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Intensity-dependent impact of sport climbing on vascular plants and land snails on limestone cliffs

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ABSTRACT

Limestone cliffs in the Jura Mountains harbour species-rich plant and animal communities including rare species. Sport climbing has recently increased in popularity in this habitat and several studies have reported damage to cliff biodiversity. However, so far how damage levels vary with climbing intensity has not been investigated. We evaluated the effects of climbing intensity on the diversity of vascular plants and land snails in 35 limestone cliff sectors in the Northern Swiss Jura Mountains. Mixed-effects models were used to examine whether species richness of plants and land snails differ between cliff sectors with low and high climbing intensity and unclimbed cliff sectors (controls) taking into account potential influences of cliff characteristics (aspect, cliff height, rock microtopography). At the cliff base, the best fit model revealed that plant species richness was affected by climbing intensity and cliff aspect. Plant species richness was reduced by 12.2% and 13.1%, respectively, in cliff sectors with low and high climbing intensity compared to unclimbed cliff sectors. On the cliff face, plant species richness was only influenced by climbing intensity (species richness reduction by 24.3% and 28.1%). Combining data from cliff base, face and plateau, the best fit model revealed that land snail species richness was only affected by climbing intensity (species richness reduction by 2.0% and 13.7%). In both organism groups, species composition was increasingly altered by increasing climbing intensity. Our study provides evidence that even low climbing intensity reduces cliff biodiversity and that damage becomes more pronounced with increasing climbing intensity.

Keywords: Biodiversity, Human disturbance, Gastropod, Impact assessment, Rocky habitat

1. Introduction

Outdoor recreational activities including sport climbing, bouldering (a form of rock climbing on boulders), hiking, and mountain biking have increased enormously in popularity over recent decades (Kuntz and Larson, 2006; Holzschuh, 2016; Tessler and Clark, 2016). Some of these activities are performed in historically inaccessible habitats and thereby increasingly disturb the biota. However, studies assessing the impact of various outdoor activies on the local biodiversity are still rare and their results are inconclusive, partly due to lack of proper controls (Holzschuh 2016).

Limestone cliffs are globally a rare habitat supporting highly specialized and distinct biotas including lichens, bryophytes, vascular plants, insects and gastropods (Larson et al., 2000; Schilthuizen et al., 2003). The high species richness, large number of rare species and rarity of the habitat type give limestone cliffs a high conservation value (Wassmer, 1998; Baur, 2003; Ursenbacher et al., 2010). The Fauna-Flora-Habitat guidelines of the European Union consider limestone cliffs as habitats of "European importance" (Council Directive 92/43/EEC, 1992). In contrast to large rocky areas of the Alps and other high-elevation mountains, the cliffs of the Jura Mountains in Switzerland are small and isolated, and mostly surrounded by beech forests or xerothermic oak forests (Fig. S1), which have been partly cleared and subsequently used as pasture for some centuries (Moor, 1972). In this landscape at low elevation, the rocky habitats represent islands of special environmental conditions. A variety of organisms living on these cliffs are inter- or post-glacial relics with a recent Mediterranean or Arctic–Alpine distribution (Walter and Straka, 1970).

Rock climbing is very popular in the Jura Mountains in the region of Basel, Switzerland, where this sport can be performed during the entire year (Hanemann, 2000). More than 2000 sport-climbing routes with fixed protection bolts have been installed on 48 rock cliffs of this region (Andrey et al., 1997). Approximately 70% of these sport-climbing routes were opened between 1985 and 1999 (Andrey et al., 1997). The enormous number of climbers has led to conflicts between the goals of nature conservation and recreation activities (Wassmer, 1998; Baur, 2003).

Damage to vascular plants and lichens due to rock climbing has been recorded on limestone cliffs of the Swiss Jura Mountains (Müller et al., 2004; Rusterholz et al., 2004; Baur et al., 2007), and on other types of rocky cliffs in Germany (Herter, 1993, 1996) and North America (Nuzzo, 1995, 1996; Kelly and Larson, 1997; Camp and Knight, 1998; Farris, 1998; McMillan and Larson, 2002; Clark and Hessl, 2015). Damage includes a reduction of vegetation cover, alterations in the composition of the plant community and local extinction of species sensitive to disturbance and of specialists adapted to these extreme habitats. Clearing of soil from crevices and erosion of the cliff edge and face have also been recorded (McMillan and Larson, 2002; Kuntz and Larson, 2006). Furthermore, human trampling has reduced the above-ground vegetation cover at the base of cliffs and caused significant shifts in plant species composition (Rusterholz et al., 2011).

Climbing-related effects on invertebrate communities have received less attention. McMillan et al. (2003) found that species richness and density of land snails were lower along climbing routes than in unclimbed areas of the Niagara escarpment, and that snail community composition differed between climbed and unclimbed sites. In the Swiss Jura mountains, Baur et al. (2017) found that species richness of live rock-dwelling snails was 61% less in sampling plots along climbing routes than in nearby control plots on unclimbed rock faces, and abundance was 71% less. The complexity of the rock surface had little influence on snail species richness and abundance.

Not all parts of a cliff might be affected in the same way by sport climbing. At the cliff base (or talus), trampling by climbers and people securing the climbers destroys the ground vegetation, reduces the litter layer and the abundance of invertebrates living in it, and compacts the soil (Rusterholz et al., 2011; Fig. S2). On the cliff face, climbers may remove soil, damage vegetation and crush snails when establishing a new route and during ascents (Nuzzo, 1995; Farris, 1998; Adams and Zaniewski, 2012; Fig. S3). The magnitude of these disturbances may depend partly on the microtopography of the cliff face, because soil volume and vegetation abundance increase with the number and size of microtopographic features, such as crevices, cracks, pockets and ledges (Holzschuh, 2016). The cliff plateau is normally not accessed by climbers, because sport climbing routes typically end at the top of the face (Andrey et al., 1997; Fig. S4).

In a recent review of the impact of rock climbing, Holzschuh (2016) criticised the lack of proper controls in some studies and argued that potential differences in slope, aspect, insolation and microtopography between climbed and unclimbed areas were not always considered. Holzschuh (2016) also noted that no study had investigated how climbing effects vary with climbing intensity. Such studies would facilitate improved management of rock climbing areas that are rich in biodiversity and harbour rare and threatened species.

In our study, in the Northern Swiss Jura Mountains, we used a multi-taxon approach (vascular plants and land snails) to examine whether limestone cliffs with low or high climbing intensity differed in species richness, species composition and abundance, and whether they differed from unclimbed cliffs, considering confounding effects of aspect and microtopography of the cliffs. We recorded species richness and species composition of vascular plants and shelled gastropods (land snails) at the base, on the face and on the plateau of 35 cliff sectors. We also examined whether unclimbed cliff sectors and cliff sectors with low and high climbing intensity differ in abiotic factors (complexity of the rock surface, aspect of cliff face, etc.) and in visitor-related aspects (distance to nearest parking area, distance to the city).

In particular, we tested the following hypotheses:

1) The impact of sport climbing on both plant and snail species richness becomes more pronounced with increasing climbing intensity.
2) Plants growing on the plateau are less impacted than those at the cliff base and on the face.
3) Different plant and land snail species are unequally affected by climbing activities. Species-specific responses of plants and snails can be explained by particular life-history traits (or combination of traits).

2. Material and methods

2.1. Study sites

The study was carried out at eight isolated limestone cliffs in the Northern Swiss Jura Mountains, 10–20 km S–SE of Basel (47° 35'N, 7° 35'E; Fig. S5). The cliffs are at elevations of 470–700 m above sea level and 1–25 km apart from each other (Table S1; Fig. S5). They mainly consist of Jurassic coral chalks (Bitterli-Brunner, 1987). The cliff bases are covered by stands of deciduous forests belonging to Fagetum and Tilietum associations (Burnand and Hasspacher, 1999). In this region, the annual temperature averages 9.6 °C and annual precipitation is 1021 mm (MeteoSwiss, 2012).

In the Jura Mountains, most of the cliffs are naturally subdivided by canyons, rock falls or steep forested slopes into several sectors. We investigated the plant and snail diversity in 35 cliff sectors belonging to the eight cliffs (Table S1).

For each cliff sector the following ecological variables were recorded: aspect of the cliff face (in degrees from north using a compass), elevation at the base (in metres above sea level, measured by a GPS receiver and checked against 1 : 25,000 topographical maps, geographical coordinates (measured with the GPS receiver), average height of the cliff (in m; data extracted from Andrey et al. 1997), and the length of the cliff sector (measured in m at the cliff base).

To assess the complexity of the rock surface (hereafter microtopography) in a cliff sector, we determined the number of fissures (any 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 roughly circular cavities extending into the rock surface) in 15 plots each measuring 50 cm × 50 cm. Three plots were arranged in a vertical line at heights of 1 m, 1.75 m and 2.5 m, and the five vertical lines were evenly distributed over the length of the cliff sector. We used a semi-quantitative scale of cumulative scores to express rock surface complexity 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, each plot received a score ranging from 0 (no structure in the rock surface) to 6 (highly structured rock surface). To characterize the microtopography of a cliff sector, we added the scores of the three plots in a vertical line resulting in total scores ranging from 0 to 18 and presented the mean score of the five vertical lines per cliff sector. Our measure of the rock face microtopography relates only to the lower part of the cliff (height 0.5–2.5 m). In contrast, the difficulty grade for climbing (see below) relates to the entire climbing route (length 12–30 m).

Information on the number of climbing routes (indicated by the presence of fixed protection bolts) and their difficulty grade for climbing (French scale) was obtained from Andrey et al. (1997). Information on climbing intensity (three categories) in the different cliff sectors was obtained from climbers (Knecht 1999): (0) no climbing, (1) low or moderate sport climbing activity (hereafter low climbing activity), and (2) intense sport climbing activitiy (hereafter high climbing activity). Unclimbed cliffs were mainly situated in nature reserves, in which climbing is not allowed. The categories low and high climbing intensity consider the number of climbing attempts per year on the various routes in each sector (Knecht 1999). High climbing activity means that a cliff sector is visited almost daily for climbing.

We measured the walking distance from the nearest parking area to each cliff sector using 1 : 5,000 topographical maps. As a proxy for cliff remoteness, we determined the travelling distance from the centre of the city of Basel (Spalentor) to the parking area of each cliff using Google maps route planner.

2.2. Plant survey and plant traits

Plant surveys were conducted in 2002–2007. The richness of vascular plants (presence/absence) was recorded at the base (a 5 m wide strip along the baseline of the cliff), on the face and on the plateau (a 5 m wide strip along the edge of the cliff face) of each cliff sector. To obtain the species richness in a standardized manner, the strip at the base, the face (with the help of binoculars) and the strip on the plateau were each searched for 45 min and all plant species were recorded, and identified following Binz and Heitz (1991).

In five sectors, the leaf litter layer at the cliff base was extremely thick (>20 cm), preventing the growth of any ground vegetation. The plateau of one sector was not accessible and in one sector the entire cliff face could not be surveyed. Thus, plant data were obtained from the base of 30 cliff sectors, the face of 34 sectors and the plateau of 34 sectors.

Information on threatened plant species was obtained from the Red List of Switzerland (Bornand et al., 2016). Data on rock specificity of plants were obtained from Wassmer (1998). Information on plant functional types (Grime, 2001) was extracted from the BiolFlor database (Klotz et al., 2002).

2.3. Snail survey and snail traits

We sampled snails in 2002–2007. We used two methods to assess the species richness and relative abundance of land snails at the base, in the lower part of the cliff face and on the plateau (a 3 m-wide strip along the edge of the cliff face) of each cliff sector. First, we searched visually for living snails and empty shells on the ground, in the leaf litter and under stones in a 2 m wide strip along the cliff base and on the rock face (to a height of 2.5 m) for 90 min. and on the plateau along the edge of the cliff face (3 m wide strip) for 30 min. in each cliff sector (Oggier et al., 1998). After species identification, we released living snails at the spot were they were found. Second, we collected soil samples including leaf litter (up to 2 cm depth, in total a volume of 3 l per cliff sector: 2 l at the cliff base and 1 l on the plateau). For the extraction of snails, samples were washed out using a set of sieves (mesh sizes 5 and 0.5 mm) and later examined under a binocular microscope. The combination of the two methods allows the detection of both large-sized taxa that often occur at low density and micro-species that are cryptic and litter-dwelling (Oggier et al., 1998). Slugs are not adequately sampled with this procedure and were not considered in this study. Nomenclature of snails followed Turner et al. (1998).

For data analyses, we combined data of living snails and empty shells of the same species, because in species with small shells we could not determine whether individuals were alive or dead when they were sampled. Furthermore, we combined data on snails collected at the base, on the face and the plateau, because empty shells of species exclusively living on the face and the plateau can be found at the cliff base.

Data on the snails' life-history traits (adult shell size, age at sexual maturity, longevity, egg size and clutch size) were obtained from Falkner et al. (2001) and Bengtsson and Baur (1993). Information on threatened snail species was obtained from the Red List of Switzerland (Rüetschi et al., 2012). Species were considered as threatened if they were listed as endangered, vulnerable or nearly threatened.

2.4. Data analyses

Climbing intensity was considered as a categorical predictor. Aspect of a cliff sector (direction in which the cliff faced) was assigned to one of four categorical predictors: north (N), east (E), south (S) and west (W). Cliff sectors with an intermediate aspect were assigned to the nearest main aspect. If the statistical analysis required a numerical input, then aspect was coded as a dummy variable. We considered elevation, height, length and microtopography of cliff sectors as well as the distance from each cliff sector to the nearest parking area and the distance from the city centre to the parking area as continuous predictors. As plant species richness was recorded in three different parts of each cliff sector (base, face and plateau; hereafter cliff habitat type), we considered cliff habitat type as a categorical predictor in the analyses of plant data. Cliff identity was used as a random factor in some statistical models.

For statistical analyses, the French scale of difficulty grade of climbing routes (e.g. 7b+) was replaced by a score ranging from 1 (lowest difficulty grade corresponding to 3a on the French scale) and 28 (highest difficulty grade corresponding to 8c+ on the French scale), and considered as a continuous predictor.

We used variance inflation factors (VIFs) to check collinearity of predictor variables. Analysis of variance (ANOVA), Tukey and chi-square tests were used to examine differences in abiotic and visitor-related characteristics among unclimbed cliff sectors and cliff sectors with low and high climbing intensity. We applied Constrained Analysis of Principal Coordinates (CAP; Anderson and Willis, 2003) with Sørensen distance to assess the overall separation of unclimbed cliff sectors and sectors with different climbing intensity using standardized variables. We ran an ANOVA-like permutation to test the significance of the separation of climbing routes under different climbing intensity.

Linear mixed-effects (LME) models were used to examine whether plant species richness and species richness and abundance of snails were influenced by climbing intensity and environmental variability (aspect, elevation, height, length and microtopography) of the cliff sectors. The best-fit models were selected using an information theoretic approach based on the Akaike Information Criterion corrected for the number of cases and parameters estimated (AICc) and Akaike weights (Garamszegi and Mundry, 2014). Delta AICc indicates the difference in the fit between a particular model considered and that of the best fit model. Models with delta AICc < 3 are shown in the Results section. AIC weight was calculated among all possible models.

The impact of climbing intensity on threatened species was assessed in two different ways. First, generalized linear mixed (GLM) models were applied to test the effect of climbing intensity on the richness of threatened species (richness of threatened species was modelled by using a Poission distribution, cliff identity was regarded as random factor, while climbing intensity was considered as categorical predictor). These analysis provided information on whether the number of threatened species was influenced by climbing intensity. Second, LME models were used to test whether the proportion of threatened species (number of threatened species in relation to the total number of species in a particular sector) was impacted by climbing intensity. In this approach the proportion of threatened species was modelled using a Gaussian distribution, cliff identity was regarded as random factor, while climbing intensity was considered as categorical predictor. This analysis provided information on whether the response of threatened species was similar to that of the remaining (not threatened) species. Similar LME models were used to examine whether the proportion of plant species with a particular trait was influenced by climbing intensity.

We used constrained analysis of principal coordinates to examine whether the species composition of plant and snail communities differed among cliff sectors with different climbing intensity. We ran ANOVA-like permutations to test for a significant separation of cliff sectors with different climbing intensities.

Correlation analysis showed that adult shell size, age at sexual maturity, longevity, egg size and clutch size of snails were all intercorrelated (in all cases, $P < 0.001$). Consequently, we used adult shell size as a surrogate for all other life-history traits in snails.

Analyses were run in the R statistical environment (R Core Team, 2016) using the *car* (Fox and Weisberg, 2011), *faraway* (Faraway, 2016), *lme4* (Bates et al., 2015), *MASS* (Venables and Ripley, 2002), *nlme* (Pienheiro et al., 2016), *multcomp* (Hothorn et al., 2008), *MuMIn* (Barton, 2016), and *vegan* (Oksanen et al., 2016) packages.

3. Results

3.1. Abiotic and visistor-related characteristics of cliff sectors

Unclimbed cliff sectors and sectors with either low or high climbing intensity did not differ in cliff face aspect ($\chi^2 = 8.214$, df = 6, $P = 0.221$), cliff height (ANOVA, $F_{2,32} = 0.853$, $P = 0.435$) and microtopography (ANOVA, $F_{2,32} = 2.775$, $P = 0.077$). However, cliff sectors with different climbing activities differed in elevation of where they were located (ANOVA, $F_{2,32} = 4.311$, $P = 0.022$). This was mainly because unclimbed cliff sectors were at higher elevations (average elevation 636 m) than cliff sectors with high climbing activity (average elevation 546 m) (Tukey test: estimate = -90.67, s.e. = 31.72, $t = -2.858$, $P = 0.019$).

Unclimbed cliff sectors and sectors with low and high climbing intensity did not differ in distance from the nearest parking area (ANOVA, $F_{2,32} = 0.913$, $P = 0.411$), but differed in distance from the city (ANOVA, $F_{2,32} = 6.666$, $P = 0.004$). Unclimbed cliff sectors were farthest from the city (mean distance 26.6 km), while cliff sectors with low and high climbing intensity were situated closer to the city (21.3 and 18.3 km, respectively). Considering all abiotic and visitor-related characteristics together, CAP revealed that there were no overall differences among cliff sectors with no, low and high climbing activities (ANOVA-like permutation: $F = 1.374$, $P = 0.209$).

Finally, ANOVA showed that the difficulty grades of climbing routes were lower in cliff sectors with high climbing intensity compared to those of routes in sectors with low climbing intensity (ANOVA, $F_{1,390} = 16.595$, $P < 0.001$), suggesting that fewer sport climbers try and master the extremely difficult routes.

3.2. Species richness of vascular plants

Altogether 240 vascular plant species were recorded (Table S2), 203 species at the cliff base, 171 on the face and 197 on the plateau. Plant species richness ranged among sectors from 40 to 143 species (mean 93.4). The cliff bases and plateaus hosted more species (mean: 58.8 and 57.7 species per cliff sector, respectively) than the faces (45.2 species per cliff sector; ANOVA, $F_{2,95} = 6.576$, $P = 0.002$).

The best fit model (with the lowest AICc) revealed that plant species richness was influenced by climbing intensity, aspect and length of the cliff sector and by the type of cliff habitat (Table 1A). Alternative and still pausible statistical models emphasized the importance of several predictors, and particularly the effect of cliff habitat type. We therefore analyzed plant community data for each habitat type separately.

At the base of the cliffs, plant species richness was affected by climbing intensity and cliff aspect in the best fit model (Table 1B). Multiple comparisons showed that unclimbed cliff sectors harboured the highest species richness and cliff sectors with low climbing intensity had lower richness (Fig. 1A). Compared to unclimbed cliff sectors, plant richness at the base was 12.2% less in low climbing intensity sectors and 13.1% less in high climbing intensity sectors. Species richness was highest at the base of south- and west-facing sectors and lowest at the base of north-facing sectors (Fig. S6). Some alternative statistical models also highlighted the importance of cliff height (Table 1B).

On the face of the cliffs, the most likely statistical model revealed that plant species richness was only influenced by climbing intensity (Table 1C). Compared to unclimbed cliff sectors, plant species richness was significantly reduced by 24.3% in cliff sectors with low climbing intensity and by 28.1% in cliff sectors with high climbing intensity (Fig. 1). Alternative statistical models also indicated the importance of the height, length and microtopography of the cliff sectors and the elevation at which they are situated (Table 1C).

On the plateaus, species richness was influenced by the length of the cliff sectors and their elevation in the best fit model (Table 1D), but not by climbing intensity (Fig. 1). Climbing intensity was also not considered in alternative statistical models (Table 1D).

Nine of the 240 plant species (3.8%) are of conservation importance. The number and proportion of Red-listed plant species were reduced by climbing intensity on the cliff face (number of Red-listed [RL] plants: GLM: ANOVA, $\chi^2 = 6.604$, df = 2, $P = 0.037$; proportion of RL-plants: LME, ANOVA, $F_{2,21} = 3.562$, $P = 0.044$), but not at the cliff base (number of RL-plants: GLM, ANOVA, $\chi^2 = 3.566$, df = 2, $P = 0.037$; proportion of RL-plants: LME, ANOVA, $F_{2,21} = 0.976$, $P = 0.393$).

3.3. Species richness and abundance of land snails

In total, 44,416 individuals representing 66 land snail species were recorded in the 35 cliff sectors (Table S3). Species richness of land snails was highest in cliff sectors with no rock climbing activity (Fig. 1B). Compared with these control sectors, species richness was 2.0% less in sectors with low climbing intensity and 13.7% less in sectors with high climbing intensity. The best fit model (with the lowest AICc) revealed that species richness was only affected by climbing intensity (Table 2). Delta AICc values and Akaike weights did not support any alternative model (Table 2). Multiple comparisons showed that snail species richness differed between cliff sectors with no climbing (control areas) and those with high climbing intensity (Fig. 1B).

The best fit models revealed that the abundance of land snails was affected by climbing intensity and microtopography (Table 2). Multiple comparisons showed that cliff sectors with low climbing intensity supported lower snail abundance than sectors with no climbing (Fig. S7). However, sectors with high climbing intensity did not differ significantly from sectors with no climbing and low climbing intensity. The best fit model also showed that snail abundance increased with microtopographical complexity of the rock face (Table 2, Fig. S8). Alternative but still plausible statistical models (Table 2) revealed that not only climbing intensity and microtopography, but also the size of climbing sectors (indicated by the length at the base) may influence snail abundance, although the relationship between abundance and sector length was not significant (Fig. S9).

Thirteen of the 66 snail species (19.7%) are of conservation importance. However, the proportion of Red-listed snail species was not affected by climbing intensity (LME: ANOVA, $F_{2,21} = 1.129$, $P = 0.339$).

3.4. Community composition

Constrained analysis of principal coordinates showed that cliff sectors with different climbing intensities differed in plant and snail species compositions (Fig. 2; ANOVA-like permutations, plants: $F_{2,95} = 3.743$, $P < 0.001$; snails: $F_{2,32} = 4.291$, $P < 0.001$). The compositions of the plant communities in sectors with different climbing intensity was separated by the first CAP-axis (Fig. 2A), that of the snail communities by the first two CAP-axes (Fig. 2B).

3.5. Climbing intensity-related changes in traits

The proportion of rock-specific plant species found on the cliff face was influenced by climbing intensity (LME: ANOVA, $F_{2,24} = 3.533$, $P = 0.045$). Pairwise comparisons revealed that cliff faces in sectors with low and high climbing intensity harboured slightly but not significantly reduced proportions of rock-specific plants than did faces of unclimbed sectors (Fig. S10). No climbing-related differences in proportion of plant species with rock specificity were recorded at the cliff base (LME: ANOVA, $F_{2,21} = 0.956$, $P = 0.400$).

Considering plant functional types, the proportion of stress-tolerant species (S-strategists) was affected by climbing intensity at the base (LME: ANOVA, $F_{2,21} = 3.733$, $P = 0.041$) and on the face of cliffs (LME: ANOVA, $F_{2,24} = 4.766$, $P = 0.018$). In both habitat types, the proportion of S-strategists was lower in cliff sectors with high climbing intensity (Fig. 11A). The proportions of C-, R-, and CSR-strategists appeared not to be influenced by climbing intensity (Fig. 11B).

The average shell size of snail species recorded in cliff sectors decreased with climbing intensity (LME: ANOVA, $F_{2,25} = 4.143$, $P = 0.028$). Cliff sectors with high climbing intensity had species with significantly smaller shells than sectors with low climbing intensity or no climbing (Fig. S12).

4. Discussion

Our study showed that climbing intensity affected the extent of damage to plant and land snail communities on limestone cliffs. In both groups of organisms the reduction in species richness was more pronounced in cliff sectors with high climbing intensity than in sectors with low climbing intensity.

The three categories of climbing intensity used in our study are coarse. Nonetheless, the extent of climbing-related damage increased as climbing intensity increased. The only abiotic difference between unclimbed cliff sectors and sectors with low or high climbing intensity was that the former were situated at a higher elevation. All other abiotic variables (aspect, microtopography, cliff height and length) did not differ significantly among the three categories. This is important because potential differences in aspect and microtopography between climbed and unclimbed cliffs have been considered as an alternative explanation for reported differences in species richness between the two types of cliffs (Holzschuh, 2016).

Climbing intensity was higher in cliff sectors with routes of low and moderate difficulty than in sectors with extremely difficult routes. This is probably because fewer climbers climb extremely difficult routes. During weekdays, numerous climbers like to spend some hours climbing in the late afternoon or evening and may therefore prefer cliffs that can be reached with a short travel time. Indeed, climbed cliffs were located closer to the city than unclimbed cliffs.

4.1. Plants

Several studies have demonstrated negative effects of sport climbing on cliff vegetation (reviewed by Holzschuh, 2016). However, the present study is to our knowledge the first that considered diverse impacts of different climbing intensities on the extent of damage to the vegetation.

Climbing-related damage to vegetation was differenly expressed in different cliff habitats. We found no differences in plant diversity and species composition between the plateaus of climbed and unclimbed cliff sectors, presumably because the plateaus are normally not accessed by climbers. In contrast, at the cliff base, trampling by climbers and the people securing the climbers reduces both the vegetation cover and litter layer (Fig. S2). At the base of several cliffs even trampling-tolerant plant species had been unintentionally introduced (Rusterholz et al., 2011). Reduction of plant species richness was most pronounced on cliff faces. Species with high rock specificity appear to suffer most from disturbance, becoming locally extinct on climbing routes. The repeated removal of plants and soil from crevices prevents a re-colonization. March-Salas et al. (2018) also reported a climbing-related reduction in plant species richness, which was mainly a result of a decrease in generalist but not specialist species on climbing routes. Various possibilities should be considered when interpreting contrasting findings. The studies may differ in rock type, spatial scale of the investigation, range of climbing intensity, regional climate and composition of the plant and animal communities. The reduction in the proportion of stress-tolerant plant species found on the cliff faces of our study indicates that these plant species are adapted to extreme abiotic conditions (low nutrient conditions, high temperature variation), but might be vulnerable to mechanical disturbance by climbers.

4.2. Snails

Limestone cliffs provide a variety of 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 and in fissures, pockets and shallow crevices 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 exists exclusively on rock faces (i.e., rock-dwelling species). These snails are resistant to drought and their specialized radulae enable them to graze epi- and endolithic lichens and cyanobacteria growing on rock faces (Baur et al., 1992; Baur et al., 1994; Fröberg et al., 2011). The snails are active during periods of high air humidity, otherwise they rest attached to the exposed rock surface or in small fissures (Baur and Baur, 1991). These snails are exposed to the risk of being crushed by climbers, which results in reduced density in climbed areas (Baur et al., 2017). Our results showed that both species richness and abundance of land snails were negatively affected by sport climbing and that the impact increased with climbing intensity.

The sensitivity of an organism to the type of disturbance exerted by climbers may be related among other things to its size and, in animals, to their behaviour. Sport climbing is mainly performed under dry conditions, which correspond to periods when the snails are resting. Therefore, the size of the snails and their resting site preference might be of importance. Baur et al. (2017) showed that species with small shells were less sensitive to disturbance, as were species that preferred to rest in small fissures and underneath overhangs, i.e. in microsites that are not touched by climbers. Species with large shells (adult shell height 7.2–10.8 mm) and a preference for resting on smooth rock faces, showed a more pronounced decrease in abundance. Similarly, in our study the average shell size of snail species occurring on cliffs decreased with increasing climbing intensity.

5. Conclusions and management implications

Cliff faces are among the few remaining habitats on earth that are largely unchanged by direct human disturbance (Larson et al., 2000). Cliffs harbour unique communities of highly specialized plants and animals, many of them rare and threatened. The increase in popularity of sport climbing, however, is bringing greater numbers of people to these previously untouched cliffs (Holzschuh, 2016).

Our study showed that rock climbing significantly reduces the species richness of both plants and land snails and that the impact increases with climbing intensity. It is, however, questionable whether a reduction of climbing intensity is a suitable measure to minimize damage to plants and animals, because decreased species richness was even recorded at low climbing intensity. Our results suggest that that the prohibition of sport climbing on cliffs or cliff sectors with a high number of specialized plant and invertebrate species and the establishment of climbing-free protection zones in popular areas are the most effective and necessary 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 with the aim of educating the climbers and increasing their compliance with such measures.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://xxxxxxx

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Table 1

Best fit LME models explaining the species richness of vascular plants in sectors with different climbing intensity for entire cliff sectors (A), and for the cliff base (B), face (C) and plateau (D) separately. Only models with delta AICc < 3 are displayed.

Predictors	df	AICc	delta	weight
A: *entire cliff sectors*				
climbing + aspect + habitat + cliff length	11	799.0	0.00	0.096
climbing + habitat type	7	800.1	1.07	0.056
aspect + habitat type + cliff length	9	800.3	1.31	0.050
climbing + elevation + aspect + habitat type + cliff length	12	800.6	1.60	0.043
climbing + elevation + habitat type + cliff length	9	800.7	1.71	0.041
climbing + aspect + habitat type	10	801.0	1.95	0.036
climbing + elevation + habitat type	8	801.0	1.97	0.036
climbing + aspect + habitat type + cliff length + microtopography	12	801.1	2.07	0.034
habitat type	5	801.2	2.18	0.032
climbing + habitat type + cliff length	8	801.3	2.25	0.031
climbing + elevation + habitat type + cliff height + cliff length	10	801.3	2.32	0.030
climbing + aspect + habitat type + cliff height + cliff length	12	801.6	2.60	0.026
climbing + habitat type + cliff height	8	801.7	2.72	0.025
B: *cliff base*				
climbing + aspect	8	243.5	0.00	0.186
cliff height	4	244.5	0.91	0.118
climbing + cliff height	6	244.8	1.30	0.097
aspect	6	245.2	1.65	0.082
climbing + aspect + cliff height	9	245.9	2.35	0.058
climbing + elevation + cliff height	7	246.0	2.44	0.055
elevation + cliff height	5	245.2	2.65	0.050
aspect + cliff height	7	246.5	2.97	0.042
C: *cliff face*				
climbing	5	259.4	0.00	0.208
(only intercept model)	3	270.9	1.54	0.096
climbing + cliff length	6	271.2	1.84	0.083
climbing + cliff height	6	271.5	2.11	0.072
cliff length	4	272.1	2.71	0.057
climbing + elevation	6	272.3	2.89	0.049
climbing + microtopography	6	272.3	2.89	0.049
D: *cliff plateau*				
elevation + length	5	298.1	0.00	0.301
length	4	299.2	1.15	0.169
(only intercept model)	3	299.4	1.36	0.152
elevation	4	300.8	2.72	0.077
elevation + height + length	6	301.0	2.89	0.071

Table 2

Best fit LME models explaining the species richness and abundance of land snails in cliff sectors with different climbing intensity. Only models with delta AICc < 3 are displayed.

Response variable	Predictors	df	AICc	delta	weight
species richness	climbing	5	200.6	0.00	0.319
	climbing + microtopography	6	203.1	2.41	0.096
	climbing + cliff height	6	203.4	2.78	0.079
	climbing + elevation	6	203.5	2.82	0.078
	climbing + cliff length	6	203.5	2.87	0.076
abundance	climbing + microtopography	6	541.0	0.00	0.116
	climbing	5	541.5	0.59	0.087
	climbing + cliff length	6	541.7	0.71	0.082
	microtopograpgy	4	542.6	1.61	0.052
	climbing + cliff length + microtopography	7	542.6	1.62	0.052
	cliff length	4	543.0	2.06	0.041
	climbing + cliff length + microtopography	7	543.1	2.12	0.040
	(only intercept model)	3	543.3	2.31	0.037
	climbing + cliff height + cliff length	7	543.4	2.40	0.035
	cliff lenght + microtopography	5	543.4	2.40	0.035
	climbing + elevation + microtopography	7	543.7	2.71	0.030
	climbing + cliff height	6	543.8	2.84	0.028

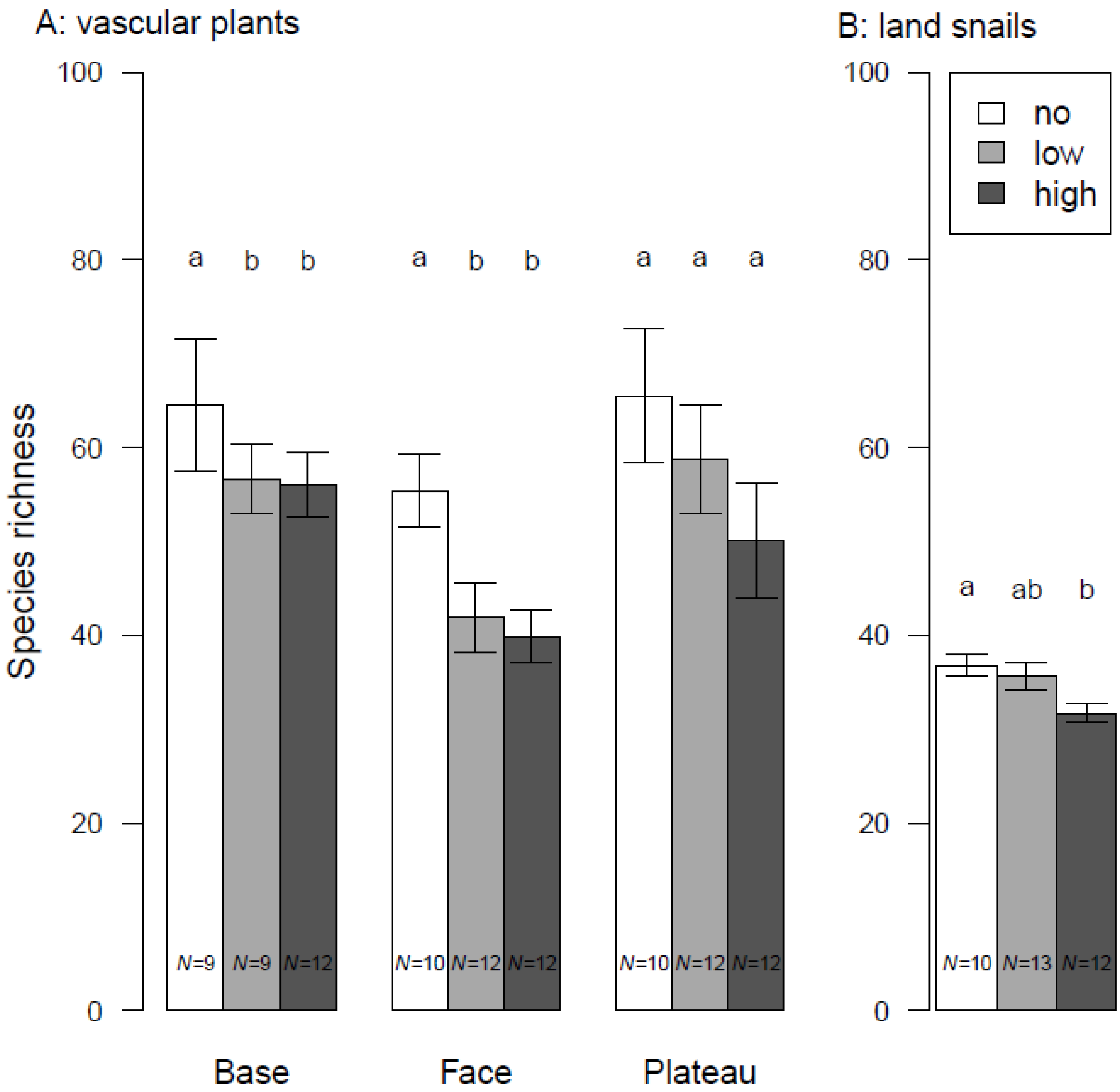

Fig. 1. Effect of climbing intensity on the species richness of vascular plants in different parts of cliffs (A), and of land snails on the entire cliffs (B). Bars indicate mean values, whiskers standard errors. Different letters indicate significant differences between climbing levels (Tukey test, Bonferroni-adjusted *P* value at $P = 0.05$).

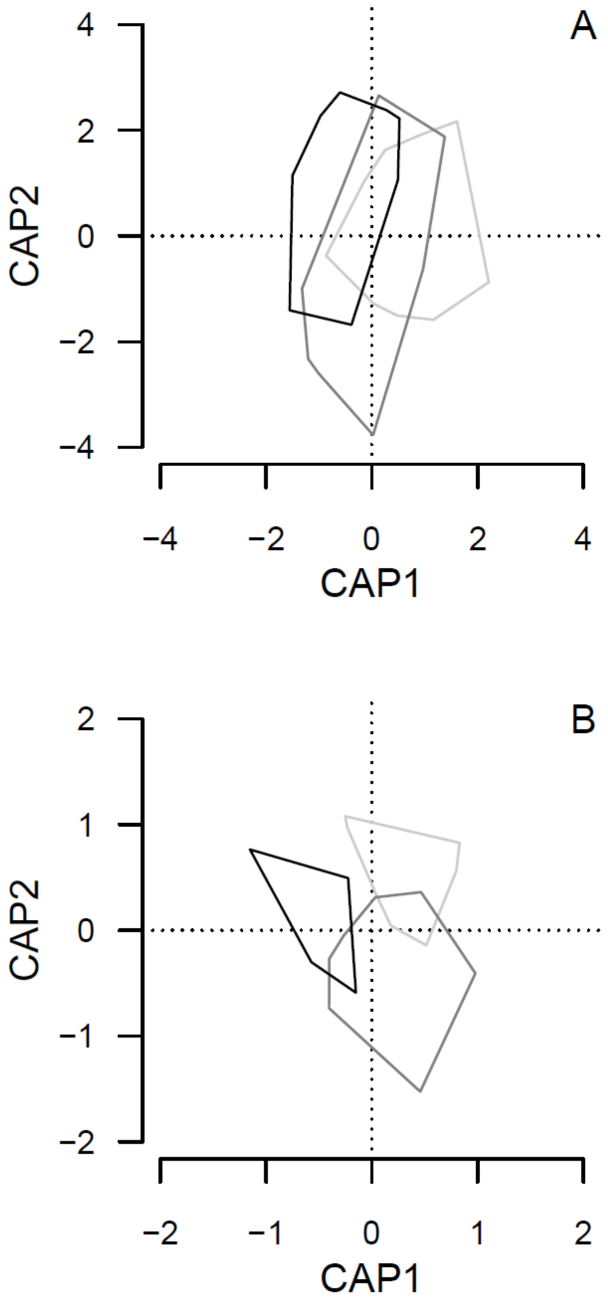

Fig. 2. Results of constrained analyses of principal coordinates visualizing similarities in the species compositions of plants (A) and land snails (B) in cliff sectors with no climbing (light grey), and in sectors with low (dark grey) and high (black) climbing intensity.