Lichen-dominated soil crusts as arthropod habitat in warm deserts

J.S. Lalley[a,*], H.A. Viles[a], J.R. Henschel[b], V. Lalley[c]

[a]Oxford University Centre for the Environment, Dyson Perrins Building, South Parks Road, Oxford OX1 3QY, UK
[b]Gobabeb Training and Research Centre, P.O. Box 953, Walvis Bay, Namibia
[c]University of Binghamton, Biological Sciences Department, P.O. Box 6000, Binghamton, NY 13902, USA

Abstract

Soil crust lichens can be the dominant vegetation in arid lands, yet their importance as habitat to secondary producers is relatively unknown. This study examines the distribution of arthropod communities in the northern Namib Desert to evaluate whether a lichen-rich area is more or less productive than adjacent habitats in terms of the consumers each supports. Arthropods are diverse and highly endemic in the Namib Desert and lichens dominate this desert's extensive gravel plains. We sampled lichen-rich, dwarf shrub, and unvegetated sites and found distinct arthropod assemblages in the lichen-dominated sites, including species unique to lichen sites. Arthropod assemblages in two of the lichen sites were similar to those found in the dwarf shrub site. In a canonical correspondence analysis, crustose lichens and overall lichen cover were key in driving the variance in arthropod assemblages within the lichen sites. Furthermore, lichen morphotypes, overall lichen cover and species richness, were significantly correlated with the representation of arthropod subgroups and arthropod species richness. These findings provide evidence that lichen-dominated soil crusts in the Namib Desert are important supporters of secondary production, warranting more in-depth studies into the ecology and conservation of this lichen-rich habitat in warm deserts.
© 2006 Elsevier Ltd. All rights reserved.

Keywords: Biological soil crusts; Desert ecology; Namib Desert; Pitfall trapping

*Corresponding author. Tel.: +44 1865 271919; fax: +44 1865 271929.
E-mail addresses: j.s.lalley@worc.oxon.org (J.S. Lalley), heather.viles@ouce.ox.ac.uk (H.A. Viles).

1. Introduction

The structure and functions of biological soil crusts in arid environments have received attention by ecologists, as the biological components of these crusts can be the primary fixers of nitrogen in deserts (Rogers and Lange, 1966; Zaady et al., 1998; Evans and Belnap, 1999), sinks for carbon (Beymer and Klopatek, 1991), and play critical roles in soil stabilization and the prevention of erosion (Belnap and Gillette, 1998; Eldridge and Leys, 2003). Soil crust lichens contribute significantly to all of these roles, but while there is plenty of evidence of primary production in soil crust lichen communities, there is little knowledge of soil crust lichens as basal organisms supporting secondary production, as pointed out by Shepherd et al. (2002) in reference to arthropods. Most desert food web studies have focused on higher plants, looking at shrub patches as local biodiversity hotspots with little consideration of the effect of the surrounding biological soil crusts (Wharton, 1980; Robinson, 1981; Sanchez and Parmenter, 2002). Given the dominance of lichens in large areas of deserts where hyperarid conditions exclude higher plants, are patches of dense lichen growth serving as "islands of fertility" in these low-energy systems?

Few studies have examined the influence of terricolous lichen communities on consumer organisms in warm deserts, which is surprising considering the dependence of many animals on epiphytic and terricolous lichens in cold deserts. Lichens fill an important niche in both cold and warm deserts where extreme climatic conditions lead to an absence or seasonal inaccessibility of higher plants. In cold deserts, reindeer are well known for their dependence on lichen growth (Storeheier et al., 2002) and arthropods depend on these lower plants in regions of Antarctica and the Arctic (Block and Convey, 1995; Hodkinson and Wookey, 1999). In warm deserts there is limited evidence that animals feed on lichens in years of drought (Noy-Meir, 1974; Wessels, 1986). Furthermore, few studies link desert micro-fauna to lichens, despite the focus of many ecologists on the unique invertebrate and reptile communities found in warm deserts.

Shepherd et al. (2002) report the large void in arthropod—biological soil crust research and conducted a study on moss-dominated soil crusts in the southwest United States showing a clear association of both micro- and macro-arthropods with biological soil crusts. One study in the semi-arid Negev Desert compared spider communities on shrub patches with those found on biological soil crusts, and found distinct communities occurring on each (Whitehouse et al., 2002). In the Namib Desert where this study takes place, lichens are the dominant vegetation in large areas, yet only two invertebrate studies have examined the lichen-rich soil crust niche. Wessels (1986) reported on the common fruticose lichen species *Teloschistes capensis* in Namibia, and found 17 species of mite associated with this one species. Furthermore, Wessels et al. (1979) reported on two lichen-feeding tenebrionid beetle species, one of which showed selective eating behaviour on *T. capensis*. Despite the fact that invertebrates make up 91% of Namibia's overall terrestrial biodiversity (Barnard, 1998), there have been no further studies linking arthropod populations with the Namib Desert's most widespread vegetation type, lichens.

Arthropod populations in the Namib Desert, where this study took place, have a high rate of endemism and niche specialization so are recognized as being unique by entomologists worldwide (Koch, 1962; André et al., 1997). Identifying the associations, or lack of, between these communities and the widespread lichen-rich soil crusts, would be a strong indicator as to whether or not lichen communities are vital components of desert food webs. Given the ongoing discovery of new arthropod species in the Namib Desert

(Simmons et al., 1998), there is also a tremendous need for improved knowledge on the basal organisms and habitats of these populations. This need coincides with a prioritization of desert lichen research in Namibia, where human activities have caused considerable damage to lichen-dominated soil crusts along the Namibian coastline (Wessels and van Vuuren, 1986; Schieferstein and Loris, 1992; Lalley and Viles, 2005).

The complexities of soil crust lichen communities are relatively unknown, but lichens have been found to be extremely slow to recover after human-induced disturbances, so this habitat type requires special consideration (Brotherson et al., 1983; Evans and Belnap, 1999). Lalley and Viles (in press) report recovery rates ranging from 5 to over 500 years in the northern and central Namib Desert, depending on the lichen soil crust type. The currently limited knowledge of the organisms associated with lichen cover has made it difficult to assess the cascading impacts from disturbances to these fragile components of deserts. But the diversity of lichen species and the mosaic distribution of some communities, suggest that there is a strong patch dynamic linked to lichen growth. Stronger evidence of such links will help determine whether lichen-dominated areas of deserts should be regarded as an important habitat type for heterotrophs and given the necessary conservation protection.

We hypothesize that lichen-rich soil crusts in warm deserts serve as key providers of food and refuge to micro-fauna, which we aim to test in an assessment of arthropod assemblages and abundances within and outside of lichen soil crust areas of the Namib Desert. We test the influence of different lichen soil crust characteristics (growth density, species richness, and representation of lichen morphogroups) on arthropod assemblages. Specifically, this research examines two questions: (i) Is there a significant difference between arthropod assemblages in lichen-dominated soil crust areas and those found in unvegetated and dwarf shrub areas? (ii) Does lichen community structure influence arthropod assemblages that are present in lichen-dominated soil crusts?

2. Materials and methods

2.1. Study area

The Namib Desert extends from South Africa, through Namibia, and into Angola, covering roughly 2000 km of Africa's southwest coastline (Goudie, 2002) (Fig. 1). The majority of the desert falls within Namibia. It is one of the driest deserts in the world, receiving a mean annual rainfall of 19 mm along the coast (Lancaster et al., 1984; Southgate et al., 1996). However, fog moisture penetrates inland between 30 and 200 days in a year (Lancaster et al., 1984). Fog intensity varies considerably along both latitudinal and longitudinal gradients, but mean annual fog precipitation has been estimated to range between 37 and 87 mm (Hachfeld, 2000; Lancaster et al., 1984; Olivier, 1992). Similar climatic conditions occur in only two other deserts in the world, the Atacama Desert in Chile, and the Sonoran Desert in Baja California, Mexico.

Regular fog events sustain most life in the Namib, creating an isolated environment conducive to high rates of species diversity and endemism in comparison with other hyperarid regions of the world (van Zinderen Bakker, 1975; Seely, 1978; Southgate et al., 1996; Simmons et al., 1998). However, the moisture deposited by a fog event is not enough to initiate the germination of higher plants, except for isolated areas of water run off such as rock crevices and drainage lines. This study was conducted in the remote northern
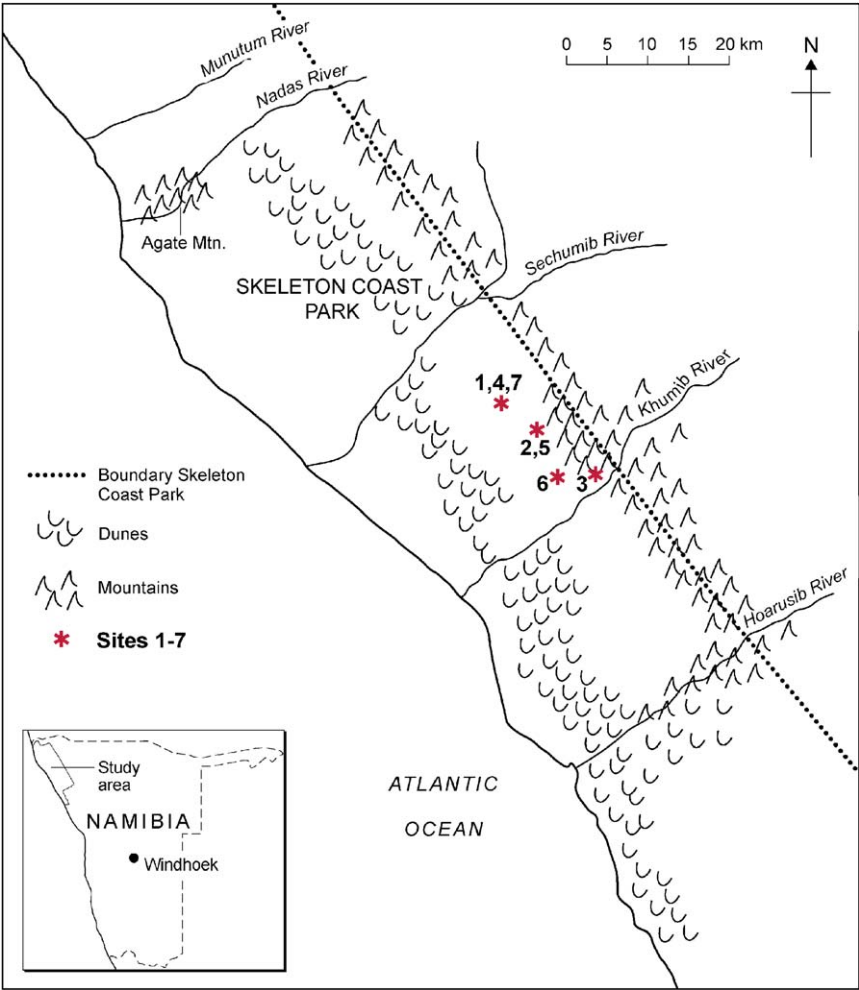
Fig. 1. Map of study area, demarcating each sampling site.

Namib Desert where habitats include coastal plains, mountains, sand dune fields, and gravel plains interspersed with ephemeral stream channels. Gravel plains here are largely dominated by lichen-rich soil crusts that vary in lichen cover and species richness on several geographic scales (Schieferstein and Loris, 1992; Lalley and Viles, 2005). Lichen species that form biological soil crusts in the Namib Desert include species from three morphological groups, crustose (growing flat and adnate to the substrate), foliose (leafy or lobulous), and fruticose (shrub-like), all of which entangle both soil sediments and gravel. The sediments and gravel thus become the aggregates of the biological soil crusts.

2.2. Field study

In this study, we focused sampling efforts to seven sites in the northern Namib Desert, between 15 and 30 km inland, inside the Skeleton Coast National Park where accessibility

is limited (Fig. 1). Sites 1–3 were gravel plains with three different biological soil crust types with varying degrees of lichen cover, community composition and lichen species richness, and varying soil surface structures (Table 1). All three sites have unsorted gravel cover, and lichens adhere to the soil sediments and small gravel stones, forming the perimorphic layer of the biological soil crust (Evans and Johansen, 1999). Sites 1 and 2 fell within a large lichen-covered soil crust matrix and site 3 was a small isolated montane community. Sites 4–7 represented four different habitat types that are devoid of lichen cover. Site 4 was a large bare patch within a lichen-covered soil crust matrix. Site 5 was a barren area 9 m from a lichen soil crust area. Site 6 was a river terrace 1.5 km from lichen soil crust areas, that was barren except for roots of past annual grass growth (site 6); and site 7 was an ephemeral stream channel with sparse dwarf shrub patches. Dwarf shrub patches in the northern Namib are restricted primarily to washes and ephemeral stream channels, and many are dominated by desert daisy (*Tripteris* sp., family Asteraceae), as was the case in site 7. This site fell in close proximity to lichen site 1 (15 m away) and the unvegetated site 4 (20 m away). These three sites were chosen in close proximity so that any distinctions found in arthropod assemblages between the sites could be more confidently linked to vegetation cover and not to geographic isolation.

Lichen species cover within sites 1–3 was sampled following Lalley and Viles (2005), using a grid measuring 0.5 m × 0.5 m at 20 locations within each site, five of which fell adjacent to the pitfall traps. Overall cover and the cover of individual species were assessed independent of one another as a percentage of the 100 subdivisions within the grid. Any lichen growth within a subdivision counted as 1%, and only lichens growing on the surface of biological soil crusts were counted. Lichens that did not contribute to the aggregation of the soil surface were excluded.

2.2.1. Pitfall trapping and line transect sampling

Sampling of arthropods took place in the dry winter month of July 2003 when there was a lower chance of any grass cover forming possible corridors between the sampling sites or any grass growing within the lichen-rich areas. This cool and dry period is not ideal for capturing arthropods because of their low activity, but it was important to sample different habitat types when lichen-rich areas were void of seasonal vegetation. Our aim was to sample arthropod assemblages in distinct habitat types and not to record the overall diversity of species for the area. Within each site, we carried out pitfall trapping of arthropods and line-transect sampling to detect arthropod activity.

Despite questions about its efficiency, pitfall trapping is recognized as the most cost-effective sampling method and suitable for estimating differences in relative abundance and community composition (Olivier and Beattie, 1996; Duelli et al., 1999). Here, pitfall trapping followed standard methods (Abensperg-Traun and Steven, 1995; Weeks and McIntyre, 1997; Whitehouse et al., 2002; Woinarski et al., 2002) placing five traps in each site in a randomly chosen location. Traps were placed 5 m apart to ensure independent sampling within each trap. In the ephemeral stream channel, traps were also placed at least 2 m from shrubs, as the intention was not to sample the small vegetation patches as island habitats for invertebrates, but to rather sample stream channels as a habitat characterized by patches of higher plant cover. Following studies by Abensperg-Traun and Steven (1995) and Woinarski et al. (2002), a large trap diameter was used (18 cm) in hopes of increasing the likelihood of trapping a large range of arthropods, including rare and larger species. Traps were steep-sided and 30 cm deep to prevent capture losses, and the bottom of each

Table 1
Descriptions of sites 1–7 including vegetation characteristics, soil structures, lichen community descriptors, and arthropod species richness estimations

Site	Lichen cover or proximity of lichens to site border	Vascular plant occurrence or proximity of plants to site border	Soil structure	Arthropod sp. richness (sum)	Species richness estimation (jackknife)	Arthropod sp. unique to site (total)	Lichen sp. richness (sum)	Fruticose cover (%)	Foliose cover (%)	Crustose cover (%)
1	28.6% lichen cover	Site border 15 m from dwarf shrub & grass patches	Sandy with thin crust; calcrete patches	20	35±3.61	5	12	3	28.2	7.3
2	67.4% lichen cover	Site border 25 m from dwarf shrub & grass patches	Thin to thick soil crust with silt sediments; gypsum patches	16	29±3.35	5	15	15.5	62.4	4
3	86.9% lichen cover	Site border 12 m from dwarf shrub & grass patches	Thick soil crust with gypsum	17	25±2.33	4	14	65.2	83	10.6
4	Site border 2 m from lichen-rich area	Site border 20 m from dwarf shrub & grass patches	Thin crust over loose sand sediments	13	19±2.60	1	0	0	0	0
5	Site border 9 m from lichen-rich area	Site border 17 m from dwarf shrub & grass patches	Loose sand sediments	13	21±3.44	1	0	0	0	0
6	Site border 1500 m from lichen-rich area	Sparse dry grass roots	Thin calcrete crust over loose sediments; sand patches	8	9±1.35	3	0	0	0	0
7	Site border 15 m from lichen-rich area	Dwarf shrubs & grass patches	Loose sand sediments	23	39±3.64	8	0	0	0	0

trap was covered in $+2$ cm of sand to provide some protection to captured specimens from predation. No baiting was used. If the area on the periphery of the trap was disturbed during the burying of the traps, this was carefully rehabilitated. In order to access the traps for sampling, the same route and footprints were followed each time to minimize the area of disturbance.

Traps were emptied every 48 h over a period of 15 days. Trapped arthropod specimens were recorded to the genus or species level where possible, based on comparisons of voucher specimens. Each arthropod species was also categorized into one of four subgroups: ant (Hymenoptera), beetle (Coleoptera), arachnid (Araneae, Acari, Scorpiones, Solifugae), and a fourth subgroup comprising miscellaneous insects (i.e. Thysanoptera, Thysanura). Live specimens were released outside of the collection areas to avoid recapture and ensure the independence of each sample of each trap.

Observations of arthropod activity were made in each site along two parallel line transects measuring 50 m and spaced 10 m apart. Signs of arthropod activity, namely entrances to insect and arachnid burrows or traps, spider webs, and ant nests, were recorded within 1 m on either side of the transect.

2.3. Data analysis

Pitfall trap data were divided into two data sets, both of which used the total collection of each bucket as one sample. The first data set consisted of all arthropod species that could be confidently differentiated from other specimens across the seven sites. The second set consisted of the four arthropod subgroups in which all collected specimens could be divided regardless of genus. The analysis of arthropod subgroups was used to guide interpretations of the arthropod—lichen associations and CCA analysis. Line transect observations were qualitatively assessed in order to further explain findings from the pitfall trap sampling.

2.3.1. Comparative analysis—lichen vs. non-lichen sites

The comparative analysis used qualitative and quantitative methods to compare lichen sites against non-lichen sites based on the sampled arthropod communities. Qualitative comparisons were made of the overall species richness values for each site, the number of unique species in each site (occurring only in that site), and the number of arthropod burrows, webs, or nests counted along the line transects. Given the limitations of the sampling, as well as the diverse nature of arthropod communities in the Namib Desert and the variations in ground cover (lichen or other), it was unlikely that site sampling would have equal capture rates or that all species would have equal detectability. This was confirmed through species accumulation assessments for each site. To account for incomplete species lists, a jackknife species richness estimator was used in Species Diversity and Richness software version 2.65, to extrapolate a projected species number from the sample data for each site (Burnham and Overton, 1979). The jackknife estimator takes the heterogeneous nature of species detectability into consideration, and has been shown to be one of the least biased estimators when sample sizes are small or, in this case, dominated by values of zero (Hellmann and Fowler, 1999).

Arthropod assemblages were tested for similarities between sites using Sørensen's coefficient of similarity in Community Analysis Package software version 2.04, which

measures the extent to which two sites or samples have species in common based on presence and absence data (Kent and Coker, 1992).

2.3.2. Arthropod associations with lichen community structure

All arthropod samples and species data for the three lichen sites were ordinated against lichen characteristics (environmental variables) using canonical correspondence analysis (CCA) in CANOCO software version 4.5 (ter Braak, 1988). CCA ordination is useful for large species data sets $(10+)$ and uses weighted averaging to assess the association of environmental variables with species occurrence in samples, and ordinates the samples and species accordingly. The environmental variables consisted of cover percentage of three different lichen morphogroups (crustose, foliose, and fruticose), total lichen cover, and lichen species richness (total number of lichen species in the biological soil crusts of each site).

Using the subgroup data set, arthropod subgroup abundance values for each bucket sample were tested for correlations with overall lichen cover, the cover of the three lichen morphogroups (crustose, foliose, and fruticose), and lichen species richness found at each sampling site. Spearman's rank correlation was used in SPSS software version 11.5 (Kinnear and Gray, 2000).

3. Results

3.1. Arthropod species richness and assemblages

Across the 245 samples of the 35 pitfall traps, 1090 specimens were collected, from which 54 arthropod species were recorded. Ants were the only subgroup that was not separated into species, as all specimens were morphologically similar, and it was not within the scope of this research to differentiate between these specimens. The species accumulation assessments indicated that the sampling effort used in this study did not capture all potential species in the arthropod communities of lichen sites 1–3 and the shrub site 7, which were the only vegetated sites and the sites with the highest arthropod species richness values (Table 1). The highest total number of species and the highest estimated species richness values were found in the ephemeral stream channel with shrub patches (site 7), followed closely by site 1 with lichen cover (Table 1). The lowest species number was found in the seasonal grassland where no lichen or shrub patches occurred, and where only dry grass roots remain (site 6). The highest number of unique species, those occurring in one site, was found in the shrub site (site 7), followed by the lichen-rich sites 1 and 2 (Table 1). Of the 19 species of beetle collected, seven were unique to lichen sites, the majority of which fell in the Tenebrionidae family. Of the arachnid group, there was a similar number of unique species found in the lichen sites (1–3), unvegetated sites (4–6), and shrub site (site 7). Ants were most abundant in the shrub site, and the miscellaneous insect group revealed several unique species in the lichen and shrub sites.

The similarity index revealed that species assemblages in site 7 with shrubs, and sites 1 and 2 with lichen cover, were similar in nature, as shown by the Sørensen's similarity coefficient values (Table 2). Complete similarity was found between the unvegetated sites 5 and 6, and high similarity values were found between the lichen sites 1 and 2. The lowest similarity coefficient was found between lichen site 3 and the two unvegetated sites (sites 5 and 6).

Table 2
Sørensen's coefficient values, indicating the similarity between sites based on arthropod species presence or absence

Site no.	1	2	3	4	5	6
2	0.9091					
3	0.75	0.6667				
4	0.5	0.6667	0.3333			
5	0.5714	0.5	0.4	0.8		
6	0.5714	0.5	0.4	0.8	1	
7	0.7273	0.8333	0.4444	0.6667	0.5	0.5

Coefficient value of 1 indicates total similarity and 0 indicates total dissimilarity.

3.2. Arthropod activity

The arthropod activity observed along line transects in each of the sites is illustrated in Fig. 2. The largest number of insect burrows was found in the unvegetated site with the remnants of annual grass (site 6). It is likely that these holes were from termite activity, as these communities are commonly associated with grass roots (Whitford et al., 1992). The next highest number of insect burrows was found in lichen-rich site 1. Spider webs were most frequently found in the lichen and shrub areas. Of the three lichen areas, site 3 with dense lichen cover had the lowest count of insect burrows as well as spider webs.

3.3. Arthropod associations with lichen community structures

In a CCA, all arthropod species were ordinated according to five lichen community characteristics: the cover percentage of the three lichen morphogroups, the total cover percentage of lichen growth and the lichen species richness values (total number of species in site). The ordination highlighted the cover of crustose lichen species (eigenvalue = −0.6003) as the dominant environmental variable driving the variance in arthropod assemblages on the first axis, followed by overall lichen cover on the second axis (eigenvalue = −0.4758) (Table 3; Fig. 3). The first axis explained 62.2% of the overall variance, and the second axis explained an additional 37.5%. The centroids of the sampled sites are shown in Fig. 3, illustrating the association of specific species with the three sites. Several beetle species were associated with sites one and three, while arachnids and miscellaneous insects were associated with site 2.

To supplement the analysis of arthropod species—lichen associations, we used the arthropod subgroup data set and arthropod species richness values to test for correlations between the five lichen community variables using Spearman's rank correlation analysis. The beetle subgroup and arthropod species richness values were positively correlated with all lichen community variables except lichen species richness, with the most significant correlations occurring with the crustose and fruticose lichen morphogroups (Table 3). Arachnids were positively correlated with lichen species richness. The miscellaneous insect group was negatively correlated with lichen cover and the foliose and fruticose lichen morphogroups (Table 3). Ants showed no significant correlations with any of the lichen community variables.
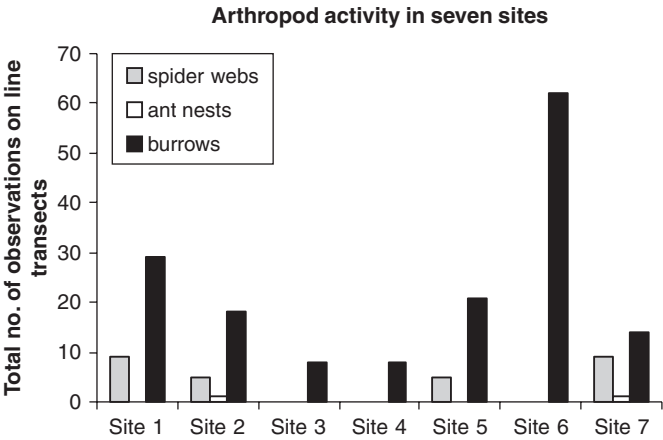
Arthropod activity in seven sites

Fig. 2. Arthropod activity observed along two line transects in each of the seven sampling sites. Sites 1–3 are lichen-rich sites, site 7 is a shrub site, and sites 4–6 are unvegetated.

Table 3
Spearman's rank correlation coefficients and significance (two tailed) for correlations between lichen community variables and the abundance of arthropod subgroups and arthropod species richness within the three lichen sites ($N = 15$)

	Correlation coefficient & significance	Arthropod sp. richness	Ants	Arachnids	Beetles	Misc. insects
Lichen cover	r_s	0.598	0.322	0.267	0.550	−0.514
	p	0.019*	0.243	0.336	0.034*	0.050*
Lichen sp. richness	r_s	0.028	0.132	0.648	−0.266	−0.286
	p	0.920	0.638	0.009**	0.339	0.301
Crustose	r_s	0.598	0.322	0.267	0.550	−0.516
	p	0.019*	0.243	0.336	0.034*	0.050*
Foliose	r_s	0.591	0.302	0.278	0.519	−0.511
	p	0.020*	0.275	0.317	0.047*	0.052
Fruticose	r_s	0.598	0.322	0.267	0.550	−0.514
	p	0.019*	0.243	0.336	0.034*	0.050*

Significance: *$p < 0.05$; **$p < 0.01$.

4. Discussion

The dissimilarities found in arthropod assemblages between lichen sites, unvegetated sites and shrub sites, and the number of unique species found within the lichen-dominated sites, suggest that soil lichen cover in the Namib Desert provides an important habitat to
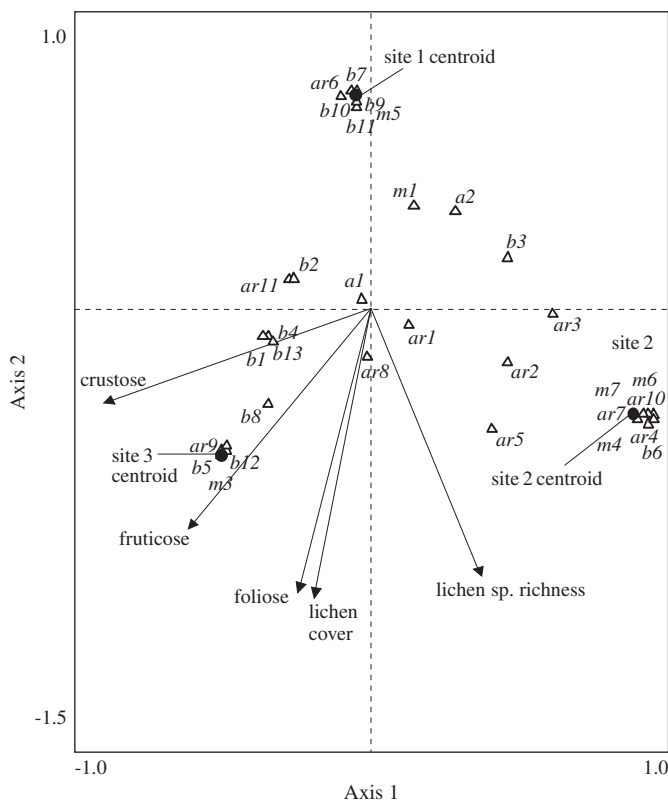
Fig. 3. CCA ordination biplot of lichen community variables driving arthropod species assemblages. a = ants; ar = arachnids; b = beetles; m = misc. insects.

arthropods. A larger, cross-seasonal sampling effort would provide larger sample sizes that may reveal even stronger associations of species with lichen-rich areas, as would variations in traps that increase capture rates and reduce possible capture losses. The sampling in this study was also limited by the chosen season when arthropods are less active. Nevertheless, there were clear associations of arthropods with the sampled lichen sites.

Similarities in arthropod assemblages between the dwarf shrub site and two lichen-rich sites (Table 2) suggest that lichen-rich habitats may play several significant roles for secondary producers, as commonly recorded for shrub patches in warm deserts (Sanchez and Parmenter, 2002). Lichens offer protection from extreme environmental conditions, but they may also be key in providing a food source to omnivores, a prey base to carnivorous arthropods through lichen-associated mites and other lichen-feeding arthropods, collectors of wind-blown detritus for detritivores, and structures for web-building spiders. If confirmed, the importance of lichen growth in the coastal Namib Desert would exceed that of shrub patches, given the vast areas in which lichen growth dominate.

The additional analyses of lichen sites and sampled arthropod communities, shed some light on how lichen sites are utilized by arthropods. A qualitative examination of the

unique arthropod species found in the three studied lichen sites shows a representation of omnivorous (possibly lichen-feeding), carnivorous, and detritivorous species. The number of webs found within the lichen sites also suggests that lichens provide enough structure for spider web construction and an adequate prey base. The lichen sites also supported unusual species such as the flightless grasshopper, which was found only in lichen sites. Along with lichen-feeding mites and tenebrionid beetles (Wessels et al., 1979), these large omnivores may also be consumers of lichen thalli, as suggested by Seely (1992).

Arthropod assemblages varied considerably between the three lichen sampling sites where lichen community structures differed (lichen cover and species composition), suggesting that the variations occurring in lichen soil crusts influence the suitability of the site for different arthropods. The CCA ordination weighted the crustose lichen morphogroup and overall lichen cover as key in explaining the variance in arthropod assemblages (Fig. 3).

The influence of crustose species may be soil-related. As part of a biological soil crust, this morphogroup can grow flat and adnate on soil or gravel surfaces and is often associated with hardened soil surfaces such as gypsum crusts (Eldridge and Koen, 1998; Lalley and Viles, 2005; St. Clair et al., 1993). Some crustose species are also associated with well-developed lichen communities, because the soil stabilizing hyphae and filamentous growths of some species can support the growth of others (Schulten, 1985). This hardened soil surface would be avoided by any burrowing arthropod species without strong digging appendages (Crawford, 1981). At the same time, the soil stability would be beneficial to equipped species that form long-term burrows and nests in stable surfaces, as seen under shrub canopies where plant roots stabilize the surface (Whitford, 2002). The positive correlation between crustose species and the beetle subgroup may be indicative of this association. Also, the variation in insect and arachnid burrows found in the three lichen areas (Fig. 2) suggests that differences in soil substrates and soil stabilizing lichen densities (Table 1) could be governing arthropod assemblages, following soil correlations found in other desert arthropod studies (Crawford, 1988; Tigar and Osborne, 1997).

The importance of lichen cover in the CCA (Fig. 3) may also indicate a link with soil hardness, but more directly it can influence the number of edible lichen thalli, the detritus trapping potential of the area, and the sheltering ground cover. The correlation of beetles with overall lichen cover (Table 3) may be explained by all of these roles, as they are dependent on detritus (Seely and Mitchell, 1987), lichen thalli (Wessels et al., 1979), and shelter from high temperatures and predators (Gerson, 1973; Seely and Mitchell, 1987; Crawford, 1988). The significant correlation between beetles and fruticose and foliose lichens further suggests that this is the case (Table 3). The shrub-like thalli of fruticose lichens are known to be food sources for some tenebrionid beetles (Wessels et al., 1979). The erect structure of both fruticose and foliose lichens would also increase the detritus—trapping potential of the lichen community and offer shelter.

The correlation of arthropod species richness with lichen cover and morphogroup representation is most probably due to the diversity of microhabitat offered by different lichen community types. The lichen site with the lowest growth density had the highest number of arthropod species, abundances, and activity (burrows, nests, webs) (Table 1; Fig. 2). This may be explained by the patchy mosaic of lichen cover in the low density site, which consisted of harder soil surfaces beneath the lichen growth and looser sand or thin physical soil crusts between the lichen patches (Table 1). Assuming that a diversity of microhabitats leads to a diversity of species (Gardner et al., 1995; Hansen, 2000), a mosaic

of hard and soft soil surfaces and variations in lichen cover should reveal a greater diversity of arthropods. The negative correlation between Misc. insects and lichen cover variables (overall and morphotypes) may also be linked to this diversity of microhabitats.

Ants showed no significant correlation with any of the lichen variables and arachnids were only correlated with lichen species richness. Arachnid associations with lichen species numbers may be due to the mite prey base found on different lichen thalli (Wessels, 1986). A more diverse community of lichens would presumably support a more diverse range of mites (not sampled here) and omnivores. Spiders may also be attracted to a more diverse range of lichen morphotypes for web-building purposes and ambushing. Web-constructing spiders in deserts are known to be selective in the vegetation they use for web support (Robinson, 1981). Here, the lichen site with the densest lichen cover had the lowest incidence of spider webs, which may indicate that bare ground between web-supporting structures is optimal.

Further investigations into niche specialization in lichen-rich habitats of deserts would strengthen evidence for lichen soil crusts as important supporters of secondary production in desert ecosystems, either as food, shelter, or food sources (lichen thalli, detritus or thallus-inhabiting mites). While this study is only preliminary to what is needed, the findings indicate that variations in lichen community types are key in dictating arthropod assemblages in warm deserts, and lichens may be vital supporters of secondary producers in hyperarid regions such as the Namib Desert.

5. Conclusion

Lichen-dominated soil crusts form one of the largest vegetation bases in the Namib Desert and in several other hyperarid regions of the world. Our results suggest that there are distinct populations of arthropods associated with this habitat type. Comparisons with a dwarf shrub site in the Namib Desert showed similarities with lichen sites in terms of arthropod species richness and assemblages, which warrants further investigation into lichen-rich areas as biodiversity hotspots where shrub patches are absent. This leaves many questions as to how arthropod species utilize this habitat type, i.e. as thermo-regulated shelter, a direct food source, a trap for detritus, or a source of prey species (mites). Answers to such questions will shed light on the possible cascading impacts of lichen soil crust removal on micro-fauna, which should have considerable ramifications for land-use planning. Lichen-rich habitats will require greater conservation attention in the future as human activities in deserts increase and as the biodiversity of deserts is unveiled, particularly in the understudied regions of the Namib Desert.

References

Abensperg-Traun, M., Steven, D., 1995. The effects of pitfall drap diameter on ant species richness (Hymenoptera: formicidae) and species composition of the catch in a semi-arid eucalypt woodland. Australian Journal of Ecology 20, 282–287.

André, H.M., Noti, M.-I., Jacobson, K.M., 1997. The soil microarthropods of the Namib Desert: a patchy mosaic. Journal of African Zoology 111, 499–517.

Barnard, P., 1998. Biological Diversity in Namibia—a Country Study. Ministry of Environment and Tourism, Windhoek.

Belnap, J., Gillette, D.A., 1998. Vulnerability of desert biological soil crusts to wind erosion: the influences of crust development, soil texture, and disturbance. Journal of Arid Environments 39, 133–142.

Beymer, R.J., Klopatek, J.M., 1991. Potential contribution of carbon by microphytic crusts in Pinyon–Juniper Woodlands. Arid Soil Research and Rehabilitation 5, 187–198.

Block, W., Convey, P., 1995. The biology, life cycle and ecophysiology of the Antarctic mite *Alaskozetes antarcticus*. Journal of Zoology 236, 431–499.

Brotherson, J.D., Rushforth, S.R., Johansen, J.R., 1983. Effects of long-term grazing on cryptogam crust cover in Navajo National Monument, Arizona. Journal of Range Management 36, 579–581.

Burnham, K.P., Overton, W.S., 1979. Robust estimation of population size when capture probabilities vary among animals. Ecology 60, 927–936.

Crawford, C.S., 1981. The Biology of Desert Invertebrates. Springer, New York.

Crawford, C.S., 1988. Surface-active arthropods in a desert landscape: influences of micro-climate, vegetation, and soil texture on assemblage structure. Pedobiologia 32, 373–385.

Duelli, P., Obrist, M.K., Schmatz, D.R., 1999. Biodiversity evaluation in agricultural landscapes: above-ground insects. Agriculture Ecosystems & Environment 74, 33–64.

Eldridge, D.J., Koen, T.B., 1998. Cover and floristics of microphytic soil crusts in relation to indices of landscape health. Plant Ecology 137, 101–114.

Eldridge, D.J., Leys, J.F., 2003. Exploring some relationships between biological soil crust, soil aggregation and wind erosion. Journal of Arid Environments 53, 457–466.

Evans, R.D., Belnap, J., 1999. Long-term consequences of disturbance on nitrogen dynamics in an arid ecosystem. Ecology 80, 150–160.

Evans, R.D., Johansen, J.R., 1999. Microbiotic crusts and ecosystem processes. Critical Reviews in Plant Sciences 18 (2), 183–225.

Gardner, S.M., Cabido, M.R., Valladares, G.R., Diaz, S., 1995. The influence of habitat structure on arthopod diversity in Argentine semi-arid Chaco forest. Journal of Vegetation Science 6, 349–356.

Gerson, U., 1973. Lichen-arthropod associations. Lichenologist 5, 434–443.

Goudie, A., 2002. Great Warm Deserts of the World: Landscapes and Evolution. Oxford University Press, New York, pp. 152–182.

Hachfeld, B., 2000. Rain, fog and species richness in the Central Namib Desert in the exceptional rainy season of 1999/2000. Dinteria 26, 113–146.

Hansen, R.A., 2000. Effects of habitat complexity and composition on a diverse litter microarthopod assemblage. Ecology 81, 1120–1132.

Hellmann, J.J., Fowler, G.W., 1999. Bias, precision, and accuracy of four measures of species richness. Ecological Applications 9, 824–834.

Hodkinson, I.D., Wookey, P.A., 1999. Functional ecology of soil organisms in tundra ecosystems: towards the future. Applied Soil Ecology 11, 111–126.

Kent, M., Coker, P., 1992. Vegetation Description and Analysis—A Practical Approach. Belhaven Press, London.

Kinnear, P.R., Gray, C.D., 2000. SPSS for Windows Made Simple. Psychology Press, East Sussex.

Koch, C., 1962. The Tenebrionidae of Southern Africa. Annals of the Transvaal Museum 24, 61–106.

Lalley, J.S., Viles, H.A., 2005. Terricolous lichens in the northern Namib Desert of Namibia: distribution and community composition. Lichenologist 37, 77–91.

Lalley, J.S., Viles, H.A., in press. Recovery of lichen-dominated soil crusts in a hyper-arid desert. Biodiversity and Conservation.

Lancaster, J., Lancaster, N., Seely, M.K., 1984. Climate of the central Namib Desert. Madoqua 14, 5–61.

Noy-Meir, I., 1974. Desert ecosystems: higher trophic levels. Annual Review of Ecology and Systematics 5, 195–214.

Olivier, J., 1992. Some spatial and temporal aspects of fog in the Namib. South African Geographer 19, 106–126.

Olivier, I., Beattie, A.J., 1996. Designing a cost-effective invertebrate survey: a test of methods for rapid assessment of biodiversity. Ecological Applications 6, 594–607.

Robinson, J.V., 1981. The effects of architectural variation in habitat on a spider community: an experimental field study. Ecology 62, 73–80.

Rogers, R.W., Lange, R.T., 1966. Nitrogen fixation by lichens of arid soil crusts. Nature 209, 96–97.

Sanchez, B.C., Parmenter, R.R., 2002. Patterns of shrub-dwelling arthropod diversity across a desert shrubland-grassland ecotone: a test of island biogeographic theory. Journal of Arid Environments 50, 247–265.

Schieferstein, B., Loris, K., 1992. Ecological investigations on lichen fields of the Central Namib. Vegetatio 98, 113–128.

Schulten, J.A., 1985. Soil aggregation by cryptogams of a Sand Prairie. American Journal of Botany 72, 1657–1661.

Seely, M.K., 1992. The Namib. Shell Namibia Ltd., Namibia.

Seely, M.K., 1978. The Namib Dune Desert: an unusual ecosystem. Journal of Arid Environments 1, 117–128.

Seely, M.K., Mitchell, D., 1987. Is the subsurface environment a thermal haven for chthonic beetles? South African Journal of Zoology 2, 57–61.

Shepherd, U.L., Brantley, S.L., Tarleton, C.A., 2002. Species richness and abundance patterns of microarthropods on cryptobiotic crusts in a pinon-juniper habitat: a call for greater knowledge. Journal of Arid Environments 52, 349–360.

Simmons, R.E., Griffin, M., Griffin, R.E., Marais, E., Kolberg, H., 1998. Endemism in Namibia: patterns, processes and predictions. Biodiversity and Conservation 7, 513–530.

Southgate, R.I., Masters, P., Seely, M.K., 1996. Precipitation and biomass changes in the Namib Desert dune ecosystem. Journal of Arid Environments 33, 267–280.

St. Clair, L.L., Johansen, J.R., Rushforth, S.R., 1993. Lichens of soil crust communities in the Intermountain Area of the western United States. Great Basin Naturalist 53, 5–12.

Storeheier, P.V., Mathiesen, S.D., Tyler, N.J.C., Olsen, M.A., 2002. Nutritive value of terricolous lichens for reindeer in winter. Lichenologist 34, 247–257.

ter Braak, C.F.J., 1988. CANOCO—an extension of DECORANA to analyze species–environment relationships. Vegetatio 75, 159–160.

Tigar, B.J., Osborne, P.E., 1997. Patterns of arthropod abundance and diversity in an Arabian desert. Ecography 20, 550–558.

van Zinderen Bakker, E.M., 1975. The origin and palaeoenvironment of the Namib Desert biome. Journal of Biogeography 2, 65–73.

Weeks, R.D., McIntyre, N.E., 1997. A comparison of live versus kill pitfall trapping techniques using various killing agents. Entomologia Experimentalis et Applicata 82, 267–273.

Wessels, D.C.J., 1986. Lichens in the central Namib Desert, SWA/Namibia. Report to Department of Nature Conservation, Windhoek.

Wessels, D.C.J., van Vuuren, D.R.J., 1986. Remote sensing—its possible use in mapping the distribution of major lichen communities in the Namib Desert, South West Africa. Madoqua 14, 369–374.

Wessels, D.C.J., Wessels, L.A., Holzapfel, W.H., 1979. Preliminary report on lichen-feeding *Coleoptera* occurring on *Teloschistes capensis* in the Namib Desert, South West Africa. Bryologist 82, 270–273.

Wharton, R.A., 1980. Insects and arachnids associated with *Zygophyllum simplex* (Zygophyllaceae) in the central Namib Desert. Madoqua 12, 131–139.

Whitehouse, M.E.A., Shochat, E., Shachak, M., Lubin, Y., 2002. The influence of scale and patchiness on spider diversity in a semi-arid environment. Ecography 25, 395–404.

Whitford, W.G., 2002. Ecology of Desert Systems. Academic Press, London.

Whitford, W.G., Ludwig, J.A., Noble, J.C., 1992. The importance of subterranean termites in semi-arid ecosystems of south-eastern Australia. Journal of Arid Environments 22, 82–91.

Woinarski, J.C.A., Andersen, A.N., Churchill, T.B., Ash, A.J., 2002. Response of ant and terrestrial spider assemblages to pastoral and military land use, and to landscape position, in a tropical savanna woodland in northern Australia. Australian Ecology 27, 324–333.

Zaady, E., Groffman, P., Shachak, M., 1998. Nitrogen fixation in macro- and microphytic patches in the Negev Desert. Issue Series Title: Soil Biology & Biochemistry 30, 449–454.