1						
Bupleurum falcatum	4		1							
Campanula rotundifolia	4		2	1				2	1	
Campanula trachelium	1			2						
Cardamine heptaphylla	1	2		2						
Carduus defloratus s.l.	2				1					
Carex digitata	1					1				
Carpinus betulus	1									1
Coronilla coronata	1			1						
Cystopteris fragilis	3								1	
Draba aizoides	2		3							
Fagus sylvatica	1								1	
Fraxinus excelsior	1			1						
Galium pumilum	4			2		3				
Geranium robertianum	5							1		
Hedera helix	1		1	1				1	1	3
Helleborus foetidus	1		1							
Hieracium humile	3	1	1	1						
Hieracium murorum	1	1	1	2		2	1	1	1	
Hippocrepis emerus	1		2							
Hypericum montanum	1							1		
Kernera saxatilis	2					2				
Lamium galeobdolon	1							1	1	1
Lonicera xylosteum	1			1						
Melica ciliata	4				1					
Melica nutans	1			1						
Mercurialis perennis	1			1				1		2
Moehringia muscosa	1					1		1	1	
Mycelis muralis	1	1		4	1				1	2
Origanum vulgare	4		1							
Poa nemoralis	1		1							
Quercus petraea	1			1						1
Ribes uva-crispa	1	1								
Sedum album	3								1	
Sesleria caerulea	2		2	1		2		2		
Sonchus asper	5		1		1					
Sorbus aucuparia	1		1							1
Taxus baccata	1						1			
Thlaspi montanum	3							2	3	1
Vincetoxicum hirudinaria	1									1

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Chapter 5

Temporal and spatial patterns of overgrowing forest around limestone cliffs in the northern Swiss Jura mountains

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Abstract

The limestone cliffs of the northern Swiss Jura mountains harbour a diverse flora with several relict populations of arctic-alpine and Mediterranean plant species. Overgrowing forests increasingly threatens rare, relict plant species with high light demand on cliffs, because traditional forms of forest use, including the collection of firewood and grazing by goats, were abandoned. We examined the temporal and spatial patterns of overgrowing forest at six cliffs in the northern Swiss Jura mountains by analysing tree cover on time-series of air photographs made between 1951 and 2000. We developed stereo models of the cliffs and estimated tree cover in 25 m x 25 m grids. Overall tree cover increased from 60% to 85% at the six cliffs examined between 1951 and 1964 and afterwards levelled off. The increase in tree cover showed a distinct spatial pattern. It was significant in the talus (bottom of the cliff) and on the cliff face, but not on the plateau (at the top of the cliffs). These findings correspond to the overall increase in the wood stock in the Swiss Jura mountains. Our results confirm the assumption that the cliff forests became denser during the last decades. Forestry practises such as selective thinning or controlled grazing by goats are suggested to promote the threatened relict plant species.

Keywords: Air photographs, ERDAS, cliff ecology, light conditions, time-series

Introduction

Cliffs provide unique habitats for many specialised organisms (Larson et al. 2000). Dryness, high temperature amplitude, scarcity of nutrients and high insolation are general characteristics of exposed limestone cliff faces. The combined effects of drought and low nutrient availability, light and gravity limit plant growth in these extreme habitats (Coates and Kirkpatrick 1992). The structural complexity of cliff faces causes microclimatic and edaphic differences on a very small scale. Exposed patches are generally hotter and drier than protected ones, fractures are colder and wetter than ledges, and overhangs shadow deeper situated parts (Ashton and Webb 1977). The taluses of limestone cliffs provide dynamic, relatively unstable habitats, which are characterized by the displacement of debris and microclimatic differences like cold air drainage and exposure to sun. On the plateaus of limestone cliffs, the insolation is less extreme, but the porousness of the calcareous rock and the exposure to winds lead to dry conditions comparable to those of ruderal plains. All these effects lead to a highly diverse mosaic of microhabitats, which allow the existence of specialised chamaephytes and slowly growing trees (Escudero 1996, Larson et al. 2000).

The vegetation of limestone cliffs in the Swiss Jura mountains consists of plants of arctic-alpine, continental and Mediterranean origin (Wassmer 1998). For several alpine and arctic plant species, these cliffs serve as peripheral refugia which formed a periglacial steppe together with continental plants during the Pleistocene glacier advancements from the Alps and the Black Forest (Walter 1986). The arctic-alpine plant species and the xerothermic oak forest species (*Quercetalia pubescenti-petraeae*) colonised the south-exposed taluses and the plateaus of the Jura Mountains during postglacial warm periods (Ellenberg 1986). Due to the establishment of beech-forests under more temperate climate conditions, they were displaced towards the wood-free cliff sites. On the plateaus, these plant communities intersperse with beech and pine communities adapted to the arid conditions (*Molinio-Pinetum, Carici-Fagetum*; Ellenberg 1986).

Grazing goats and timber harvesting influenced the forests surrounding the limestone cliffs in northern Switzerland for many centuries. During the middle ages and until the 19th century, the steep slopes at the cliff bases were predominantly managed as coppice forests for the production of firewood, charcoal, bedding and raw materials for craftsmen and as temporal pasture (Stuber and Bürgi 2002a, Stuber and Bürgi 2002b). During the 18th and 19th centuries, the forests of the taluses were intensively managed for the production of timber and firewood, which was used for heating and in iron- and glassworks, two important branches of the regional economy at the beginning of industrialisation (Bloechlinger 1995). As a result of these human activities, the canopy of the forest surrounding limestone cliffs was open providing good light and temperature conditions for the relict plant species.

Because of the excessive exploitation of the forests, governmental decrees prohibited pasturing and bedding at the end of the 19th century (Suter 1971, Blöchlinger 1995, Stuber and Bürgi 2002a, Stuber and Bürgi 2002b). Additionally, the demand for firewood decreased dramatically after 1950. Nowadays, the cliff bases are exclusively used as timber forests, usually under a shelterwood system (Hendry 1998). As a result of the less intensive forestry, the forests become older and denser (Schiess and Schiess-

Bühler 1997, Wohlgemuth et al. 2002). The enhanced shadowing reduces the quality and size of the habitats for light-demanding species. This is particularly true for relict plants on limestone cliffs and at their base (Wassmer 1998) and for reptiles (Jäggi and Baur 1999).

There is empirical evidence for negative effects of the overgrowing forests on relict plant species on the taluses of limestone cliffs (Ewald 2000, Fachstelle Naturschutz Kanton Zürich 2004). Overgrowing forests lead to a decrease in the abundance of cliff plants with a high light demand and are therefore in some cases the main factor for the local extinction of threatened or rare species like *Dianthus gratianopolitanus, Daphne cneorum* or *Kernera saxatilis* (Wassmer 1998, Käsermann 1999). However, quantitative data on the extent and spatial pattern of overgrowing forest at limestone cliffs are presently not available, especially on the landscape scale. In the present study, we quantify the extent of overgrowing forest and examine its spatial pattern on six limestone cliffs in the northern Swiss Jura mountains by analysing time series of air photographs. Knowledge on the extent and spatial patterns of overgrowing forests can help to set priorities for the management of the species-rich habitats with high conservation value.

Materials and methods

Investigation sites

We examined overgrowing forest at six limestone cliffs in the northern Swiss Jura mountains (cantons of Solothurn and Basel-Landschaft) in an area of 30 km x 30 km (Fig. 1). The cliffs are located at elevations ranging from 350 to 1150 m above sea level (Table 1). They mainly consist of Jurassic coral chalks (Bitterli-Brunner 1987). The characteristic plant community of the predominantly south-facing cliffs belongs to the Potentillo-Hieracietum association (Richard 1972).

Analysis of air photographs

We used air photographs to examine different stages of overgrowing forest. Two requirements have to be fulfilled for a quantitative analysis of temporal and spatial changes in tree cover: First, air photographs should be available in spatially overlapping series. A three dimensional view allows better assessment of the extent of tree cover than 2D orthophotographs. Second, air photographs from different years have to be available and corrected for differences in radiographic techniques and relief due to different points of take.

Analogue black and white photos were obtained from the Swiss Federal Office of Topography (swisstopo). They were made in spring 1951, 1964, 1982 and 2000 on a scale ranging between ~1:15’000 and ~1:30’000. A total of 54 photos were scanned at a resolution of 14 µm and the stereo models have a root mean squared (RMS) error of <3 m after aerial triangulation.

A photo interpreter estimated the tree cover in raster cells of 25 m x 25 m (Fig. 2) using a 3D stereo softcopy station (ERDAS 8.3, Stereoanalyst; Leica Geosystems 2000). Schematic illustrations of different cover levels (Ahrens 2001) were used to assign squares to 10%-steps on an ordinal scale. We investigated the entire cliff areas, if stereo models where available. Only squares present at each time step were included in the data analysis. Squares with a tree cover of 100% at each time were assumed as forest and excluded from the data analyses. During the estimation of tree cover, stereo models were randomised to exclude an observational bias.

Statistical analysis

Medians of tree cover per time were plotted against the date of photographs to examine temporal changes. To evaluate any differences between the four times, a two-way analysis of variance (ANOVA) with the factors cliff and year was performed. We evaluated differences in vegetation cover between successive periods using Tukey's post-hoc test.

Analyses of variance were also used to examine the impact of the position at the cliff face on vegetation cover. Following Larson *et al.* (2000), we assigned the squares to different sections of the cliff: talus, cliff face and plateau. A three-way ANOVA was performed with the factors cliff, cliff section (nested in factor cliff) and year (nested in factor section). To examine whether there is a horizontal spatial pattern in overgrowing forest in the talus, we assigned raster cells to groups of 250 m width (= distance classes) beginning at the western end of each cliff. Statistical analyses were conducted using SAS version 8.02.

Results

Vertical pattern of tree cover

Tree cover could be assessed in a total of 1’769 25 m x 25 m plots distributed over the six cliffs. Considering the repeated air photographs, a total of 7’076 plots were examined.

Overall tree cover of the cliffs increased significantly from 60% to 85% (mean value of cliff medians) between 1951 and 1964 (Tukey's post hoc test,

$P < 0.05$) and thereafter levelled off (Fig. 3). However, single cliffs differed in the increase of overall tree cover ($F_{5,7086} = 350.73$, $P < 0.0001$).

The change in overall tree cover was most pronounced at Gerstelfluh (40% increase between 1951 and 1964), Ravelle (30% increase between 1951 and 1964), and Klus (20% increase between 1951 and 1964). In contrast, at the Holzfluh, the Mont Raimeux and the Muggenberg, overall tree cover did not increase in the same period (Table 2).

In the talus, mean tree cover increased from 62% to 80% between 1951 and 1964 and remained at this level since then (Fig. 4). The corresponding values on the cliff face were 55% in 1951 and 73% in 1964 and thereafter levelled-off. On the plateau, mean tree cover slightly increased from 74% to 79% between 1951 and 2000. However, this difference was not statistically significant ($P = 0.73$).

Considering single cliffs, the difference in tree cover of the talus ranged from an increase of 37% (Gerstelfluh) to a decrease of 4% (Muggenberg) between 1951 and 1964 (Table 2). On the cliff face differences in tree cover ranged from an increase of 40% (Gerstelfluh) to a decrease of 4% (Muggenberg) and on the plateau from an increase of 16% (Klus) to a decrease of 10% (Holzfluh).

Horizontal pattern of tree cover

Two of the six cliffs showed a horizontal spatial pattern of overgrowing forest between 1951 and 1964 (Fig. 5). At Gerstelfluh, the increase in tree cover on the talus was significantly higher in the western part than in the eastern part. Tree cover increased by 60% at the western end of this cliff and by 19% at the eastern end (unpaired t-test between the two distance classes: $t = 6.11$, df =

42, $P < 0.0001$). At Muggenberg, tree cover increased only in the central part of the cliff (distance classes 5 and 6 in Fig. 5). The cliff of Muggenberg has the shape of a “V”. An increase in tree cover was recorded in the part of the cliff, in which the exposition changes from south-east to north-east. In this section the cliff receives the highest insolation. No horizontal spatial pattern in overgrowing forest was found in the remaining four cliffs between 1951 and 1964.

Discussion

Our study provides quantitative evidence that cliff forests in the northern Swiss Jura mountains became denser during the last decades, and confirms a so far empirically unsupported assumption (Schiess and Schiess-Bühler 1997, Wohlgemuth et al. 2002). The increase in tree cover during the first decades after the Second World War is mainly a result of the abandonment of both forestry practices and the use of it as temporal pasture at the steep slopes. With the economic revival of the 1950ies, heating oil squeezed firewood out of the market as energy source in Switzerland. For example, in the forests of Schöntal near the investigated cliff Gerstelfluh, the use of firewood peaked during the Second World War until 1946 but no more firewood was sold after 1960 (H.-P. Rusterholz, *unpubl. data*). The stock of wood in the forests of Schöntal increased from 100 m^3/ha in 1928 to 280 m^3/ha in 1968. The progression of the stock of wood also manifests the decreasing importance of wood as energy source and building material.

Several studies showed that the abandonment of traditional forest practices such as its use as wooded pasture or the collecting of leaf litter and firewood resulted in a decrease in the abundance and number of plant and invertebrate species (Keller and Hartmann 1986, Egloff 1991, Schiess and Schiess-Bühler 1997). Egloff (1991) compared the present-day flora with that 100 years ago on the cliffs of Lägern in Switzerland and found that 74 plant species have become locally extinct during the past century. Keller and Hartmann (1986) reported extinction rates of 4% to 8% for several forests in northern Switzerland. Furthermore, Schiess and Schiess-Bühler (1997) interpreted the observed decline of butterfly species in a formerly intensively used forest as a result of the abandonment of traditional forestry practice. All these authors considered an increase in shadowing as the main factor for the observed species loss.

The dramatic reduction in timber and firewood use in the past decades not only led to an increase in standing biomass, it also led to an accumulation of nutrients in the soil. This in turn amplifies the growth of the vegetation in the talus and promotes plants with high nutrient demands. The large increase in the tree cover in the talus recorded between 1951 and 1964 is probably the result of a more extensive forestry practice or no forestry at all. This is exemplified at the cliff of Gerstelfluh, where the increase in tree cover between 1951 and 1964 was signifantly higher in the western part of the cliff than in the eastern part. The western part of the cliff is adjacent to the village of Waldenburg and thus was more frequently visited by harvesting people.

The present study also showed that tree cover on the plateau did not increase between 1951 and 1964. At the cliffs examined, tree cover on the plateau averaged 76% already in 1951. Timber and firewood harvesting was largely reduced on the cliff plateaus due to the limited accessibility, resulting in closed canopies.

Relatively large differences in the increase of tree cover were not only apparent within, but also between cliffs. The fact that three cliffs did not show any significant increase in tree cover between 1951 and 1964 (Table 2) deserves further consideration. Due to their remote location and special tree species composition, the cliffs of Muggenberg and Mont Raimeux most probably were less suitable for intensive forestry and/or pasturing. In contrast, the cliff of Holzfluh is situated in close proximity to human settlements and resembles the other cliffs in terms of microclimatic and edaphic conditions as well as in tree species composition. However, the talus of the Holzfluh is not well accessible due to its steepness and therefore this cliff forest was not a preferred site for firewood harvesting.

We did not observe any significant increase in tree cover at any cliff after 1964. This could be either the result of a self-thinning effect in the denser forests or an effect of methodology, e.g. the increase was not detectable with the chosen ordinal scale of 10%-steps.

The finding that the overgrowing forest was most pronounced in the talus and on the cliff face and relatively weak on the plateau is partly due to habitat-related differences in climatic and edaphic conditions between the three cliff sections. High insolation and nutrient and water input from the cliff face and plateau allow a fast plant growth on the talus. In contrast, the vegetation on the plateau is limited by the availability of water and nutrients which are scarce due to the porousness of the limestone. The observed increase in tree vegetation on the cliff face can result from trees growing at the cliff base or, alternatively, reflect a change in vegetation composition on the cliff face itself. The latter is rather implausible, because trees and shrubs grow very slowly on the cliff face (Escudero 1996, Larson *et al.* 1999).

The overgrowing forest in the talus leads to an enhanced shadowing of the lower cliff parts. Together with the cliff edge (zone from the cliff face to the plateau), this area constitutes the key habitat for several relict plant species (Morisset 1971, Wassmer 1998). Forestry practices that keep the supply of light on a high level at the lower parts of the cliffs are required to preserve the relict plant species. Selective thinning at the talus results in relatively large plots with good light conditions and therefore promotes the rare, relict plant species with high light demands (Schütz 1999, Müller et al. *in press*). Another measure to manage the lower parts of cliffs could be their use as temporal pasture for goats. Other human activities in these rocky habitats that threaten the sensitive cliff vegetation, such as sport climbing, should be prevented (Müller *et al.* 2004, Rusterholz *et al.* 2004).

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Legends to the figures:

Figure 1: Map of the examined cliffs in the Northern Jura mountains of Switzerland. For a description of the cliffs see Table 1.

Figure 2: Air photograph of the cliff Gerstelfluh with raster cells of 25 m x 25 m used for the analysis. Photograph taken on 8 June 2000.

Figure 3: Tree cover (%) of the examined cliffs between 1951 and 2000. Median values per year of 6 cliffs ± SE are shown. Different letters indicate significant differences between years (Tukey's test; $p < 0.05$).

Figure 4: Changes in tree cover between 1951 and 2000 shown separately for each talus, cliff face and plateau. Different letters indicate significant differences between years (Tukey's test; $p < 0.05$).

Figure 5: Horizontal spatial pattern in tree cover increase between 1951 and 1964 in the talus of the six cliffs examined. The raster cells were assigned to groups of 250 m width (= distance class) beginning at the western end of each cliff. Mean values ± SE are shown.

Fig. 1

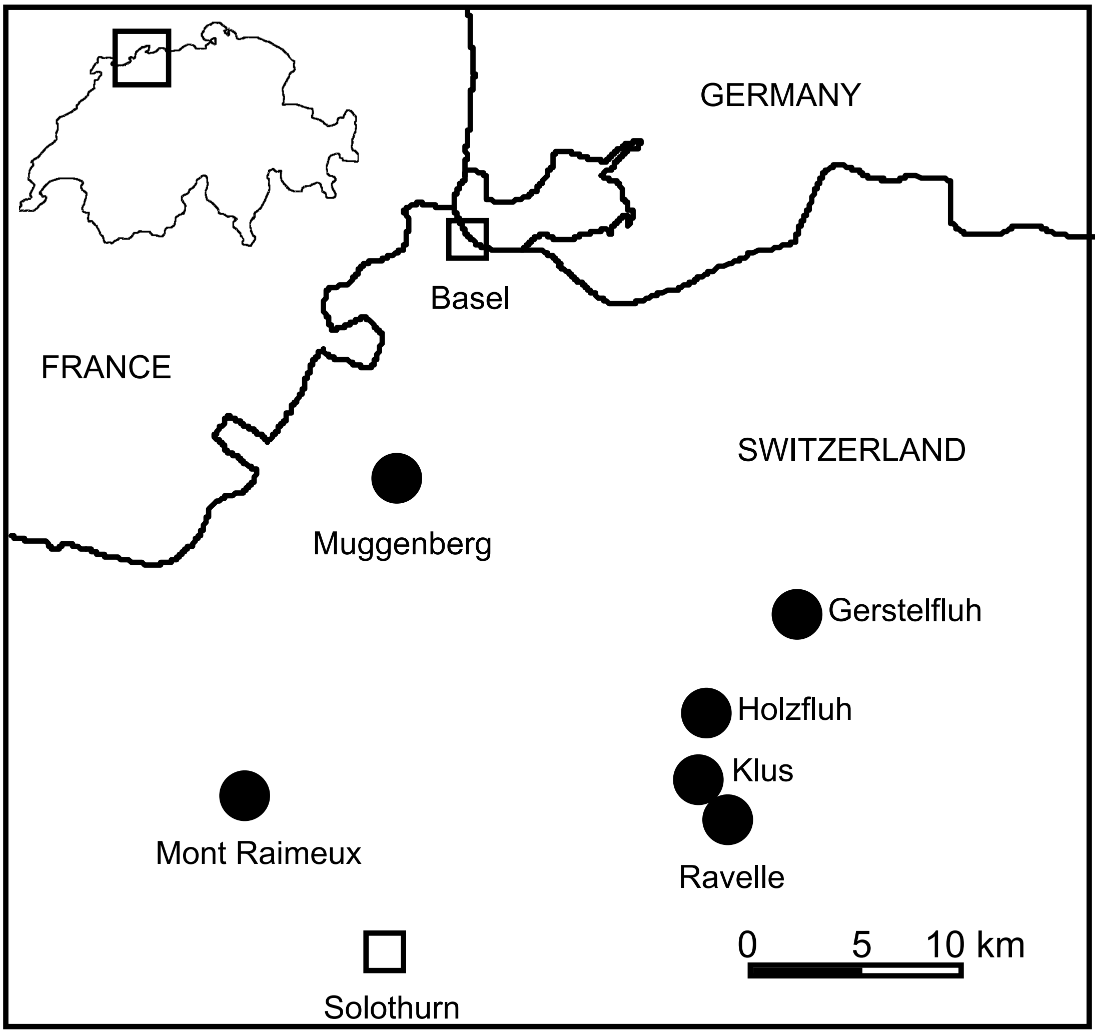

GERMANY
Basel
FRANCE
SWITZERLAND
Muggenberg
Gerstelfluh
Holzfluh
Klus
Mont Raimeux
Ravelle
Solothurn
0
5
10 km

Fig. 2

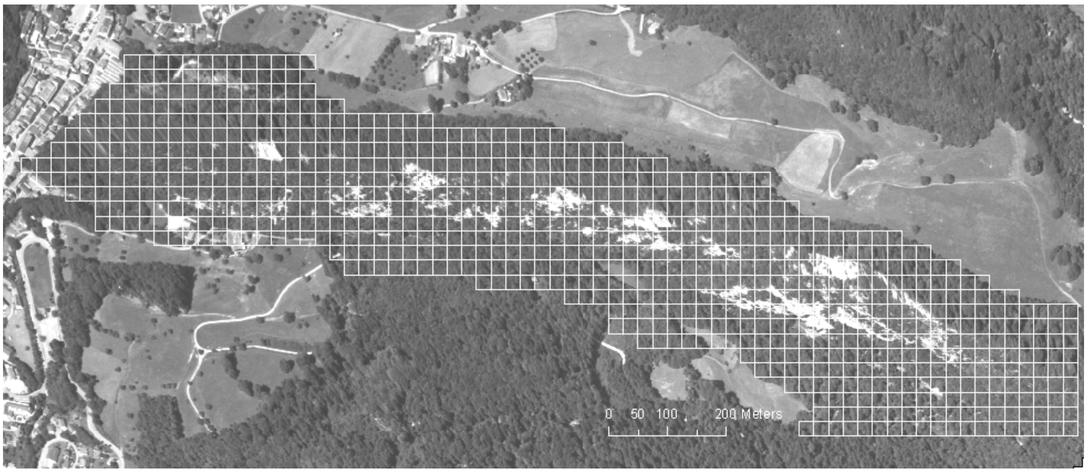


Fig. 3

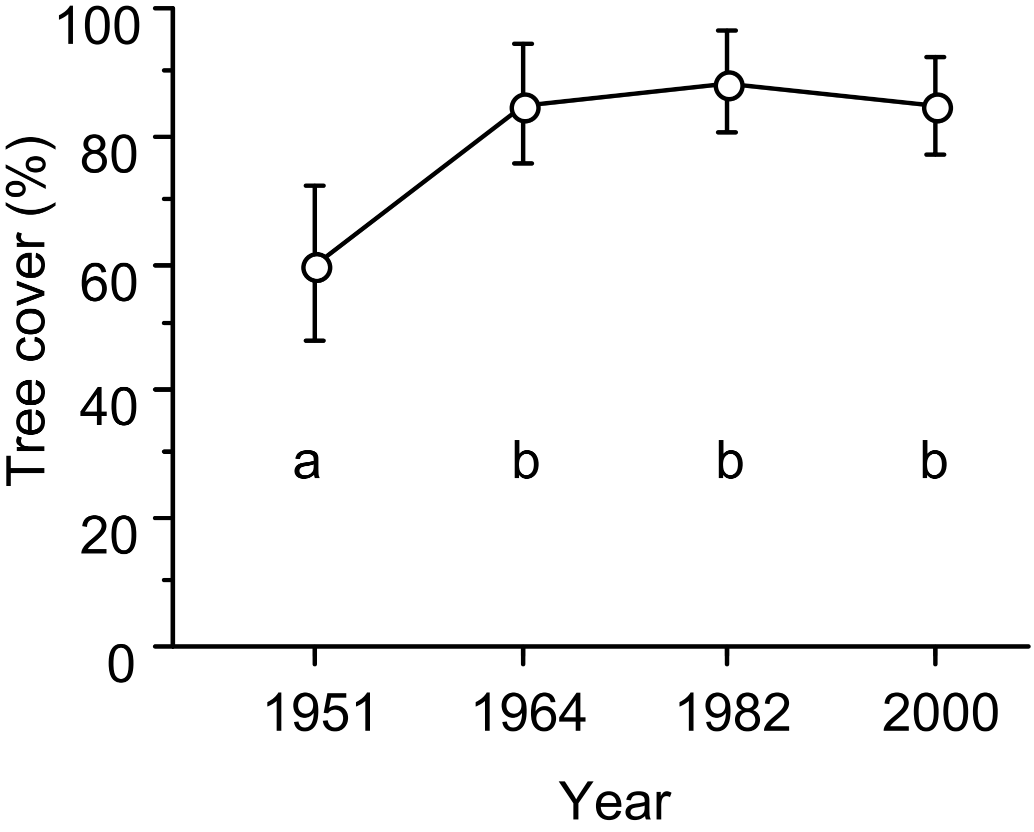
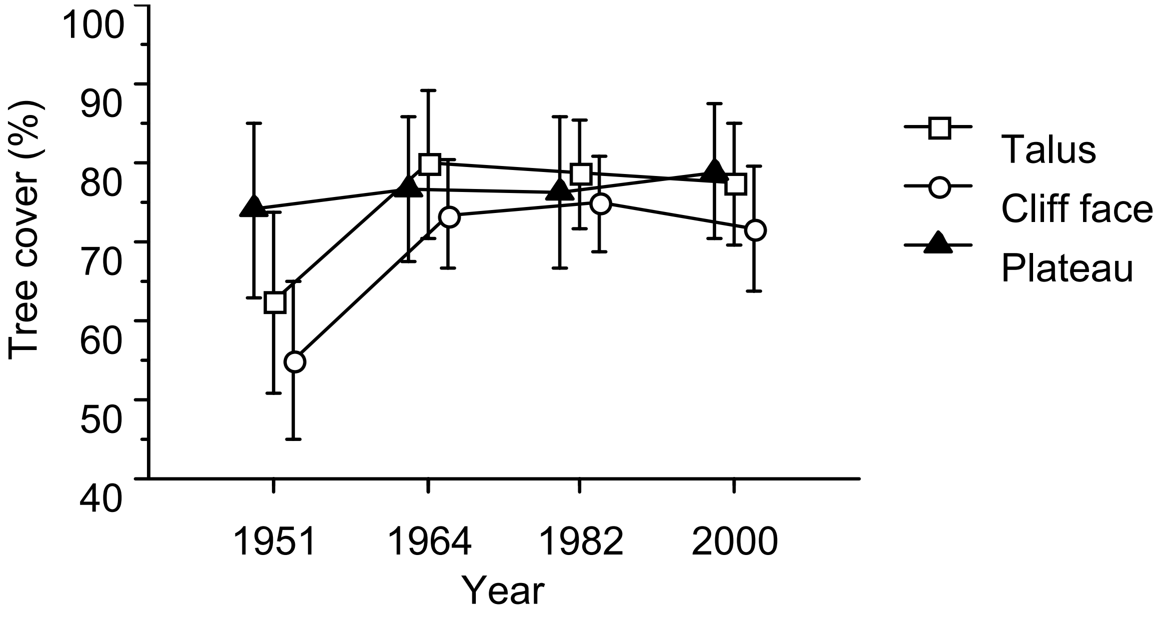
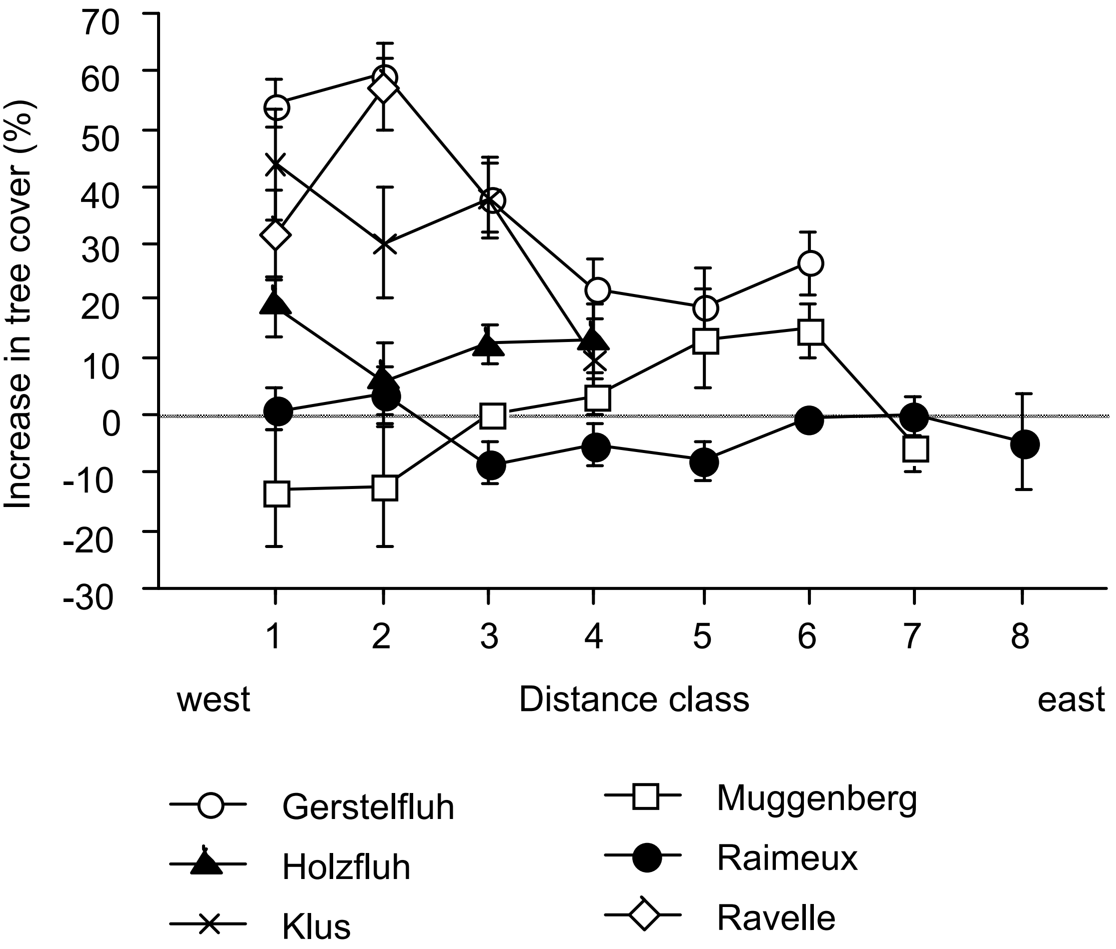


Fig. 4



Talus	a	b	b	b
Cliff face	a	b	b	b
Plateau	a	a	a	a

Fig. 5



Increase in tree cover (%)
70
60
50
40
30
20
10
0
-10
-20
-30
1
2
3
4
5
6
7
8
west
Distance class
east
Gerstelfluh
Holzfluh
Klus
Muggenberg
Raimeux
Ravelle

Table 1: Description of the cliffs investigated in the northern Swiss Jura mountains

Cliff	Elevation (m a.s.l.)	Exposure	Maximum height (m)	Cliff length (m)
Ravelle	490 - 620	SSE	80	550
Klus	500 - 790	SW - S - NE	140	1100
Holzfluh	500 - 660	S	160	900
Gerstelfluh	740 - 930	SSW	120	450
Mont Raimeux	800 - 1150	S	350	4500
Muggenberg	350 - 460	SE - S - NE	90	600

Table 2: Changes in tree cover (in %) of six investigated cliffs over three time periods.

Values are differences in the medians of 25 m x 25 m raster cells for the three sections of each cliff.

Cliff	1951 - 1964			1964 - 1982			1982 - 2000		
	Plateau	Cliff face	Talus	Plateau	Cliff face	Talus	Plateau	Cliff face	Talus
Ravelle	20	50	60	10	0	0	0	-10	0
Klus	5	50	30	10	0	0	0	-20	-10
Holzfluh	-10	10	10	0	10	20	0	0	0
Gerstelfluh	-10	60	50	10	0	0	-30	-30	-10
Mont Raimeux	10	0	0	0	0	-10	0	0	0
Muggenberg	-10	0	0	-15	0	0	25	10	0
Mean	0.8	28.3	25.0	2.5	1.7	1.7	-0.8	-8.3	-3.3

Chapter 6

Nunatak survival and mediaeval human activity influence the genetic population structure of relict plant species in the northern Jura mountains

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Manuscript

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Abstract

The genetic population structures of plants growing on isolated cliffs in the Jura mountains are of particular interest because in numerous species the plants are separated from their main distribution area in the Alps and the Mediterranean, they are living in highly fragmented habitats, and some of them might be influenced by human activities since centuries. We examined possible effects of isolation, the presumed colonisation history of cliffs and anthropogenic activities on the genetic population structure of two plant species with different life-histories in the northern Swiss Jura mountains. We assessed RAPD-polymorphisms in 14 populations of *Draba aizoides* L. and 12 populations of *Melica ciliata* L. living on isolated limestone cliffs and compared them with samples from the Alps. Analysis of molecular variance revealed a high among-population variation of each 27% in the gene pools of both species. A clear isolation-by-distance pattern and a separation of populations from the Jura mountains and the Alps was found in *D. aizoides*. This provides evidence for glacial relict endemism of this species, resulting from nunatak survival in the Jura mountains. In *M. ciliata*, UPGMA-analysis showed clusters of populations growing on cliffs with castles with shared historical incidents, indicating zoochorical dispersal related to human settlements. Future management actions should pay particular attention to isolated limestone cliffs with arctic-alpine plant species and should consider the preservation of mediaeval monuments.

Keywords: *Draba aizoides* - *Melica ciliata* - plant conservation - RAPD - isolation-by-distance - glaciation

Introduction

Genetic differentiation as a result of fragmented distribution is characteristic for many relict plant species (Ellenberg 1986, Le Corre, Dumoulin-Lapegue & Kremer, 1997). Partial extinctions, recurrent (re-)immigration, different migration routes, long-distance dispersal events, bottleneck situations, founder effects, *in situ* survival in refugia and genetic drift are crucial processes for the genetic differentiation and evolution of populations (Ellstrand, 1992; Luijten et al., 2000; Lutz, Schneller & Holderegger, 2000). Within the historical context of a species, factors like the breeding system, the ability and the mode of dispersal and clonal growth of the species affect the genetic structure of plant populations (Loveless & Hamrick, 1984, Vogel Rumsey & Russel, 1999). The relative importance of these factors influencing the species-specific capability to (re)colonise a region and to establish viable populations is a mainly unknown part within the mosaic of plant biogeography. For the conservation of relict plant populations, detailed knowledge about the interactions between life-history traits and historical circumstances is required (Hamrick & Godt, 1995).

During the Pleistocene glaciations the advancing glaciers caused a fragmented distribution patterns in many plant species. Due to the capacious knowledge about the geological and climatic history and the accessibility of the mountains, the Alps offer an especially suitable framework for investigations of both phylogeography and evolutionary mechanisms at the species level (Stehlik *et al.,* 2002) and of the processes during the Pleistocene climatic oscillation. For example, a high intraspecific chloroplast DNA (cpDNA) variation (but no firmed phylogenetic affinities between populations) was found in *Draba aizoides* L. (Widmer & Baltisberger, 1999). Strong geographical patterns of genetic diversity have been reported for isolated alpine relict populations of *Saxifraga cernua* L. (Bauert et al., 1998), *Saxifraga paniculata* Mill. (Reisch, Poschlod & Wingender, 2003), *Erinus alpinus* L. (Stehlik, Schneller & Bachmann, 2002) and *Eritrichium nanum* (L.) Gaudin (Stehlik *et al.*, 2002).

For the Jura Mountains and other low mountain ranges north of the Alps, an intensive debate on the origin of arctic-alpine plant populations has proceeded since the beginning of the twentieth century. Several biogeographic hypotheses about the origin of species like *D. aizioides*, *Dryas octopetala* L. or *S. paniculata* have been suggested (Lutz, Schneller & Holderegger, 2000): (1) the present-day populations of these species descended from populations that occurred in glacial refugia on nunataks (ice-free mountain peaks within the ice shield) and survived glaciation *in situ*; (2) the present-day populations descended either from populations that grew on forefields and moraines of glaciers during the ice ages or from remnant populations along the recolonisation routes of the species after the last glaciation; and (3) the present-day populations originated from long-distance dispersal after glaciation. The Jura Mountains have been postulated to serve as peripheral refugia for several alpine and arctic plant species, which formed a periglacial steppe together with continental plants during the Pleistocene glacier advances from the Alps and the Black Forest (Walter, 1986). Hantke (1978) also suggested that mountain tops in the southern part of the Jura Mountains surmounted the ice shield and therefore were potential nunataks.

Based on this hypothetical framework, genetic studies investigating the biogeographic history of relict plant species in the Jura Mountains are rare.

The cliffs of the northern Swiss Jura Mountains harbour several relict plant species with a highly fragmented distribution due to the geological and climatic history. In addition to the arctic-alpine plant species, xerothermic oak forest species (*Quercetalia pubescenti-petraeae*) colonised the south-exposed slopes of the Jura Mountains from refuges in Southern France and, particularly, from the Balkans during the postglacial warm periods (Ellenberg, 1986). Because of the establishment of beech-forests in the recent, temperate climate conditions, the relict plant species were displaced towards the wood-free cliff sites. Nowadays, the cliffs of the Jura mountains are mostly surrounded by deciduous forest, which has been partly cleared and subsequently used as pasture or hay meadow for some centuries. Today, the vegetation of these limestone cliffs consists of a mosaic of arctic-alpine, continental and mediterranean plant species, which all show a highly fragmented distribution pattern.

The cliff vegetation of the Jura Mountains is influenced by human activities since several centuries. Castles were established on cliffs at strategic points near passes to provide protection against raids in the early middle ages. In the following centuries, the steep slopes were managed as coppice forests (Burnand & Hasspacher, 1999) and temporarily even grazed by goats. In the twentieth century, this mixed form of land use disappeared gradually (Suter, 1971) and timber forest developed again. As a result, the habitats of the relict plant species gradually decreased in size.

In the present study, we examined the genetic structure of two relict plant species with different breeding and dispersal modes, *Draba aizoides* and *Melica ciliata* (L.). In particular, we addressed the following questions: (1) is there genetic evidence for nunatak or periglacial survival of these relict plant species in the Jura Mountains? (2) are isolated plant populations of the two species on Jura cliffs genetically distinguishable from each other and from populations of the recent species' distribution centre? (3) do cliff plants with different breeding and dispersal modes exhibit different genetic population structures? (4) are their recent genetic population structures influenced by former human activities?

Material and methods

Species

Draba aizoides (Brassicaceae) is a cespitose, perennial rosette plant. In the Swiss Jura mountains, flower buds are visible in December and flowering takes place between February and middle of April. The yellow flowers are strongly protogynous and pollinated by a wide variety of insects including bees, bumble bees, flies and butterflies (Kay & Harrison, 1970). *Draba aizoides* is supposed to be mainly outcrossing, with automatic self-pollination probably occurring when the flowers close in bad weather (Kay & Harrison, 1970). There is no vegetative reproduction and vegetative spread is limited to increase the size of the cushion, which takes place by the production of axillary rosettes at the base of the flowering stem (Kay & Harrison, 1970). The heavy seeds are dispersed over short distances implicating that the majority of them germinate near the maternal plant (Frey et al., 1995). However, seeds can be dispersed over distances of a few metres within the rocky habitats by wind and rain-splash (Kay & Harrison, 1970). *Draba aizoides* is widely distributed in Continental Europe, particularly from the Pyrenees through the Alps to the Carpathians (Hegi, 1920). In Switzerland, the species lives in rock crevices at the montane and alpine level of both the Jura mountains and the Alps (Welten & Sutter, 1982).

Melica ciliata is a hemicryptophytic, rhizomatous, tuft-forming grass species with pronounced xerophylic adaptions, flowering from May to July (Landolt, 1977). The inflorescence is a scarcely branched panicle consisting of hermaphroditic and sterile flowers (Tyler, 2004). The mature lemmas of the dispersal units are covered by long hairs and are easily dispersed by wind (Hensen & Müller, 1997). Furthermore, zoochorous dispersal of seeds and sterile flowers has been observed in the field (Müller SW, unpubl. data). *Melica ciliata* is widely distributed in Southern and Central Europe, Northern Africa and the Near East between Turkey and Iran (Tyler, 1993). In Switzerland, the species is restricted to exposed limestone cliffs, quarries and stone walls in the Jura mountains, in the calcareous northern and southern Prealps and in alpine valleys (Welten & Sutter, 1982).

Study area and sampling localities

The present study was carried out in the northern Swiss Jura mountains in the region of the canton of Solothurn in an area measuring 50 x 40 km. Parallel mountain chains run from south-west to north-east with an altitudinal range from 350 to 1450 m a.s.l.. Villages and areas of intensive agriculture are abundant at the bottom of the valleys, whereas the slopes are mainly covered by forest and interspersed meadows and rocky cliffs.

We sampled leaf material from 183 *D. aizoides* plants at 14 localities (8 – 18 plants per locality) and from 156 *M. ciliata* plants at 12 localities (10 – 16 plants per locality) in summer 2001 (Fig. 1, Table 1). To avoid repeated sampling from the same individual, the minimum distance between two sampled individuals was set to 2 m for *D. aizoides* and 5 m for *M. ciliata*. The distance between two populations ranged from 2.0 to 38.1 km (mean 18.5 km) in *D. aizoides* and from 1.8 to 36.2 km (mean 18.2 km) in *M. ciliata*.

Outgroup specimens of both species were also sampled at two localities in the main distribution areas (Fig. 1): *D. aizoides* on the Pilatus mountain and the Mythen mountain in the northern Prealps (Central Switzerland), *M. ciliata* at the base of the Rigi mountain and near the town of Massa Marittima (Tuscany, Italy).

An exact estimation of the population size was not possible because of the clonal growth of the species and the inaccessibility of large parts of the cliffs (vertical cliff walls). Cliff size, expressed as estimated total area of bare rock, was therefore used as an indirect measure of population size in the data analyses.

DNA isolation and PCR amplification

Samples of 5 *D. aizoides* and 5 *M. ciliata* were screened for decamere primers (MWG-Biotech). Primers that did not produce well-amplified, clearly distinguishable bands or reproducable fingerprints were excluded. To reach a high repeatability in the analyses, prior to the analyses of the whole sample set, five individuals of each species were examined five times using selected primers. Primers with inconsistent bands within individuals were excluded from the analysis.Out of the 40 primers examined, we selected six primers for *D. aizoides* and five primers for *M. ciliata* (Table 2).

DNA was isolated using a modified extraction protocol of Doyle (1991). Modifications were 3% CTAB [w/v] instead of 2%, addition of 20 μl 1% proteinase [w/v] to isolation buffer, and no ammonium acetate in wash buffer. After quantification in an agarose gel, a DNA working solution of ca. 3 ng/μL was prepared. A 25 μL amplification reaction mix contained ca. 15 ng template DNA, 0.2 μM primer, 200 μM of each dNTP (Promega), 0.5 units Taq polymerase (Promega), 2.5 mM $MgCl_2$ and 1 x PCR buffer. The PCR reaction mixtures were overlaid with mineral oil and amplified in a PTC-100 thermocyler (MJ Research Inc.) which was programmed for an initiating heating step (5 min at 93°C) followed by 45 cycles of 1 min at 94°C, 1 min at 36°C, and 2 min at 72°C. After the last cycle, samples were kept for another 7 min at 72°C and then at 4°C prior to analysis. Amplification products were size-fractioned on 1.2% agarose gels which run in 0.5 x TBE, stained with ethidium bromide and visualised by illumination with ultraviolet light (312 nm). Molecular weights were estimated using the amplisize DNA standard from Bio-Rad.

Data analysis

We calculated genetic distances among populations (Nei, 1978) using Popgene Version 1.32 (Yeh, Yang & Boyle, 1997). Mantel tests were performed using XLStat (Addinsoft, New York). An analysis of molecular variance (AMOVA, Excoffier et al., 1992) was calculated using GenAlEx V5 (Peakall & Smouse, 2001). UPGMA-cluster analyses were performed using TFPGA (Miller 1997). Spearman rank correlations were used to examine possible associations between cliff size and proportion of polymorphic loci in both species. For these purposes, proportions of polymorphic loci were corrected for sample size with a division by the square root of (n - 1).

Results

PCR-amplification resulted in 85 polymorphic bands with a length ranging from 330 to 1230 bp in *D. aizoides* and 79 polymorphic bands with a length ranging from 330 to 1440 bp in *M. ciliata*. Considering all individuals, the mean band frequency was 27.3% (SD: 24.9%, range: 0.6-84.7%) in *D. aizoides* and 27.6% (SD: 25.6, range: 0.7-92.9%) in *M. ciliata*. The two species differed in proportion of polymorphic bands within populations: 45.1% (SD: 9.8, range 28-60) in *D. aizoides* and 38.5% (SD: 10.6, range: 20-63) in *M. ciliata* (t = 2.43, d.f. = 22, *P* = 0.024). In neither species, the number of polymorphic bands was correlated with sample size (*D. aizoides*: r = 0.12, *N* = 14, *P* = 0.12; *M. ciliata*: r = 0.46, *N* = 12, *P* = 0.13). Furthermore, we found no correlation between cliff size and the proportion of polymorphic loci (corrected for sample size; *D. aizoides*: r = 0.20, *N* = 13, *P* = 0.49; *M. ciliata*: r = -0.07, *N* = 11, *P* = 0.82).

Genetic distances (Nei, 1978) among populations were positively correlated with geographical distances in *D. aizoides* (Mantel-test: r = 0.33, *N* = 78, *P* = 0.013) but not in *M. ciliata* (Mantel-test: r = -0.04, *N* = 55, *P* = 0.37). The results of the AMOVA showed that in both species the within-population variation accounted for 73% of the total variation and the among-population variation for 27% (Table 3).

The UPGMA cluster analysis based on mean Nei distances (Nei, 1978) revealed different patterns for the two species. In *D. aizoides*, the easternmost situated population (FB) and the high-altitude population (ROE) branched off first from the remaining populations (Fig. 2A). The analysis revealed further different clusters of geographically neighboured populations.

In *M. ciliata* we found no clear geographical pattern. The UPGMA-clustering, however, showed possible relationships between populations due to historical connections. The upper-most cluster (Fig. 2B, populations BM, FB, AB) consists of three populations growing on ruins of castles of the dukes of Froburg or families in partnership, which were all inhabited between the tenth and thirteenth century. The neighbour cluster consists of two populations on cliffs not affected by human settlements (HC, RM) and two populations growing on ruins of castles of the dukes of Thierstein, built in the thirteenth century (DO, TH). Such a pattern could emerge when seeds of *M. ciliata* were exchanged among related families, e.g. by passive dispersal on sheep and goats grazing in the close surroundings of the castles. Concerning the genetic variability, however, no difference between populations on cliffs with or without castles was found (number of polymorphic loci corrected for sample size: t = 0.35, d.f. = 9, *P* = 0.74).

Discussion

Genetic diversity and structure

The main factors that influence the levels of genetic diversity and divergence and the distribution of genetic variability within and among plant populations have usually been interpreted as the result of a balanced combination between reproductive system and the past history of the species under study (Loveless & Hamrick, 1984, Segarra-Moragues & Catalan, 2003). Outcrossing perennials like *D. aizoides* generally exhibit higher levels of genetic diversity and lower levels of population differentiation (Segarra-Moragues & Catalan, 2003). In contrast, a lower amount of genetic diversity and higher levels of population differentiation would be expected for plants like *M. ciliata*, with a high amount of clonal growth and/or self-pollination. The results of our study support this expectation: populations of *D. aizoides* exhibited a higher genetic diversity than populations of *M. ciliata*. The observed levels of polymorphisms (polymorphic bands per population) of 28 - 60% for *D. aizoides* and of 20 - 63% for *M. ciliata* resembled those of other, comparable RAPD-studies with relict species. Hensen & Oberprieler (2005) found proportions of polymorphic bands per population of 40 - 61% in *Dictamnus albus* L. in central Germany and Reisch, Poschlod & Wingender (2003) reported proportions of 12 - 54% in *Saxifraga paniculata* in central Europe. However, the levels of population differentiation found in the present study are not congruent with theoretical assumptions. For both species, the AMOVA-analyses revealed an among-population variation of 27%. This indicates that dispersal by vegetative parts of individuals, particularly splitting-off rosettes (as reported by Kay & Harrison (1970)) is highly relevant even in *D. aizoides*, a species with a limited ability of clonal growth, living on isolated cliffs in the Jura Mountains.

A positive correlation between measures of genetic variation and population size has been reported in several plant species (Fischer & Matthies, 1998; Luijten et al., 2000; Reisch, Poschlod & Wingender, 2003; Hensen & Oberprieler, 2005; Hensen, Oberprieler & Wesche, 2005). No similar correlation was found in either species of the present study. We used cliff size as a surrogate of plant population size, because parts of the cliffs were not accessible for a detailed count of plant individuals. Furthermore, the clonal growth of the species makes any determination of individual plants difficult. Both factors may confound the relationship between genetic variation and population size in the plant species examined.

Glacial relict endemism

The isolation-by-distance pattern, the UPGMA-cluster with a clear distinction of populations from the Jura mountains and the Alps and the isolated position of two possible nunatak populations indicate that *D. aizoides* survived glaciations *in situ*. Lutz, Schneller & Holderegger (2000) investigated the population genetics of *Saxifraga aizoides* in the lowland and lower mountains north of the Alps without being able to trace the species' biogeographic history. The distinct genetic structures found on a very small geographic scale in *D. aizoides*, the long-term isolation of the populations of the Jura mountains from those of the Alps, and the high degree of variation among populations suggest that natural founder events did not occur on the cliffs of the northern Jura mountains. Most probably, the forestation of the entire area prohibited dispersal. For other arctic-alpine species with large, heavy seeds, a similar history of populations can be assumed.

In *M. ciliata*, the absence of an isolation-by-distance pattern and the incomplete separation of populations from the Jura mountains and the Alps suggest that the species colonized the Jura mountains after glaciation. The grouping of population HO together with the outgroup populations (VI and MM) in the UPGMA-cluster could in fact have a historical background. For example, in 1374, a goods transport to the city of Basel was assaulted near the cliff of Holzfluh (HO) (Sigrist, 1992). The goods, mainly saffron (and potentially also diaspores of *M. ciliata*), were concealed in the nearby castle of

Neu-Falkenstein. Such mediaeval events of trade and warfare are supposed to have contributed to seed dispersal. Dispersal of *M. ciliata*, which has been supposed to be meteorochoric (Müller-Schneider, 1986), is also zoochoric. This could lead to the conspicuous pattern of close genetic relationship of populations with resembling historical impacts. Our findings are consistent with the findings of Fischer, Poschlod & Beinlich (1996) who state that the dispersal of diaspores by animals has so far been largely underestimated.

Implications for conservation and management

Species with a fragmented distribution are particularly vulnerable to extinction when gene flow between populations is lacking. Limestone cliffs of the northern Swiss Jura mountains harbour numerous specialized and threatened lichen, plant and invertebrate species with a highly fragmented distribution and are therefore of high conservation value (Müller, Rusterholz & Baur, 2003). For example, plant species with similar life-histories as *D. aizoides*, including *Saxifraga paniculata*, *Kernera saxatilis* (L.) Sweet, *Erinus alpinus* L. and *Alyssum montanum* L., may also be affected by the isolation of suitable rock cliffs and therefore exhibit discrete genetic reservoirs in the Jura mountains. Therefore, adequate management actions should be developed and implemented. These actions should specially attend to cliffs with numerous arctic-alpine plant species to protect them from mechanic disturbances by sport climbing and hiking (Kelly & Larson, 1997; MacMillan & Larson 2002; Müller, Rusterholz & Baur, 2004; Rusterholz, Müller & Baur, 2004). Furthermore, the quality and size of the cliffs should not be reduced by overgrowing forest and the resulting increase in shadowing.

The presumed interrelation between human settlements and the genetic structure of *M. ciliata* suggests that a part of the cliff vegetation is affected by human activities since many centuries. Interestingly, the protection of castles and ruins in their original state for historical and cultural reasons may also contribute to preserve genetic aspects of biodiversity. The preservation of mediaeval sites also connotes the conservation of plant populations of species introduced into the area during the time of human activities on these sites. Monument preservation and nature conservation are in that case synergetic.

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Table 1. Characteristics of the sampling localities. Cliff size is indicated as rank number for both plant species (see Methods).

Locality	Abbreviation	Altitude (m a.s.l.)	Presence of a castle / ruin	Species sampled		Cliff size (rank)	
				D. aizoides		*D. aizoides*	
Hohle Felse	HE	470	Yes		X		9
Dorneck	DO	500	Yes		X		11
Schartenfluh	SF	750	No	X		12	
Hofstetter Chöpfli	HC	490	Yes	X	X	9	8
Rämel	RM	830	No	X	X	8	6
Roti Flue	RF	740	No	X	X	5	4
Thierstein	TH	490	Yes	X	X	6	5
Balmchopf	BC	640	No	X		4	
Stallflue	ST	1380	No	X		1	
Balm	BM	650	Yes	X	X	2	1
Röti	ROE	1390	No	X		7	
Chamben	CN	1240	No	X		11	
Holzflue	HO	730	Yes		X		3
Ravelle	RV	610	No	X	X	13	10
Alt Bechburg	AB	800	Yes		X		7
Bölchen	BOE	1040	No	X		10	
Froburg	FB	820	Yes	X	X	3	2

Table 2. Primers applied and number of bands obtained in the PCR analysis.

Species Primer name	Nucleotide sequence	Number of bands	Size range of scorable bands
Draba aizoides			
X2	5' – GTG AGG CGT C – 3'	17	330 - 940
X4	5' – GGT GAC GCA G – 3'	22	330 - 1210
X7	5' – CTC GCG GCT A – 3'	16	350 - 950
X14	5' – GAT GAC CGC C – 3'	15	330 - 1230
X20	5' – CCT GGC GAC C – 3'	19	360 - 1160
H4	5' – GGA AGT CGC C – 3'	14	340 - 810
Melica ciliata			
X3	5' – ACC CGG TCA C – 3'	17	420 - 1210
X5	5' – TCC GCT CTG G – 3'	15	360 - 1200
X8	5' – ACC CAT GCG G – 3'	6	470 - 620
X11	5' – GTG TGC CCC A – 3'	15	330 - 1220
X18	5' – CGT CCG TCA G – 3'	14	430 - 1320
H1	5' – GGT CGG AGA A – 3'	12	440 - 1440

Table 3. Summary of analysis of molecular variances (AMOVA). The level of significance is based on 1000 random permutations.

Species Level of variation	df	SS	MS	% Total	P
Draba aizoides					
Among populations	12	1166.3597.20	26.8	<0.01	
Within populations	167	2680.50	16.01	73.2	<0.01
Melica ciliata					
Among populations	10	962.41	96.24	27.0	<0.01
Within populations	154	2263.5714.70	73.0	<0.01	

Legends to the figures

Figure 1. Sampling localities in the northern Swiss Jura mountains (right), in Central Switzerland (left, upper part) and in Italy (left, lower part). Plants from the latter sites served as outgroups.

Figure 2. UPGMA analysis for *D. aizoides* (A) and *M. ciliata* (B) based on Nei distances (Nei 1978) between populations. Numbers below branches indicate bootstrap support (percentage) based on 1000 bootstrap replications. Letters indicate castles of the dukes of Froburg and relatives (f) and those of the dukes of Thierstein and relatives (t).

Fig. 1

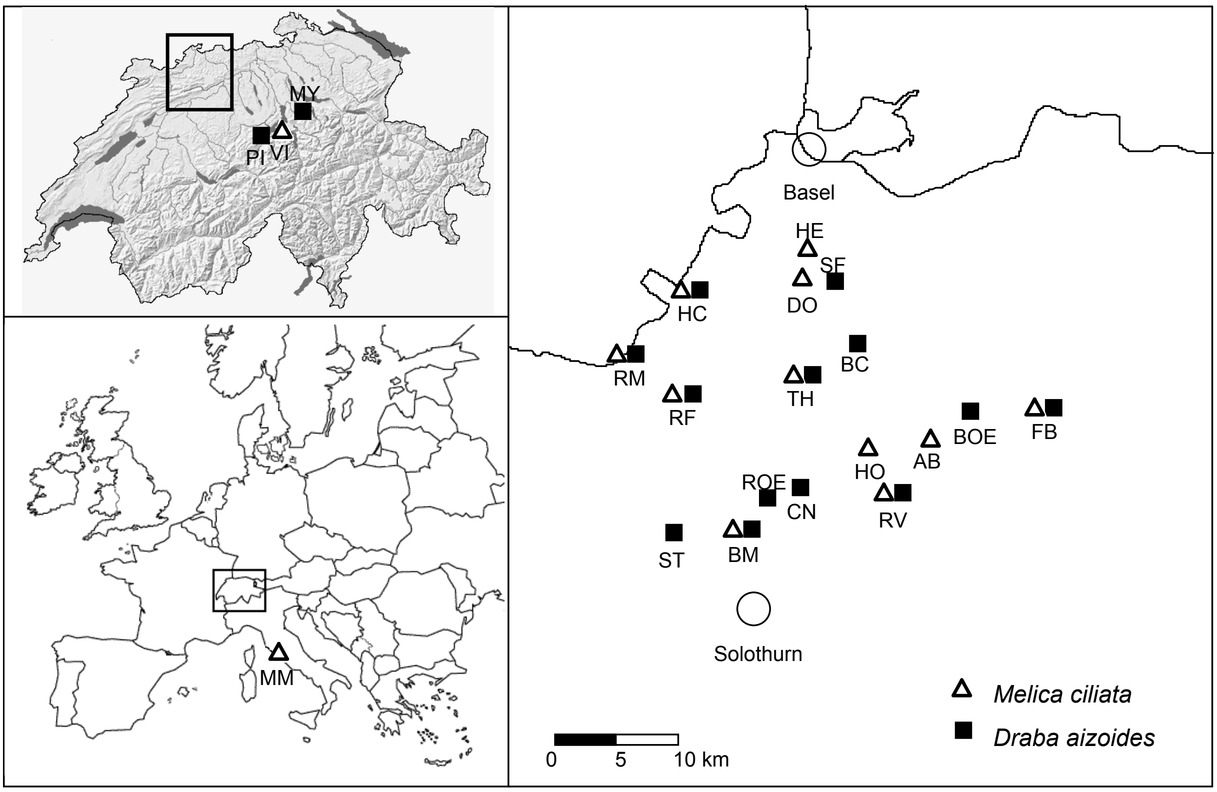
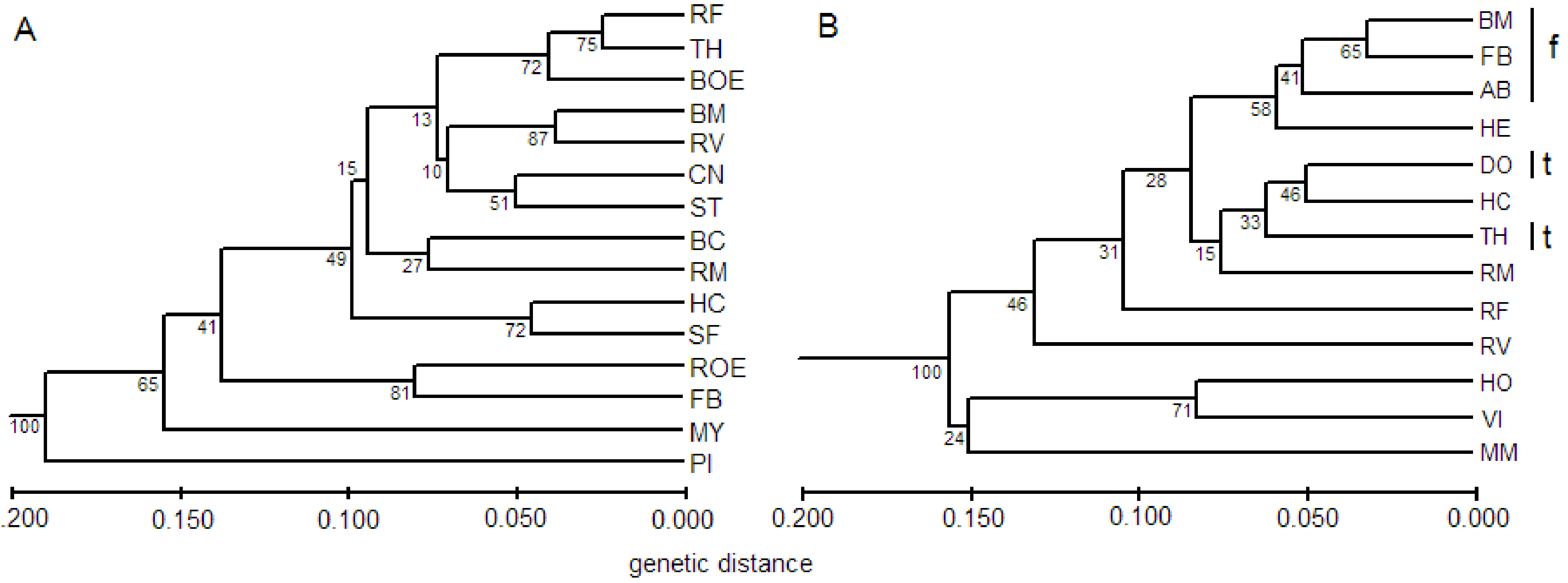

MY
PI
VI
MM
Basel
HE
SF
DO
HC
RM
BC
TH
RF
BOE
FB
AB
HO
ROF
CN
RV
ST
BM
Solothurn
Melica ciliata
Draba aizoides
0
5
10 km

Fig. 2


A
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genetic distance
B
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t
t
65
41
58
28
46
33
15
31
46
100
71
24
0.200
0.150
0.100
0.050
0.000

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Ich erkläre, dass ich die Dissertation

„Human impact on the vegetation of limestone cliffs in the northern Swiss Jura mountains“

nur mit der darin angegebenen Hilfe verfasst und bei keiner anderen Universität und keiner anderen Fakultät der Universität Basel eingereicht habe.

Stefan Müller