

## Snail herbivory decreases cyanobacterial abundance and lichen diversity along cracks of limestone pavements

LARS FRÖBERG,<sup>1</sup> PETER STOLL,<sup>2,†</sup> ANETTE BAUR,<sup>2</sup> AND BRUNO BAUR<sup>2</sup>

<sup>1</sup>Botanical Museum, Department of Biology, Östra Vallgatan 18, SE-223 61 Lund, Sweden

<sup>2</sup>Section of Conservation Biology, Department of Environmental Sciences, University of Basel, St. Johans-Vorstadt 10, CH-4056 Basel, Switzerland

**Abstract.** Herbivores are known to decrease plant species diversity in ecosystems with low productivity. Limestone pavements are low-productive habitats harboring specialized communities of cyanobacteria, and endo- and epilithic lichens exposed to extreme temperature and humidity fluctuations. Pavements of the Great Alvar (Öland, Sweden) are covered by free-living cyanobacteria giving the rock surface a dark color. Based on cyanobacterial abundance along the edges, two types of cracks intersecting the pavements have been described: Type one with abundant cyanobacteria and type two without cyanobacteria resulting in light-colored edges. Erosion and different lengths of inundation by melt water have been suggested to cause the conspicuous differences in community composition and hence color between cracks. We hypothesized that this pattern results from the grazing activity of the cyanobacteria- and lichen-feeding snail *Chondrina clienta*, which reduces cyanobacterial cover along light-colored cracks and facilitates endolithic lichens. Three dark and three light-colored cracks were investigated at each of three localities. Crack characteristics (i.e., aspect, width, depth and erosion) and snail density were assessed at the crack level. Cyanobacterial cover and lichen diversity were recorded in 1-cm sections, sampled every 5 cm along eight 160-cm-long transects per crack. Model selection was applied to estimate effects of snail density and distance from crack edges on cyanobacterial abundance and lichen diversity. Crack characteristics explained no differences in cyanobacterial cover or lichen diversity. However, cyanobacterial cover decreased towards the edges of cracks with high snail densities. A transplant experiment supported the correlational evidence. The abundant cyanobacterial cover on pieces of stone placed close to cracks with high snail densities was completely grazed within 19 months. By contrast, cyanobacteria recolonized initially completely grazed pieces of stone when fixed near cracks without snails. Abundance and diversity of endolithic lichens increased along cracks with high compared to low snail densities but decreased in epilithic lichens and lichens with cyanobacterial symbionts. However, the presence of the gastropod herbivore decreased overall lichen diversity. Comparing presence-absence matrices with null models revealed that species co-occurred less frequently than expected. Taken together, we provide evidence that herbivory indirectly released endolithic lichens from competition for light by reducing cyanobacterial cover.

**Key words:** bioweathering; cyanobacteria; epilithic lichen; herbivory; spatial pattern.

**Received** 20 December 2010; revised 30 January 2011; accepted 1 February 2011; final version received 7 March 2011; **published** 30 March 2011. Corresponding Editor: D. P. C. Peters.

**Citation:** Fröberg, L., P. Stoll, A. Baur, and B. Baur. 2011. Snail herbivory decreases cyanobacterial abundance and lichen diversity along cracks of limestone pavements. *Ecosphere* 2(3):art38. doi:10.1890/ES10-00197.1

**Copyright:** © 2011 Fröberg et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits restricted use, distribution, and reproduction in any medium, provided the original author and sources are credited.

† **E-mail:** peter.stoll@unibas.ch

## INTRODUCTION

Indirect interactions occur when changes in one species or a group of species affect others through a chain of intermediate species. Ecologists increasingly recognize that indirect interactions can be very important and lead to significant changes of communities (Strauss 1991, Rooney and Waller 2003, White et al. 2006). Diversity of primary producers is influenced by large-scale processes such as dispersal, disturbances and isolation but also by small-scale processes such as interactions between organisms of the same or different trophic levels and by indirect effects. Particularly, herbivory and competition may interact to increase or decrease diversity depending on the competitive ability, defense mechanisms and regeneration ability of primary producers, the size and selectivity of herbivores, nutrient availability and hence productivity of ecosystems (Bakker et al. 2006).

Herbivory is a key factor shaping plant communities. Substantial evidence suggests that the mechanisms by which herbivores influence primary producers do not differ fundamentally among terrestrial, limnic, and marine ecosystems (Huntly 1991). In general, diversity will increase if the impact of grazers reduces the competitive ability of dominant plant species but will decrease if inferior competitors are negatively influenced (e.g., Lubchenco and Gaines 1981, Pacala and Crawley 1992, Carson and Root 2000). For example, in low-productive habitats, high grazing pressure usually decreases plant diversity while high grazing pressure often increases diversity in highly productive habitats (Proulx and Mazumder 1998, Hillebrand 2003). However, diversity within specific functional groups may not obey this general dynamic because they show differential responses to grazing depending on the characteristics of the system. Thus, generalizations of herbivore effects on plant diversity may be unwarranted as supported by many exclusion experiments with mixed results (Crawley 1997). It has been suggested that if herbivory reduces competition among plant species, it may be more important than competition in structuring communities of primary producers (Sih et al. 1985, Hulme 1996). In contrast to the well-studied direct effects (e.g., consumption) of vertebrates on plant species

diversity, the impact of invertebrate herbivory on the diversity of lichen communities are largely unexplored with few exceptions. For example, the absence of *Lobaria amplissima*, an epiphytic lichen on lower parts of tree trunks in deciduous forests in Norway, has been explained by intensive gastropod grazing (Asplund et al. 2010). Nevertheless, indirect effects (e.g., competitive release) of invertebrates on the diversity of lichens have so far not been investigated.

Limestone pavements in the steppe-like Great Alvar (Öland, Sweden) harbor diverse lichen communities consisting of foliose, epi- and endolithic lichens together with microscopic, free-living cyanobacteria (family Chroococaceae) giving the rock surface its characteristic dark color. The myco- and photobiont layers of endolithic lichens occur at depths between 0 and 7 mm in the rock, while in epilithic and foliose lichens the tissue is above the rock surface. The pavements are intersected by 1–50 cm wide cracks most of which are entirely filled with soil and plant debris or cushions of bryophytes occasionally hosting a few vascular plants. However, open cracks are frequently found in certain restricted areas of the alvar (Königsson 1977). Around some of these open cracks, the cover of free-living cyanobacteria is reduced resulting in a conspicuous light zone on both sides of the cracks (Fig. 1A). Fröberg (1989) hypothesized that these light zones could be caused by snow cover, inundation in spring and/or erosion near the cracks' edges. However, investigating the dispersal pattern of the land snail *Chondrina clienta* (Westerlund) in various rocky habitats, Baur and Baur (1995) found that this species inhabited some of the cracks (Fig. 1C). Moreover, the lichen- and cyanobacteria-feeding snails were observed to forage on the horizontal surface of the pavements on rainy days. As soon as the rock surface becomes dry they return to sheltered sites in the cracks (Baur and Baur 1995). This suggests that gastropod grazing may reduce cyanobacterial cover (Fig. 1D) along the cracks. Lichens are protected against herbivores by a number of mechanisms. The presence of different secondary metabolites, together with other features, such as nutrient content, surface toughness, type of photobiont, growth form (epilithic, endolithic, foliose) and other morphological characteristics might ac-

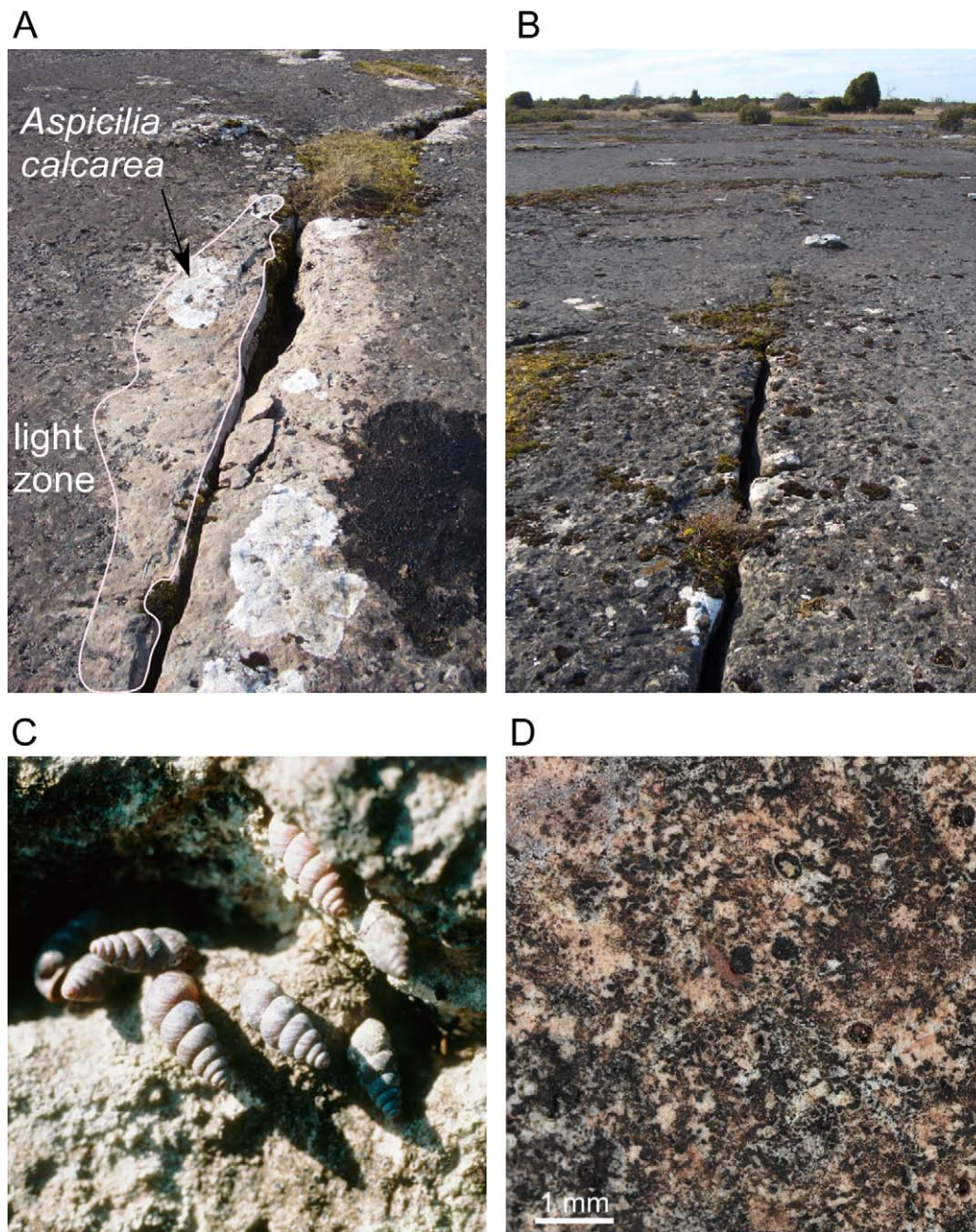


Fig. 1. (A) Crack with conspicuous light zone on a limestone pavement at Bårby on the Baltic island of Öland, Sweden. During hot and dry conditions, resting snails (*Chondrina clienta*) are attached to the vertical wall of cracks. The snails become active during periods of high air humidity and graze cyanobacteria, algae and lichens from rock faces with their specialized radulae. Cyanobacteria are grazed in the light zone (circled) but the endolithic lichen *Clauzadea immersa* and the white epilithic lichen *Aspicilia calcarea* still occur. (B) Crack without conspicuous light zone. (C) *Chondrina clienta*. (D) A close-up of microscopic cyanobacteria growing in small flakes (the larger black dots are apothecia of *Clauzadea immersa* overgrown by cyanobacteria).

count for differential preferences shown by land snails (Fröberg et al. 1993, Baur et al. 1994, Hesbacher et al. 1996).

We use the cyanobacteria-lichen-snail model system on limestone pavements to investigate direct and indirect effects of consumers on diversity of primary producers. However, our model system may be more complicated than anticipated at first glance. Autotrophic bacteria, algae and lichens have been implicated in both chemical and physical weathering processes (Friedmann 1982, Büdel et al. 2004, Matthews and Owen 2008) leading to increased substrate heterogeneity. Thus, feed-backs between primary producers and the environment and bottom-up effects may explain diversity differences better than top-down effects of consumers. Microorganisms often aggregate and mineralize to create biocrusts (Viles 1995), leading to surface protection rather than increasing erosion. Similarly, crustose lichens have intimate associations with their substrate, the epilithic ones being attached by a large number of fungal hyphae forming the thallus base and the endolithic ones being completely embedded in the substrate. The action of grazers may thus increase erosion by removing protective structures. Finally, interactions among primary producers may further complicate the picture. Negative species interactions have recently been demonstrated in stressful environments (Bowker et al. 2010b) and cyanobacteria may very well shade endolithic lichens. Grazers feeding on free-living cyanobacteria and epilithic lichens may thus decrease competition pressure allowing a high diversity of endolithic lichens. In contrast, cyanobacteria as initial colonizers of bare rocks may increase colonization success of other species but may eventually be out-competed by algae and fungi (both lichenized and non-lichenized) which develop surface crusts (Doppelbauer 1959, Omeilon et al. 2007).

We aimed to elucidate the effects of snail grazing on cyanobacterial abundance and on the diversity and abundance of the lichens occurring on limestone pavements. We hypothesized that a dense cover of cyanobacterial colonies reduces light availability for photosynthesis of endolithic lichens. Consequently, reduced cyanobacterial cover as a result of gastropod grazing should increase abundance or diversity of endolithic

lichens and lead to a positive relationship between abundance or diversity of endolithic lichens and snail density. Since our model system has low productivity, the overall effect of snail grazing on lichen diversity should be negative.

## MATERIAL AND METHODS

### *Study system and sampling design*

Field work was carried out from 1995 to 1997 in the Great Alvar in the southern part of the Baltic island of Öland, Sweden (56°30' N; 16°30' E). The area is a calcareous grassland sometimes grazed by sheep or cattle. The bedrock is exposed as limestone pavements in c. 1% of the 300 km<sup>2</sup> large Great Alvar. The annual mean temperature is 7°C (July mean = 16°C; January mean = -1°C) and the annual mean precipitation varies from 450 mm to around 500 mm. The Great Alvar is a UNESCO World Heritage Site since 2000. Geomorphology, climate and vegetation have been described in detail by Krahulec et al. (1986 and references therein).

We selected pavements at three localities (4.5–8 km apart): (1) Bårby-källan (measuring 40 × 60 m), c. 1 km N of the crossing between the road connecting Södra Bårby with Alby and the border of Mörbylånga and Hulterstad parishes (= Bårby), (2) Vickelby (60 × 80 m), 3 km ESE of Vickelby church, and (3) Ekelunda (80 × 80 m), c. 1 km S of Ekelunda. All pavements contained numerous open cracks. To ensure independence of cracks, exclude uncontrolled confounding and edge effects, we selected cracks fulfilling the following criteria: separated from each other by at least 2 m, fully exposed to the sun (no shading by shrubs), free of accumulating soil, distance to the edge of the pavement exceeding 1 m and at least 2 m long. At each locality about 50 cracks fulfilled these criteria. We randomly selected six at each of the three localities, making sure that three of them had a conspicuous light zone (Fig. 1A) and three had no light zone indicating dense cyanobacterial colonies (Fig. 1B). Cracks were selected in July 1995 before snail density (see below) was quantified in August 1995 and 1996.

Temperatures were measured at the sites where lichens occur and where individuals of *C. clienta* forage (horizontal surface), rest, estivate and overwinter (crack) (Appendix A: Fig. A1). Winter temperatures were higher and never fell

below  $-4^{\circ}\text{C}$  in cracks compared to the surface of the limestone pavements. Summer temperatures had high maxima on the surface, reaching values close to  $40^{\circ}\text{C}$ , but never exceeding  $27^{\circ}\text{C}$  in the cracks.

#### *Snail herbivores*

Seventeen land snail species have been recorded on the Ekelunda pavement and in the surrounding grassland, four of them being lichen feeders (Baur 1987). In cracks, *Chondrina clienta* (Fig. 1C) is by far the most abundant (>99%) lichen-feeding species (Baur 1988, Baur and Baur 1995). The cylindro-conical shell of adult *C. clienta* has a height of 5.5–7 mm (Baur 1988). Individuals become sexually mature at an age of 4–6 years and live for another 5–10 years, suggesting that densities should not vary too much from year to year. The snails are well adapted to rocky habitats, and whilst resistant to drought their activities are confined to periods of high air humidity. Their specialized radulae enable them to graze cyanobacteria, algae and lichens from rock faces (Baur et al. 2000). Individuals of *C. clienta* grazed on 18 of 27 lichen species offered in laboratory experiments (Fröberg et al. 1993). Sometimes even the outermost layer of stones is removed and gastropods may contribute to the erosion of rocky surfaces (Shachak et al. 1987).

A pilot study showed that the majority of *C. clienta* (78%) are resting attached to the vertical wall of cracks at a depth of 6–20 cm, another 18% of the snails in the uppermost 5 cm of the cracks and the remaining 4% occur at depths ranging from 21 to 35 cm (B. Baur, unpublished data). In the present study, the abundance of *C. clienta* resting in cracks was estimated by counting the number of juvenile and adult snails found to a depth of 20 cm within 2 min. searching time by one of us (B.B.). A small mirror was used to detect the snails in narrow fissures. Density estimates were conducted exclusively under conditions of dry weather, when the snails are at rest (Baur and Baur 1991), because this method reveals reliable density estimates for rock-dwelling land snails (Baur et al. 1995, Armbruster et al. 2007). In each crack, density estimates were based on three replicate searches made in August 1995 and six made in August 1996. However, density estimates were remarkably similar in

1995 ( $20.1 \pm 3.3$ , mean  $\pm$  SE,  $n = 54$ ) and 1996 ( $18.3 \pm 2.3$ ,  $n = 108$ ). Consequently, snail density estimates of the two years were pooled and averaged across  $n = 9$  replicates per crack and location.

#### *Field survey*

The width and depth of cracks were measured and their aspect determined with a compass. The crack edges were eroded to different extents and some edges had a stair-like shape being lowest at the edge of the crack. The extent of erosion was estimated by measuring the vertical distances between a horizontally stretched string connecting the uneroded pavement surface on either side of a crack and the eroded surface at the crack edge. These distances were measured at intervals of 5 cm along one randomly chosen transect (described below). The amount of rock eroded was expressed as the vertical area (in  $\text{cm}^2$ ) removed between string and rock surface.

Eight transects (160 cm long and separated by 10 cm) were placed perpendicular to each crack, and marked with a string. We examined sixteen 1-cm long sections every 5 cm along each transect extending 80 cm on both sides of the crack. Another four 1-cm long sections situated on the vertical crack walls at depths of 5 and 10 cm (two on either side) were examined on each transect. Thus, a total of 36 sections of 1 cm were examined on each transect. The positions of the sections are given as the distance from the edge of the crack, with negative values for sections on the vertical crack wall. Abundances of cyanobacterial colonies and the presence of different lichen species, bryophytes, vascular plants and algae were recorded within each 1-cm section. Note that bryophytes, plants and algae were not abundant enough to be analysed from a single taxa perspective but used in the community-level comparisons. Lichens were determined to the species level (for exceptions see Appendix C, taxonomical remarks) using a lens (magnification  $\times 20$ ). Lichens that could not be identified in situ were collected for microscopical identification. Within a 1-cm section more than one taxon (two or, in a few cases, three) could be recorded. Altogether 5024 observations or point records within 1-cm long sections were made (1728 in Bårby, 1696 in Vickleby and 1600 in Ekelunda). To exclude any possible influence from nearby-

situated cracks or from the vegetation at the edge of the pavement, transects of one crack at Vickleby were only 140 cm long and transects of two cracks at Ekelunda were only 120 cm long leading to somewhat lower numbers of point records at Vickleby and Ekelunda. The lichen and cyanobacterial surveys were conducted between 26 July and 12 October 1995, 18 May and 16 October 1996, and 29 July and 17 October 1997 by one of us (L.F.).

The abundance of microscopic cyanobacteria was estimated using a four-point scale: 0, 0–20% of the area covered by cyanobacteria; 1, 21–40%; 2, 41–60%; and 3, more than 60% of the area covered. Typically the cyanobacterial cover consisted of a mosaic of *c.* 0.2-mm-wide flakes resulting in a maximum cover of 80% (Fig. 1D). Preliminary analyses revealed that the response of cyanobacterial colonies to snail grazing was independent of abundance class used. Abundance classes 2 and 3 showed similar and both complementary responses to abundance classes 0 and 1. Consequently, abundance classes 2 and 3 were pooled and abundance classes 0 and 1 omitted from further analyses.

Cyanobacterial species were identified in four randomly chosen samples of 1–4 mm<sup>2</sup> situated along each crack. The most common species were *Gloeocapsa alpina* (Nägeli) Brand and *G. rupestris* Kützing (Geitler 1932). However, identification for all point records where cyanobacteria occurred was not feasible and statistical analyses could not take any species-level information into account.

#### Transplant experiment

A transplant experiment was designed on the pavement at Bårby to examine the grazing pressure on microscopic cyanobacteria transplanted to the edge of cracks with known snail abundance, and to assess the recolonization of cyanobacteria on completely grazed stone surfaces transplanted to cracks with no snails. Pieces of stone (surface area: 4–6 cm<sup>2</sup>, *n* = 11) covered with microscopic cyanobacteria were transferred from two cracks with no snails to two grazed cracks with snail densities of 50.4 and 45.3 individuals collected within 2 min. The pieces were fixed with modelling clay at the cracks' edges on 11 August 1996. On the same day, pieces of stone with a completely grazed surface

(area: 4–6 cm<sup>2</sup>, *n* = 10) were transferred from the same two cracks with high snail densities to the same two cracks with no snails and fixed with modelling clay. On each piece of stone the abundance of microscopic cyanobacteria was assessed prior to the transplantation and after 19 months (on 11 March 1998) to determine the change in cyanobacterial cover.

#### Statistical analyses: single taxa perspective

Our main interest concerned differences among localities, and relationships of snail density and distance to crack edge (independent variables) with abundance of cyanobacterial colonies, individual lichen species and lichen diversity (dependent variables). However, these relationships could be non-linear and the spatial scales at which potential effects could be expected were unknown. Therefore, we adopted an information-theoretic approach to address potential non-linearities and sensitivity to spatial scale (see below). A set of seven candidate models of increasing complexity was constructed (Table 1). The first model (1) contained locality (as a factor with three levels), snail density and distance to crack edge. Model 2 added the interaction between snail density and distance and models 3 to 7 added polynomials of distance and snail density testing for deviations from linearity. Best fitting models were then selected using Akaike's information criterion (Burnham and Anderson 2002) corrected for sample size

Table 1. Set of candidate models used in the model selection approach to analyze variation in abundance of cyanobacterial colonies, lichen species and lichen diversity associated with locality, snail density and distance to crack edge on limestone pavements on the Baltic island of Öland, Sweden.

Model	Fitted model terms	<i>K</i>
1	locality + snail density (S) + distance (D)	5
2	locality + snail density + distance + S × D	6
3	locality + snail density + distance + D <sup>2</sup> + S × D	7
4	locality + snail density + distance + S <sup>2</sup> + S × D	7
5	locality + snail density + distance + D <sup>2</sup> + D <sup>3</sup> + S × D	8
6	locality + snail density + distance + D <sup>2</sup> + S <sup>2</sup> + S × D	8
7	locality + snail density + distance + D <sup>2</sup> + D <sup>3</sup> + S <sup>2</sup> + S × D	9

Notes: *K* gives the number of fitted parameters and equals the number of fitted terms + 2, because locality was fitted as a factor with three levels.

(Hurvich and Tsai 1989).

All candidate models were tested at two spatial scales. A small scale using the original raw data (5 cm between point records) and a large scale pooling five adjacent point records. Since our dependent variables were expressed as relative number of point records (%) or diversity per crack, our basic sampling unit was the crack (not the transect or point records). Thus, the sample size for the small scale was  $n = 18 \text{ cracks} \times 18 \text{ distances} = 324$ , but  $n = 18 \times 4 = 72$  for the larger scale. The large scale did not work out with even numbers of points and the last segment (that most distant from the crack edges) contained only three adjacent point records. Results for the analyses of abundance are given for the small scale in the main text and for the large spatial scale in Appendix D.

Best fitting models were then used to produce filled contour plots showing discrete classes of dependent variables as a function of snail density and distance to crack edge. The intercept was taken as average across the three localities. These contour plots were projected into three-dimensional plots of the raw data using colors to identify the cracks of different localities and covered the horizontal plane spanned by snail density and distance to crack edge.

Squared correlation coefficients ( $R^2$ -values) of snail density with dependent variables at different distances are given in Appendix D as post-hoc tests assessing spatial extent and scale of snail density effects. Bonferroni corrections ( $P < \alpha/\text{number of distances}$ , i.e., 18 and 4 for small and large scale) were used to adjust for the number of simultaneous tests (Rice 1989).

We used correlations to examine relationships between characteristics of cracks (i.e., aspect, width, depth and extent of erosion) and estimates of cyanobacterial and lichen abundance, or their diversity at various distances. Shannon's  $H'$  was calculated as  $-\sum(p_i \times \log p_i)$ , with  $p_i$  as the relative number of point records per lichen species  $i$ , distance and crack. Evenness was calculated as  $H'/\log(S)$ , with  $S = \text{number of species per distance and crack}$ . Analyses of diversity are reported for the larger scale (i.e., five adjacent point records pooled) rendering diversity measures most reliable because of the higher number of species included compared to the smaller scale. However, it may have missed

small-scale patterns because of its low resolution. Therefore, results for the small spatial scale are given in Appendix D.

The Mardia-Watson-Wheeler test (Batschelet 1981) was used to examine differences in aspect of cracks, and analysis of variance to test for differences in dimensions and snail densities of cracks with or without conspicuous light zones. To test whether abiotic crack characteristics rather than snail densities correlated with dependent variables, all correlations were also run with width, depth or erosion of cracks rather than snail density. However, none of these correlations were significant at a Bonferroni corrected significance level of  $P < 0.05/18 = 0.0028$  with one exception. Diversity (i.e., Shannon's  $H'$  and evenness) of foliose cyanolichens (lichens with cyanobacteria as photobiont) was positively correlated with erosion at 15 cm distance.

Conventional models (i.e., normal errors, constant variance) were used following arc-sine transformations ( $\sin^{-1} \sqrt{[0.01 \times p]}$ , where  $p$  is percent cover) for the analyses of percentage cover (Crawley 2005) performed for cyanobacterial colonies and the most abundant lichen species. For the analyses of diversity measures (i.e., number of species, Shannon's  $H'$  and evenness) of epilithic and endolithic lichens and cyanolichens, distributional assumptions were met and hence no transformation was necessary. However, snail density was square-root transformed for all analyses to meet the assumptions of normal errors and homoscedasticity.

All analyses (except C-Scores, see below) were performed using R (version 2.8.1, R Development Core Team 2008). Model selection statistics, parameter estimates and significance tests of selected model, single distance correlations with snail density and Bonferroni corrected significances for all dependent variables and the two spatial scales are given in Appendix D.

#### *Statistical analyses: community-level comparisons*

Null model analysis of co-occurrence (Gotelli 2000) was used to estimate biotic interaction strength at the community level. Presence-absence matrices, where each row represents a species and each column transects at specific distances, were constructed for each crack. Segments of three adjacent point records were taken into account (e.g., at 0, 5 and 10 cm away

from crack edges) covering a band of 15 cm width across all transects, and because we sampled eight transects on either side of the cracks, our presence-absence matrices had 48 columns and 116 rows (cyanobacterial colonies, 84 lichen, two algae, three vascular plant and 26 bryophyte species). Checkerboard scores (C-scores) were calculated for each species pair as  $(R_i - S)(R_j - S)$ , where  $R_i$  and  $R_j$  are the total number of occurrences of species  $i$  and  $j$ , and  $S$  is the number of point records in which both species occur (Stone and Roberts 1990). The final score is then given as the average over all possible pairs in the matrix. C-scores have been shown to be insensitive to the presence of noise in the data and to have good statistical properties (Gotelli 2000). To determine the strength of co-occurrence in the data, C-scores were compared to null models serving as baseline representing communities unstructured by interactions. Null models were generated using a sequential swap algorithm with fixed rows and equiprobable columns retaining species frequencies in the random matrices. This null model has been recommended for standardized samples collected in homogeneous habitats (Gotelli 2000). C-scores depend on the number of species and co-occurrences at each crack. Therefore, we obtained standardized effect sizes as  $(I_{obs} - I_{sim})/S_{sim}$  where  $I_{obs}$  is the observed value of the C-score, and  $I_{sim}$  and  $S_{sim}$  are the mean and standard deviation, respectively, of the index obtained from 5000 null communities. Consequently, values higher and lower than 0 (expressed as differences in units of standard deviation to C-scores of randomized matrices) indicate prevailing spatial segregation and aggregation among the species within the community, respectively. Assuming that neither limited dispersal nor habitat selection are the main drivers of the observed patterns, C-scores higher than 0 suggest the dominance of competitive interactions. Null model analyses were conducted with Ecosim 7.72 (Gotelli and Entsminger 2006).

## RESULTS

### *Crack characteristics and snail density*

Cracks at the three localities did not differ in aspect (Table B1; Mardia-Watson-Wheeler-test,  $P > 0.5$ ), width, depth and in the extent of erosion

at their edges (ANOVA,  $F_{2,12}$  in all cases with  $P > 0.11$ ). There were also no significant differences in crack characteristics among cracks with or without a conspicuous light zone ( $F_{1,12}$  in all cases with  $P > 0.11$ ).

Relative snail density varied from 0 to  $55.7 \pm 11.9$  adult individuals of *Chondrina clienta* (Table B1). Snail density differed significantly among localities ( $F_{2,12} = 33.0$ ,  $P < 0.0001$ ) and between cracks with or without conspicuous light zones ( $F_{1,12} = 351.0$ ,  $P < 0.0001$ ). Snail density was lowest at Vickieby. Averaged across localities, relative snail density was 50 times higher in cracks with a light zone compared to cracks without a light zone ( $37.0 \pm 19.9$  vs  $0.8 \pm 0.9$  individuals). Snail density of cracks with a light zone, however, was lower at Vickieby compared to Bårby or Ekelunda (interaction  $F_{2,12} = 13.5$ ,  $P < 0.001$ ). Snail density was not correlated with any of the quantified characteristics of the cracks.

### *Cyanobacterial cover*

Cyanobacterial colonies almost completely covered the pavements of all three localities at distances more than 50 cm away from crack edges (Fig. 2). However, at distances less than 25 cm and snail densities higher than 5–10 individuals, cyanobacterial colonies were almost completely absent. At snail densities lower than five individuals, cyanobacterial colonies could be found up to the crack edges and even on the vertical walls of cracks down to 10 cm. All models without a squared distance term (models 1, 2 and 4) had Akaike weights close to zero and model 3 was selected as the most parsimonious one explaining 61.3% of the variability in the cover of cyanobacterial colonies (Table 2). Parameter estimates revealed that Ekelunda had the lowest overall abundance of cyanobacterial colonies followed by Bårby and Vickieby which did not significantly differ from each other. Snail density was negatively, and distance positively, correlated with cover of cyanobacterial colonies (Table 3). However, the increase with distance was not linear and the significant negative effect of distance squared showed that cover reached 100% beyond 50 cm. The significant interaction between snail density and distance indicated that the effect of snail density was spatially limited and vanished with increasing distance from crack edges. The negative correlation of cyanobacterial



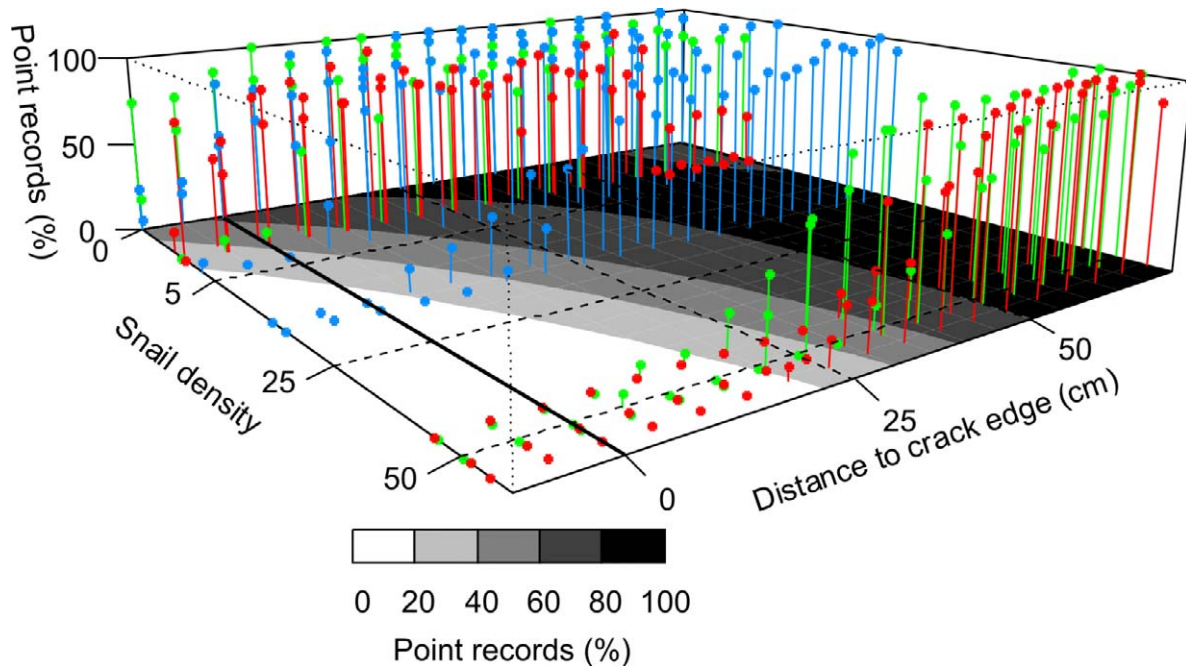


Fig. 2. Cover of cyanobacterial colonies (point records in %) as function of snail density and distance to crack edge (indicated by the black line at distance 0 cm, negative distances refer to vertical crack walls) at three localities (green; Bårby, blue: Vickleby, red: Ekelunda) on the Baltic island of Öland, Sweden. Best fitting models were used to produce filled contours projected onto the horizontal plane spanned by snail density (sqrt-transformed) and distance to crack edge. Filled contours represent discrete classes of point records (indicated on the horizontal scale bar) occupied by cyanobacterial colonies with more than 40% cover (pooled abundance class 2 and 3). Thus, 80–100% indicates that 12.6–16 point records (16 being the maximum because we had 8 transects on either side of each crack) were occupied with cyanobacterial colonies covering more than 40% of a point records section of 1 cm. The best fitting model was selected from a set of candidate models using Akaike's information criterion (see Table 3).

Table 2. Model selection statistics of a set of candidate models fitted to the cover of cyanobacterial colonies at various distances from crack edges with different snail densities on limestone pavements at three localities on the Baltic island of Öland, Sweden. Bold values highlight the best fitting model.

Model	$K$	$R^2$	Delta	Weight
1	5	42.0	129.4	0.000
2	6	57.4	30.8	0.000
3	7	<b>61.3</b>	<b>0.0</b>	<b>0.389</b>
4	7	57.4	31.6	0.000
5	8	61.3	1.3	0.203
6	8	61.4	0.7	0.268
7	9	61.4	2.1	0.139

Notes: See Table 1 for definitions of models 1 to 7. Abbreviations:  $K$ , number of fitted model parameters;  $R^2$ , adjusted  $R^2$  in %; Delta, difference in Akaike information criterion ( $AIC_c$ ); Weight, model probabilities or Akaike weights.

Table 3. Parameter estimates and corresponding significance tests for the best fitting model in Table 2. Bold values highlight  $P < 0.05$  (except for Bårby which is the overall intercept).

Term	$t$	$P$	Sig
Bårby	17.9	0.000	
Vickleby	0.0	0.993	
Ekelunda	<b>-3.1</b>	<b>0.002</b>	--
Snail density	<b>-14.1</b>	<b>0.000</b>	---
Distance	<b>6.2</b>	<b>0.000</b>	+++
Distance <sup>2</sup>	<b>-5.8</b>	<b>0.000</b>	---
Distance <sup>3</sup>			
Snail density <sup>2</sup>			
Interaction	<b>11.3</b>	<b>0.000</b>	+++

Notes: Abbreviations:  $t$ ,  $t$ -value of fitted model term with  $324 - K$  degrees of freedom;  $P$ ,  $P$ -value; Sig, significance code using 1, 2 or 3 + or - signs to indicate the direction of the correlations and the conventional significance levels of 0.05, 0.01 and 0.001, respectively.

cover with snail density with some  $R^2$ -values > 80% could be detected up to 30 cm from crack edges on both spatial scales (Appendix D: Tables D1–D3). The snail density effect was also negative at the larger spatial scale and the adjusted  $R^2$  rose to 71.7% albeit with a significant distance-cubed term (model 5).

#### *Lichen species richness*

A total of 84 lichen taxa were recorded along the cracks in the three limestone pavements representing 77% of the 108 calcicolous lichens reported in the Great Alvar (Fröberg 1989, Appendix C). Fifty-one lichen taxa were found on the pavement at Bårby, 65 in Vickleby and 53 in Ekelunda. Thirty-six (43.4%) of the lichen taxa were found on all three pavements, 14 (16.9%) species on two of the three pavements and 33 (39.8%) on only one of the three pavements. Lichen species similarity, analysed by Sørensen's similarity coefficient, was 72.4% for the comparison Bårby vs Vickleby, 71.2% for Bårby vs Ekelunda and 72.9% for Vickleby vs Ekelunda. Of all lichen records (3755), lichens with green algae as photobionts were dominant (34.6% endolithic, 34.3% epilithic) followed by lichens with cyanobacteria as photobionts (15.6% epilithic, 14.5% foliose). Thus, endo- and epilithic lichens with green algae as well as epilithic and foliose lichens with cyanobacteria were abundant enough to be analyzed as groups. However, to obtain comparable numbers of species and records in different groups, epilithic and foliose lichens with cyanobacterial photobionts were combined to cyanolichens (17 taxa with 1127 records).

Endolithic lichen species richness increased with snail density and decreased with distance to the cracks; the best fitting model explained 65.6% of the variability (Table 4). The three localities did not differ from each other in the number of endolithic lichen species (Table 5). The best fitting model included a positive effect of snail density independent of the spatial scale or selected best fitting model (Appendix D: Tables D4–D6). However, at the small scale, the negative distance effect was replaced by higher order polynomials of distance indicating more complex non-linear patterns. For example, at high snail density, the number of endolithic lichen species first increased and then decreased going from the vertical crack walls, to the edge and further away from crack edges. Correlations

of the number of endolithic lichen species with snail density at single distances were strongest close to crack edges and positive on both spatial scales and the quadratic snail density effect increased  $R^2$  from 47.5 to 71.6% (Fig. 3A).

Epilithic lichen species richness was best fitted by model 4 without non-linear distance but with a negative quadratic snail density term (Table 4). Ekelunda harbored fewer epilithic lichen species compared to Bårby or Vickleby (Table 5). The number of epilithic lichen species decreased with increasing distance at the large spatial scale. However, at the small spatial scale, higher order polynomials were significant indicating that the number of epilithic lichen species first increased but then decreased with increasing distance from crack edges (Appendix D: Tables D7–D9). Correlations with snail density at single distances confirmed the negative effects of snail density on the number of epilithic lichen species (Fig. 3B).

Cyanolichen species richness responded similarly but stronger to snail density than epilithic lichens. Model 3 was best fitting and explained 38.2% of the variability (Table 4). The three localities did not differ in number of cyanolichen species but snail density had a negative effect (Table 5). Distance effects were positive but the negative non-linear distance effect indicated that the number of cyanolichen species first increased and then decreased with increasing distance from crack edges on both spatial scales (Appendix D: Tables D10–D12). However, a positive quadratic snail density effect was found at the small scale indicating decreasing number of cyanolichen species with increasing snail density as a desaturating function. In fact, at snail densities larger than 25 individuals and distances less than 10 cm there were almost no cyanolichen species present. Correlations with snail density at single distances were negative at small distances. Snail density alone explained 60.5% of the variability in the number of cyanolichen species at distances from –10 to 10 cm to the crack edges (Fig. 3C).

Treating all lichen species as one group, model 6 without a cubic distance effect was slightly favored over model 7 (Table 4). Lichen species richness did not differ between localities (Table 5). Both quadratic distance and snail density effects were negative indicating that the number of lichen species first increased and then de-

Table 4. Model selection statistics of a set of candidate models fitted to the number of lichen species in different groups at various distances from crack edges with different snail densities on limestone pavements at three localities on the Baltic island of Öland, Sweden. Bold values highlight the best fitting models.

Model	K	Lichen species group											
		endolithic			epilithic			cyanolichens			all lichen species		
		R <sup>2</sup>	Delta	Weight	R <sup>2</sup>	Delta	Weight	R <sup>2</sup>	Delta	Weight	R <sup>2</sup>	Delta	Weight
1	5	60.0	6.8	0.011	40.9	7.8	0.009	9.3	25.0	0.000	41.0	3.8	0.058
2	6	63.0	2.5	0.093	46.2	2.3	0.147	15.9	20.8	0.000	41.3	4.7	0.037
3	7	64.0	1.9	0.124	45.8	4.2	0.058	<b>38.2</b>	<b>0.0</b>	<b>0.539</b>	44.5	2.1	0.137
4	7	64.6	0.7	0.230	<b>48.9</b>	<b>0.0</b>	<b>0.475</b>	15.3	22.7	0.000	43.9	2.8	0.096
5	8	64.0	3.3	0.061	45.9	5.5	0.030	37.4	2.4	0.165	44.5	3.5	0.070
6	8	<b>65.6</b>	<b>0.0</b>	<b>0.323</b>	48.6	1.9	0.184	37.9	1.7	0.229	<b>47.2</b>	<b>0.0</b>	<b>0.398</b>
7	9	65.6	1.4	0.158	48.7	3.2	0.097	37.1	4.2	0.067	47.3	1.3	0.203

Notes: For the analyses of species number, five adjacent point records made at 5 cm distances were pooled. See Table 1 for definitions of models 1 to 7 and Table 2 for abbreviations.

Table 5. Parameter estimates and corresponding significance tests for the best fitting models in Table 4. Bold values highlight  $P < 0.05$  (except for Bårby which is the overall intercept).

Term	Lichen species group											
	endolithic			epilithic			cyanolichens			all lichen species		
	t	P	Sig	t	P	Sig	t	P	Sig	t	P	Sig
Bårby	6.0	0.000		11.7	0.000		8.7	0.000		12.6	0.000	
Vickleby	-0.3	0.783		0.4	0.673		0.3	0.778		0.7	0.499	
Ekelunda	-0.4	0.726		<b>-2.2</b>	<b>0.028</b>	-	-0.3	0.735		-1.0	0.322	
Snail density	<b>3.7</b>	<b>0.000</b>	+++	0.8	0.444		<b>-4.0</b>	<b>0.000</b>	---	1.8	0.084	
Distance	<b>-3.5</b>	<b>0.001</b>	---	<b>-6.4</b>	<b>0.000</b>	---	<b>4.4</b>	<b>0.000</b>	+++	-0.4	0.723	
Distance <sup>2</sup>	1.7	0.092					<b>-5.0</b>	<b>0.000</b>	---	<b>-2.2</b>	<b>0.029</b>	-
Distance <sup>3</sup>												
Snail density <sup>2</sup>	<b>-2.0</b>	<b>0.048</b>	-	<b>-2.1</b>	<b>0.038</b>	-				<b>-2.1</b>	<b>0.043</b>	-
Interaction	<b>-2.6</b>	<b>0.011</b>	-	<b>2.8</b>	<b>0.006</b>	++	<b>2.9</b>	<b>0.005</b>	++	1.2	0.220	

Notes: For the analyses of species number, five adjacent point records made at 5 cm distances were pooled. See Table 3 for abbreviations but t-values of fitted model terms now have 72 - K degrees of freedom because of the pooled distances.

creased with increasing snail density. At the small spatial scale, linear distance effects became positive, indicating that the number of lichen species increased and then decreased with increasing distance (Appendix D: Tables D13–D15). Correlations of lichen species number with single distances were never significant. However, the correlation including a non-linear quadratic snail density effect explained 41.5% of the variability in number of lichen species (Fig. 3D).

#### Lichen species diversity

Model 7 was selected as best model explaining 54.0% of the variability in Shannon's diversity index of endolithic lichens (Appendix D: Tables D16–D18). The relationship between endolithic lichen diversity and snail density was non-linear with highest diversity recorded at intermediate snail densities. Endolithic lichen diversity de-

creased with increasing distance from crack edges independent of the best model and spatial scale. Correlations at single distances were significant only at the small spatial scale and positive correlations were found on the vertical crack walls. Epilithic lichen diversity was best modeled without any non-linear term (model 2) and decreased with snail density and distance (Appendix D: Tables D19–D21). At the small spatial scale, however, diversity first increased and then decreased with increasing snail density. Strong negative correlations of epilithic lichen diversity with snail density were found right on the crack edge and up to distances of 30 cm. Diversity of cyanolichens showed more pronounced responses to snail density than diversity of epilithic lichens (Appendix D: Tables D22–D24). Model 3 was supported indicating that non-linear distance but no snail density effects

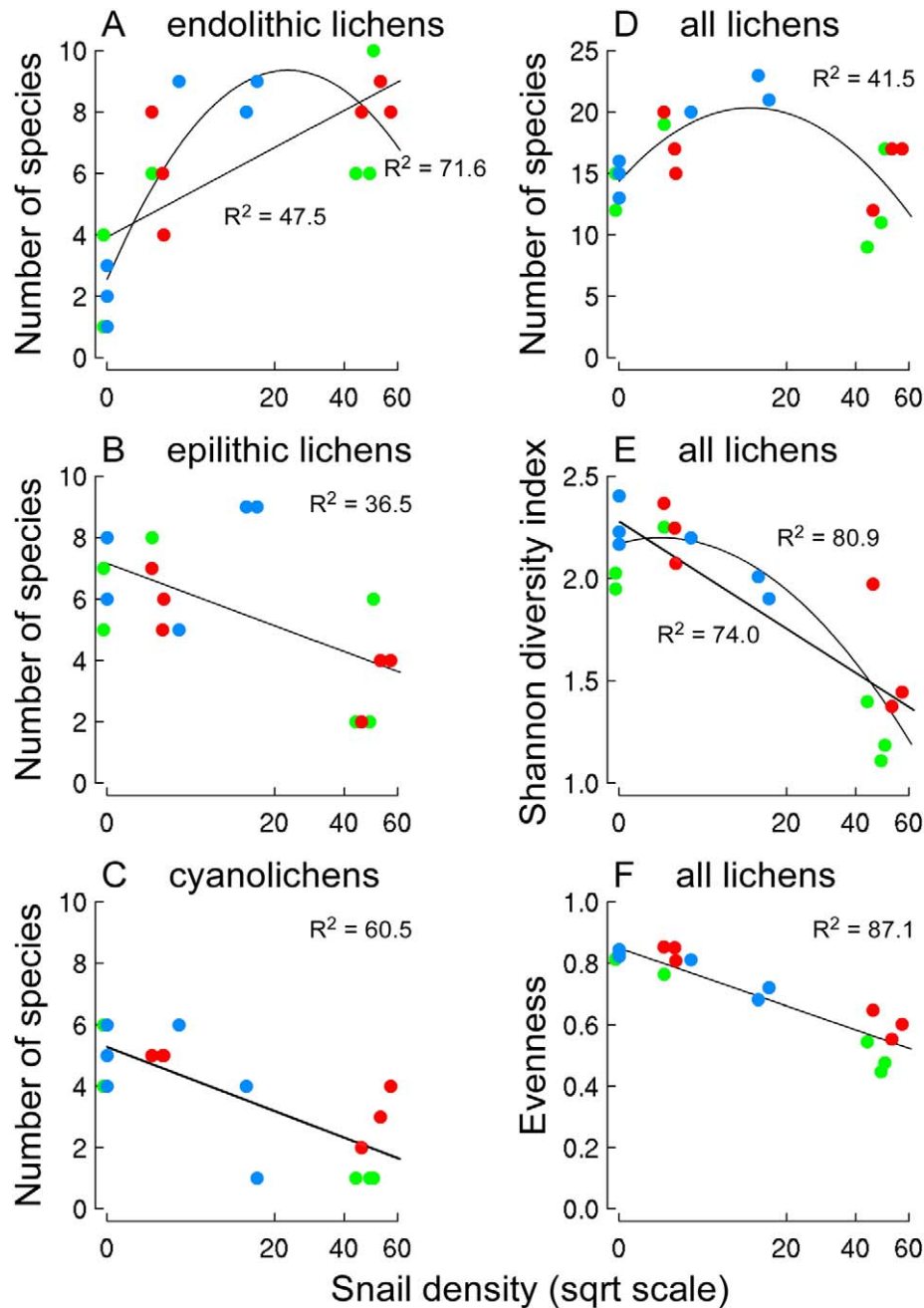


Fig. 3. Number of lichen species in different groups (A–C) and number and diversity of all lichen species (D–F) as a function of snail density in six cracks of limestone pavements at three localities (green: Bårby, blue: Vickleby, red: Ekelunda) on the Baltic island of Öland, Sweden. (A) Endolithic, (B) epilithic with green algal photobiont, (C) cyanolichens, i.e., epilithic or foliose lichens with cyanobacterial photobiont, and (D) all lichen species. (E) Shannon diversity index and (F) evenness of all lichen species. Point records of species were made along transects (8 on either side of each crack) every 5 cm and five adjacent point records were pooled. The distance range at which the strongest correlations (highest  $R^2$ ) were found started 10 cm on vertical crack walls within cracks and extended 10 cm onto the horizontal limestone pavements away from crack edges for number of species (A–D) and from 15 to 35 cm for Shannon diversity and Evenness (E & F). Linear, and non-linear regression lines with a squared snail density term are given as thin lines together with corresponding  $R^2$ -values if  $P < 0.05$  and as thick lines if  $P < 0.001$ . If symbols completely overlapped (e.g., at 0 snail density), they have been slightly relocated.

were important. Cyanolichen diversity decreased with snail density but first increased and then decreased with distance independent of spatial scale. At the small spatial scale, quadratic snail density was positive indicating highest diversity of cyanolichens at intermediate snail densities. Correlations of cyanolichen diversity with snail densities at single distances were negative up to a distance of 30 cm with  $R^2$ -values exceeding 40%. Diversity of all lichen species decreased with increasing snail density at both scales. Model 5 without a non-linear snail density effect explained 33.1% of the variability (Appendix D: Tables D25–D27) and there was no difference among localities. Diversity decreased with distance from crack edges but snail density and distance interacted indicating more pronounced snail density effects at small distances. Lichen diversity was negatively correlated with snail density at distances <40 cm and with  $R^2$ s of up to 70%. Although the quadratic snail density effect was not significant in the full model, it was significant and increased  $R^2$  from 74 to 81% if only snail density was correlated with the diversity of all lichen species at distances from 10 to 35 cm from crack edges (Fig. 3E).

Evenness of endolithic lichens was not influenced by snail density (Appendix D: Tables D28–D30) but decreased with distance. However, at the small spatial scale, evenness of endolithic lichens increased with increasing snail density. For epilithic lichens, correlations with snail density or distance were generally weak but positive at distance ranges from –10 to 10 cm (Appendix D: Tables D31–D33). Evenness of cyanolichens decreased with increasing snail density independent of the spatial scale (Appendix D: Tables D34–D36). Taken together, evenness of all lichen species decreased significantly with increasing snail density (Fig. 3F) and the negative correlations were very strong at both scales within distances of up to 60 cm (Appendix D: Tables D37–D39).

#### Community-level comparison

Average standardized effect sizes of C-scores were considerably larger than 0 at distances of 0 to 10 cm (Fig. 4A) and 40 to 50 cm (Fig. 4B) away from crack edges. Close to crack edges, C-scores were significantly higher along cracks with a conspicuous light zone ( $F_{1,12} = 6.1$ ,  $P = 0.029$ ) at

Bårby and Ekelunda though not at Vickelby. At larger distances, no similar differences were observed ( $F_{1,12} = 0.1$ ,  $P = 0.740$ ) and there were no significant differences between localities.

#### Cover of most abundant lichens

The four most abundant lichens made up almost half (46.2%) of all lichen records. *Clauzadea immersa* (Fig. C1), the most abundant endolithic species with green algae (975 or 75.1% of 1298 records), was common at high snail densities and 0 to 25 cm from crack edges (Fig. 5A). Parameter estimates of the best model (adjusted  $R^2 = 71.0\%$ , Appendix D: Tables D40–D42) showed that *C. immersa* was more abundant at Bårby compared to Vickelby and Ekelunda. Snail density and distance effects were positive but the negative quadratic and positive cubic distance effect indicated first increasing, then decreasing abundance with increasing distance from crack edges. The quadratic snail density effect indicated that the increase of *C. immersa* abundance with snail density was stronger than linear. The negative interaction between snail density and distance indicated a pronounced distance effect at high snail densities. Finally, *C. immersa* abundance was positively correlated with snail density up to 35 cm from crack edges. These patterns were confirmed at both spatial scales.

*Verrucaria nigrescens* (Fig. C2), the most abundant epilithic species with green algae (606 or 47.1% of 1287 records), was common at intermediate snail densities and distances (Fig. 5B). The species was completely absent on vertical crack walls with snails and the abundance was lowest at cracks of Bårby and Ekelunda with high snail densities. Model 7 outperformed simpler models (Appendix D: Tables D43–D45). Compared to abundances of cyanobacterial colonies and *C. immersa*, the adjusted  $R^2$  of 33.2% was relatively low. While the abundance of *V. nigrescens* first increased with snail density, the negative effect of quadratic snail density (which was positive for *C. immersa*) indicated that *V. nigrescens* abundance decreased non-linearly with increasing snail density. The interaction term of snail density with distance was positive (i.e., the distance effect was much more pronounced at low or intermediate compared to high snail densities). The negative effect of snail density on *V. nigrescens* abundance was strongest right at the

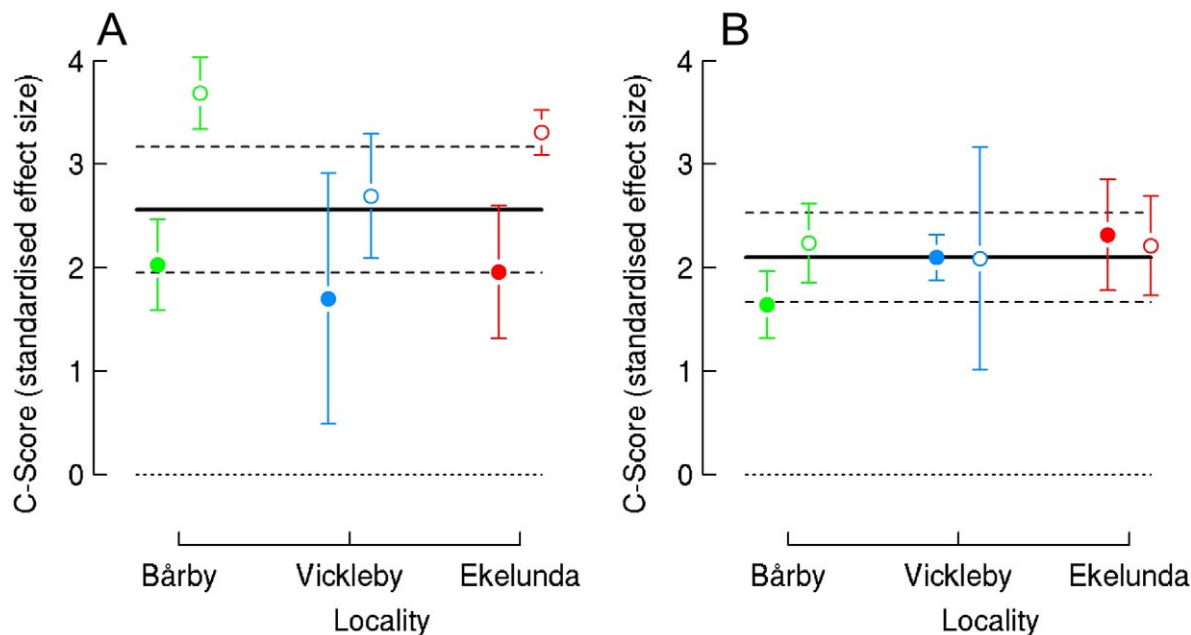


Fig. 4. Standardised effect size of checkerboard scores (C-score) of cyanobacterial and lichen communities at distances (A) 0–10 cm and (B) 40–50 cm away from crack edges on three pavements on the Baltic island of Öland, Sweden. Each point represents the mean ( $\pm 1$  S.E) of three replicated cracks with (open symbols) or without (closed symbols) conspicuous light zones per locality. The horizontal black lines give the overall mean  $\pm 95\%$  confidence interval (dashed lines,  $n = 18$ ).

crack edge and spatially restricted. The patterns were confirmed at the larger spatial scale at which the cubic distance effect disappeared and the adjusted  $R^2$  rose to 48%.

The two most common lichens with cyanobacterial photobionts, *Placynthium nigrum* s. lat. (203 or 34.8% of 584 records, Fig. C3) and *Collema fuscovirens* (250 or 46.0% of 543 records), were less abundant than either *C. immersa* or *V. nigrescens*. Both species were more abundant at Vickleby and Ekelunda than at Bårby. For *P. nigrum* s. lat., model 3 fitted best (adjusted  $R^2 = 35.6\%$ , Appendix D: Tables D46–D48) and for *C. fuscovirens*, model 7 was selected (adjusted  $R^2 = 11.6\%$ , Appendix D: Tables D49–D51). *P. nigrum* s. lat. was almost completely absent in the presence of snails up to 25 cm away from crack edges (Fig. 5C). *C. fuscovirens* was somewhat less affected by the presence of snails (Fig. 5D). The filled contours indicated that both species had very low abundances up to distances of 25 cm from crack edges when snails were present.

#### Transplant experiment

Changes in abundance of cyanobacterial colo-

nies differed between pieces of stone placed near cracks with high snail densities or without snails (Kruskal-Wallis rank-sum test on change in abundance class,  $\chi^2 = 16.4$ ,  $df = 1$ ,  $P \ll 0.001$ ). Five out of eleven pieces with abundant cyanobacterial colonies (abundance class 2 or 3) were completely grazed and six were heavily grazed (abundance class 1) within 19 months when placed near cracks with high snail densities. In contrast, eight out of ten stones without cyanobacteria showed cyanobacterial colonies (abundance class 1) after 19 months when placed near cracks without snails.

## DISCUSSION

### Direct effects of herbivore presence

The present study showed that cyanobacterial cover was nearly completely removed along the edges of cracks inhabited by gastropods and that endolithic lichen abundance, as well as diversity increased in close association with high snail densities. On the other hand, abundant cyanobacterial colonies could be observed even within cracks uninhabited by snails. Herbivorous snails

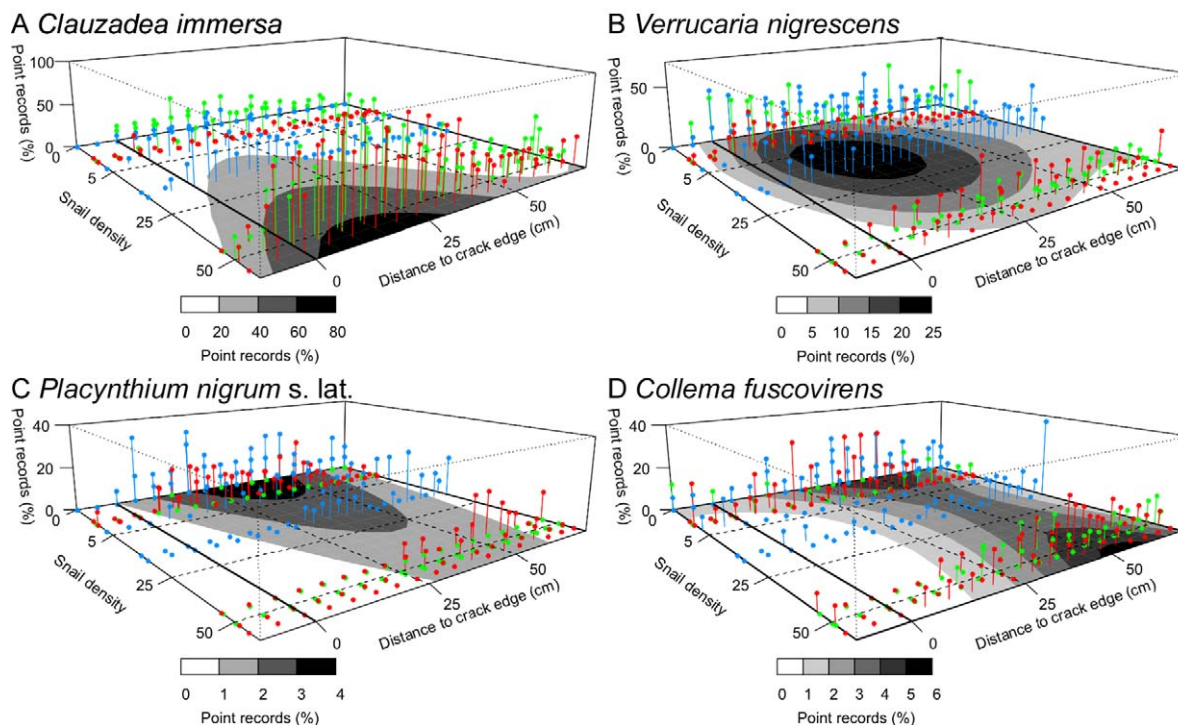


Fig. 5. Cover (point records in %) of most abundant lichen species as a function of snail density and distance to crack edge (indicated by the black line at distance 0 cm, negative distances refer to vertical crack walls) on three pavements (green: Bårby, blue: Vickleby, red: Ekelunda) on the Baltic island of Öland, Sweden. (A) *Clauzadea immersa*; (B) *Verrucaria nigrescens*; (C) *Placynthium nigrum* s. lat.; (D) *Collema fuscovirens*. Best fitting models were used to produce filled contours projected onto the horizontal plane spanned by snail density (sqrt-transformed) and distance to crack edge. Levels of filled contours represent discrete classes of point records (indicated on the horizontal scale bar) occupied by the different lichen species. Thus, 80–100% indicates that 12.6–16 point records (16 being the maximum because we had 8 transects on either side of each crack) were occupied with a given species. The best fitting model was selected from a set of candidate models using Akaike's information criterion (Appendix D: Tables D40–D51). Note the different scaling of the z-axes.

(*C. clienta*) rest in cracks but graze cyanobacteria and various lichens on the horizontal rock surface under periods of high air humidity. Cracks providing shelter against extreme winter and summer temperature fluctuations allow the snails to survive in this rather harsh environment (Appendix A: Fig. A1).

Our results clearly showed that the conspicuous light zones along the cracks of the limestone pavements can be explained by the presence of herbivorous gastropods and not as previously hypothesized by abiotic crack characteristics. This interpretation is further supported by the results of our transplant experiment although full recolonization of coccoid cyanobacteria may take several years (Pentecost and Whitton 2000). In addition, cyanobacteria constitute a main food

source for *C. clienta*. Experiments testing the quality of different food types revealed that juvenile *C. clienta* kept on a diet of cyanobacteria grew faster than those kept on lichen diets (Baur et al. 1992, 1994). Groups of *C. clienta* and the competing land snail *Balea perversa* were raised successfully over 1–2 generations in dishes containing small pieces of stone covered with cyanobacteria and lichens (Baur and Baur 1990, 2000). Laboratory experiments with lichen-feeding snails revealed differential grazing damage in different calcicolous lichen species (Fröberg et al. 1993, Baur et al. 1994). Individuals of *C. clienta* grazed on 18 out of 27 lichen species offered and damage was significantly larger in epilithic lichens than in endolithic lichens (Fröberg et al. 1993). Grazing damage was also recorded in 33

of 52 lichen species examined on limestone walls in the grassland Great Alvar (Baur et al. 1995).

In the field, the extent of gastropod grazing on lichens varies temporally and spatially (Gauslaa et al. 2006, Asplund et al. 2010). In the present study, grazing damages were observed exclusively in lichens near cracks inhabited by *C. clienta* (L. Fröberg, unpublished data). Most interestingly, grazing damage was most concentrated in lichen individuals growing less than 20 cm from the crack edges and predominantly to epilithic lichens with green algae as symbionts. On horizontal surfaces of limestone pavements, the gastropod *C. clienta* is most probably the exclusive herbivore, while on the nearby situated limestone walls with a much higher abundance of foliose lichens specialized oribatid mites and larvae of Lepidoptera also graze on lichens together with *B. perversa* and *C. clienta* (Fröberg et al. 1996, Baur and Baur 1997). On the top of two stone walls studied in the grassland Great Alvar, 39.5% of the thallus area of *Aspicilia calcarea* was severely damaged by snail grazing (Fröberg et al. 2006). Corresponding figures were 3.5–22.5% for *Verrucaria nigrescens* and 6.0–11.5% for *Tephromela atra*. However, lichen regeneration should be taken into account when quantifying grazing damage. The regenerative capacity of three calcicolous lichen species damaged by the snail *Balea perversa* has been examined in a controlled field experiment (Fröberg et al. 2006). On horizontal rock surfaces, slightly damaged thalli of *A. calcarea*, *V. nigrescens* and *T. atra* were regenerated after 1 year when further snail grazing was prevented. Severely damaged lichen thalli of *A. calcarea* regenerated 3 years after snail grazing, but they were thinner than ungrazed (control) thalli (Fröberg et al. 2006). Under natural field conditions grazing and regeneration of lichens occur simultaneously.

So far, major grazing impacts have rarely been documented in natural lichen communities, apart from sites with large reindeer populations (den Herder et al. 2003). The present study provides evidence for a significant grazing impact of gastropods in a natural cyanobacteria-lichen community of a low-productive environment.

#### *Indirect effects*

The abundance and diversity of endolithic lichens was higher along cracks with high snail

density but lower in cyanolichens and epilithic lichens with green algae as photobionts. Thus, the removal of cyanobacteria and epilithic lichens, in particular crustose ones, indirectly favored endolithic lichens releasing them from competition for light. Such an interpretation is supported by Omelon et al. (2007) showing that rocks hosting communities dominated by cyanobacteria lack surface crusts and have fewer endolithic lichens. Moreover, the community-level comparison clearly showed that competition as inferred by co-occurrences was important in structuring the observed patterns. But the finding that community-wide competition was stronger in the presence of snails seems to refute our hypothesis. On the other hand, endolithic lichens were almost completely absent where cyanobacteria dominate and snails were absent. However, if grazing snails remove cyanobacteria and release endolithic lichens from competition, C-scores may not quantify competition among cyanobacteria and endolithic lichens but competition within endolithic lichens, which in turn may lead to higher C-scores compared to communities at cracks with low snail densities or further away from cracks with high densities where endolithic lichens are completely excluded by cyanobacteria.

The use of primary producers by herbivores is often determined by nutritional value and quality and quantity of host-plant defense (e.g., Thompson 1999). Lichen species differ in growth form, type of photobiont, surface toughness, texture, energy and nutrient content and composition and concentration of secondary chemical compounds. Secondary compounds are mainly located in the upper cortex and/or in the medullary layer of the lichen (Gauslaa 2009). The cortical lichen compounds protect the lichen against excess solar radiation, whereas the medullary compounds cause feeding deterrence or even acute toxicity in herbivores (Gauslaa 2009). Lichens with the ability to fix N show, with a few exceptions, low concentrations of lichen compounds (Gauslaa 2009). The majority of lichen species occurring on the pavements do not contain any feeding deterring compounds suggesting that species-specific chemical defense might be of minor importance for explaining the distribution of lichens recorded in the present study.



The presence of snails could not be explained by any of the crack characteristics examined in this study. During three winters different cracks were filled with snow depending on the wind direction during heavy snowfall events (B. Baur, unpublished). Cracks with *C. clienta* were filled with snow as often as cracks without snails. Melt water from the surrounding grassland creates small streams for short periods in spring. Water discharge in cracks depends on the amount of snow and does not occur every year. We observed that water discharge occurred exclusively in cracks, which are free of *C. clienta*. Thus, hibernating snails attached to the vertical rock surface of cracks and in fissures may be dislodged by running water. It is therefore possible that the absence of snails in certain cracks could be explained by repeated events of water discharge extirpating any newly founded population. This hypothesis could be tested by transplanting snails to uninhabited cracks and recording their densities, the potential water discharges, and the abundances of cyanobacteria and lichens over a period of 10–15 years.

#### *Patterns of different lichen groups and species*

The response of the most abundant species in each lichen group was similar to that of the whole group. The most abundant epilithic lichen with green algae (*Verrucaria nigrescens*) and the cyanolichens (*Placynthium nigrum* s. lat. and *Collema fuscovirens*) responded negatively to the presence of snails, whereas the most abundant endolithic lichen (*Clauzadea immersa*) responded positively. By retaining water, cyanobacteria have the ability to prolong photosynthesis and respiration during dry periods (Lange et al. 1998, Lange 2000). This pronounced water-holding capacity may partly explain the higher abundance of cyanolichens at cracks with lower snail densities. Certain endolithic lichens have broad temperature optima of net photosynthesis and still reach one-third of their maximum rates at 2°C (Weber et al. 2007). Endolithic lichens are thus well adapted to varying microclimatic conditions (e.g., Garvie et al. 2008) but are presumably not competitive against cyanobacteria and crustose or foliose epilithic species (Tretiach and Pecchiari 1995). *C. immersa* produces a light grey or whitish grey endolithic thallus and immersed apothecia within pits. It is rather

common and dominates the vegetation at the edge of weathered cracks contributing to the distinct light coloration (Fröberg 1989). Based on our results we now interpret the increased abundance of *C. immersa* along the edges of cracks as a result of snail grazing on cyanobacteria and the associated competitive release.

#### *Scale dependence*

Grazing can alter the spatial heterogeneity of vegetation, influencing ecosystem processes and biodiversity depending on spatial patterns (Bergelson 1990) and on various spatial scales (e.g., Sarnelle et al. 1993, Sommer 1999, 2000, Adler et al. 2001). The scale of observation is defined at the lower end by the unit of sampling and at the upper end by the overall extent of the study area. In our case, the highest resolution was at 5 cm between sampling units and this high resolution was important. Many of the relatively small scale effects of the gastropod grazers would not have been detected if sampling units would have been too large (>15 cm). For example, the positive effect of snail density on evenness of endolithic lichens were detected on the smaller but not the larger spatial scales. On the other hand, sampling larger areas allowed us to show that the number of epilithic lichen species first increased but then decreased with increasing distance from the cracks independent of snail density. It also allowed detecting various non-linear effects of either snail density or distance. The most pronounced effects, however, the negative effects of snail presence on the abundance of cyanobacteria, diversity and evenness of all lichen species or cyanolichens only, were independent of spatial scale of the sampling units. Finally, although crack characteristics did not explain the observed large-scale patterns, small-scale differences in abiotic factors such as small depressions in the rock surface could nevertheless explain the microdistribution of cyanobacteria and certain species or groups of lichens on the pavements.

#### *General conclusions*

Limestone pavements are rare, threatened worldwide and have a high conservation value (Ward and Evans 1976, Usher 1980). We demonstrate high species richness of lichens including several rare species on the pavements. Lichens dominate low-productive, dry and/or cold hab-

itats under conditions too harsh to sustain a dense cover of vascular plants. Our study is as far as we know the first demonstrating any influence of land snails on the diversity of endo- and epilithic lichen communities. Our results complement evidence that lichen-feeding gastropods shape epiphytic communities in boreal forests (Asplund and Gauslaa 2008, Gauslaa 2008) and increase our knowledge of herbivory effects on diversity. Recently, biodiversity research extended to biological crusts as model systems to uncover general ecological principles (Walker and Pace 2007, Gorbushina and Broughton 2009, Bowker et al. 2010a, 2010b). We added effects of herbivory and therefore an additional trophic level. We also provide empirical support for a general ecological principle. As in our limestone pavements, negative effects of grazers on diversity of primary producers are commonly found in low-productive ecosystems (Proulx and Mazumder 1998, Hillebrand 2003).

#### ACKNOWLEDGMENTS

We thank B. Büdel for determining samples of microscopic cyanobacteria, N. Cronberg for determining samples of bryophytes, and J. Asplund, M. Bowker, Y. Gauslaa, and D. M. Newbery for comments on earlier drafts. P. Frödén took the cyanobacteria picture in Fig. 1D and the lichen pictures in Appendix C. Financial support was received from the Swiss National Science Foundation (grant to BB).

#### LITERATURE CITED

- Adler, P. B., D. A. Raff, and W. K. Lauenroth. 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128:465–479.
- Armbruster, G. F. J., M. Hofer, and B. Baur. 2007. Effect of cliff connectivity on the genetic population structure of a rock-dwelling land snail species with frequent self-fertilization. *Biochemical Systematics and Ecology* 35:325–333.
- Asplund, J., and Y. Gauslaa. 2008. Mollusc grazing limits growth and early development of the old forest lichen *Lobaria pulmonaria* in broadleaved deciduous forests. *Oecologia* 155:93–99.
- Asplund, J., P. Larsson, S. Vatne, and Y. Gauslaa. 2010. Gastropod grazing shapes the vertical distribution of epiphytic lichens in forest canopies. *Journal of Ecology* 98:218–225.
- Bakker, E. S., M. E. Ritchie, H. Olff, D. G. Milchunas, and J. M. H. Knops. 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology Letters* 9:780–788.
- Batschelet, E. 1981. *Circular statistics in biology*. Academic Press, London.
- Baur, A., and B. Baur. 1991. The effect of hibernation position on winter survival of the rock-dwelling land snails *Chondrina clienta* and *Balea perversa* on Öland, Sweden. *Journal of Molluscan Studies* 57:331–336.
- Baur, A., B. Baur, and L. Fröberg. 1992. The effect of lichen diet on growth-rate in the rock-dwelling land snails *Chondrina clienta* (Westerlund) and *Balea perversa* (Linnaeus). *Journal of Molluscan Studies* 58:345–347.
- Baur, A., B. Baur, and L. Fröberg. 1994. Herbivory on calcicolous lichens—different food preferences and growth rates in two coexisting land snails. *Oecologia* 98:313–319.
- Baur, B. 1987. Richness of land snail species under isolated stones in a karst area on Öland, Sweden. *Basteria* 51:129–133.
- Baur, B. 1988. Microgeographical variation in shell size of the land snail *Chondrina clienta*. *Biological Journal of the Linnean Society* 35:247–259.
- Baur, B., and A. Baur. 1990. Experimental evidence for intra- and interspecific competition in two species of rock-dwelling land snails. *Journal of Animal Ecology* 59:301–315.
- Baur, B., and A. Baur. 1995. Habitat-related dispersal in the rock-dwelling land snail *Chondrina clienta*. *Ecography* 18:123–130.
- Baur, B., and A. Baur. 1997. *Xanthoria parietina* as a food resource and shelter for the land snail *Balea perversa*. *Lichenologist* 29:99–102.
- Baur, B., and A. Baur. 2000. Social facilitation affects longevity and life time reproductive success in a self-fertilizing land snail. *Oikos* 88:612–620.
- Baur, B., L. Fröberg, and A. Baur. 1995. Species diversity and grazing damage in a calcicolous lichen community on top of stone walls in Öland, Sweden. *Annales Botanici Fennici* 32:239–250.
- Baur, B., L. Fröberg, A. Baur, R. Guggenheim, and M. Haase. 2000. Ultrastructure of snail grazing damage to calcicolous lichens. *Nordic Journal of Botany* 20:119–128.
- Bergelson, J. 1990. Spatial patterning in plants—opposing effects of herbivory and competition. *Journal of Ecology* 78:937–948.
- Bowker, M. A., F. I. Maestre, and C. Escolar. 2010a. Biological crusts as a model system for examining the biodiversity-ecosystem function relationship in soils. *Soil Biology & Biochemistry* 42:405–417.
- Bowker, M. A., S. Soliveres, and F. T. Maestre. 2010b. Competition increases with abiotic stress and regulates the diversity of biological soil crusts. *Journal of Ecology* 98:551–560.
- Büdel, B., B. Weber, M. Kuhl, H. Pfanzer, D. Sultemeyer,

- and D. Wessels. 2004. Reshaping of sandstone surfaces by cryptoendolithic cyanobacteria: bioalkalization causes chemical weathering in arid landscapes. *Geobiology* 2:261–268.
- Burnham, K. P., and D. J. Anderson. 2002. Model selection and multimodel inference. A practical information-theoretic approach. Second edition. Springer, New York, USA.
- Carson, W. P., and R. B. Root. 2000. Herbivory and plant species coexistence: Community regulation by an outbreaking phytophagous insect. *Ecological Monographs* 70:73–99.
- Crawley, M. J. 1997. Plant-herbivore dynamics. Pages 401–474 in M. J. Crawley, editor. *Plant ecology*. Blackwell Scientific Publications, Oxford, UK.
- Crawley, M. J. 2005. *Statistics. An introduction using R*. John Wiley & Sons, Chichester, UK.
- den Herder, M., M. M. Kytoviita, and P. Niemela. 2003. Growth of reindeer lichens and effects of reindeer grazing on ground cover vegetation in a Scots pine forest and a subarctic heathland in Finnish Lapland. *Ecography* 26:3–12.
- Doppelbaur, H. W. 1959. Studien zur Anatomie und Entwicklungsgeschichte einiger endolithischen pyrenocarpen Flechten. *Planta* 53:246–292.
- Friedmann, E. I. 1982. Endolithic microorganisms in the antarctic cold desert. *Science* 215:1045–1053.
- Fröberg, L. 1989. The calcicolous lichens on the Great Alvar of Öland. Sweden. Dissertation. University of Lund, Sweden.
- Fröberg, L., A. Baur, and B. Baur. 1993. Differential herbivore damage to calcicolous lichens by snails. *Lichenologist* 25:83–95.
- Fröberg, L., A. Baur, and B. Baur. 2006. Field study on the regenerative capacity of three calcicolous lichen species damaged by snail grazing. *Lichenologist* 38:491–493.
- Fröberg, L., T. Solhøy, A. Baur, and B. Baur. 1996. Hornkvalster (Oribatida) knutna till lavar på Ölands Stora Alvar. *Entomologisk Tidskrift* 117:161–164.
- Garvie, L. A. J., L. P. Knauth, F. Bungartz, S. Klonowski, and T. H. Nash. 2008. Life in extreme environments: survival strategy of the endolithic desert lichen *Verrucaria rubrocincta*. *Naturwissenschaften* 95:705–712.
- Gauslaa, Y. 2008. Mollusc grazing may constrain the ecological niche of the old forest lichen *Pseudocyphellaria crocata*. *Plant Biology* 10:711–717.
- Gauslaa, Y. 2009. Ecological functions of lichen compounds. Pages 95–108 in Bayerische Akademie der Wissenschaften, editor. *Rundgespräche der Kommission für Ökologie: ökologische Rolle der Flechten*. Verlag Dr. Friedrich Pfeil, München, Germany.
- Gauslaa, Y., H. Holien, M. Ohlson, and T. Solhøy. 2006. Does snail grazing affect growth of the old forest lichen *Lobaria pulmonaria*? *Lichenologist* 38:587–593.
- Geitler, L. 1932. Cyanophyceae. Rabenhorst's Kryptogamen-Flora. Eduard Kummer Verlag, Leipzig, Germany.
- Gorbushina, A. A., and W. J. Broughton. 2009. Microbiology of the atmosphere-rock interface: How biological interactions and physical stresses modulate a sophisticated microbial ecosystem. *Annual Review of Microbiology* 63:431–450.
- Gotelli, N. J. 2000. Null model analysis of species occurrence patterns. *Ecology* 81:2606–2621.
- Gotelli, N. J., and G. L. Entsminger. 2006. Ecosim: Null model software for ecology. Version 7. Acquired Intelligence Inc. & Kesey-Bear, Jericho, Vermont 05465, USA. (<http://garyentsminger.com/ecosim/index.htm>)
- Hesbacher, S., L. Fröberg, A. Baur, B. Baur, and P. Proksch. 1996. Chemical variation within and between individuals of the lichenized ascomycete *Tephromela atra*. *Biochemical Systematics and Ecology* 24:603–609.
- Hillebrand, H. 2003. Opposing effects of grazing and nutrients on diversity. *Oikos* 100:592–600.
- Hulme, P. E. 1996. Herbivory, plant regeneration, and species coexistence. *Journal of Ecology* 84:609–615.
- Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics* 22:477–503.
- Hurvich, C. M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. *Biometrika* 76:297–307.
- Königsson, L.-K. 1977. Weathering in the fissure systems in southern Öland. *Geologiska Föreningens i Stockholm Förhandlingar* 99:384–394.
- Krahulec, F., E. Rosén, and E. van der Maarel. 1986. Preliminary classification and ecology of dry grassland communities on Ölands Stora Alvar (Sweden). *Nordic Journal of Botany* 6:797–809.
- Lange, O. L. 2000. Photosynthetic performance of a gelatinous lichen under temperate habitat conditions: long-term monitoring of CO<sub>2</sub> exchange of *Collema cristatum*. Pages 307–332 in B. Schroeter, M. Schlensog, and T. G. A. Green, editors. *Bibliotheca Lichenologica*. J. Cramer in der Gebrüder Bornträger Verlagsbuchhandlung, Berlin-Stuttgart, Germany.
- Lange, O. L., J. Belnap, and H. Reichenberger. 1998. Photosynthesis of the cyanobacterial soil-crust lichen *Collema tenax* from arid lands in southern Utah, USA: role of water content on light and temperature response of CO<sub>2</sub> exchange. *Functional Ecology* 12:195–202.
- Lubchenco, J., and S. D. Gaines. 1981. A unified approach to marine plant-herbivore interactions. 1. Populations and communities. *Annual Review of*

- Ecology and Systematics 12:405–437.
- Matthews, J. A., and G. Owen. 2008. Endolithic lichens, rapid biological weathering and Schmidt Hammer R-values on recently exposed rock surfaces: Storbreen glacier foreland, Jotunheimen, Norway. *Geografiska Annaler Series a, Physical Geography* 90A:287–297.
- Omelon, C. R., W. H. Pollard, and F. G. Ferris. 2007. Inorganic species distribution and microbial diversity within high arctic cryptoendolithic habitats. *Microbial Ecology* 54:740–752.
- Pacala, S. W., and M. J. Crawley. 1992. Herbivores and plant diversity. *American Naturalist* 140:243–260.
- Pentecost, A., and B. A. Whitton. 2000. Limestones. Pages 257–279 in B. A. Whitton and M. Potts, editors. *The ecology of cyanobacteria—Their diversity in time and space*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Proulx, M., and A. Mazumder. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* 79:2581–2592.
- R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* 181:165–176.
- Santesson, R., R. Moberg, A. Nordin, T. Tønsberg, and O. Vitikainen. 2004. Lichen-forming and lichenicolous fungi of Fennoscandia. SBF-förlaget, Uppsala.
- Sarnelle, O., K. W. Kratz, and S. D. Cooper. 1993. Effects of an invertebrate grazer on the spatial arrangement of a benthic microhabitat. *Oecologia* 96:208–218.
- Shachak, M., C. G. Jones, and Y. Granot. 1987. Herbivory in rocks and the weathering of a desert. *Science* 236:1098–1099.
- Sih, A., P. Crowley, M. McPeck, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities - a review of field experiments. *Annual Review of Ecology and Systematics* 16:269–311.
- Sommer, U. 1999. The impact of herbivore type and grazing pressure on benthic microalgal diversity. *Ecology Letters* 2:65–69.
- Sommer, U. 2000. Benthic microalgal diversity enhanced by spatial heterogeneity of grazing. *Oecologia* 122:284–287.
- Stone, L., and A. Roberts. 1990. The checkerboard score and species distributions. *Oecologia* 85:74–79.
- Strauss, S. Y. 1991. Indirect effects in community ecology—their definition, study and importance. *Trends in Ecology & Evolution* 6:206–210.
- Thompson, J. 1999. What we know and do not know about coevolution: insect herbivores and plants as a test case. Pages 7–30 in H. Olff, V. K. Borwn, and R. H. Drent, editors. *Herbivores: between plants and predators; the 38th symposium of the British Ecological Society in cooperation with The Netherlands Ecological Society held at the Wageningen Agricultural University, 1997*. Blackwell Science, Oxford.
- Tretiach, M., and M. Pecchiari. 1995. Gas exchange rates and chlorophyll content of epi- and endolithic lichens from the Trieste Karst (NE Italy). *New Phytologist* 130:585–592.
- Usher, M. B. 1980. An assessment of conservation values within a large site of special scientific interest in North Yorkshire. *Field Studies* 5:323–348.
- Viles, H. 1995. Ecological perspectives on rock surface weathering—toward a conceptual model. *Geomorphology* 13:21–35.
- Walker, J. J., and N. R. Pace. 2007. Endolithic microbial ecosystems. *Annual Review of Microbiology* 61:331–347.
- Ward, S. D., and D. F. Evans. 1976. Conservation assessment of British limestone pavements based on floristic criteria. *Biological Conservation* 9:217–233.
- Weber, B., C. Scherr, H. Reichenberger, and B. Büdel. 2007. Fast reactivation by high air humidity and photosynthetic performance of alpine lichens growing endolithically in limestone. *Arctic Antarctic and Alpine Research* 39:309–317.
- White, E. M., J. C. Wilson, and A. R. Clarke. 2006. Biotic indirect effects: a neglected concept in invasion biology. *Diversity and Distributions* 12:443–455.

## APPENDIX A

### *Temperature profiles on the surface and different depths of a crack on a limestone pavement*

The air temperature on the horizontal rock surface and at different depths (10, 30, 60, and 85 cm) of a 15-cm wide crack on the limestone pavement of Bårby was measured with Tinytalk

temperature loggers (Gemini Data Loggers, Chichester, UK). Loggers were fixed directly on the rock surface or at given depths in the crack using a string. Temperatures were recorded every 3 hours for 12 months (from 15 October 1996 to 14 October 1997). We picked the depth of 60 cm, the

surface of the pavement and one control to illustrate representative temperature profiles. The actual sites of measurement corresponded to the sites where lichens occur and individuals of *C. clienta* forage (horizontal surface), rest, estivate and overwinter (crack). For comparison, two loggers measuring air temperature under standard conditions (at a height of 1.5 m in the shade) were set up 30 m away from the limestone pavement.

Winter temperatures were damped by snow cover on the pavement and higher in cracks compared to the surface or control without snow

cover (Fig. A1). At depths of 60 cm within the crack, temperature was stable and never fell below  $-4^{\circ}\text{C}$ . In summer, night temperatures on the surface of the pavement were similar to control temperatures (Fig. A1). Day temperatures of sunny days regularly reached values above  $30^{\circ}\text{C}$  on the surface with a maximum of  $39.4^{\circ}\text{C}$ . Temperatures within the crack were damped and did not fall as low in the night as temperatures on the surface of the pavement or the control. During hot and sunny days, temperatures at 60 cm within cracks never exceeded  $27^{\circ}\text{C}$ .

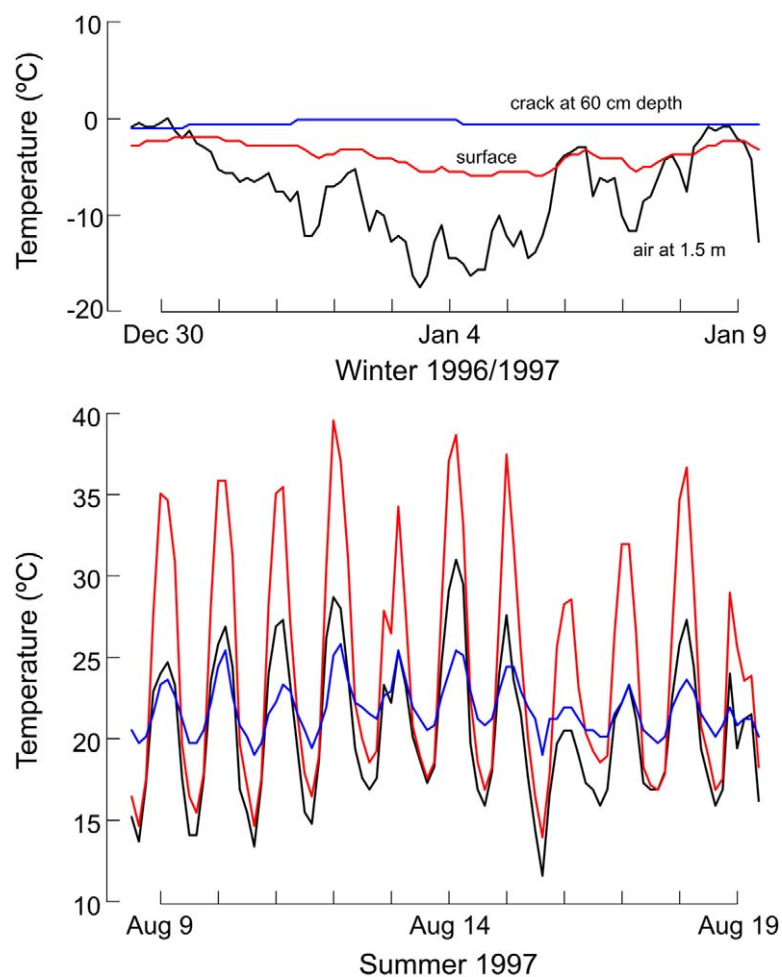


Fig. A1. Air temperature profiles on the surface (red), in a crack at a depth of 60 cm (blue), and from a control (black, measured 1.5 m above the surface in the shade) of a limestone pavement near Bårby (Baltic island of Öland, Sweden). Representative periods of 10 days around the coldest day in winter 1996/1997 (top panel) and the hottest day in summer 1997 (bottom panel) are shown. The damping effects of cracks on both winter and summer temperature extremes allow the herbivore (*C. clienta*) to exist on pavements.

## APPENDIX B

Table B1. Aspect, crack dimensions and relative density of the snail *Chondrina clienta* in cracks with or without conspicuous light zones indicating poor or dense cyanobacterial cover in limestone pavements at three localities on the Baltic island of Öland, Sweden.

Locality	Conspicuous light zone	Aspect	Width (cm)†		Depth (cm)†		Erosion‡ (cm <sup>2</sup> )	Snail density§	
			Mean	SD	Mean	SD		Mean	SD
Bårby	present	WNW-ESE	5.8	1.2	71.1	1.1	156.5	50.4	12.8
		W-E	4.4	1.3	60.5	0.5	77.0	45.3	18.1
		WNW-ESE	8.0	2.5	73.6	6.4	98.8	51.9	16.8
	absent	WSW-ESE	5.8	1.3	121.3	17.2	165.0	0.0	
		WNW-ESE	3.5	1.0	51.8	4.3	89.3	0.0	
		WNW-ESE	4.3	1.7	12.6	1.2	54.3	1.7	1.9
Vickleby	present	SW-NE	7.5	1.5	110.5	0.7	89.3	3.7	2.8
		SSW-NNE	7.1	0.3	26.8	2.1	108.0	13.8	6.9
		SW-NE	10.3	4.4	47.8	7.0	65.5	16.0	6.4
	absent	WNW-ESE	2.8	1.1	25.5	6.1	35.0	0.0	
		SSW-NNE	5.8	1.8	107.4	2.1	66.3	0.0	
		SW-NE	8.8	2.2	141.6	2.5	460.0	0.0	
Ekelunda	present	SE-NW	7.0	0.7	87.4	1.2	75.8	51.7	11.8
		SE-NW	6.4	0.7	74.9	1.2	110.5	55.7	11.9
		WSW-ESE	6.3	0.8	70.1	3.6	144.8	44.7	5.6
	absent	SE-NW	10.0	0.5	52.5	4.7	48.3	2.0	2.0
		SSW-NNE	2.6	0.7	39.8	2.8	174.5	1.2	2.0
		SE-NW	6.8	2.3	25.1	1.4	63.5	1.9	1.9

† N = 8 measurements per crack

‡ Total erosion at both sides of the crack

§ Mean number of adult snails collected in 9 replicated searches of 2 minutes

## APPENDIX C

*Taxonomical remarks*

Nomenclature of lichens follows Santesson et al. (2004), except for *Placynthium tremniacum* (A. Massal.) Jatta. *Aspicilia contorta* includes two subspecies (*ssp. contorta* and *ssp. hoffmanniana*) but intermediates occur frequently. The intermediates were considered as a separate taxon. The status of the species in the genus *Bagliettoa* is uncertain and therefore these species were not distinguished. The *Caloplaca velana* group includes *C. dolomiticola* and *C. glomerata*, distinguished on the basis of spore characteristics. Specimens without spores were referred to as *C. velana* s. lat. The genus *Lempholemma* needs revision. A few specimens that deviated from *L. isidiodes* were still included in this species. In the *Lecanora dispersa* group, five species have been

recorded. Most specimens of this group found on the limestone pavements were too small for a proper identification and thus were referred to as *L. dispersa* s. lat. Similarly, small specimens of the genus *Placynthium* were referred to *Placynthium nigrum* s. lat (203 point records). Adding *Placynthium nigrum* (79 point records) and *Placynthium tremniacum* (95 point records) to *Placynthium nigrum* s. lat. increased R<sup>2</sup>-values and lowered the P-values of the correlations with snail densities at single distances below the Bonferroni-corrected significances, but did not qualitatively change the results obtained from the analyses using exclusively the 203 point records. One undetermined squamulose species is referred to as “unidentified”.

Table C1. Frequency of lichens with green algae as photobionts in and along cracks on three limestone pavements in the grassland Great Alvar on the Baltic island of Öland, Sweden. The number of records at cracks are given with a conspicuous light zone present (p) or absent (a), their total ( $\Sigma$ , n = 3 cracks per locality and crack type) and their overall total for all three sites (P, A and  $\Sigma$  respectively). Abbreviations are: endolithic (Type: endo), epilithic (epi), fruticose (fru) and foliose (fol).

Type	Species	Location									P	A	$\Sigma$
		Bårby			Vickleby			Ekelunda					
		p	a	$\Sigma$	p	a	$\Sigma$	p	a	$\Sigma$			
endo	<i>Clauzadea immersa</i>	371	131	502	106	12	118	348	7	355	825	150	975
	<i>Ionaspis melanocarpa</i>	8	0	8	7	0	7	53	5	58	68	5	73
	<i>Thelidium decipiens</i>	17	2	19	8	1	9	21	4	25	46	7	53
	<i>Protoblastenia calva</i>	8	1	9	8	0	8	12	1	13	28	2	30
	<i>Verrucaria calciseda</i>	2	3	5	11	2	13	3	4	7	16	9	25
	<i>Polyblastia deminuta</i>	3	1	4	12	0	12	2	6	8	17	7	24
	<i>Lecanora dispersa</i> s. lat.	0	1	1	6	10	16	0	2	2	6	13	19
	<i>Staurothele caesia</i>	3	2	5	6	0	6	6	2	8	15	4	19
	<i>Bagliettoa</i> sp.	3	5	8	0	1	1	7	2	9	10	8	18
	<i>Staurothele guestphalica</i>	6	1	7	5	0	5	5	0	5	16	1	17
	<i>Protoblastenia incrustans</i>	1	0	1	4	0	4	3	0	3	8	0	8
	<i>Rinodina immersa</i>	2	1	3	1	0	1	2	1	3	5	2	7
	<i>Verrucaria dufourii</i>	4	0	4	1	0	1	2	0	2	7	0	7
	<i>Farnoldia jurana</i>				4	0	4				4	0	4
	<i>Thelidium incavatum</i>	1	0	1	1	0	1	2	0	2	4	0	4
	<i>Candelariella aurella</i>				0	3	3				0	3	3
	<i>Caloplaca crenulatella</i>				0	2	2				0	2	2
	<i>Catillaria lenticularis</i>	0	2	2							0	2	2
	<i>Clauzadea metzleri</i>	0	1	1	1	0	1				1	1	2
	<i>Caloplaca alociza</i>							1	0	1	1	0	1
	<i>Clauzadea monticola</i>							0	1	1	0	1	1
	<i>Polyblastia albida</i>	0	1	1							0	1	1
	<i>Porina</i> sp.							1	0	1	1	0	1
	<i>Rinodina bischoffii</i>				0	1	1				0	1	1
	<i>Staurothele rupifraga</i>				1	0	1				1	0	1
epi	<i>Verrucaria nigrescens</i>	44	146	190	178	115	293	54	69	123	276	330	606
	<i>Aspicilia calcarea</i>	23	47	70	76	74	150	18	75	93	117	196	313
	<i>Mycobilimbia lurida</i>	18	16	34	15	16	31	15	32	47	48	64	112
	<i>Aspicilia contorta</i> s. lat.	5	9	14	25	30	55	0	16	16	30	55	85
	<i>Agonimia tristicula</i>	1	3	4	4	18	22	8	13	21	13	34	47
	<i>Aspicilia contorta</i> ssp. <i>hoffmanniana</i>	2	2	4	6	4	10	0	4	4	8	10	18
	<i>Verrucaria fuscula</i>	1	7	8	4	3	7				5	10	15
	<i>Verrucaria obscura</i>	3	0	3	6	0	6	1	3	4	10	3	13
	<i>Caloplaca dolomiticola</i>	0	5	5	0	5	5				0	10	10
	<i>Aspicilia contorta</i> ssp. <i>contorta</i>	0	4	4	0	4	4	1	0	1	1	8	9
	<i>Verrucaria glaucina</i>	1	3	4	4	0	4	0	1	1	5	4	9
	<i>Acarospora glaucocarpa</i>	0	1	1	1	2	3	0	3	3	1	6	7
	<i>Protoblastenia rupestris</i>	1	4	5	1	1	2				2	5	7
	<i>Verrucaria muralis</i>	1	0	1	0	3	3				1	3	4
	<i>Caloplaca variabilis</i>				3	0	3				3	0	3
	<i>Verrucaria caerulea</i>	3	0	3							3	0	3
	<i>Verrucaria viridula</i>				1	2	3				1	2	3
	<i>Acarospora macrospora</i>	0	2	2							0	2	2
	<i>Caloplaca glomerata</i>				2	0	2				2	0	2
	<i>Caloplaca velana</i> s. lat.							1	1	2	1	1	2
	<i>Lobothallia radiosa</i>				0	1	1	0	1	1	0	2	2
	<i>Polyblastia fuscoargillacea</i>				1	0	1	1	0	1	2	0	2
	<i>Rinodina lecanorina</i>	1	1	2							1	1	2
	<i>Sagirolechia protuberans</i>				1	0	1	0	1	1	1	1	2
	<i>Toninia sedifolia</i>	1	1	2							1	1	2
	<i>Caloplaca chalybaea</i>	1	0	1							1	0	1
	<i>Ionaspis rhodopis</i>				0	1	1				0	1	1
	unidentified				0	1	1				0	0	1
	<i>Lecidella stigmatea</i>	1	0	1							1	0	1
	<i>Rhizocarpon umbilicatum</i>							1	0	1	1	0	1
	<i>Rinodina calcarea</i>							0	1	1	0	1	1
	<i>Squammarina cartilaginea</i>				0	1	1				0	1	1
fru	<i>Cladonia pocillum</i>							0	10	10	0	10	10
	<i>Cladonia symphyocarpia</i>				0	1	1	0	1	1	0	2	2
fol	<i>Dermatocarpon leptophyllum</i>				2	2	4	0	1	1	2	3	5

Table C2. Frequency of lichens with cyanobacteria as photobiont in and along cracks on three limestone pavements in the grassland Great Alvar on the Baltic island of Öland, Sweden. The number of records at cracks are given with a conspicuous light zone present (p) or absent (a), their total ( $\Sigma$ , n = 3 cracks per locality and crack type) and their overall total for all three sites (P, A and  $\Sigma$  respectively). Abbreviations are: endolithic (Type: endo), epilithic (epi) and foliose (fol).

Type	Species	Location									P	A	$\Sigma$
		Bårby			Vickleby			Ekelunda					
		p	a	$\Sigma$	p	a	$\Sigma$	p	a	$\Sigma$			
endo	<i>Petractis clausa</i>							1	1	2	1	1	2
epi	<i>Placynthium nigrum</i> s. lat.				47	74	121	24	58	82	71	132	203
	<i>Synalissa symphorea</i>	13	19	32	24	25	49	19	9	28	56	53	109
	<i>Placynthium tremniacum</i>	7	19	26	48	6	54	9	6	15	64	31	95
	<i>Lempholemma isidiodes</i>	21	28	49	7	15	22	18	0	18	46	43	89
	<i>Placynthium nigrum</i>	7	39	46	9	7	16	2	15	17	18	61	79
	<i>Lempholemma degelianum</i>	1	1	2	2	1	3	2	0	2	5	2	7
	<i>Psorotichia schaeveri</i>				2	0	2				2	0	2
fol	<i>Collema fuscovirens</i>	25	26	51	39	60	99	43	57	100	107	143	250
	<i>Thyrea confusa</i>	7	47	54	0	1	1	18	1	19	25	49	74
	<i>Collema cristatum</i>	4	16	20	4	21	25	7	18	25	15	55	70
	<i>Collema multipartitum</i>	8	11	19	5	27	32	2	5	7	15	43	58
	<i>Leptogium lichenoides</i>	0	9	9	7	25	32	2	4	6	9	38	47
	<i>Collema parvum</i>	5	5	10	8	1	9	18	4	22	31	10	41
	<i>Collema auriculatum</i>				0	1	1				0	1	1
	<i>Collema tenax</i>				0	1	1				0	1	1
	<i>Peltigera rufescens</i>				0	1	1				0	1	1

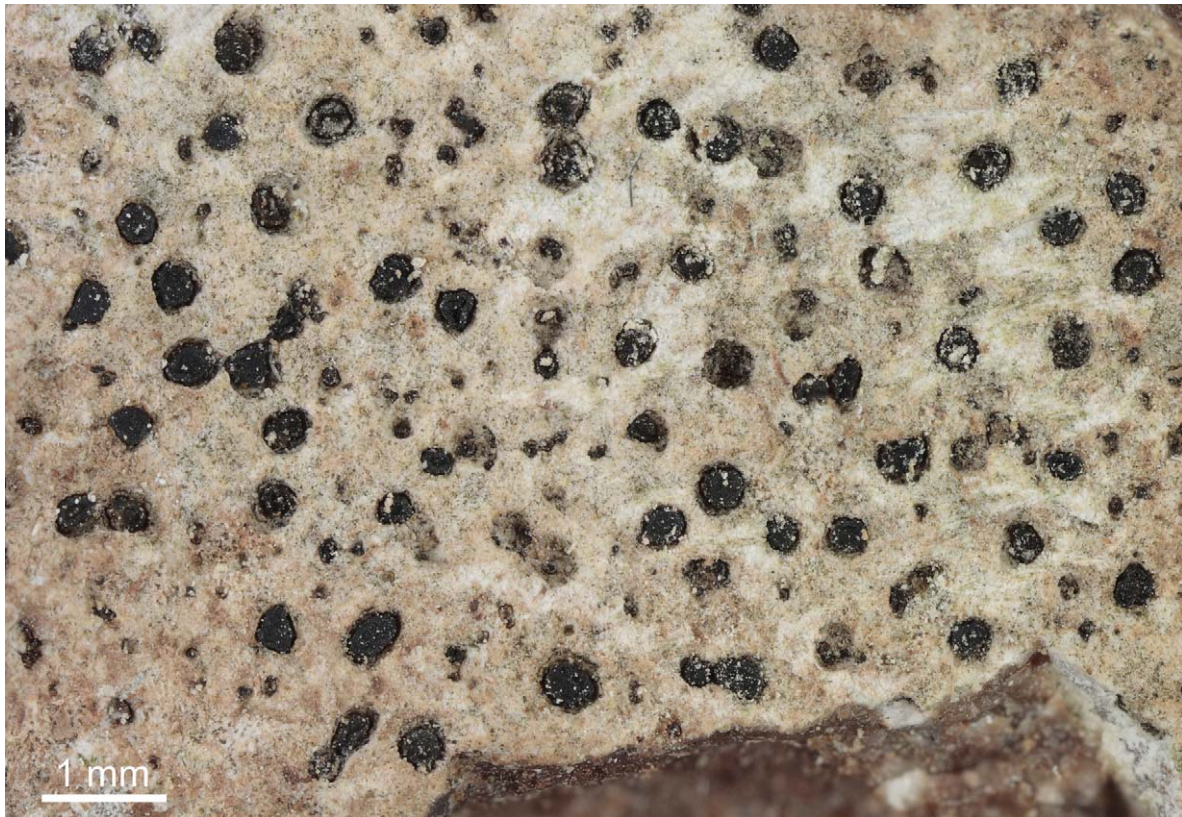


Fig. C1. *Clauzadea immersa* with an endolithic light thallus and apothecia immersed in pits.





Fig. C2. *Verrucaria nigrescens* with an epilithic, dark and smooth thallus that is divided into minute areolae.

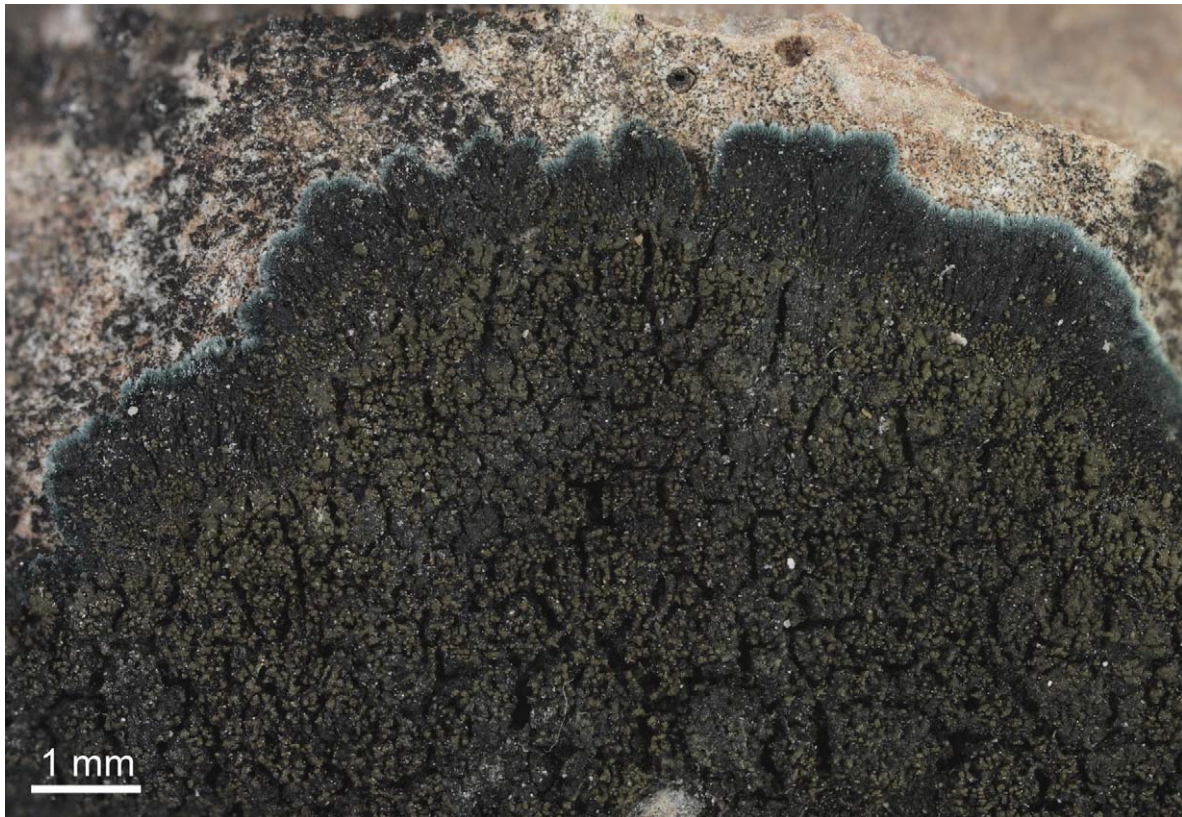


Fig. C3. *Placynthium nigrum* with an epilithic blackish thallus having a granular surface and a dark greenish border.

## APPENDIX D

Comprehensive results of dependent variables (i.e. abundances of cyanobacterial colonies, number of lichen species, Shannon diversity index, Evenness and abundance of most common lichen species) at two different spatial scales (5 and 25 cm). The larger scale pools five adjacent point records originally made every 5 cm along 8 transects on either side of 6 cracks on limestone pavements at three localities (Bårby, Vickleby and Ekelunda) on the Baltic island of Öland, Sweden. The sample size,  $n$ , on the original scale was 324 and on the larger scale 72 (3 localities  $\times$  6 cracks  $\times$  4 segments of 25 cm length along transects).

Tables of model selection give comprehensive statistics (i.e. adj.  $R^2$ , delta  $AIC_c$ , AIC weights and weight or evidence ratios relative to the best fitting model) for all models. The column 'Model' refers to particular regression models with K parameters. Model 1 contained locality (as factor

with three levels), snail density and distance to crack edge. Model 2 added the interaction between snail density and distance and models 3 to 7 added various polynomials of distance and snail density to test for potential deviations from linearity in the relations of dependent variables with snail density and distance (see Table 1 in the main text).

Tables of parameter estimates and corresponding significance tests ( $t$ - and  $P$ -values coded using + and - signs to indicate the direction of the correlations using 1, 2 or 3 characters indicating the conventional significance levels of 0.05, 0.01 and 0.001, respectively) are given for the best fitting model.

Tables of correlations give the results ( $R^2$ ,  $t$ - and  $P$ -values) of correlations with snail densities at single distances and Bonferroni corrected significance levels (Bon). At the original scale

with the highest resolution the Bonferroni corrected  $\alpha$  was 0.05/18 distances = 0.003 giving a + or a -. Corresponding levels at 0.01 and 0.001 were 0.0006 and 0.00006 giving ++/-- or +++/--- respectively. At the larger spatial scale, the Bonferroni corrected  $\alpha$  was 0.05/4 = 0.0125. Distances were pooled as follows: -10, -5, 0, 5, 10; 15, 20, 25, 30, 35; 40, 45, 50, 55, 60; and 65, 70, 75.

Table D1. Model selection, cyanobacterial colonies (abundance class 2 and 3).

Model	K	Scale, i.e. number of pooled adjacent point records							
		1 (n = 324)				5 (n = 72)			
		adj. $R^2$	Delta	Weight	Ratio	adj. $R^2$	Delta	Weight	Ratio
1	5	42.0	129.4	0.000	>10 <sup>6</sup>	20.0	70.6	0.000	>10 <sup>6</sup>
2	6	57.4	30.8	0.000	>10 <sup>6</sup>	42.6	48.1	0.000	>10 <sup>6</sup>
3	7	<b>61.3</b>	<b>0.0</b>	<b>0.389</b>	<b>1</b>	69.8	3.1	0.129	5
4	7	57.4	31.6	0.000	>10 <sup>6</sup>	41.9	50.3	0.000	>10 <sup>6</sup>
5	8	61.3	1.3	0.203	2	<b>71.7</b>	<b>0.0</b>	<b>0.607</b>	<b>1</b>
6	8	61.4	0.7	0.268	1	69.6	5.1	0.047	13
7	9	61.4	2.1	0.139	3	71.4	2.1	0.217	3

Table D2. Parameter estimates of selected model in Table D1.

Term	Scale, i.e. number of pooled adjacent point records					
	1 (n = 324)			5 (n = 72)		
	<i>t</i>	<i>P</i>	Sig	<i>t</i>	<i>P</i>	Sig
Bårby	17.9	0.000		12.0	0.000	
Vickleby	0.0	0.993		-0.3	0.769	
Ekelunda	-3.1	0.002	--	-2.1	0.044	-
Snail density	-14.1	<b>0.000</b>	---	-9.1	<b>0.000</b>	---
Distance	<b>6.2</b>	<b>0.000</b>	+++	0.6	0.538	
Distance <sup>2</sup>	-5.8	<b>0.000</b>	---	1.1	0.288	
Distance <sup>3</sup>				-2.3	<b>0.026</b>	-
Snail density <sup>2</sup>						
Interaction	<b>11.3</b>	<b>0.000</b>	+++	<b>7.4</b>	<b>0.000</b>	+++

Table D3. Correlations of cyanobacterial colonies with snail densities at single distances.

Distance to crack edge (cm)	Scale, i.e. number of pooled adjacent point records							
	1 (n = 324)				5 (n = 72)			
	$R^2$	<i>t</i>	<i>P</i>	Bon	$R^2$	<i>t</i>	<i>P</i>	Bon
-10	42.0	-3.4	0.004					
-5	<b>61.7</b>	-5.1	<b>0.000</b>	--				
0	<b>66.1</b>	-5.6	<b>0.000</b>	---	<b>81.7</b>	-8.4	<b>0.000</b>	---
5	<b>82.3</b>	-8.6	<b>0.000</b>	---				
10	<b>82.2</b>	-8.6	<b>0.000</b>	---				
15	<b>81.2</b>	-8.3	<b>0.000</b>	---				
20	<b>84.6</b>	-9.4	<b>0.000</b>	---				
25	<b>71.3</b>	-6.3	<b>0.000</b>	---	<b>78.1</b>	-7.6	<b>0.000</b>	---
30	<b>48.4</b>	-3.9	<b>0.001</b>	-				
35	31.0	-2.7	0.016					
40	22.5	-2.2	0.047					
45	5.9	-1.0	0.332					
50	11.0	-1.4	0.179		2.6	-0.7	0.521	
55	1.0	-0.4	0.695					
60	9.6	1.3	0.212					
65	19.5	2.0	0.067					
70	9.5	1.3	0.214		12.3	1.5	0.154	
75	19.0	1.9	0.070					

Table D4. Model selection, number of species, endolithic lichens.

Model	K	Scale, i.e. number of pooled adjacent point records							
		1 (n = 324)				5 (n = 72)			
		adj. $R^2$	Delta	Weight	Ratio	adj. $R^2$	Delta	Weight	Ratio
1	5	37.8	16.6	0.000	3985	60.0	6.8	0.011	30
2	6	39.9	6.4	0.020	24	63.0	2.5	0.093	3
3	7	39.8	8.0	0.009	56	64.0	1.9	0.124	3
4	7	40.1	6.4	0.019	25	64.6	0.7	0.230	1
5	8	<b>41.4</b>	<b>0.0</b>	<b>0.476</b>	<b>1</b>	64.0	3.3	0.061	5
6	8	40.0	8.1	0.008	58	<b>65.6</b>	<b>0.0</b>	<b>0.323</b>	<b>1</b>
7	9	41.6	0.0	0.469	1	65.6	1.4	0.158	2

Table D5. Parameter estimates of selected model in Table D4.

Term	Scale, i.e. number of pooled adjacent point records					
	1 (n = 324)			5 (n = 72)		
	$t$	$P$	Sig	$t$	$P$	Sig
Bårby	6.5	0.000		6.0	0.000	
Vickleby	0.1	0.906		-0.3	0.783	
Ekelunda	-0.7	0.476		-0.4	0.726	
Snail density	<b>9.2</b>	<b>0.000</b>	+++	<b>3.7</b>	<b>0.000</b>	+++
Distance	1.5	0.125		<b>-3.5</b>	<b>0.001</b>	---
Distance <sup>2</sup>	<b>-3.2</b>	<b>0.001</b>	--	1.7	0.092	
Distance <sup>3</sup>	<b>3.2</b>	<b>0.002</b>	++			
Snail density <sup>2</sup>				<b>-2.0</b>	<b>0.048</b>	-
Interaction	<b>-3.6</b>	<b>0.000</b>	---	<b>-2.6</b>	<b>0.011</b>	-

Table D6. Correlations of number of species, endolithic lichens with snail densities at single distances.

Distance to crack edge (cm)	Scale, i.e. number of pooled adjacent point records							
	1 (n = 324)				5 (n = 72)			
	$R^2$	$t$	$P$	Bon	$R^2$	$t$	$P$	Bon
-10	<b>45.7</b>	<b>3.7</b>	<b>0.002</b>	+				
-5	<b>55.9</b>	<b>4.5</b>	<b>0.000</b>	++				
0	29.2	2.6	0.021		<b>47.5</b>	<b>3.8</b>	<b>0.002</b>	++
5	22.3	2.1	0.048					
10	22.1	2.1	0.049					
15	26.8	2.4	0.028					
20	8.8	1.2	0.231					
25	22.1	2.1	0.049		28.0	2.5	0.024	
30	39.5	3.2	0.005					
35	39.1	3.2	0.005					
40	17.5	1.8	0.084					
45	30.6	2.7	0.017					
50	27.5	2.5	0.025		27.6	2.5	0.025	
55	<b>59.6</b>	<b>4.9</b>	<b>0.000</b>	++				
60	35.9	3.0	0.009					
65	<b>50.0</b>	<b>4.0</b>	<b>0.001</b>	+				
70	37.5	3.1	0.007		<b>40.4</b>	<b>3.3</b>	<b>0.005</b>	+
75	<b>47.6</b>	<b>3.8</b>	<b>0.002</b>	+				

Table D7. Model selection, number of species, epilithic lichens.

Model	K	Scale, i.e. number of pooled adjacent point records							
		1 (n = 324)				5 (n = 72)			
		adj. $R^2$	Delta	Weight	Ratio	adj. $R^2$	Delta	Weight	Ratio
1	5	12.7	81.6	0.000	>10 <sup>4</sup>	40.9	7.8	0.009	50
2	6	17.0	66.5	0.000	>10 <sup>4</sup>	46.2	2.3	0.147	3
3	7	26.6	27.9	0.000	>10 <sup>4</sup>	45.8	4.2	0.058	8
4	7	20.1	55.0	0.000	>10 <sup>4</sup>	<b>48.9</b>	<b>0.0</b>	<b>0.475</b>	<b>1</b>
5	8	29.8	14.2	0.001	1201	45.9	5.5	0.030	16
6	8	29.8	14.5	0.001	1407	48.6	1.9	0.184	3
7	9	<b>33.1</b>	<b>0.0</b>	<b>0.998</b>	<b>1</b>	48.7	3.2	0.097	5

Table D8. Parameter estimates of selected model in Table D7.

Term	Scale, i.e. number of pooled adjacent point records					
	1 (n = 324)			5 (n = 72)		
	<i>t</i>	<i>P</i>	Sig	<i>t</i>	<i>P</i>	Sig
Bärby	13.4	0.000		11.7	0.000	
Vickleby	0.9	0.364		0.4	0.673	
Ekelunda	-1.4	0.153		-2.2	0.028	-
Snail density	1.7	0.083		0.8	0.444	
Distance	<b>5.1</b>	<b>0.000</b>	+++	<b>-6.4</b>	<b>0.000</b>	---
Distance <sup>2</sup>	<b>-5.5</b>	<b>0.000</b>	---			
Distance <sup>3</sup>	<b>4.1</b>	<b>0.000</b>	+++			
Snail density <sup>2</sup>	<b>-4.0</b>	<b>0.000</b>	---	<b>-2.1</b>	<b>0.038</b>	-
Interaction	<b>4.6</b>	<b>0.000</b>	+++	<b>2.8</b>	<b>0.006</b>	++

Table D9. Correlations of number of species, epilithic lichens with snail densities at single distances.

Distance to crack edge (cm)	Scale, i.e. number of pooled adjacent point records							
	1 (n = 324)				5 (n = 72)			
	$R^2$	<i>t</i>	<i>P</i>	Bon	$R^2$	<i>t</i>	<i>P</i>	Bon
-10	3.6	-0.8	0.449					
-5	16.1	-1.8	0.098					
0	<b>63.0</b>	<b>-5.2</b>	<b>0.000</b>	--	<b>36.5</b>	<b>-3.0</b>	<b>0.008</b>	-
5	40.0	-3.3	0.005					
10	<b>46.6</b>	<b>-3.7</b>	<b>0.002</b>	-				
15	27.2	-2.4	0.027					
20	21.4	-2.1	0.053					
25	34.5	-2.9	0.010		<b>34.3</b>	<b>-2.9</b>	<b>0.011</b>	-
30	34.1	-2.9	0.011					
35	14.1	-1.6	0.125					
40	13.7	-1.6	0.131					
45	0.6	-0.3	0.760					
50	2.1	-0.6	0.568		6.9	-1.1	0.291	
55	0.1	-0.1	0.899					
60	0.0	0.0	0.997					
65	2.3	0.6	0.548					
70	3.9	0.8	0.433		0.3	0.2	0.830	
75	0.6	0.3	0.760					

Table D10. Model selection, number of species, cyanolichens.

Model	K	Scale, i.e. number of pooled adjacent point records							
		1 (n = 324)				5 (n = 72)			
		adj. $R^2$	Delta	Weight	Ratio	adj. $R^2$	Delta	Weight	Ratio
1	5	22.1	38.6	0.000	>10 <sup>4</sup>	9.3	25.0	0.000	>10 <sup>4</sup>
2	6	23.8	32.8	0.000	>10 <sup>4</sup>	15.9	20.8	0.000	>10 <sup>4</sup>
3	7	29.8	7.4	0.014	40	<b>38.2</b>	<b>0.0</b>	<b>0.539</b>	<b>1</b>
4	7	25.6	26.2	0.000	>10 <sup>4</sup>	15.3	22.7	0.000	>10 <sup>4</sup>
5	8	29.9	7.8	0.011	50	37.4	2.4	0.165	3
6	8	<b>31.6</b>	<b>0.0</b>	<b>0.539</b>	<b>1</b>	37.9	1.7	0.229	2
7	9	31.7	0.4	0.437	1	37.1	4.2	0.067	8

Table D11. Parameter estimates of selected model in Table D10.

Term	Scale, i.e. number of pooled adjacent point records					
	1 (n = 324)			5 (n = 72)		
	$t$	$P$	Sig	$t$	$P$	Sig
Bårby	8.7	0.000		8.7	0.000	
Vickleby	3.2	0.001	++	0.3	0.778	
Ekelunda	1.3	0.191		-0.3	0.735	
Snail density	<b>-4.5</b>	<b>0.000</b>	---	<b>-4.0</b>	<b>0.000</b>	---
Distance	<b>6.5</b>	<b>0.000</b>	+++	<b>4.4</b>	<b>0.000</b>	+++
Distance <sup>2</sup>	<b>-5.4</b>	<b>0.000</b>	---	<b>-5.0</b>	<b>0.000</b>	---
Distance <sup>3</sup>						
Snail density <sup>2</sup>	<b>3.1</b>	<b>0.002</b>	++			
Interaction	<b>3.0</b>	<b>0.003</b>	++	<b>2.9</b>	<b>0.005</b>	++

Table D12. Correlations of number of species, cyanolichens with snail densities at single distances.

Distance to crack edge (cm)	Scale, i.e. number of pooled adjacent point records							
	1 (n = 324)				5 (n = 72)			
	$R^2$	$t$	$P$	Bon	$R^2$	$t$	$P$	Bon
-10	9.4	-1.3	0.215					
-5	31.1	-2.7	0.016					
0	<b>51.2</b>	<b>-4.1</b>	<b>0.001</b>	-	<b>60.5</b>	<b>-4.9</b>	<b>0.000</b>	---
5	34.6	-2.9	0.010					
10	36.5	-3.0	0.008					
15	25.3	-2.3	0.034					
20	3.0	-0.7	0.491					
25	<b>55.5</b>	<b>-4.5</b>	<b>0.000</b>	--	32.5	-2.8	0.013	
30	<b>44.0</b>	<b>-3.5</b>	<b>0.003</b>	-				
35	5.1	-0.9	0.369					
40	18.4	-1.9	0.076					
45	2.7	-0.7	0.512					
50	0.1	0.1	0.884		16.8	-1.8	0.092	
55	2.8	-0.7	0.510					
60	0.3	-0.2	0.828					
65	0.1	0.1	0.910					
70	1.2	0.4	0.672		1.2	0.4	0.660	
75	3.3	-0.7	0.470					

Table D13. Model selection, number of species, all lichen species.

Model	K	Scale, i.e. number of pooled adjacent point records							
		1 (n = 324)				5 (n = 72)			
		adj. $R^2$	Delta	Weight	Ratio	adj. $R^2$	Delta	Weight	Ratio
1	5	3.5	53.4	0.000	>10 <sup>4</sup>	41.0	3.8	0.058	7
2	6	4.2	52.2	0.000	>10 <sup>4</sup>	41.3	4.7	0.037	11
3	7	16.8	7.7	0.011	47	44.5	2.1	0.137	3
4	7	4.3	52.7	0.000	>10 <sup>4</sup>	43.9	2.8	0.096	4
5	8	<b>19.0</b>	<b>0.0</b>	<b>0.527</b>	<b>1</b>	44.5	3.5	0.070	6
6	8	16.9	8.1	0.009	56	<b>47.2</b>	<b>0.0</b>	<b>0.398</b>	<b>1</b>
7	9	19.2	0.3	0.453	1	47.3	1.3	0.203	2

Table D14. Parameter estimates of selected model in Table D13.

Term	Scale, i.e. number of pooled adjacent point records					
	1 (n = 324)			5 (n = 72)		
	<i>t</i>	<i>P</i>	Sig	<i>t</i>	<i>P</i>	Sig
Bårby	15.2	0.000		12.6	0.000	
Vickleby	3.0	0.003	++	0.7	0.499	
Ekelunda	0.3	0.764		-1.0	0.322	
Snail density	-1.2	0.215		1.8	0.084	
Distance	<b>5.4</b>	<b>0.000</b>	+++	-0.4	0.723	
Distance <sup>2</sup>	<b>-4.6</b>	<b>0.000</b>	---	<b>-2.2</b>	<b>0.029</b>	-
Distance <sup>3</sup>	<b>3.1</b>	<b>0.002</b>	++			
Snail density <sup>2</sup>				<b>-2.1</b>	<b>0.043</b>	-
Interaction	<b>2.0</b>	<b>0.049</b>	+	1.2	0.220	

Table D15. Correlations of number of species, all lichen species with snail densities at single distances.

Distance to crack edge (cm)	Scale, i.e. number of pooled adjacent point records							
	1 (n = 324)				5 (n = 72)			
	$R^2$	<i>t</i>	<i>P</i>	Bon	$R^2$	<i>t</i>	<i>P</i>	Bon
-10	9.5	1.3	0.214					
-5	5.0	0.9	0.371					
0	1.8	-0.5	0.596		2.2	-0.6	0.557	
5	11.0	-1.4	0.179					
10	24.4	-2.3	0.037					
15	2.7	-0.7	0.511					
20	7.1	-1.1	0.284					
25	41.0	-3.3	0.004		2.2	-0.6	0.561	
30	27.8	-2.5	0.025					
35	0.2	0.2	0.865					
40	11.6	-1.5	0.166					
45	0.8	0.4	0.731					
50	6.6	1.1	0.305		0.1	-0.1	0.923	
55	13.7	1.6	0.131					
60	2.1	0.6	0.565					
65	6.8	1.1	0.296					
70	8.7	1.2	0.235		4.2	0.8	0.416	
75	0.1	0.1	0.911					

Table D16. Model selection, Shannon diversity index, endolithic lichens.

Model	K	Scale, i.e. number of pooled adjacent point records							
		1 (n = 324)				5 (n = 72)			
		adj. $R^2$	Delta	Weight	Ratio	adj. $R^2$	Delta	Weight	Ratio
1	5	28.5	18.1	0.000	8389	47.8	3.4	0.084	6
2	6	31.4	5.7	0.023	17	47.1	5.8	0.026	18
3	7	31.5	6.2	0.018	23	49.2	4.2	0.057	8
4	7	<b>32.8</b>	<b>0.0</b>	<b>0.400</b>	<b>1</b>	49.4	4.0	0.064	7
5	8	31.6	6.8	0.013	30	51.6	2.2	0.154	3
6	8	32.9	0.5	0.312	1	51.5	2.2	0.152	3
7	9	33.0	1.1	0.234	2	<b>54.0</b>	<b>0.0</b>	<b>0.464</b>	<b>1</b>

Table D17. Parameter estimates of selected model in Table D16.

Term	Scale, i.e. number of pooled adjacent point records					
	1 (n = 324)			5 (n = 72)		
	$t$	$P$	Sig	$t$	$P$	Sig
Bårby	3.0	0.003		6.5	0.000	
Vickleby	0.9	0.363		0.8	0.454	
Ekelunda	0.5	0.624		1.2	0.231	
Snail density	<b>5.0</b>	<b>0.000</b>	+++	<b>2.3</b>	<b>0.024</b>	+
Distance	<b>-3.7</b>	<b>0.000</b>	---	<b>-3.6</b>	<b>0.001</b>	---
Distance <sup>2</sup>				<b>2.4</b>	<b>0.021</b>	+
Distance <sup>3</sup>				<b>-2.1</b>	<b>0.040</b>	-
Snail density <sup>2</sup>	<b>-2.8</b>	<b>0.006</b>	--	<b>-2.1</b>	<b>0.041</b>	-
Interaction	<b>-3.8</b>	<b>0.000</b>	---	-0.2	0.833	

Table D18. Correlations of Shannon diversity index, endolithic lichens with snail densities at single distances.

Distance to crack edge (cm)	Scale, i.e. number of pooled adjacent point records							
	1 (n = 324)				5 (n = 72)			
	$R^2$	$t$	$P$	Bon	$R^2$	$t$	$P$	Bon
-10	<b>45.9</b>	<b>3.7</b>	<b>0.002</b>	+				
-5	<b>49.2</b>	<b>3.9</b>	<b>0.001</b>	+				
0	14.8	1.7	0.115		3.1	0.7	0.486	
5	6.1	1.0	0.324					
10	9.2	1.3	0.221					
15	11.3	1.4	0.172					
20	0.8	0.4	0.730					
25	11.2	1.4	0.175		0.2	0.2	0.862	
30	21.3	2.1	0.054					
35	31.4	2.7	0.016					
40	7.2	1.1	0.280					
45	13.8	1.6	0.129					
50	8.2	1.2	0.250		4.0	0.8	0.426	
55	<b>55.7</b>	<b>4.5</b>	<b>0.000</b>	++				
60	18.7	1.9	0.073					
65	8.2	1.2	0.248					
70	2.4	-0.6	0.544		10.4	1.4	0.192	
75	0.0	0.0	1.000					



Table D19. Model selection, Shannon diversity index, epilithic lichens.

Model	K	Scale, i.e. number of pooled adjacent point records							
		1 (n = 324)				5 (n = 72)			
		adj. $R^2$	Delta	Weight	Ratio	adj. $R^2$	Delta	Weight	Ratio
1	5	11.5	70.0	0.000	>10 <sup>4</sup>	36.9	0.7	0.202	1
2	6	15.0	58.1	0.000	>10 <sup>4</sup>	<b>38.6</b>	<b>0.0</b>	<b>0.286</b>	<b>1</b>
3	7	22.7	28.4	0.000	>10 <sup>4</sup>	38.5	1.5	0.135	2
4	7	17.9	47.7	0.000	>10 <sup>4</sup>	38.5	1.5	0.133	2
5	8	26.6	12.5	0.002	518	39.6	1.6	0.127	2
6	8	25.7	16.7	0.000	4220	38.4	3.1	0.061	5
7	9	<b>29.6</b>	<b>0.0</b>	<b>0.998</b>	<b>1</b>	39.5	3.3	0.056	5

Table D20. Parameter estimates of selected model in Table D19.

Term	Scale, i.e. number of pooled adjacent point records					
	1 (n = 324)			5 (n = 72)		
	<i>t</i>	<i>P</i>	Sig	<i>t</i>	<i>P</i>	Sig
Bårby	10.5	0.000		11.4	0.000	
Vickleby	1.1	0.284		0.8	0.406	
Ekelunda	-0.8	0.403		-1.9	0.063	
Snail density	1.6	0.108		-2.2	<b>0.033</b>	-
Distance	<b>5.1</b>	<b>0.000</b>	+++	<b>-5.2</b>	<b>0.000</b>	---
Distance <sup>2</sup>	<b>-5.6</b>	<b>0.000</b>	---			
Distance <sup>3</sup>	<b>4.3</b>	<b>0.000</b>	+++			
Snail density <sup>2</sup>	<b>-3.8</b>	<b>0.000</b>	---			
Interaction	<b>4.1</b>	<b>0.000</b>	+++	1.7	0.094	

Table D21. Correlations of Shannon diversity index, epilithic lichens with snail densities at single distances.

Distance to crack edge (cm)	Scale, i.e. number of pooled adjacent point records							
	1 (n = 324)				5 (n = 72)			
	$R^2$	<i>t</i>	<i>P</i>	Bon	$R^2$	<i>t</i>	<i>P</i>	Bon
-10	7.6	-1.1	0.268					
-5	18.0	-1.9	0.079					
0	<b>61.6</b>	<b>-5.1</b>	<b>0.000</b>	--	19.5	-2.0	0.067	
5	36.3	-3.0	0.008					
10	41.0	-3.3	0.004					
15	26.7	-2.4	0.028					
20	17.9	-1.9	0.080					
25	43.5	-3.5	0.003		<b>33.8</b>	<b>-2.9</b>	<b>0.011</b>	-
30	<b>46.6</b>	<b>-3.7</b>	<b>0.002</b>	-				
35	14.8	-1.7	0.115					
40	11.0	-1.4	0.179					
45	0.0	0.0	0.963					
50	1.0	-0.4	0.695		12.1	-1.5	0.158	
55	1.3	-0.5	0.652					
60	1.4	-0.5	0.643					
65	0.4	0.3	0.795					
70	12.4	1.5	0.152		0.7	0.3	0.740	
75	0.4	-0.3	0.802					

Table D22. Model selection, Shannon diversity index, cyanolichens.

Model	K	Scale, i.e. number of pooled adjacent point records							
		1 (n = 324)				5 (n = 72)			
		adj. $R^2$	Delta	Weight	Ratio	adj. $R^2$	Delta	Weight	Ratio
1	5	21.2	33.2	0.000	>10 <sup>4</sup>	3.5	22.1	0.000	>10 <sup>4</sup>
2	6	22.5	28.7	0.000	>10 <sup>4</sup>	16.9	12.7	0.001	566
3	7	28.2	5.2	0.039	13	<b>31.6</b>	<b>0.0</b>	<b>0.465</b>	<b>1</b>
4	7	23.9	24.1	0.000	>10 <sup>4</sup>	17.2	13.7	0.000	949
5	8	28.3	5.7	0.031	17	30.5	2.5	0.132	4
6	8	<b>29.6</b>	<b>0.0</b>	<b>0.521</b>	<b>1</b>	32.2	0.8	0.316	1
7	9	29.7	0.5	0.409	1	31.1	3.4	0.086	5

Table D23. Parameter estimates of selected model in Table D22.

Term	Scale, i.e. number of pooled adjacent point records					
	1 (n = 324)			5 (n = 72)		
	<i>t</i>	<i>P</i>	Sig	<i>t</i>	<i>P</i>	Sig
Bårby	6.7	0.000		9.3	0.000	
Vickleby	<b>2.7</b>	<b>0.007</b>	++	0.3	0.774	
Ekelunda	1.2	0.216		0.1	0.946	
Snail density	<b>-4.0</b>	<b>0.000</b>	---	<b>-4.0</b>	<b>0.000</b>	---
Distance	<b>6.4</b>	<b>0.000</b>	+++	<b>3.1</b>	<b>0.003</b>	++
Distance <sup>2</sup>	<b>-5.2</b>	<b>0.000</b>	---	<b>-3.9</b>	<b>0.000</b>	---
Distance <sup>3</sup>						
Snail density <sup>2</sup>	<b>2.7</b>	<b>0.008</b>	++			
Interaction	<b>2.7</b>	<b>0.008</b>	++	<b>3.8</b>	<b>0.000</b>	+++

Table D24. Correlations of Shannon diversity index, cyanolichens with snail densities at single distances.

Distance to crack edge (cm)	Scale, i.e. number of pooled adjacent point records							
	1 (n = 324)				5 (n = 72)			
	$R^2$	<i>t</i>	<i>P</i>	Bon	$R^2$	<i>t</i>	<i>P</i>	Bon
-10	9.7	-1.3	0.207					
-5	16.2	-1.8	0.097					
0	25.7	-2.4	0.032		<b>45.2</b>	<b>-3.6</b>	<b>0.002</b>	--
5	25.7	-2.4	0.032					
10	33.2	-2.8	0.012					
15	17.3	-1.8	0.086					
20	0.4	-0.3	0.801					
25	<b>56.2</b>	<b>-4.5</b>	<b>0.000</b>	--	4.9	-0.9	0.376	
30	<b>44.2</b>	<b>-3.6</b>	<b>0.003</b>	-				
35	3.3	-0.7	0.470					
40	15.6	-1.7	0.104					
45	3.1	-0.7	0.485					
50	0.5	0.3	0.789		1.9	-0.6	0.585	
55	10.8	-1.4	0.183					
60	0.2	-0.2	0.872					
65	0.7	0.3	0.749					
70	2.0	0.6	0.574		5.1	0.9	0.368	
75	2.6	-0.7	0.519					

Table D25. Model selection, Shannon diversity index, all lichen species.

Scale, i.e. number of pooled adjacent point records									
Model	K	1 (n = 324)				5 (n = 72)			
		adj. $R^2$	Delta	Weight	Ratio	adj. $R^2$	Delta	Weight	Ratio
1	5	3.4	41.9	0.000	>10 <sup>4</sup>	16.2	12.1	0.001	435
2	6	6.0	34.3	0.000	>10 <sup>4</sup>	27.2	3.3	0.104	5
3	7	<b>15.7</b>	<b>0.0</b>	<b>0.476</b>	<b>1</b>	28.2	3.7	0.087	6
4	7	5.7	36.2	0.000	>10 <sup>4</sup>	26.5	5.4	0.037	15
5	8	15.6	1.3	0.245	2	<b>33.1</b>	<b>0.0</b>	<b>0.553</b>	<b>1</b>
6	8	15.5	1.9	0.185	3	27.5	5.8	0.030	18
7	9	15.4	3.2	0.094	5	32.5	2.2	0.187	3

Table D26. Parameter estimates of selected model in Table D25.

Scale, i.e. number of pooled adjacent point records						
Term	1 (n = 324)			5 (n = 72)		
	<i>t</i>	<i>P</i>	Sig	<i>t</i>	<i>P</i>	Sig
Bärby	17.8	0.000		15.6	0.000	
Vickleby	<b>2.9</b>	<b>0.004</b>	++	2.0	0.051	
Ekelunda	0.6	0.568		0.2	0.868	
Snail density	<b>-3.5</b>	<b>0.001</b>	---	<b>-3.9</b>	<b>0.000</b>	---
Distance	<b>4.1</b>	<b>0.000</b>	+++	<b>-2.4</b>	<b>0.019</b>	-
Distance <sup>2</sup>	<b>-6.1</b>	<b>0.000</b>	---	<b>2.2</b>	<b>0.034</b>	+
Distance <sup>3</sup>				<b>-2.4</b>	<b>0.019</b>	-
Snail density <sup>2</sup>						
Interaction	<b>3.3</b>	<b>0.001</b>	++	<b>3.5</b>	<b>0.001</b>	+++

Table D27. Correlations of Shannon diversity index, all lichen species with snail densities at single distances.

Scale, i.e. number of pooled adjacent point records								
Distance to crack edge (cm)	1 (n = 324)				5 (n = 72)			
	$R^2$	<i>t</i>	<i>P</i>	Bon	$R^2$	<i>t</i>	<i>P</i>	Bon
-10	5.9	1.0	0.332					
-5	2.7	0.7	0.517					
0	11.6	-1.4	0.167		<b>34.2</b>	<b>-2.9</b>	<b>0.011</b>	-
5	28.6	-2.5	0.022					
10	<b>54.6</b>	<b>-4.4</b>	<b>0.000</b>	--				
15	34.4	-2.9	0.011					
20	28.3	-2.5	0.023					
25	<b>71.8</b>	<b>-6.4</b>	<b>0.000</b>	---	<b>74.0</b>	<b>-6.7</b>	<b>0.000</b>	---
30	<b>53.8</b>	<b>-4.3</b>	<b>0.001</b>	--				
35	16.1	-1.8	0.098					
40	16.1	-1.7	0.099					
45	2.0	-0.6	0.578					
50	7.7	1.2	0.266		15.2	-1.7	0.110	
55	4.9	0.9	0.376					
60	3.6	0.8	0.449					
65	5.9	1.0	0.332					
70	10.6	1.4	0.188		4.6	0.9	0.391	
75	0.8	0.4	0.718					

Table D28. Model selection, evenness, endolithic lichens.

Model	K	Scale, i.e. number of pooled adjacent point records							
		1 (n = 324)				5 (n = 72)			
		adj. $R^2$	Delta	Weight	Ratio	adj. $R^2$	Delta	Weight	Ratio
1	5	22.6	6.8	0.019	31	<b>26.6</b>	<b>0.0</b>	<b>0.382</b>	<b>1</b>
2	6	23.5	4.0	0.076	7	27.2	0.7	0.273	1
3	7	23.3	5.9	0.029	20	26.1	3.1	0.082	5
4	7	<b>24.7</b>	<b>0.0</b>	<b>0.567</b>	<b>1</b>	26.3	2.9	0.090	4
5	8	23.1	7.8	0.011	49	28.2	2.4	0.113	3
6	8	24.5	2.0	0.214	3	25.2	5.4	0.026	15
7	9	24.3	3.8	0.084	7	27.3	4.8	0.035	11

Table D29. Parameter estimates of selected model in Table D28.

Term	Scale, i.e. number of pooled adjacent point records					
	1 (n = 324)			5 (n = 72)		
	$t$	$P$	Sig	$t$	$P$	Sig
Bårby	4.2	0.000		6.1	0.000	
Vickleby	-0.2	0.860		1.3	0.186	
Ekelunda	-0.5	0.603		1.0	0.309	
Snail density	<b>4.2</b>	<b>0.000</b>	+++	-0.2	0.875	
Distance	<b>-3.7</b>	<b>0.000</b>	---	<b>-5.2</b>	<b>0.000</b>	---
Distance <sup>2</sup>						
Distance <sup>3</sup>						
Snail density <sup>2</sup>	-2.5	0.015	-			
Interaction	-2.2	0.027	-			

Table D30. Correlations of evenness, endolithic lichens with snail densities at single distances.

Distance to crack edge (cm)	Scale, i.e. number of pooled adjacent point records							
	1 (n = 324)				5 (n = 72)			
	$R^2$	$t$	$P$	Bon	$R^2$	$t$	$P$	Bon
-10	<b>50.6</b>	<b>4.0</b>	<b>0.001</b>	+				
-5	<b>47.3</b>	<b>3.8</b>	<b>0.002</b>	+				
0	7.2	1.1	0.280		3.4	-0.8	0.461	
5	1.8	0.5	0.591					
10	7.6	1.1	0.269					
15	9.1	1.3	0.225					
20	0.0	-0.1	0.951					
25	11.8	1.5	0.162		5.0	-0.9	0.372	
30	28.9	2.5	0.021					
35	26.1	2.4	0.030					
40	2.8	0.7	0.506					
45	10.2	1.4	0.195					
50	8.2	1.2	0.250		0.3	-0.2	0.832	
55	<b>57.0</b>	<b>4.6</b>	<b>0.000</b>	++				
60	19.9	2.0	0.064					
65	8.2	1.2	0.248					
70	2.4	-0.6	0.544		10.4	1.4	0.192	
75	0.0	0.0	1.000					

Table D31. Model selection, evenness, epilithic lichens.

Model	K	Scale, i.e. number of pooled adjacent point records							
		1 (n = 324)				5 (n = 72)			
		adj. $R^2$	Delta	Weight	Ratio	adj. $R^2$	Delta	Weight	Ratio
1	5	9.7	52.6	0.000	$>10^4$	23.1	2.1	0.156	3
2	6	11.9	45.8	0.000	$>10^4$	22.0	4.4	0.049	9
3	7	20.0	15.4	0.000	2190	25.6	2.3	0.139	3
4	7	13.4	41.4	0.000	$>10^4$	21.2	6.4	0.018	25
5	8	22.7	5.3	0.065	14	<b>29.4</b>	<b>0.0</b>	<b>0.439</b>	<b>1</b>
6	8	21.5	10.3	0.005	175	24.9	4.4	0.049	9
7	9	<b>24.2</b>	<b>0.0</b>	<b>0.929</b>	<b>1</b>	28.7	2.2	0.150	3

Table D32. Parameter estimates of selected model in Table D31.

Term	Scale, i.e. number of pooled adjacent point records					
	1 (n = 324)			5 (n = 72)		
	$t$	$P$	Sig	$t$	$P$	Sig
Bärby	9.7	0.000		8.8	0.000	
Vickleby	<b>2.0</b>	<b>0.050</b>	+	-0.2	0.868	
Ekelunda	-0.7	0.512		<b>-2.6</b>	<b>0.010</b>	-
Snail density	1.0	0.312		1.0	0.317	
Distance	<b>4.9</b>	<b>0.000</b>	+++	-1.6	0.124	
Distance <sup>2</sup>	<b>-4.8</b>	<b>0.000</b>	---	1.8	0.081	
Distance <sup>3</sup>	<b>3.5</b>	<b>0.001</b>	+++	<b>-2.1</b>	<b>0.039</b>	-
Snail density <sup>2</sup>	<b>-2.7</b>	<b>0.007</b>	--			
Interaction	<b>3.2</b>	<b>0.001</b>	++	-0.2	0.807	

Table D33. Correlations of evenness, epilithic lichens with snail densities at single distances.

Distance to crack edge (cm)	Scale, i.e. number of pooled adjacent point records							
	1 (n = 324)				5 (n = 72)			
	$R^2$	$t$	$P$	Bon	$R^2$	$t$	$P$	Bon
-10	9.8	-1.3	0.205					
-5	17.1	-1.8	0.088					
0	<b>52.6</b>	<b>-4.2</b>	<b>0.001</b>	-	<b>50.2</b>	<b>4.0</b>	<b>0.001</b>	++
5	7.5	-1.1	0.273					
10	20.5	-2.0	0.059					
15	25.2	-2.3	0.034					
20	10.8	-1.4	0.184					
25	35.8	-3.0	0.009		4.1	-0.8	0.418	
30	<b>60.2</b>	<b>-4.9</b>	<b>0.000</b>	--				
35	11.3	-1.4	0.174					
40	12.3	-1.5	0.154					
45	0.3	0.2	0.819					
50	0.8	-0.4	0.721		0.1	-0.1	0.917	
55	6.1	-1.0	0.324					
60	1.9	-0.6	0.590					
65	1.2	0.4	0.672					
70	13.6	1.6	0.132		1.3	0.5	0.649	
75	1.6	-0.5	0.622					

Table D34. Model selection, evenness, cyanolichens.

Model	K	Scale, i.e. number of pooled adjacent point records							
		1 (n = 324)				5 (n = 72)			
		adj. $R^2$	Delta	Weight	Ratio	adj. $R^2$	Delta	Weight	Ratio
1	5	17.4	40.1	0.000	$>10^4$	-3.0	10.2	0.002	165
2	6	21.4	25.3	0.000	$>10^4$	9.6	2.1	0.109	3
3	7	27.5	0.2	0.323	1	<b>13.9</b>	<b>0.0</b>	<b>0.318</b>	<b>1</b>
4	7	21.6	25.2	0.000	$>10^4$	10.9	2.4	0.096	3
5	8	27.4	1.7	0.152	2	12.8	2.3	0.099	3
6	8	<b>27.8</b>	<b>0.0</b>	<b>0.358</b>	<b>1</b>	15.3	0.2	0.289	1
7	9	27.7	1.5	0.167	2	14.2	2.6	0.087	4

Table D35. Parameter estimates of selected model in Table D34.

Term	Scale, i.e. number of pooled adjacent point records					
	1 (n = 324)			5 (n = 72)		
	$t$	$P$	Sig	$t$	$P$	Sig
Bärby	8.7	0.000		9.4	0.000	
Vickleby	1.8	0.076		0.5	0.621	
Ekelunda	0.8	0.448		0.5	0.601	
Snail density	<b>-3.3</b>	<b>0.001</b>	--	<b>-2.7</b>	<b>0.009</b>	--
Distance	<b>5.7</b>	<b>0.000</b>	+++	1.3	0.197	
Distance <sup>2</sup>	<b>-5.3</b>	<b>0.000</b>	---	<b>-2.1</b>	<b>0.042</b>	-
Distance <sup>3</sup>						
Snail density <sup>2</sup>	1.5	0.134				
Interaction	<b>4.3</b>	<b>0.000</b>	+++	<b>3.3</b>	<b>0.002</b>	++

Table D36. Correlations of evenness, cyanolichens with snail densities at single distances.

Distance to crack edge (cm)	Scale, i.e. number of pooled adjacent point records							
	1 (n = 324)				5 (n = 72)			
	$R^2$	$t$	$P$	Bon	$R^2$	$t$	$P$	Bon
-10	10.0	-1.3	0.201					
-5	16.2	-1.8	0.097					
0	26.8	-2.4	0.028		25.3	-2.3	0.033	
5	21.9	-2.1	0.050					
10	40.5	-3.3	0.004					
15	6.0	-1.0	0.325					
20	1.0	-0.4	0.695					
25	<b>53.5</b>	<b>-4.3</b>	<b>0.001</b>	-	27.7	2.5	0.025	
30	32.4	-2.8	0.014					
35	4.1	-0.8	0.423					
40	4.9	-0.9	0.376					
45	9.2	-1.3	0.222					
50	0.7	0.3	0.733		<b>36.0</b>	<b>3.0</b>	<b>0.009</b>	+
55	27.9	-2.5	0.024					
60	3.4	0.8	0.463					
65	5.0	0.9	0.373					
70	4.6	0.9	0.391		8.5	1.2	0.239	
75	1.6	0.5	0.616					

Table D37. Model selection, evenness, all lichen species.

Model	K	Scale, i.e. number of pooled adjacent point records							
		1 (n = 324)				5 (n = 72)			
		adj. $R^2$	Delta	Weight	Ratio	adj. $R^2$	Delta	Weight	Ratio
1	5	3.1	20.6	0.000	>10 <sup>4</sup>	6.6	6.9	0.012	32
2	6	6.6	9.9	0.002	142	<b>16.7</b>	<b>0.0</b>	<b>0.377</b>	<b>1</b>
3	7	<b>9.7</b>	<b>0.0</b>	<b>0.285</b>	<b>1</b>	15.5	2.4	0.115	3
4	7	6.7	10.4	0.002	182	15.8	2.2	0.128	3
5	8	9.9	0.1	0.269	1	18.9	0.8	0.251	2
6	8	9.9	0.4	0.228	1	14.5	4.6	0.038	10
7	9	10.1	0.6	0.214	1	18.0	3.1	0.079	5

Table D38. Parameter estimates of selected model in Table D37.

Term	Scale, i.e. number of pooled adjacent point records					
	1 (n = 324)			5 (n = 72)		
	<i>t</i>	<i>P</i>	Sig	<i>t</i>	<i>P</i>	Sig
Bårby	24.3	0.000		15.1	0.000	
Vickleby	<b>2.2</b>	<b>0.031</b>	+	1.6	0.108	
Ekelunda	-0.3	0.802		0.2	0.872	
Snail density	<b>-3.8</b>	<b>0.000</b>	---	<b>-3.4</b>	<b>0.001</b>	---
Distance	<b>2.2</b>	<b>0.028</b>	+	-1.8	0.076	
Distance <sup>2</sup>	<b>-3.5</b>	<b>0.001</b>	---			
Distance <sup>3</sup>						
Snail density <sup>2</sup>						
Interaction	<b>3.6</b>	<b>0.000</b>	+++	<b>3.0</b>	<b>0.004</b>	++

Table D39. Correlations of evenness, all lichen species with snail densities at single distances.

Distance to crack edge (cm)	Scale, i.e. number of pooled adjacent point records							
	1 (n = 324)				5 (n = 72)			
	$R^2$	<i>t</i>	<i>P</i>	Bon	$R^2$	<i>t</i>	<i>P</i>	Bon
-10	1.1	0.4	0.678					
-5	0.2	0.2	0.874					
0	27.7	-2.5	0.025		<b>49.6</b>	<b>-4.0</b>	<b>0.001</b>	--
5	34.1	-2.9	0.011					
10	<b>63.0</b>	<b>-5.2</b>	<b>0.000</b>	--				
15	<b>68.9</b>	<b>-6.0</b>	<b>0.000</b>	---				
20	<b>51.1</b>	<b>-4.1</b>	<b>0.001</b>	-				
25	<b>78.2</b>	<b>-7.6</b>	<b>0.000</b>	---	<b>87.1</b>	<b>-10.4</b>	<b>0.000</b>	---
30	<b>65.6</b>	<b>-5.5</b>	<b>0.000</b>	---				
35	<b>72.9</b>	<b>-6.6</b>	<b>0.000</b>	---				
40	17.3	-1.8	0.086					
45	32.2	-2.8	0.014					
50	0.0	0.0	0.999		<b>37.0</b>	<b>-3.1</b>	<b>0.007</b>	-
55	21.0	-2.1	0.056					
60	3.4	0.8	0.464					
65	1.5	0.5	0.631					
70	12.1	1.5	0.157		2.8	0.7	0.504	
75	5.8	1.0	0.337					

Table D40. Model selection, *Clauzadea immersa* (most abundant endolithic lichen).

Model	K	Scale, i.e. number of pooled adjacent point records							
		1 (n = 324)				5 (n = 72)			
		adj. $R^2$	Delta	Weight	Ratio	adj. $R^2$	Delta	Weight	Ratio
1	5	55.0	137.6	0.000	>10 <sup>6</sup>	72.6	23.2	0.000	>10 <sup>5</sup>
2	6	56.5	128.3	0.000	>10 <sup>6</sup>	76.5	13.5	0.001	856
3	7	64.0	67.8	0.000	>10 <sup>6</sup>	79.5	4.9	0.044	12
4	7	57.1	124.7	0.000	>10 <sup>6</sup>	76.7	14.3	0.000	1299
5	8	70.3	6.4	0.039	25	<b>81.3</b>	<b>0.0</b>	<b>0.520</b>	<b>1</b>
6	8	64.6	62.9	0.000	>10 <sup>6</sup>	79.8	5.6	0.032	16
7	9	<b>71.0</b>	<b>0.0</b>	<b>0.961</b>	<b>1</b>	81.5	0.5	0.403	1

Table D41. Parameter estimates of selected model in Table D40.

Term	Scale, i.e. number of pooled adjacent point records					
	1 (n = 324)			5 (n = 72)		
	$t$	$P$	Sig	$t$	$P$	Sig
Bårby	7.8	0.000		5.0	0.000	
Vickleby	-6.2	0.000	---	-4.6	0.000	---
Ekelunda	-7.3	0.000	---	-5.4	0.000	---
Snail density	<b>2.4</b>	<b>0.018</b>	+	<b>10.8</b>	<b>0.000</b>	+++
Distance	<b>11.2</b>	<b>0.000</b>	+++	<b>3.4</b>	<b>0.001</b>	++
Distance <sup>2</sup>	<b>-10.2</b>	<b>0.000</b>	---	<b>-3.1</b>	<b>0.003</b>	--
Distance <sup>3</sup>	<b>8.4</b>	<b>0.000</b>	+++	<b>2.6</b>	<b>0.010</b>	+
Snail density <sup>2</sup>	<b>2.9</b>	<b>0.004</b>	++			
Interaction	<b>-4.1</b>	<b>0.000</b>	---	<b>-3.9</b>	<b>0.000</b>	---

Table D42. Correlations of *Clauzadea immersa* with snail densities at single distances.

Distance to crack edge (cm)	Scale, i.e. number of pooled adjacent point records							
	1 (n = 324)				5 (n = 72)			
	$R^2$	$t$	$P$	Bon	$R^2$	$t$	$P$	Bon
-10	35.6	3.0	0.009					
-5	<b>75.4</b>	<b>7.0</b>	<b>0.000</b>	+++				
0	<b>71.0</b>	<b>6.3</b>	<b>0.000</b>	+++	<b>84.0</b>	<b>9.2</b>	<b>0.000</b>	+++
5	<b>72.3</b>	<b>6.5</b>	<b>0.000</b>	+++				
10	<b>82.1</b>	<b>8.6</b>	<b>0.000</b>	+++				
15	<b>74.3</b>	<b>6.8</b>	<b>0.000</b>	+++				
20	<b>75.2</b>	<b>7.0</b>	<b>0.000</b>	+++				
25	<b>71.2</b>	<b>6.3</b>	<b>0.000</b>	+++	<b>73.6</b>	<b>6.7</b>	<b>0.000</b>	+++
30	<b>56.1</b>	<b>4.5</b>	<b>0.000</b>	++				
35	<b>63.1</b>	<b>5.2</b>	<b>0.000</b>	++				
40	32.0	2.7	0.015					
45	<b>62.4</b>	<b>5.2</b>	<b>0.000</b>	++				
50	31.8	2.7	0.015		<b>52.6</b>	<b>4.2</b>	<b>0.001</b>	++
55	<b>50.9</b>	<b>4.1</b>	<b>0.001</b>	+				
60	<b>49.9</b>	<b>4.0</b>	<b>0.001</b>	+				
65	43.0	3.5	0.003					
70	<b>66.1</b>	<b>5.6</b>	<b>0.000</b>	+++	<b>57.8</b>	<b>4.7</b>	<b>0.000</b>	++
75	27.5	2.5	0.026					



Table D43. Model selection, *Verrucaria nigrescens* (most abundant epilithic lichen).

Scale, i.e. number of pooled adjacent point records									
Model	K	1 (n = 324)				5 (n = 72)			
		adj. $R^2$	Delta	Weight	Ratio	adj. $R^2$	Delta	Weight	Ratio
1	5	8.0	99.5	0.000	>10 <sup>6</sup>	22.4	24.4	0.000	>10 <sup>4</sup>
2	6	11.6	87.7	0.000	>10 <sup>6</sup>	28.3	20.0	0.000	>10 <sup>4</sup>
3	7	23.9	40.0	0.000	>10 <sup>6</sup>	39.7	8.9	0.009	84
4	7	17.0	68.1	0.000	>10 <sup>6</sup>	36.0	13.2	0.001	723
5	8	27.6	24.8	0.000	>10 <sup>4</sup>	38.8	11.4	0.003	300
6	8	29.5	16.6	0.000	3965	<b>47.7</b>	<b>0.0</b>	<b>0.777</b>	<b>1</b>
7	9	<b>33.2</b>	<b>0.0</b>	<b>1.000</b>	<b>1</b>	46.9	2.6	0.210	4

Table D44. Parameter estimates of selected model in Table D43.

Scale, i.e. number of pooled adjacent point records						
Term	1 (n = 324)			5 (n = 72)		
	$t$	$P$	Sig	$t$	$P$	Sig
Bårby	9.0	0.000		7.7	0.000	
Vickleby	1.5	0.123		1.0	0.327	
Ekelunda	-2.8	0.006	--	-2.1	0.036	-
Snail density	<b>3.5</b>	<b>0.001</b>	+++	<b>2.1</b>	<b>0.039</b>	+
Distance	<b>6.6</b>	<b>0.000</b>	+++	1.6	0.110	
Distance <sup>2</sup>	-6.0	<b>0.000</b>	---	-3.9	<b>0.000</b>	---
Distance <sup>3</sup>	<b>4.3</b>	<b>0.000</b>	+++			
Snail density <sup>2</sup>	-5.2	<b>0.000</b>	---	-3.3	<b>0.002</b>	--
Interaction	<b>4.3</b>	<b>0.000</b>	+++	<b>3.0</b>	<b>0.004</b>	++

Table D45. Correlations of *Verrucaria nigrescens* with snail densities at single distances.

Scale, i.e. number of pooled adjacent point records								
Distance to crack edge (cm)	1 (n = 324)				5 (n = 72)			
	$R^2$	$t$	$P$	Bon	$R^2$	$t$	$P$	Bon
-10	2.1	-0.6	0.568					
-5	34.2	-2.9	0.011					
0	<b>70.4</b>	<b>-6.2</b>	<b>0.000</b>	---	<b>51.6</b>	<b>-4.1</b>	<b>0.001</b>	--
5	31.7	-2.7	0.015					
10	19.7	-2.0	0.065					
15	13.5	-1.6	0.134					
20	4.7	-0.9	0.389					
25	11.8	-1.5	0.163		13.2	-1.6	0.139	
30	31.4	-2.7	0.015					
35	0.7	-0.3	0.739					
40	0.6	-0.3	0.766					
45	0.3	-0.2	0.823					
50	0.2	-0.2	0.865		0.1	-0.1	0.886	
55	0.7	-0.3	0.734					
60	10.7	1.4	0.185					
65	1.0	0.4	0.699					
70	0.2	-0.2	0.875		0.7	0.3	0.745	
75	2.9	0.7	0.499					

Table D46. Model selection, *Placynthium nigrum* s. lat. (most abundant epilithic lichen with cyanobacterial symbiont).

Model	K	Scale, i.e. number of pooled adjacent point records							
		1 (n = 324)				5 (n = 72)			
		adj. $R^2$	Delta	Weight	Ratio	adj. $R^2$	Delta	Weight	Ratio
1	5	29.9	25.4	0.000	$>10^4$	50.1	19.6	0.000	$>10^4$
2	6	30.0	26.1	0.000	$>10^4$	51.1	19.5	0.000	$>10^4$
3	7	<b>35.6</b>	<b>0.0</b>	<b>0.476</b>	<b>1</b>	<b>63.4</b>	<b>0.0</b>	<b>0.607</b>	<b>1</b>
4	7	29.8	28.0	0.000	$>10^6$	50.4	22.0	0.000	$>10^4$
5	8	35.6	1.3	0.247	2	62.9	2.5	0.173	3
6	8	35.5	1.9	0.183	3	62.9	2.5	0.173	4
7	9	35.4	3.2	0.094	5	62.3	5.1	0.047	13

Table D47. Parameter estimates of selected model in Table D46.

Term	Scale, i.e. number of pooled adjacent point records					
	1 (n = 324)			5 (n = 72)		
	$t$	$P$	Sig	$t$	$P$	Sig
Bårby	-0.4	0.691		0.0	0.981	
Vickleby	9.3	0.000	+++	8.1	0.000	+++
Ekelunda	8.0	0.000	+++	7.1	0.000	+++
Snail density	<b>-3.4</b>	<b>0.001</b>	---	<b>-3.1</b>	<b>0.003</b>	---
Distance	<b>5.5</b>	<b>0.000</b>	+++	<b>4.2</b>	<b>0.000</b>	+++
Distance <sup>2</sup>	<b>-5.4</b>	<b>0.000</b>	---	<b>-4.8</b>	<b>0.000</b>	---
Distance <sup>3</sup>						
Snail density <sup>2</sup>						
Interaction	1.2	0.237		1.8	0.083	

Table D48. Correlations of *Placynthium nigrum* s. lat. with snail densities at single distances.

Distance to crack edge (cm)	Scale, i.e. number of pooled adjacent point records							
	1 (n = 324)				5 (n = 72)			
	$R^2$	$t$	$P$	Bon	$R^2$	$t$	$P$	Bon
-10	2.1	-0.6	0.568					
-5	0.0	0.0	1.000					
0	14.4	-1.6	0.121		28.6	-2.5	0.022	
5	22.6	-2.2	0.046					
10	23.4	-2.2	0.042					
15	36.2	-3.0	0.008					
20	24.5	-2.3	0.037					
25	18.2	-1.9	0.077		26.0	-2.4	0.031	
30	15.4	-1.7	0.107					
35	6.4	-1.0	0.311					
40	3.4	-0.8	0.464					
45	17.2	-1.8	0.087					
50	8.4	-1.2	0.245		3.5	-0.8	0.459	
55	0.0	0.0	0.992					
60	3.0	0.7	0.493					
65	0.0	0.1	0.938					
70	18.8	-1.9	0.073		4.3	-0.9	0.407	
75	2.6	-0.7	0.519					

Table D49. Model selection, *Collema fuscovirens* (most abundant foliose lichen with cyanobacterial symbiont).

Model	K	Scale, i.e. number of pooled adjacent point records							
		1 (n = 324)				5 (n = 72)			
		adj. $R^2$	Delta	Weight	Ratio	adj. $R^2$	Delta	Weight	Ratio
1	5	7.9	9.0	0.005	88	2.6	22.2	0.000	>10 <sup>4</sup>
2	6	8.3	8.7	0.005	79	4.9	21.8	0.000	>10 <sup>4</sup>
3	7	10.4	2.5	0.115	3	<b>31.0</b>	<b>0.0</b>	<b>0.396</b>	<b>1</b>
4	7	8.7	8.5	0.006	69	4.0	23.8	0.000	>10 <sup>4</sup>
5	8	11.2	0.3	0.338	1	32.0	0.4	0.327	1
6	8	10.7	2.2	0.135	3	30.6	1.9	0.154	3
7	9	<b>11.6</b>	<b>0.0</b>	<b>0.397</b>	<b>1</b>	31.6	2.3	0.123	3

Table D50. Parameter estimates of selected model in Table D49.

Term	Scale, i.e. number of pooled adjacent point records					
	1 (n = 324)			5 (n = 72)		
	$t$	$P$	Sig	$t$	$P$	Sig
Bårby	2.7	0.007		3.4	0.001	
Vickleby	3.0	0.003	++	2.0	0.047	+
Ekelunda	3.4	0.001	+++	2.0	0.052	
Snail density	<b>-2.1</b>	<b>0.037</b>	-	-2.0	0.055	
Distance	0.6	0.530		<b>4.4</b>	<b>0.000</b>	+++
Distance <sup>2</sup>	1.3	0.180		<b>-5.1</b>	<b>0.000</b>	---
Distance <sup>3</sup>	<b>-2.0</b>	<b>0.042</b>	-			
Snail density <sup>2</sup>	1.5	0.124				
Interaction	1.5	0.127		1.9	0.061	

Table D51. Correlations of *Collema fuscovirens* with snail densities at single distances.

Distance to crack edge (cm)	Scale, i.e. number of pooled adjacent point records							
	1 (n = 324)				5 (n = 72)			
	$R^2$	$t$	$P$	Bon	$R^2$	$t$	$P$	Bon
-10	2.1	-0.6	0.566					
-5	8.5	-1.2	0.242					
0	4.9	-0.9	0.377		17.0	-1.8	0.089	
5	11.7	-1.5	0.165					
10	2.0	-0.6	0.580					
15	6.8	-1.1	0.295					
20	2.3	0.6	0.544					
25	7.4	-1.1	0.276		3.2	-0.7	0.478	
30	3.3	-0.7	0.469					
35	4.0	-0.8	0.426					
40	4.1	0.8	0.420					
45	0.1	0.1	0.924					
50	0.1	0.1	0.925		3.6	-0.8	0.451	
55	15.7	-1.7	0.104					
60	6.9	-1.1	0.292					
65	6.5	1.1	0.307					
70	2.0	0.6	0.574		5.5	1.0	0.348	
75	3.4	0.8	0.464					