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Impact assessment of intense sport climbing on limestone cliffs: response of rock-dwelling land snails

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ABSTRACT

Exposed limestone cliffs in the Swiss Jura Mountains harbour a diverse gastropod community with some rare species. Sport climbing has recently increased in popularity on these cliffs. We examined the effects of sport climbing and microtopographical features of rock faces on terrestrial gastropods by assessing species diversity and abundance on climbing routes and in unclimbed areas of seven isolated cliffs in the Northern Swiss Jura Mountains. We considered exclusively living individuals resting attached to rock faces. In total, 19 gastropod species were recorded. Six of them were specialized rock-dwelling species, whose individuals spend their entire life on rock faces, feeding on algae and lichens. Plots along climbing routes harboured fewer species of rock-dwelling snails as well as other gastropod species (usually living in the leaf litter layer at the cliffs' base) than plots in unclimbed control areas. Similarly, both the density of individuals and frequency of occurrence in plots were reduced in both groups of snails on climbing routes. The complexity of the rock surface had little influence on the species richness and abundance of gastropods. *Pyramidula pusilla*, the species with the smallest shell and a preference to rest underneath overhangs, was less affected by sport climbing than snail species with larger shells and a preference to rest on exposed smooth rock surface. Our findings indicate land snail diversity and abundance are suitable indicators for impact assessment in rocky habitats. Future management plans and actions should therefore not only rely on plants; they ought to consider also gastropods and other invertebrates. 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.

Keywords: Biodiversity, Climbing, Disturbance, Gastropod, Impact assessment

1. Introduction

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). 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, which have been partly cleared and subsequently used as pasture for some centuries (Moor, 1972; see also Fig. S1). In this landscape, the rocky habitats represent islands of special environmental conditions (Wilmanns, 1993). 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). 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).

During past decades, however, recreational activities including sport climbing, bouldering (a form of rock climbing on boulders), hiking, and mountain biking, are increasingly threatening the sensitive cliff biota. Rock climbing is popular in these mountain areas at low elevation, 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 the Jura mountains 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 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 reduced the aboveground 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) examined living snails and empty shells in soil samples from climbed and unclimbed cliff sections at the edge, cliff face and talus of the Niagara escarpment. They did not distinguish between different groups of snails, but found that species richness and density of snails were lower along climbing routes than in unclimbed areas, and that snail community composition differed between climbed and unclimbed sites.

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 and in fissures, solution 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 very 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, 1994, 2000; Fröberg et al., 2001, 2011). The snails are active during periods of high air humidity, otherwise they rest attached to the exposed rock surface or in small fissures (Neuckel, 1981; Baur and Baur, 1991). 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. Several other gastropod species occur in the leaf litter layer and ground vegetation at the cliffs' bases. In these species some individuals forage occasionally on algae on rock faces and may rest attached to the rock surface during periods of drought.

In our study, we examined whether intense sport climbing and microtopographical features of the rock face affect gastropod species richness and abundance on limestone cliffs. We used a design that considered different cliffs with multiple climbing routes and corresponding control areas. We exclusively considered living individuals resting attached to the rock faces avoiding any bias due to empty shells dislocated from other (micro-)habitats. We analysed species richness and abundance separately for true rock-dwelling species and for gastropod species whose individuals only occasionally occur on rock faces. In particular, we addressed the following questions:

1) Are species richness, species density and abundance of terrestrial gastropods on cliffs affected by intensive sport climbing activities and by the structure of the rock face?
2) Are different gastropod species differently influenced by sport climbing?
3) Do different gastropod species differ in their preferences for resting sites on rock faces and do these preferences differ between climbed and unclimbed rock faces?
4) Can rock-dwelling land snails be used as an indicator group for impact assessment?

2. Materials and methods

2.1. Study sites

The study was carried out in the lower parts of seven isolated limestone cliffs in the northern Swiss Jura mountains 10–15 km S–SE of Basel (47º 35'N, 7º 35'E; Fig. S1). The cliffs are situated at elevations ranging from 470 to 700 m above sea level and they are 1–13 km apart from each other (Table S1). They mainly consist of Jurassic coral chalks (Bitterli-Brunner, 1987). The characteristic plant community of the predominantly east- to south-facing cliffs belongs to the Potentillo-Hieracietum association (Wassmer, 1998). The cliff bases are covered by different stands of deciduous forests belonging to Fagetum and Tilietum associations (Burnand and Hasspacher, 1999). In this region, the annual temperature averages 9.6 ^{o}C and the annual precipitation is 1021 mm (MeteoSwiss, 2012).

2.2. Field survey

We recorded the number of individuals of each species in plots set up on sport-climbed cliff faces and on undisturbed rock faces (control areas) on the same cliffs in May–September 2005. We placed three 50 cm x 50 cm plots in a vertical line with an interplot distance of 20–30 cm in selected sport climbing routes (indicated by fixed protection bolts) at a height of 0.3–2.5 m (Fig. S2). Using the same spatial arrangement, we placed another three sampling plots at a horizontal distance of 10–30 m from each focal climbing route in an unclimbed part of the same cliff face (hereafter unclimbed control area). The following criteria were used to select the unclimbed control areas: (1) both the climbing route and control area had the same aspect, (2) they were situated within 10–30 m of each other, (3) received the same insolation, (4) did not differ in forest management at the cliff base, and (5) did not differ in rock surface complexity (see below). Five pairs of climbing routes and control areas were examined at each cliff and the same procedure was repeated at seven cliffs (Table S1) resulting in a total of 210 sampling plots (105 plots in climbing routes and 105 in the corresponding control areas).

In each plot, we carefully examined the rock surface, fissures and pockets for attached gastropods using a magnifying glass (3x). We surveyed plots only in dry weather and considered exclusively living snails resting attached to the rock surface (Fig. S3, S4). After species identification, 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 aspect of the cliff face (in degrees from north) in each climbing route and control area. The elevation of the cliff's base was obtained from topographical maps. 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 cavities extending into the rock surface) in each plot. 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 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 0.3–2.5 m), i.e. to the area in which the resting gastropods were examined. In contrast, the difficulty grade for climbing relates to the entire climbing route (length 12–30 m).

Information on the year of first ascent and difficulty grade for climbing (French scale) of the routes was obtained from Andrey et al. (1997). Most of the investigated climbing routes were installed between 1980 and 1994 and range in difficulty grade from 4 (moderately difficult) to 7b (extremely difficult). Rock-surface complexity in the lower part (0.3–2.5 m) of the climbing routes was not correlated with the difficulty grade of the corresponding route (Spearman $r_s = -0.184$, $n = 35$, $P = 0.29$). However, the difficulty grade of a climbing route was negatively correlated with the age of the route (r_s = –0.406, *n* = 32, *P* = 0.021); older routes are easier to climb than recently established routes.

Climbed and control plots examined did not differ in the complexity of the rock surface (Welch two-sample *t*-test, *t* = 0.307, *n* = 210, *P* = 0.76). Furthermore, climbed and unclimbed plots did not differ in aspect (Rayleigh circular test of uniformity of differences in aspect of paired climbed and control plots around 0; test statistics = 0.856, *P* = 0.72), confirming that there was no bias in plot selection.

To examine whether the most abundant snail species differ in their preference for resting sites on the cliff faces, we recorded characteristics of their resting sites both on climbing routes and in unclimbed areas on four cliffs. The resting sites of *Chondrina avenacea*, *Abida secale*, *Pyramidula rupestris*, *Clausilia rugosa parvula* and *Cochlostoma septemspirale* were assigned to one of the following four groups: on exposed smooth vertical rock surface, underneath overhangs, in fissures, and in pockets. On climbing routes, the resting sites preferences were recorded for 1022 individuals, in unclimbed areas for 1037 individuals.

2.3. Data analyses

Analyses were conducted at two spatial levels. First, we considered individual plots (*n* = 210) as units of analysis (hereafter plot level). Second, we considered individual climbing routes and control areas (*n* = 70) as units of data analysis (hereafter route level). In these analyses, data from the three plots per route or control area were pooled. All data analyses were also conducted separately for true rock-dwelling snail species, whose individuals spend their entire life on rock faces (see Neuckel, 1981; Fröberg et al., 1993) and for the other gastropod species, whose individuals forage and rest only occasionally on rock faces.

At the plot level, generalized linear mixed-effects models (GLMMs) with Poisson distribution were used to examine whether species density (number of gastropod species recorded per plot) or individual density (number of individuals recorded per plot) of rock-dwelling and other gastropod species were affected by sport climbing (used as categorical predictor: climbing route or control area) and the complexity of the rock surface (used as continuous predictor). Cliffs (*n* = 7) and climbing routes (*n* = 5 in each cliff) were used as random factors (route nested in cliff). The minimal adequate model was selected based on Akaike's Information Criterion (AIC).

We also examined how individual species were affected by climbing and rock surface complexity. We transformed individual density data of single species to incidence data because the frequency of occurrence was extremely low in most species. Only five species occurred in at least 25% of the plots examined. We used generalized linear mixed-effects models (GLMMs) with binomial distribution to examine how the occurrence of these five species was influenced by single and joint effects of climbing (categorical predictor) and complexity of the rock surface (continuous predictor). The minimal adequate model was selected based on Akaike's Information Criterion (AIC).

At the route level, linear models (LMs) were used to examine whether species richness and the number of individuals of rock-dwelling and other gastropod species responded to single and joint effects of climbing (categorical predictor) and rock surface complexity (continuous predictor). We also investigated whether individual species were influenced by climbing and rock surface complexity at the route level. In these LMs, the log(x+1) transformed number of individuals of either of the two frequently occurring rock-dwelling species (*A. secale* and *C. rugosa parvula*) was used as response variable, while the single and joint effects of climbing (climbing route vs. control area) and rock surface complexity (the sum of the values of the three plots in the same route) were considered as predictors. Similarly to the plot level, only five species occurred in at least 25% of the routes and control areas (*n* = 70). The numbers of individuals recorded in these five species were transformed to incidence data and generalized linear models (GLMs) with binomial distribution were applied as described at the plot level.

The potential influence of the difficulty grade of a climbing route on both the number of rock-dwelling and other gastropod species and on the number of individuals of either group was examined by using Spearman rank correlation (control areas were not considered in these analyses). The age of the climbing routes was not further considered because of the intercorrelation with the difficulty grade of the corresponding climbing route (see above).

The Monte Carlo method was applied to examine the resting site preference of snails (Manly 2007). For each species found on climbing routes and in control areas, the observed number of individuals was randomly assigned to one of the following microhabitats: smooth vertical rock surface, underneath overhangs, fissures, or pockets. We repeated this procedure 10,000 times and defined the true 95% confidence interval of the generated distribution. Microhabitats were regarded as preferred if the observed number of individuals of a species fell within the upper 2.5% of the generated distribution. In contrast, a microhabitat was regarded as non-preferred if the observed number of individuals fell within the lower 2.5% of the generated distribution. We applied contingency tests to examine whether gastropod species differed in their distributions of resting sites between climbed and unclimbed rock faces.

Data analyses were run in the R statistical environment (R Core Team, 2015) using the *CircStats* (Lund and Agostinelli, 2012), *circular* (Agostinelli and Lund, 2013) and *lme4* (Bates et al., 2015) packages.

3. Results

3.1. Species richness and frequency of occurrence

In total, 4022 individuals representing 19 species (18 snails and one slug) were recorded on the 35 climbing routes and in the corresponding control areas (Table 1). Eight species (830 individuals) were found on the climbing routes, 18 species (3192 individuals) in the control areas (Table 1). The gastropod community was dominated by five rock-dwelling species (altogether 90.8% of the individuals; in decreasing order of abundance: *Pyramidula pusilla* 70.6%, *Chondrina avenacea* 11.5%, *Abida secale* 4.9%, *Clausilia rugosa parvula* 3.6%, *Neostyriaca corynodes* 0.4%). Among the other gastropod species, only *Cochlostoma septemspirale*, individuals of which frequently graze algae from rock surfaces and tree stems, was abundant (8.0% of all indidivuals). The remaining 13 species were recorded in low numbers (1–12 individuals; Table 1).

At the plot level, only the four rock-dwelling species *P. pusilla*, *C. avenacea*, *A. secale* and *C. rugosa parvula* and another species (*C. septemspirale*) were found in 52 or more of the plots examined (≥ 25% of the plots). The remaining species were rare, occurring in 1 to 14 of the 210 plots (< 7% of the plots). At the route level, only two rock-dwelling species (*P. pusilla* and *C. avenacea*) were found in more than 50% of the climbing routes and control areas. Three species, two rock-dwelling snails (*A. secale* and *C. rugosa parvula*) and *C. septemspirale*, were found in more than 25% of the climbing routes and control areas.

3.2. Effect of climbing and rock-surface complexity

At the plot level, the minimal adequate GLMM revealed that climbing had a significant negative effect on the species density of rock-dwelling snails (estimate = –1.861, s.e = 0.123, t = –15.118, $P < 0.001$), while the effect of rock surface complexity was marginally not significant (estimate = 0.123, SE = 0.060, t = 1.867, P = 0.064, Fig. 1a). The interaction between climbing and rock surface complexity was removed during the model selection procedure. Similarly, the minimal adequate model showed that climbing negatively influenced individual density of rock-dwelling species (estimate = –19.846, SE = 2.620, t = –7.435, $P <$ 0.001; Fig. 1c). Rock-surface complexity as well as the interaction between climbing and rock complexity were removed during model selection.

The species density of the other gastropods was negatively influenced by climbing (estimate = –0.732, SE = 0.069, t = –10.469, $P < 0.001$). The model also showed a weak (non-significant) influence of rock surface complexity (estimate = 0.088, SE = 0.048, t = 1.835, P = 0.068) and a marginally non-significant interaction between climbing and rock surface complexity (estimate = –0.130, SE = 0.067, t = –1.924, P = 0.056; Fig. 1b). Finally, the minimal adequate model explaining the individual density of all other gastropod species included a significant negative effect of climbing (estimate = –3.001, SE = 0.356, t = –8.421, P < 0.001), a positive effect of rock complexity (estimate = 0.524, SE = 0.255, t = 2.053, P = 0.041) and a negative interaction between climbing and rock surface complexity (estimate = –0.712, SE = 0.357, t = –1.998, P = 0.047; Fig. 1d).

Analyses performed at the route level revealed similar results. Climbing negatively affected the species richness (LM: estimate = –2.343, SE = 0.229, t = –10.200, P < 0.001) and number of individuals (estimate = –58.460, SE = 16.140, t = –3.622, P < 0.001) of rock-dwelling gastropods (Fig. 2a,c). The other factors were removed during the model selection procedure. Species richness of rock-dwelling snails on a climbing route was on average only 37.8% of that of a control area (Fig. 2a). The number of rock-dwelling individuals on a climbing route was only 28.4% compared to that in a control area (Fig. 2c). Similarly, climbing negatively influenced the species richness (LM: estimate = –1.228, SE = 0.189, t = –6.504, P < 0.001) and number of individuals of other gastropods (estimate = –9.029, SE = 2.000, t = –4.514, P < 0.001; Fig. 2b,d). The other factors were removed during the model selection procedure. Species richness of other gastropods in climbing routes averaged 10.4% of that in control areas (Fig. 2b), while the number of individuals in climbing routes was only 5.4% of that in control areas (Fig. 2d).

3.3. Difficulty grade of climbing routes

The difficulty grade of climbing routes was neither correlated with the number of rock-dwelling snail species (Spearman r_s = –0.167, n = 35, P = 0.34) nor with the number of other gastropod species recorded in the routes (r_s = –0.110, n = 35, P = 0.53). Similarly, no correlations between the difficulty grade of climbing routes and the number of individuals of either rock-dwelling snails or other gastropods were found (r_s = –0.115, n = 35, P = 0.51 and r_s

= –0.128, *n* = 35, *P* = 0.46, respectively).

3.4. Species-specific responses to climbing

At the plot level, GLMMs revealed that climbing negatively affected the occurrence of all five species examined (Table 2). Similarly, at the route level, the occurrences of all species examined were negatively influenced by climbing, while other factors were removed during the model selection (Table 3). Climbing also negatively influenced the numbers of individuals in *P. pusilla* (LM: estimate = –1.661, SE = 0.411, $t = -4.045$, $P < 0.001$) and *C. avenacea* (estimate = –0.995, SE = 0.239, $t = -4.149$, $P < 0.001$). In both cases, other factors were removed during model selection.

3.5. Species-specific resting site preferences

The resting-site preference of 2059 individuals belonging to five species was examined in climbing routes and control areas (Fig. 3). Monte Carlo simulations revealed that all five species showed a preference for using a particular microtopographical structure for resting (Fig. 3). All species except *P. pusilla* rested most frequently on smooth vertical rock surfaces; *P. pusilla* rested most frequently underneath overhangs both on climbing routes and in control areas (Fig. 3). In three of the five species, the distributions of resting sites did not differ between climbed rock faces and unclimbed faces (*A. secale:* $\chi^2 = 5.146$, $df = 3$, $P = 0.16$; *C. avenacea:* $\chi^2 = 2.616$, $df = 3$, $P = 0.46$; *C. rugosa parvula:* $\chi^2 = 0.308$, $df = 2$, $P = 0.86$). In *P. pusilla*, however, snails rested less frequently on the exposed smooth rock face on climbing routes than in control areas (Fig. 3; $\chi^2 = 188.03$, $df = 3$, $P < 0.001$). Similarly, individuals of *C. septemspirale* tended to rest less frequently on the exposed smooth rock face on climbing routes than in control areas ($\chi^2 = 7.659$, $df = 3$, $P = 0.054$).

4. Discussion

Our study showed that sport climbing significantly reduces species richness and abundance of gastropods as well as their frequency of occurrence on limestone cliffs in the Northern Swiss Jura Mountains. Both true rock-dwelling species and other gastropods, which occasionally forage and aestivate on rock faces but otherwise occur in the ground-level vegetation and leaf litter at the cliff bases, were negatively affected by sport climbing. Although potential impacts of sport climbing on cliff-face vegetation (vascular plants, bryophytes, lichens) and cliff-nesting birds have been widely studied (for an overview see Farris, 1998; Kuntz and Larson, 2006; Adams and Zaniewski, 2012; Clark and Hessl, 2015), less attention has been paid to the influence on rock-dwelling invertebrates.

Rock-dwelling snails live exclusively on rock faces. Their activity is restricted to periods of optimal temperature and sufficient moisture (Neuckel, 1981). Individuals of *C. avenacea* were active only during 11%–14% of the year on the limestone cliff Schartenflue (Neuckel, 1981), one of the cliffs examined in our study (Table S1). The remaining time they aestivate attached to the rock face, predominantly on the exposed smooth surface of rock walls (Fig. S3) and less frequently underneath overhangs, in pockets and small fissures. *Chondrina avenacea* enters aestivation very rapidly whenever their environment dries out (Kostal et al., 2013). Aestivating snails suppress their metabolism and minimize water loss using a discontinuous gas-exchange pattern (Kostal et al., 2013). On the cliff face, the snails are exposed to disturbances by sport climbers but must also cope with extreme temperatures during summer heat or during winter frosts. Hibernating individuals of *C. avenacea* rely on a supercooling strategy that allows them to survive when air temperature drops to as low as –21 ^{o}C (Kostal et al., 2013). Winter dormancy in rock-dwelling snails, however, is not deep (Schmera et al., 2015). Individuals of *P. pusilla* and *C. avenacea* were observed to graze on lichens growing on rocks under mild conditions in January (B. Baur, unpubl. data). These small animals (adult shell width or height 2–8 mm) show limited mobility. For example, distances dispersed per year ranged from 1.4 to 2.4 m in *C. avenacea* living on limestone cliffs (Baur and Baur, 1994). Thus, they are not able to escape disturbance due to sport climbing by moving to neighbouring cliffs.

The sensitivity of an organism to the type of disturbance exerted by climbers may be related among others 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. Species with small shells are expected to be less sensitive to disturbance, as are species that prefer to rest in small fissures and underneath overhangs, i.e. in microsites that are not touched by climbers. Indeed, *P. pusilla*, the snail that suffered least from the impact of sport climbing (Table 1), was the smallest of the species examined (adult shell width 2.8– 3.0 mm) and showed a preference to rest underneath overhangs (Fig. 3). The remaining rock-dwelling species were larger (adult shell height 7.2–10.8 mm) and preferred to rest on smooth rock faces. In these species, an even more pronounced decrease in abundance was found on climbing routes.

Rock-dwelling snails graze epi- and endolithic lichens and cyanobacteria growing on rock faces (Baur et al., 1995, 2000; Fröberg et al., 2001, 2006). When feeding on lichens, the snails sequester lichen compounds, which in turn may be used for their own chemical defense against predators such as birds (Baur, 1994; Hesbacher et al., 1995). As shown in our study, sport climbing reduces snail density and thus indirectly decreases the grazing pressure on lichens growing on cliff faces. A reduced grazing pressure in turn may change competitive interactions among lichen species resulting in altered species abundances (Baur et al., 2007; Fröberg et al., 2011).

Individuals of other gastropod species graze occasionally on algae and lichens on rock faces, although their main habitat is the leaf litter layer at the base of the cliffs. However, as a result of human trampling by climbers and the people securing the climbers at the cliff bases, the ground vegetation is reduced, the leaf litter layer destroyed and the soil compacted at these sites (Rusterholz et al., 2011; see also Fig. S5). Soil compaction in turn leads to an increase in soil bulk density and a decrease in soil porosity, changes the water regime, and alters the soil-nutrient composition (Kozlowski, 1999; Kissling et al., 2009). Thus, sport-climbing activities also degrade and partly destroy the habitat of leaf litter-dwelling gastropods at the cliff bases.

McMillan et al. (2003) reported that total snail species richness and density were lower along climbing routes than in unclimbed areas of the Niagara escarpment, and the community composition differed between climbed and unclimbed sites. They examined living snails and empty shells in soil samples and did not distinguish between true rock-dwelling species and species living in close proximity to cliff faces. Our study focused on living gastropods aestivating on rock faces on climbing routes, i.e. at spots where the climbers follow preinstalled, permanent bolts. The more pronounced negative impact of sport climbing on gastropod abundance and species richness found in our study may be explained by the different approaches used.

4.1. 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). These cliffs harbour unique communities of highly specialized plants and animals, many of them being rare and threatened (Hanemann, 2000). The increase in popularity of sport climbing, however, is bringing even greater numbers of people to these previously untouched cliffs (Kuntz and Larson, 2006).

Our study showed that rock climbing significantly reduces the diversity and abundance of rock-dwelling species and gastropods living in the leaf litter at the cliffs' base. 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. Larson et al., 2000; Müller et al., 2004; Rusterholz et al., 2004; Clark and Hessl, 2015). Our findings indicate that rock-dwelling land snails are a suitable indicator group to assess the impact of sport climbing on limestone cliffs. We suggest that future impact assessments, management plans and actions in rocky habitats should also include gastropods. The prohibition of sport climbing on cliffs or cliff areas 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 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 with the aim of educating the climbers and increasing their compliance with such measures.

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Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://

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Table 1
Number of individuals recorded for each gastropod species and frequency of occurrence (expressed in % of the 105 plots examined in parentheses) in climbing routes and in corresponding control areas on the faces of limestone cliffs in the Northern Jura Mountains, Switzerland.

Family	Species	Climbing routes		Control areas	
Cochlostomatidae	*Cochlostoma septemspirale* (Razoumowsky 1789)	16	(3.8)	304	(53.3)
Cochlicopidae	*Cochlicopa lubrica* (O.F. Müller 1774)	1	(1.0)	0	(0)
Orculidae	*Orcula dolium* (Draparnaud 1801)	0	(0)	3	(2.9)
Pyramidulidae	*Pyramidula pusilla* (Vallot 1801) *	675	(41.9)	2167	(76.2)
Chondrinidae	*Abida secale* (Draparnaud 1801) *	9	(5.7)	190	(58.1)
	Chondrina avenacea (Bruguière 1792) *	122	(40.0)	342	(69.5)
Buliminidae	*Merdigera obscura* (O.F. Müller 1774)	0	(0)	4	(3.8)
Discidae	*Discus rotundatus* (O.F. Müller 1774)	0	(0)	1	(1.0)
Zonitidae	*Oxychilus* juv.	0	(0)	1	(1.0)
Agriolimacidae	*Deroceras reticulatum* (O.F. Müller 1774)	0	(0)	2	(1.9)
Clausiliidae	*Macrogastra plicatula* (Draparnaud 1801)	0	(0)	1	(1.0)
	Clausilia rugosa parvula A. Férussac 1807 *	4	(1.9)	141	(60.0)
	Clausilia dubia Draparnaud 1805	0	(0)	1	(1.0)
	Cochlodina laminata (Montagu 1803)	0	(0)	4	(3.8)
	Neostyriaca corynodes (Held 1836) *	2	(1.9)	14	(10.5)
Hygromiidae	*Trichia sericea* (Draparnaud 1801)	1	(1.0)	10	(7.6)
	Monachoides incarnatus (O.F. Müller 1774)	0	(0)	2	(1.9)
Helicidae	*Helicigona lapicida* (Linnaeus 1758) *	0	(0)	4	(3.8)
	Cepaea sylvatica (Draparnaud 1801)	0	(0)	1	(1.0)

* true rock-dwelling species

Table 2

Summary output of minimal adequate GLMMs showing how climbing and rock face complexity influenced the occurrence of the five frequently encountered snail species at the plot level.

Species	Climbing				Rock surface complexity		
	Estimate	SE	*z*	**P**	Estimate	SE	*z*
Cochlostoma septemspirale	–4.736	0.778	–6.086	<0.001			
Pyramidula pusilla	–1.865	0.370	–5.037	<0.001			
Abida secale	–3.835	0.601	–6.377	<0.001			
Chondrina avenacea	–1.778	0.384	–4.630	<0.001			
Clausilia rugosa parvula	–5.590	1.056	–5.385	<0.001	0.383	0.248	1.544

Table 3

Summary output of minimal adequate GLMMs showing the effect of climbing on the occurrence of the five most frequently encountered snail species at the route level.

Species	Estimate	SE	*z*	*P*
Cochlostoma septemspirale	–3.283	0.710	–4.622	<0.001
Pyramidula pusilla	–1.760	0.632	–2.787	0.005
Abida secale	–2.792	0.603	–4.633	<0.001
Chondrina avenacea	–2.079	0.694	–2.998	0.003
Clausilia rugosa parvula	–4.595	0.874	–5.258	<0.001

Other factors and interactions were removed during model selection.

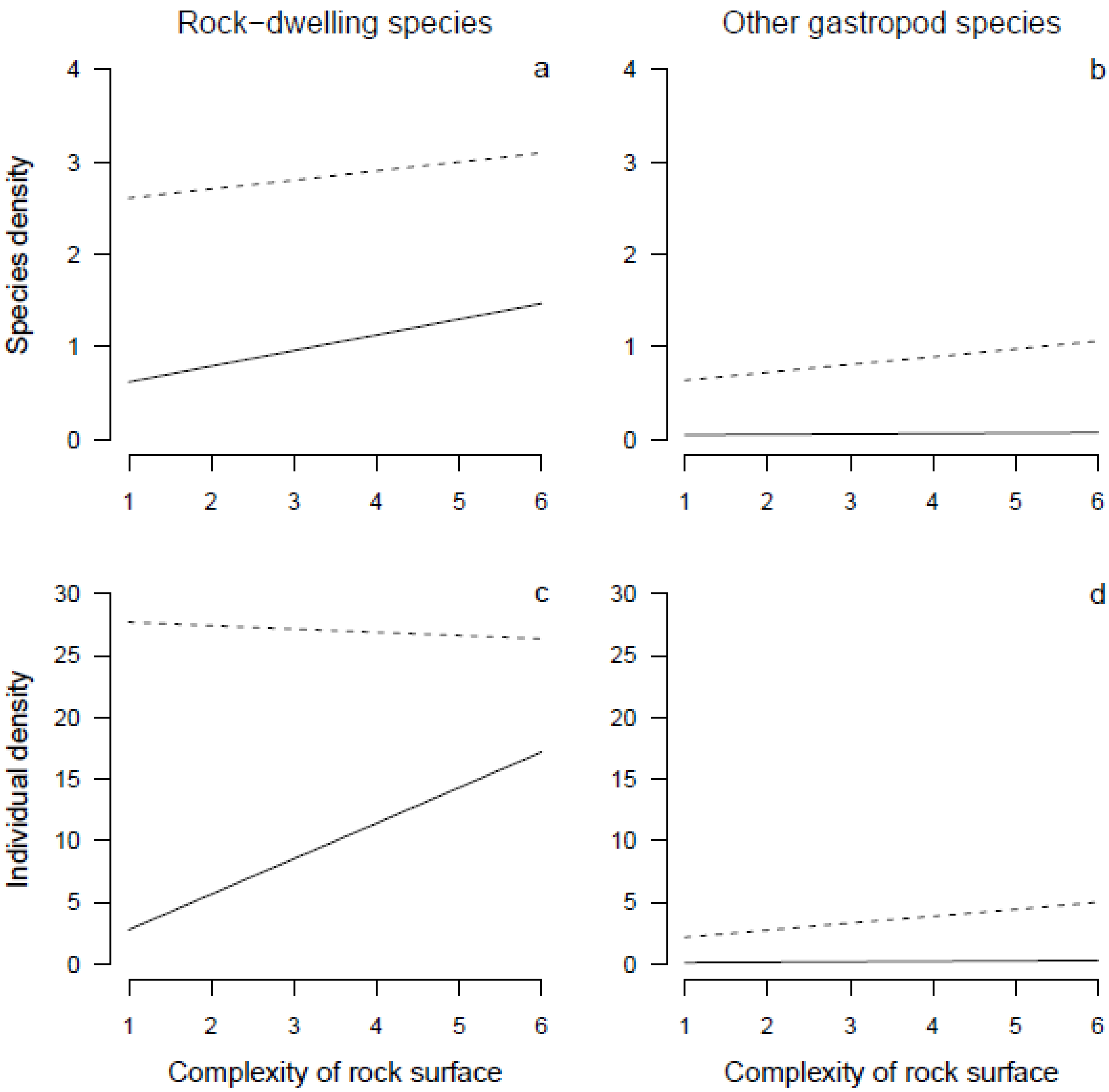

Fig. 1. Interaction plot showing the responses of species density (number of species per 0.25 m^2-plot) and individual density (number of individuals per 0.25 m^2-plot) of rock-dwelling snails and other gastropod species to rock-climbing (solid line: climbing routes; dotted line: control areas) and in relation to the complexity of the rock surface.

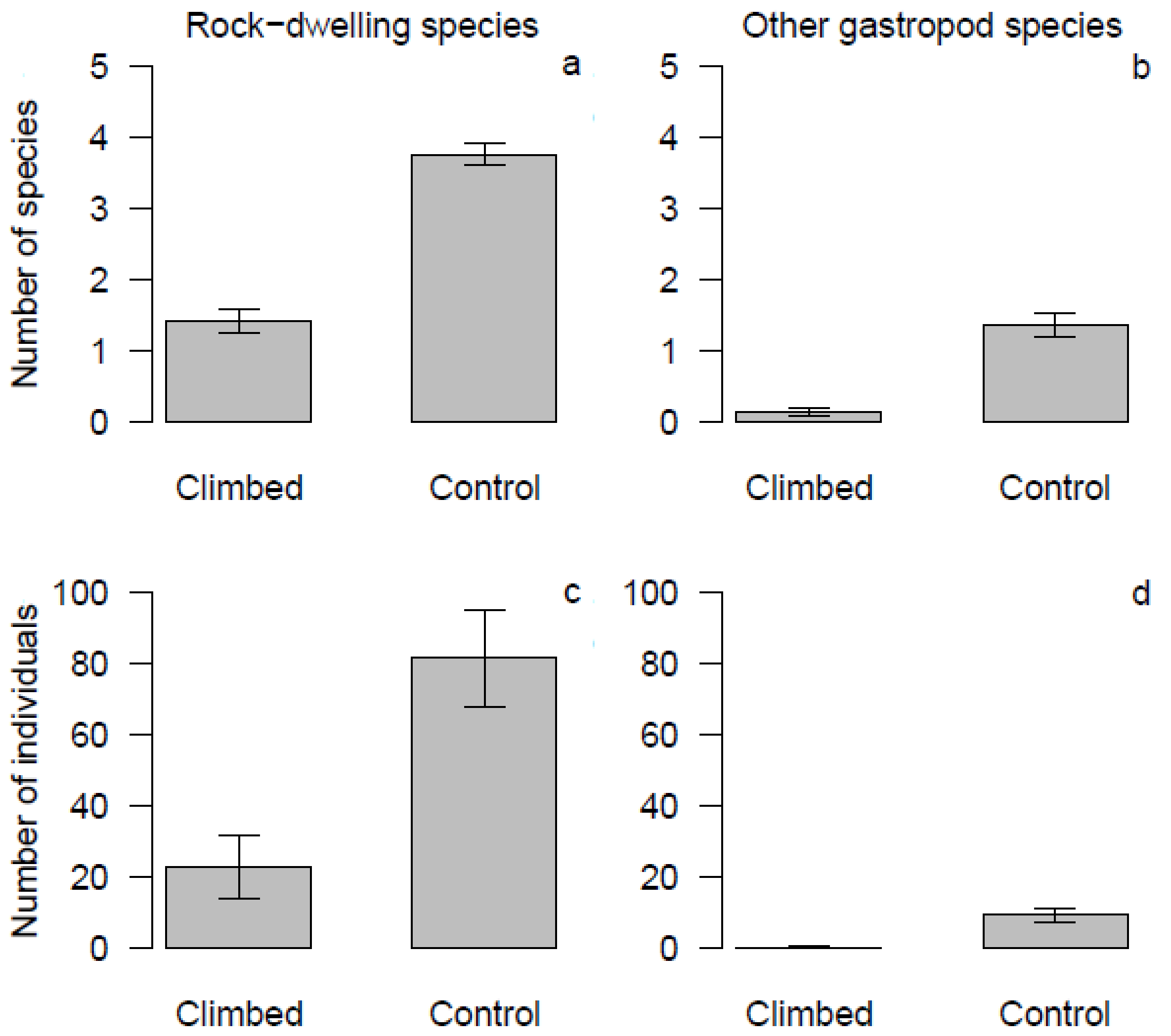

Fig. 2. Species richness (number of species) and abundance (number of individuals) of rock-dwelling snails and other gastropods recorded per climbing route or control area. Mean values ± SE are given (in each case n = 35).

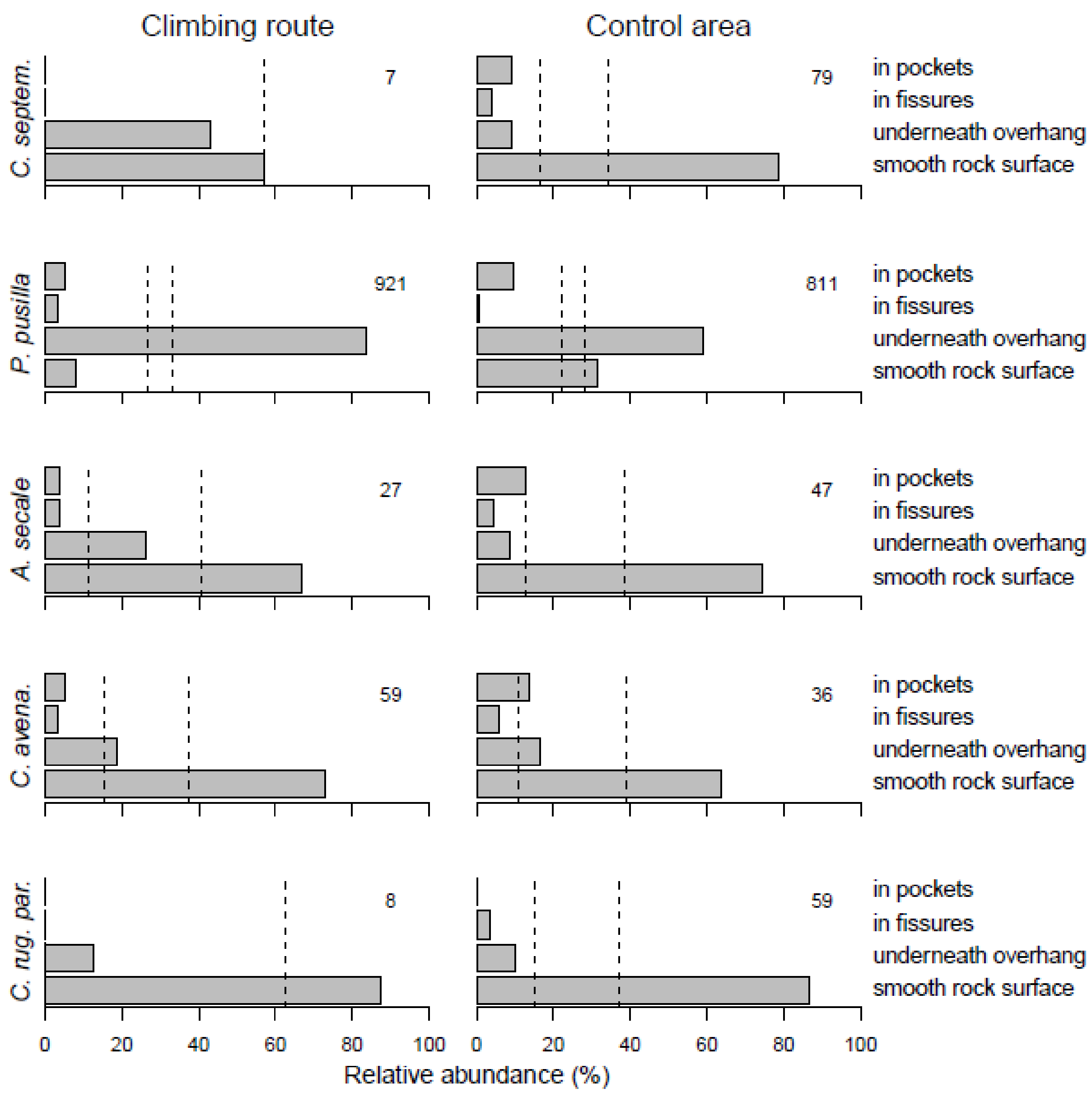

Fig. 3. Relative abundance (% of individuals) of five gastropod species resting on different microtopographical structures of rock faces on climbing routes (left) and in control areas (right). Vertical dotted lines indicate 95% confidence intervals of the generated distributions (Monte Carlo method; see Data analyses).