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Diversity of microfungal communities inside saxicolous lichens from Nahal Oren, Mount Carmel, Israel

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In this study, we examined the endolichenic fungal communities of saxicolous lichens covering the rocks in the Nahal Oren valley, northern Israel. A total of 60 fungal species belonging to 35 genera were isolated from six lichen species collected in the summer and winter on the south-facing slope (SFS) and north-facing slope (NFS) of the valley. We verified that rocks serve as a possible source for the formation of endolichenic communities because communities colonising lichen thalli and the rock surface shared 39% of species and clustered together on the SFS. On the NFS, with a comparatively favourable microclimate, lichen thalli abundantly harboured typical soil fungi such as *Clonostachys rosea* and *Fusarium* spp. in winter and summer, respectively. At the same time, more severe environmental conditions on the SFS facilitated the prevalence of melanised fungi with thick-walled and multicellular spores irrespective of season. The lowest species richness and isolate densities of endolichenic communities were registered in the thalli of *Collema cristatum*. This decrease, especially expressed in the summer, was probably associated with the antifungal effect of substances produced by its cyanobiont, as well as with the heavy dehydration of thalli during the dry season.

Key words: endolichenic fungi, lichen thallus, melanised fungi, microclimatic contrast, rock surface.

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Studie zkoumá společenstva endolichenických hub ze stélek saxikolních lišejníků, rostoucích na skalách v údolí Nahal Oren v severním Izraeli. Celkem 60 druhů z 35 rodů hub bylo izolováno ze šesti druhů lišejníků, odebraných v létě a v zimě na jižně a severně orientovaném svahu. Ukazuje se, že povrch skal je možným zdrojem hub pro endolichenická společenstva, neboť bylo zjištěno, že společenstva z lišejníků a z okolních skal sdílejí 39 % druhů a na jižním svahu se sdružila ve shlukové analýze. Na severním svahu s příhodnějším mikroklimatem stélky lišejníků často hostí typické půdní houby, v zimě *Clonostachys rosea*, v létě jsou hojné druhy rodu *Fusarium*. Naproti tomu, podíváme-li se současně na jižní svah, vlivem nehostinnějších podmínek tu bez ohledu na roční období převládají melanizované houby s tlustostěnnými vícebuněčnými sporami. Nejnižší druhová bohatost i množství izolátů endolichenických hub byly zaznamenány ve stélkách *Collema cristatum*; pokles zřejmý

zejména v letním období je pravděpodobně spojen s antifungálním účinkem látek, které produkuje cyanobiont tohoto lišejníku, jakož i se značnou dehydratací stélek v suché části sezóny.

INTRODUCTION

Lichen thalli as a substrate harbouring specific endolichenic fungal communities, has attracted the attention of mycologists during the past decades. Studies dealing with endolichenic fungi have been performed in different geographical regions and ecosystems. These studies included various lichen species and forms on a variety of substrates, and implied both culture-based and culture-independent molecular methodologies (e.g. Li et al. 2007, Peršoh et Rambold 2012, Zhang et al. 2015, Suryanarayanan et Thirunavukkarasu 2017, Suryanarayanan et al. 2017, Chakarwarti et al. 2020, Oh et al. 2020, Muggia et al. 2021, Santiago et al. 2021). Nevertheless, lichen thalli are still considered mycologically poorly explored habitats where novel fungal taxa can be found (Tripathi et Joshi 2019, Muggia et al. 2021). Furthermore, endolichenic fungi are known to be sources of bioactive secondary metabolites which makes them promising objects for study in pharmacology and biotechnology (e.g. Gao et al. 2016, Kellog et Raja 2017, Singh et al. 2017, Tripathi et Joshi 2019, Santiago et al. 2021, Wethalawe et al. 2021).

In Israel, endolichenic fungi in the thalli of saxicolous lichens have been studied in two different ecosystems: in Upper Galilee in the northern part of the country (Grishkan et Temina 2019), and in the Central Negev Desert (Grishkan et Temina 2023). During these studies, 39 and 101 endolichenic fungal species were isolated, respectively. The endolichenic communities were characterised by a complex of protective features important for inhabiting the lichen thalli with limited nutrient and water supply, restricted aeration, and potential activity of various extracellular secondary metabolites produced by host lichen species.

Our present study was conducted at Nahal Oren – a wadi (i.e. an Arabic term traditionally referring to a valley) located in the northern part of Israel. The wadi was chosen as a natural research site as part of the Evolution Canyon (EC) research programme testing the effect of environmental variability on biodiversity patterns (Nevo 1995). It consists of two opposite slopes – a north-facing (NFS) and a south-facing (SFS) one, which are characterised by sharply divergent microclimates (Pavlíček et al. 2003) regardless of the regional Mediterranean climate, display the same geology, and have similar soils, but divergent plant and animal communities (e.g. Nevo 1995, Nevo et al. 1998). The NFS, also called European slope, is temperate, cool, humid and forested, while the SFS, also called the African slope, is tropical, hot, dry, and savannah-like.

At Nahal Oren (Evolution Canyon I), the composition and spatio-temporal distribution of soil microfungal communities were examined using the culture-dependent methodology (Grishkan et al. 2000, Grishkan 2019a). The composition of mycobiota displayed remarkable relationship with edaphic and microclimatic conditions expressed in the dominance of drought-resistant melanised fungi and *Fusarium* spp. in the sun-exposed soil of the SFS and the prevalence of a complex of mesophilic *Penicillium* spp. in the under-canopy soil of the NFS.

The current research deals with the composition of endolichenic fungi inhabiting the thalli of saxicolous lichens covering the rocks at Nahal Oren. The study mainly focuses on the effect of various environmental factors (microclimatic gradient related to slope orientation, season, lichen species, its growth form, and type of photobiont) on the composition and richness of endolichenic fungal communities. Parallel to that, we studied the composition of fungal communities inhabiting the rock surface from which lichen specimens were collected, and the soil, in order to reveal possible sources of the formation of fungal assemblages colonising the lichen thalli.

MATERIAL AND METHODS

Site description. Nahal (wadi) Oren (32°43' N 34°58' E) is a deeply incised valley running from the Mount Carmel watershed westward into the Mediterranean Sea. The regional climate is Mediterranean, characterised by mild rainy winters and dry summers, with a mean annual rainfall of ca 600 mm and potential evapotranspiration of about 1700 mm. The average temperatures of the hottest (August) and coldest (January) months are 28 °C and 13 °C, respectively (Atlas of Israel 1985). The north- and south-facing slopes of the canyon have an identical geology and soil type (terra rossa soil on Upper Cenomanian limestone), but differ in topography (SFS dips 35°, NFS dips 25°; Nevo et al. 1998). The distance between the slopes is 100 m at the bottom, 400 m at the top, and 250 m in the middle. The SFS is covered by a xeric, Mediterranean, savannah-like, evergreen open park forest of *Ceratonia siliqua* and by African savannah grasses. By contrast, the NFS is covered by mesic east Mediterranean maquis (brushwood forest) of evergreen live oak, *Quercus calliprinos*, and the deciduous *Pistacia palaestina* (Nevo et al. 1999; Fig. 1a).

A climatic study at EC I (Pavlíček et al. 2003) revealed that solar radiation on the SFS was significantly (2.3–8 times) higher than on the NFS. Measurements of soil surface (0–1 cm) temperature and gravimetric moisture content conducted in July 2015 revealed a similar pattern (Grishkan 2019a), with temperatures higher on the SFS than on the NFS, and moisture lower on the SFS than on the NFS. The NFS soils are more alkaline than those of the SFS and have a significantly higher organic carbon content (see detailed soil analysis in Nevo et al. 1998).

Sampling design. Six lichen species were collected on limestone rocks in the summer (August) of 2020 and winter (February) of 2021. Rocks with lichen thalli (Fig. 1b, c) were chosen at the following three locations: two stations in the lower and middle part of the NFS and one station in the lower part of the SFS. Five different rocks with lichen thalli of each species were collected randomly at the stations in both seasons. Because the sampled lichen species were unevenly distributed on the slopes, only one species, *Caloplaca aurantia*, was collected at each station on both slopes. The other five species, *Cladonia pocillum*, *Collema cristatum*, *Solenopsora cesatii* var. *grisea*, *Squamarina*

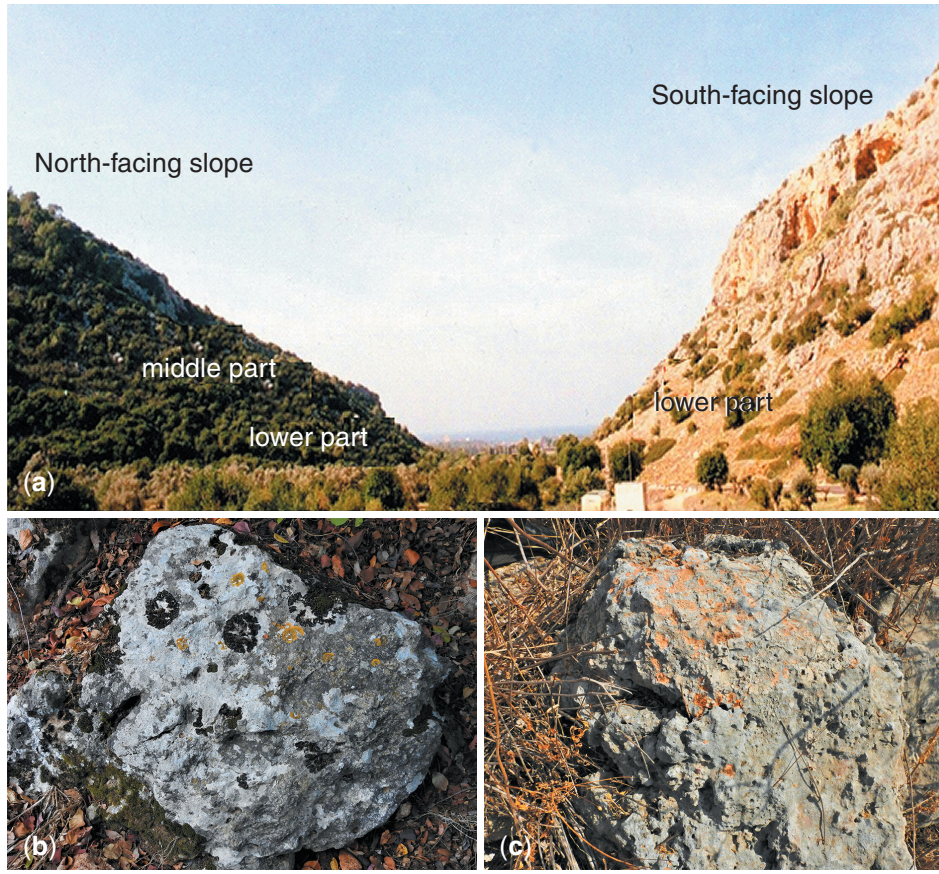

Fig. 1. General view of Nahal Oren, Mount Carmel (**a**); rocks on the ground covered by saxicolous lichens on north-facing slope (**b**) and south-facing slope (**c**).

cartilaginea var. *cartilaginea* and *Verrucaria viridula*, were only collected in the lower and middle parts of the NFS. Lichen specimens were sampled together with the substrate by cutting off rock pieces covered with lichen thalli. The samples were put into plastic bags, stored in a dry, cool place, and processed within 3–5 days after collection.

Soil samples were collected from the uppermost horizons at the same stations in the summer. The samples were collected at sunny, open localities, three samples from each locality. Samples were collected from a depth of 1–2 cm into sterile paper bags and stored in a dry, cool place before processing (1–5 days).

Measurement of rock surface temperature. The surface temperature of ten randomly selected rocks at each station was measured in an interval of 9.30 a.m. to 2.30 p.m. with a Micron Infrared Thermometer, Model M102HTL (Mikron Instrument, Oakland, NJ, USA) during the sampling of lichen thalli.

Preparation of lichen thalli. Lichen specimens were cleaned in tap water to remove soil particles and debris from their surfaces and then thoroughly washed under running tap water. The lichen thalli were surface sterilised by consecutive immersion for 1 minute in 75% ethanol, 3 minutes in 2% sodium hypochlorite and 30 seconds in 75% ethanol. The lichen thalli were then dried by placing them on sterile filter paper, exposed to ultraviolet (UV-C) light for 30 minutes for additional surface sterilisation, and cut into five fragments of approximately 1 mm^2 in size using a sterile razor blade (Grishkan et Temina 2019, 2023). From each rock containing lichen thalli, powder samples were obtained by scraping the surface with a small sterile knife.

Isolation and identification of fungal strains. The fragments of lichen thalli and rock powder were spread evenly over the surface of Malt Extract Agar (MEA; Pronadisa, Laboratorios Conda, Madrid, Spain) in Petri dishes of 90 mm diameter. Streptomycin (Spectrum Chemical, Gardens, USA) was added to the medium (100 µg/ml) to suppress bacterial growth. The plates were incubated at 25 °C in the dark for 10–30 days. Altogether, five Petri dishes with fragments of a lichen species from five rocks per station were incubated, in parallel with 10 Petri dishes containing the powder of 10 different rock fragments from a station, which were the sources of lichen thalli. For isolation of soil fungi, the soil dilution plate method (Davet et Rouxel 2000) was employed. One ml of soil suspension (1 g soil / 1000 ml sterile water) was mixed with MEA at 40 °C in Petri dishes. Streptomycin (Spectrum Chemical, Gardens, USA) was added to the medium (100 µg/ml) to suppress bacterial growth. The plates were incubated at 25 °C in the dark for 10–14 days.

After incubation, the emerging fungal colonies were transferred to MEA for purification and further taxonomic identification. To induce sporulation, all non-sporulating isolates were also grown on Oatmeal Agar (Sigma-Aldrich, St. Louis, USA) as recommended by Bills et al. (2004), and on Water Agar (agar – 20 g, water – 1000 ml). Taxonomic identification was based on morphological characteristics of fungal isolates. The following basic identification keys were used: Ellis (1971, 1976), Samson (1974), Pitt (1979), Sutton (1980), Arx et al. (1986), Kiffer et Morelet (2000), Klich (2002), Samson et Frisvad (2004), Domsch et al. (2007), Samson et al. (2007, 2010), and Xia et al. (2019). Since species identification based on morphological characteristics may be ambiguous, we presented some species names in Tab. 2 and the Electronic supplement as a 'species complex' or as 'cf.' as is accepted in taxonomy (Lucas 1986). All names of the identified species are cited according to the Species Fungorum database (www.speciesfungorum.org).

Data analysis. For each fungal species from the rock surface and the lichen thalli, relative abundance was calculated as number of isolates of a particular species in a sample divided by total number of all isolates in the sample. To analyse spatial and seasonal variations in community composition, five major groups were selected: *Penicillium* spp., consisting mainly of mesic fungi; *Aspergillus* spp., comprising thermotolerant and thermophilic fungi; mycoparasitic species (*Clonostachys* spp. and *Trichoderma* spp.); *Fusarium* spp., containing drought-resistant fungi; and melanised species covering fungi with resistance to different kinds of abiotic and biotic stresses. In the last group, melanised species with large multicellular spores were examined separately. The contribution of each group to the communities was estimated as its density – number of isolates of a particular group in a sample divided by the total number of all isolates in the sample, i.e. its relative abundance in total number of isolates in the sample. For fungal communities of each lichen species, species richness and isolate density expressed in number of colony forming units (CFU) were calculated per lichen specimen.

Statistical analysis was conducted with XLSTAT (http://www.xlstat.com). Hierarchical clustering was employed to evaluate similarity of microfungal communities isolated from the thalli of various lichen species at different localities and seasons as well as similarity of endolichenic and rock-surface fungal communities from these localities and seasons. The clustering based on relative abundance of fungal species was made by the unweighted pair-group average method with Chi-square distance as distance coefficient. We performed the non-parametric Wilcoxon signed-rank test to compare paired spatial and seasonal data of species richness and isolate density of endolichenic communities from

the same lichen species. A three-way unbalanced ANOVA with interactions was used to test the effect of slope orientation (or position of locality on the slope), season, and lichen species, separately and in interaction, on species richness and isolate density of the endolichenic communities.

RESULTS

Temperature of rock surface

Average rock surface temperatures are shown in Tab. 1. The temperatures displayed inter-slope and seasonal differences being expectedly higher on the SFS than on the NFS and in the summer than in the winter. The small differences between rock surface temperatures on the SFS and the NFS were probably caused by the fact that the SFS measurements were performed in the morning, while the NFS measurements were carried out at midday.

Tab. 1. Temperature of rock surface (°C) at sampling stations of Nahal Oren, Mount Carmel (average ± SD, n = 50). SFS = south-facing slope, NFS = north-facing slope.

Stations	Summer	Winter
SFS, lower part	35.1 ± 2.3	29.3 ± 2.2
NFS, lower part	30.3 ± 1.6	17.4 ± 2.1
NFS, middle part	34.1 ± 2.7	23.4 ± 4.3

The values were measured during the following hours: SFS, lower part 9:30–10:30 am; NFS, middle part 11–12:30 am; NFS, lower part 1–2:30 pm.

Composition of endolichenic and rock-surface fungal communities

A total of 60 identified fungal species were isolated from lichen thalli. These endolichenic fungi included *Mortierellomycota* (1 species), *Mucoromycota* (4) and *Ascomycota* (55). The species represented 35 genera; the most abundant were *Penicillium* (9 species), *Alternaria* (6), *Aspergillus* (5) and *Fusarium* (4). Six types of strains not sporulating in culture were not identified.

A total of 41 microfungal species were isolated from the rock surface, 30 of which were also endolichenic. These rock-inhabiting fungi included *Mortierellomycota* (1 species), *Mucoromycota* (2), *Ascomycota* (37) and *Basidiomycota* (1). The species represented 26 genera, the most numerous of which were *Penicillium* and *Aspergillus* (6 species), *Alternaria* (4) and *Fusarium* (3). Five types of strains not sporulating in culture were not identified.

The composition of endolichenic and rock-inhabiting microfungal communities remarkably varied between both localities and seasons. On the SFS, melanised fungi prevailed in the lichen thalli (*Caloplaca aurantia* 78.6–91.2%) as well as on the rock surface (76.5–88.7%), both in the summer and winter (Fig. 2).

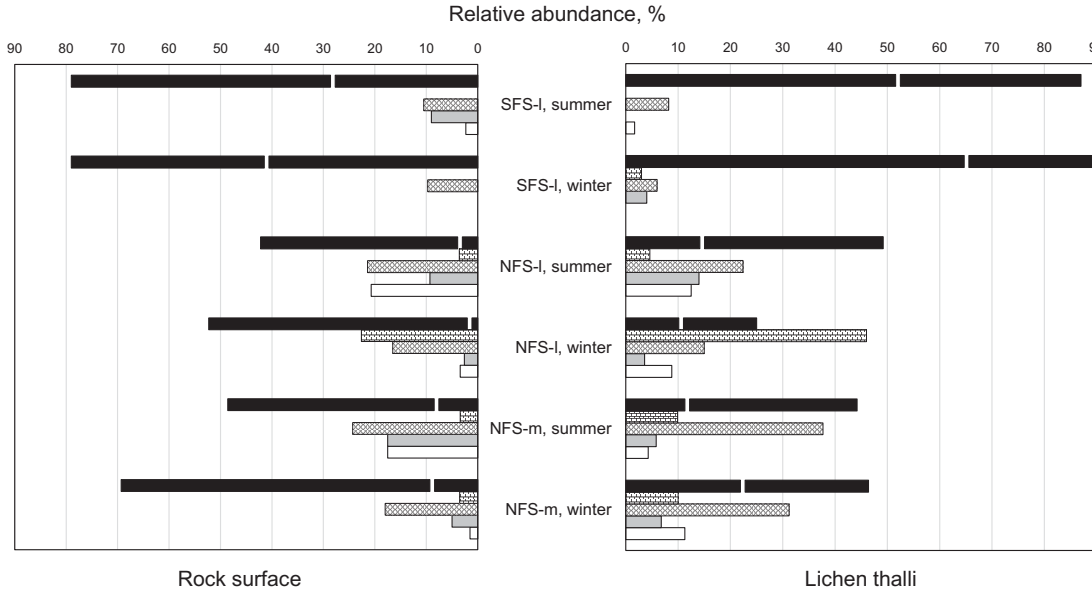

Fig. 2. Relative abundance of melanised species (■), *Penicillium* spp. (□), *Aspergillus* spp. (▒), *Fusarium* spp. (▨), and mycoparasitic spp. (▩) in lichen thalli and on rock surface at Nahal Oren, Mount Carmel. The horizontal bars represent the average values from Tab. 2. The area left (lichen thalli) and right (rock surface) of the line on bars of melanised species indicates the abundance of species with large multicellular spores.

The core of endolichenic and rock-inhabiting communities on the SFS was formed by melanised species producing large multicellular, thick-walled spores, mainly *Alternaria alternata*, *A. atra* and *Stemphylium botryosum*, followed by *Cladosporium cladosporioides* (Electronic supplement, Tab. 2). At the same time, in the summer soil of this locality, aspergilli (*A. niger* and *A. nidulans*) and penicillia (*P. simplicissimum*) prevailed (Tab. 2). Expectedly, the variations in endolichenic communities on the NFS were more clearly expressed because these communities inhabited six lichen species, which were collected in the lower and middle parts of the slope. Melanised fungi (mainly *A. alternata*, *A. phragmospora*, *C. cladosporioides* and *Aspergillus niger*) were comparatively abundant in the summer (42.5–50.4%) but less numerous in the winter (19.5–48.2%). Notably, in the lower part of the NFS in winter, the fast-growing mycoparasitic *Clonostachys rosea* was abundant or dominant in the thalli of all studied lichen species (23.3–59.3%) (Electronic supplement). *Fusarium* spp. were numerous in lichen thalli in the summer (23.4–47.9%, mainly *F. incarnatum-equiseti* complex) as well as in the winter (15,2–31.8%, mainly *F. tricinctum*). Aspergilli and penicillia were rather minor components of the NFS endolichenic communities with maximum values of 14% (lower part, in summer) and 16.2%

Tab. 2. Microfungi from thalli of saxicolous lichens, rock surface, and nearby soil at Nahal Oren, Mount Carmel, with their relative abundance (%). Melanised species are in bold; melanised species with large multicellular spores are underlined. SFS = south-facing slope, NFS = north-facing slope; l = lower part, m = middle part.

Species	Summer									Winter					
	Lichen thalli			Rock surface			Soil			Lichen thalli			Rock surface		
	SFS-l	NFS-l	NFS-m	SFS-l	NFS-l	NFS-m	SFS-l	NFS-l	NFS-m	SFS-l	NFS-l	NFS-m	SFS-l	NFS-l	NFS-m
Mortierellomycota															
Podila humilis (Linnem. ex W. Gams) Vandepol et Bonito	–	1.6	0.4	2.3	0.7	–	–	–	2.6	–	–	0.3	–	–	–
Mucoromycota															
Mucor hiemalis Wehmer	–	1.2	0.6	–	0.7	–	–	–	0.4	–	–	–	–	–	–
Mucor plumbeus Bonord.	–	3.1	–	–	–	–	–	0.4	–	–	0.3	–	–	–	–
Mucor racemosus Fresen.	–	–	–	–	–	–	–	–	–	–	3.6	–	–	–	–
Rhizopus arrhizus A. Fisch.	–	2.2	1.3	–	2.1	1.7	0.3	–	0.8	1.0	1.2	0.3	–	2.2	–
Ascomycota															
Acremonium charticola (Lindau) W. Gams	–	–	–	–	–	–	–	–	–	–	–	–	0.8	–	–
Acremonium murorum (Corda) W. Gams	–	–	–	–	–	–	–	–	–	2.0	–	–	–	–	–
Acrostalagmus luteoalbus (Link) Zare, W. Gams et Schroers	–	0.7	–	–	–	–	–	–	1.5	–	–	–	–	–	–
Alternaria alternata species complex	25.0	4.1	3.9	13.5	2.1	3.4	0.7	–	–	48.2	5.3	8.9	34.7	2.2	3.5
Alternaria atra (Preuss) Woudenb. et Crous	8.3	5.6	4.7	3.0	0.7	3.4	–	2.4	–	7.0	3.0	2.8	0.8	–	–
Alternaria chlamydospora (Preuss) Woudenb. et Crous	–	–	–	–	–	–	–	–	–	1.1	–	0.2	–	–	–
Alternaria chlamydosporigena Woudenb. et Crous	5.0	–	–	–	–	–	–	–	–	–	3.3	2.5	0.8	–	–
Alternaria phragmospora Emden	–	4.2	4.0	–	–	–	–	–	–	–	0.3	6.3	–	–	5.5
Alternaria raphani J.W. Groves et Skolko	–	–	–	–	–	–	–	–	–	–	–	1.7	–	–	–
Amerosporium concinnum Petr.	–	–	–	–	–	–	–	1.6	–	–	–	–	–	–	–
Aphanocladium album (Preuss) W. Gams	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.5
Apiotrichum sporotrichoides (Oorschot) Yurkov et Boekhout	1.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Arxotrichum succineum (L.M. Ames) A. Nováková et M. Kolařík	–	–	–	–	–	–	–	–	–	–	–	–	0.8	–	–

Species	Summer									Winter					
	Lichen thalli			Rock surface			Soil			Lichen thalli			Rock surface		
	SFS-l	NFS-l	NFS-m	SFS-l	NFS-l	NFS-m	SFS-l	NFS-l	NFS-m	SFS-l	NFS-l	NFS-m	SFS-l	NFS-l	NFS-m
Ascochyta medicaginicola Qian Chen et L. Cai	–	–	–	–	–	–	–	–	–	–	–	0.3	–	–	–
Aspergillus alliaceus Thom et Church	–	–	–	–	–	0.6	–	–	–	–	–	–	–	–	1.5
Aspergillus flavipes (Bainier et R. Sartory) Thom et Church	–	–	–	–	–	–	–	0.4	–	–	–	–	–	–	–
Aspergillus cf. *fumigatus* Fresen.	–	–	0.9	–	–	–	–	–	–	1.1	–	–	–	–	2.5
Aspergillus nidulans (Eidam) G. Winter	–	4.2	1.8	–	5.7	6.2	6.7	3.2	26.2	–	0.3	–	–	–	0.5
Aspergillus* cf. *niger Tiegh.	–	8.9	3.0	0.8	3.6	2.8	21.6	4.3	1.9	3.0	3.0	5.9	–	0.9	0.5
Aspergillus ochraceus G. Wilh.	–	0.9	–	–	–	–	–	–	–	–	–	–	–	–	–
Aspergillus terreus Thom	–	–	–	–	–	–	–	–	1.9	–	–	–	–	0.4	–
Aspergillus ustus (Bainier) Thom et Church	–	–	–	8.3	–	7.9	6.3	0.4	–	–	0.3	0.9	–	1.3	–
Aspergillus sp.	–	–	–	–	–	–	–	–	0.8	–	–	–	–	–	–
Aureobasidium pullulans (de Bary et Löwenthal) G. Arnaud	–	–	0.7	6.8	–	–	–	–	–	–	–	–	–	–	–
Bartalinia robillardoides Tassi	–	–	–	–	–	–	–	0.8	–	–	–	–	–	–	–
Boeremia exigua species complex	–	0.3	1.1	–	–	–	–	0.8	0.4	–	–	0.7	2.4	–	–
Botryotrichum murorum (Corda) X. Wei Wang et Samson	–	–	–	–	–	–	1.3	–	–	–	–	–	–	–	–
Chaetomium globosum Kunze	1.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chaetomium strumarium (J.N. Rai, J.P. Tewari et Mukerji) P.F. Cannon	1.7	0.6	–	–	–	–	–	–	–	–	–	–	–	–	–
***Chaetomium* sp. 1**	–	–	–	–	–	–	–	4.7	–	–	–	–	–	–	–
***Chaetomium* sp. 2**	–	–	2.5	–	–	–	4.0	1.6	–	–	–	–	–	–	–
Cladosporium cladosporioides species complex	16.7	9.7	13.9	33.7	33.0	27.1	7.0	21.3	17.9	15.1	5.6	12.0	33.3	38.8	56.8
Clonostachys rosea (Preuss) Mussat	–	0.9	0.7	–	2.9	2.3	0.7	4.7	–	–	37.7	2.5	–	19.6	2.1
Collariella bostrychodes (Zopf) X. Wei Wang et Samson	1.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Coleophoma empetri (Rostr.) Petr.	–	–	–	–	–	–	–	0.4	–	–	–	–	–	–	–
Curvularia clavata B.L. Jain	–	0.6	–	–	–	–	–	–	–	–	–	–	–	–	–

Species	Summer									Winter					
	Lichen thalli			Rock surface			Soil			Lichen thalli			Rock surface		
	SFS-l	NFS-l	NFS-m	SFS-l	NFS-l	NFS-m	SFS-l	NFS-l	NFS-m	SFS-l	NFS-l	NFS-m	SFS-l	NFS-l	NFS-m
Curvularia spicifera (Bainier) Boedijn	–	1.1	–	–	–	–	–	–	–	–	0.3	–	–	–	–
Cylindrocarpon didymium (Harting) Wollenw.	–	–	–	–	–	–	–	–	–	–	–	–	–	2.9	2.5
Fusarium incarnatum-equiseti species complex	8.2	20.5	31.3	10.5	21.4	22.0	4.0	8.7	4.9	3.1	5.1	–	8.1	1.3	5.0
Fusarium oxysporum species complex	–	0.5	0.6	–	–	2.3	2.1	3.2	–	–	0.8	9.9	–	–	–
Fusarium tricinctum (Corda) Sacc.	–	1.4	2.3	–	–	–	–	0.8	0.8	–	8.8	19.0	1.6	15.2	12.9
Fusarium sp.	–	0.8	3.5	–	–	–	–	–	–	3.0	0.3	2.2	–	–	–
Gymnoascus reessii Baran.	1.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lecanicillium psalliotae (Treschew) Zare et W. Gams	–	–	–	2.3	–	–	0.7	–	–	–	–	–	2.4	1.3	–
Marquandomyces marquandi (Massee) Samson, Houbraken et Luangsa-ard	1.7	–	–	3.8	–	–	–	–	–	–	–	–	–	–	–
Massarina igniaria (C. Booth) Aptroot	–	–	0.3	–	–	–	–	–	–	–	0.3	–	0.8	–	–
Metarhizium anisopliae (Metschn.) Sorokin	–	–	–	–	–	–	–	3.2	–	–	–	–	–	–	–
Microascus cirrosus Curzi	–	–	0.4	–	–	–	–	–	–	–	–	–	–	–	–
Microsphaeropsis olivacea (Bonord.) Höhn.	–	–	–	–	–	–	–	0.8	–	–	–	–	–	–	–
Monodyctis fluctuata (Tandon et Bilgrami) M.B. Ellis	–	–	–	–	–	–	–	–	–	–	–	0.8	–	–	–
Neocucurbitaria cava (Schulzer) Valenz.-Lopez, Crous, Stchigel, Guarro et Cano	–	–	0.4	–	–	–	–	–	–	–	–	–	–	–	–
Nigrospora oryzae (Berk. et Broome) Petch	–	0.8	–	–	–	–	–	–	–	–	–	–	–	–	–
Penicillium cf. *aurantiogriseum* Dierckx	–	0.8	–	–	–	1.1	–	–	1.1	–	0.3	–	–	–	–
Penicillium brevicompactum Dierckx	–	–	–	–	–	–	–	–	0.8	–	1.9	–	–	–	–
Penicillium citrinum Thom	–	–	–	–	–	–	–	–	1.1	–	–	–	–	–	–
Penicillium corylophilum Dierckx	–	1.5	–	2.3	–	–	–	–	–	–	–	–	–	–	–
Penicillium dierckxii Biourge	–	2.2	–	–	–	–	–	–	1.9	–	–	–	–	–	–
Penicillium glabrum (Wehmer) Westling	–	–	–	–	–	0.6	–	5.5	7.5	–	4.3	7.1	–	0.4	–
Penicillium restrictum J.C. Gilman et E.V. Abbott	1.7	2.0	3.4	–	–	1.7	–	–	4.9	–	–	–	–	–	–

Species	Summer									Winter					
	Lichen thalli			Rock surface			Soil			Lichen thalli			Rock surface		
	SFS-l	NFS-l	NFS-m	SFS-l	NFS-l	NFS-m	SFS-l	NFS-l	NFS-m	SFS-l	NFS-l	NFS-m	SFS-l	NFS-l	NFS-m
Penicillium scabrosum Frisvad, Samson et Stolk	–	–	–	–	–	–	–	–	–	–	–	1.3	–	–	–
Penicillium simplicissimum (Oudem.) Thom	–	6.0	0.9	–	19.9	14.1	34.7	15.8	17.6	–	3.0	2.2	–	3.0	1.5
Penicillium thomii Maire	–	–	–	–	0.7	–	–	0.8	0.8	–	0.3	0.7	–	–	–
Phoma herbarum Westend.	–	0.6	0.4	–	–	–	–	–	–	–	–	–	–	–	–
Phomatodes nebulosa (Pers.) Qian Chen et L. Cai	–	–	–	–	–	–	–	–	0.4	–	–	–	–	–	–
Scytalidium lignicola Pesante	8.2	0.2	0.6	–	–	–	0.7	6.3	–	–	–	–	–	–	–
Sordaria fimicola (Roberge ex Desm.) Ces. et De Not.	1.7	7.1	4.5	1.5	–	–	0.7	–	–	1.0	–	0.5	0.8	–	–
Stachybotrys chartarum (Ehrenb.) S. Hughes	–	0.6	–	–	–	–	–	–	–	–	–	–	0.5	2.6	–
Stemphylium botryosum Wallr.	15.0	1.1	–	10.5	–	1.7	1.1	–	–	9.0	–	1.6	4.1	–	–
Talaromyces funiculosus (Thom) Samson, N. Yilmaz, Frisvad et Seifert	–	–	–	–	–	–	–	–	1.5	–	–	–	–	–	–
Torula herbarum (Pers.) Link	–	–	1.1	0.8	–	–	6.0	–	–	–	–	–	–	–	–
Trichocladium griseum (Traaen) X. Wei Wang et Houbraken	–	–	1.1	–	0.7	–	–	4.3	–	–	2.3	1.4	–	4.3	1.5
Trichocladium seminis-citrulli (Sergeeva) X. Wei Wang et Houbraken	–	–	0.3	–	–	–	–	–	–	–	–	–	–	–	–
Trichoderma koningii species complex	–	3.6	9.2	–	0.7	1.1	1.3	3.6	1.5	3.0	8.2	7.3	–	3.0	1.5
Westerdykella capitulum (Panwar, P.N. Mathur et Thirum.) Gruyter, Aveskamp et Verkley	–	–	–	–	–	–	–	–	–	–	–	0.2	–	–	–
Zasmidium cellare (Pers.) Fr.	–	–	–	–	–	–	0.3	–	–	–	–	–	–	–	–
Zygosporium masonii S. Hughes	–	–	–	–	–	–	–	–	–	–	–	–	0.8	–	–
Basidiomycota															
Sporotrichum sp.	–	–	–	–	–	–	–	–	–	–	–	–	0.8	–	–

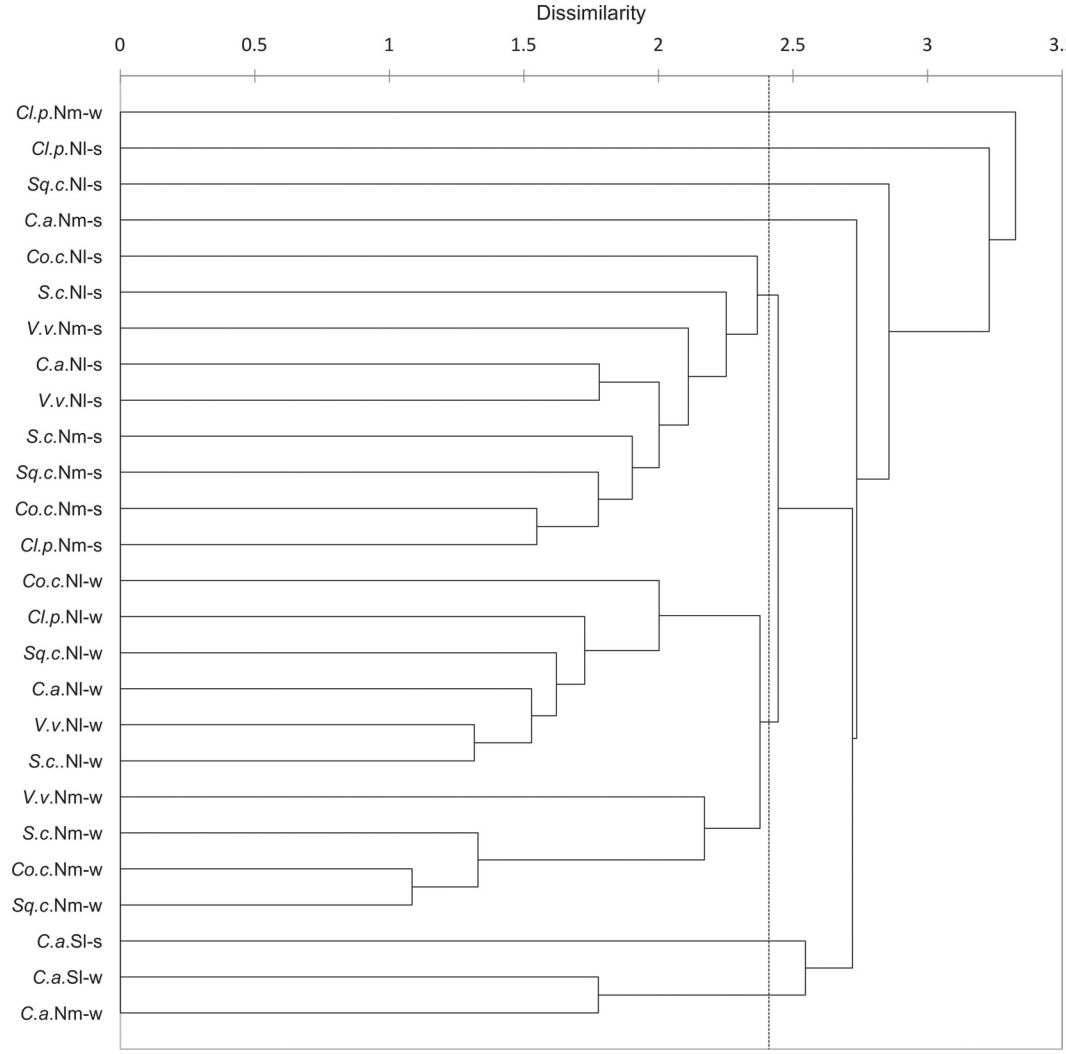

Fig. 3. Clustering of endolichenic microfungal communities from different lichen species (*C.a.* – *Caloplaca aurantia*; *Cl.p.* – *Cladonia pocillum*; *Co.c.* – *Collema cristatum*; *S.c.* – *Solenopsora cesatii*; *Sq.c.* – *Squamarina cartilaginea*; *V.v.* – *Verrucaria viridula*) collected on south-facing (S) and north-facing (N) slopes in their lower (l) and middle (m) parts in summer (s) and winter (w) at Nahal Oren, Mount Carmel, based on relative species abundance. The dotted line represents the automatic truncation, leading to three clusters and five separate classes.

(lower part, in winter), respectively (Fig. 2). On the rock surface, melanised species prevailed on the NFSin both seasons (43.5–76.4%) (Fig. 2), accompanied by *F. incarnatum-equiseti* complex in the summer, while in the summer soil, mostly *C. cladosporioides* and *P. simplicissimum* were abundant (Tab. 2).

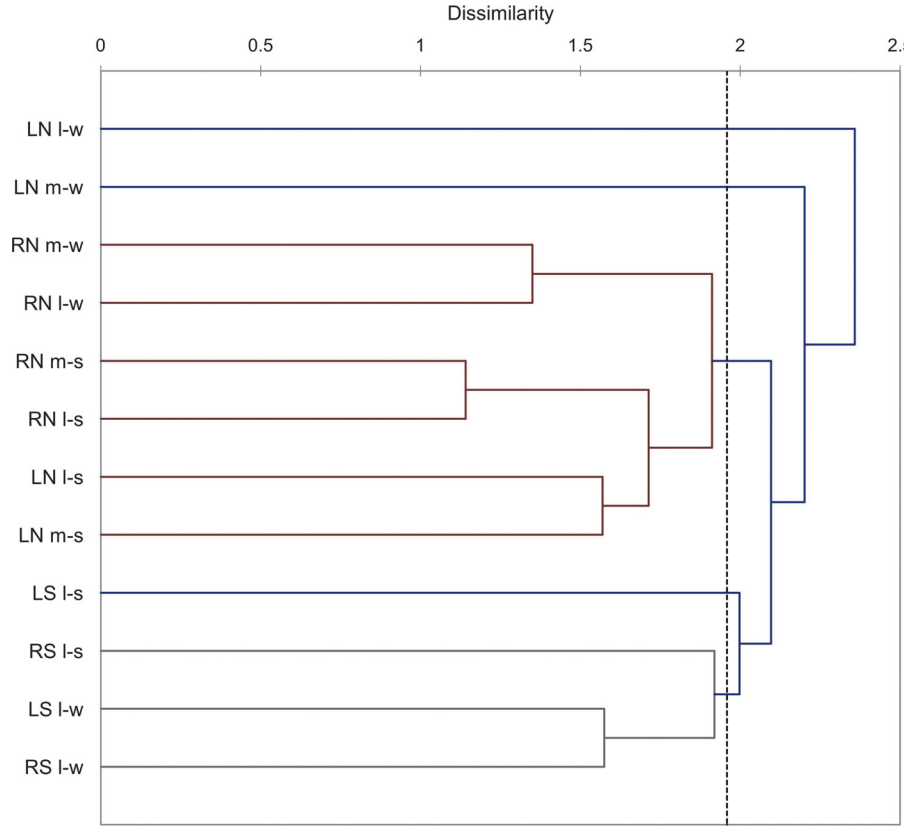

Fig. 4. Clustering of endolichenic microfungal communities from lichen thalli (L) and rocks (R) collected on south-facing (S) and north-facing (N) slopes in their lower (l) and middle (m) parts in summer (s) and winter (w) at Nahal Oren, Mount Carmel, based on relative species abundance. The dotted line represents the automatic truncation, leading to two clusters and three separate classes.

The clustering of microfungal communities from different lichen species has grouped the communities from the NFS primarily based on season (summer or winter) (Fig. 3). The winter communities were also separated according to their location on the slope (lower or middle part). Markedly, the communities from *Caloplaca aurantia* in the lower part of the SFS and the middle part of the NFS in both seasons clustered apart from other endolichenic communities. The clustering of endolichenic and rock-inhabiting communities (Fig. 4) grouped the SFS communities separately, with winter communities clustered together. On the NFS, communities inhabiting lichen thalli and the rock surface formed separate season-based groups. Overall, the endolichenic communities displayed a more heterogeneous assemblage than the rock surface communities did.

Species richness and density of microfungal isolates from lichen thalli

The number of microfungal species varied from 4.2 to 7.4 per lichen specimen followed by a variation in CFU numbers of 7.8 to 19.8 per specimen (Tab. 3). In spatial dynamics, the endolichenic communities from *Caloplaca aurantia* on the SFS and NFS did not differ significantly in species richness, while containing 1.1–1.7 times higher CFU numbers on the SFS in both seasons (Wilcoxon test, $p \leq 0.05$). With respect to seasonal variations, the summer endolichenic communities in *C. aurantia* on the SFS contained fewer species and CFUs than winter communities. On the NFS, no clear pattern could be observed in seasonal variations of species richness and isolate density. A distinct exception was found for the communities from *Collema cristatum* with a cyanobacterial photobiont, which contained the lowest number of fungal species and especially isolates in the summer. The three-way unbalanced ANOVA test did not show any significant impact of slope orientation (or position of locality), season or lichen species, either separately or in interaction, on species richness and isolate density of the endolichenic communities.

Tab. 3. Average species richness (SR/specimen) and isolate density (colony forming units, CFU/specimen) of endolichenic fungal communities from different saxicolous lichen species at Nahal Oren, Mount Carmel (n = 5). SFS = south-facing slope, NFS = north-facing slope; l = lower part, m = middle part.

Lichen species	Thallus growth form[1]	Photobiont[2]	Summer						Winter					
			SFS-l		NFS-l		NFS-m		SFS-l		NFS-l		NFS-m	
			SR	CFU	SR	CFU	SR	CFU	SR	CFU	SR	CFU	SR	CFU
Caloplaca aurantia	C	GA	5.4	12.0	5.8	10.8	5.2	8.6	6.2	19.8	5.2	12.2	6.0	14.8
Solenopsora cesatii var. *grisea*	C	GA	–	–	6.8	19.8	7.4	18.8	–	–	6.0	15.6	5.8	12.8
Squamarina cartilaginea var. *cartilaginea*	S	GA	–	–	6.6	13.6	4.2	13.2	–	–	5.2	13.4	4.6	12.4
Cladonia pocillum	S	GA	–	–	6.0	10.2	5.8	11.6	–	–	4.2	11.2	5.6	10.0
Verrucaria viridula	Cr	GA	–	–	5.4	17.2	5.0	11.2	–	–	5.8	12.8	4.8	15.0
Collema cristatum	F	CB	–	–	4.8	7.8	4.6	8.0	–	–	6.0	15.2	4.4	14.4

[1] C – crustose-placodioid, S – squamulose, Cr – cracked-areolated, F – foliose
[2] GA – green algae, CB – cyanobacteria
– = no lichen specimens collected

Discussion

Fungi residing inside lichen thalli should withstand a variety of severe environmental conditions: limited nutrient supply, low water availability, restricted aeration, rapid changes in temperature and hydration of the external environment. In addition, lichen-associated fungi should cope with the activity of various extracellular secondary metabolites excreted by the lichen mycobionts (Muggia et al. 2016). Apparently, such a combination of internal and external parameters leads to the dominance of microfungal groups, which possess appropriate adaptive traits. Melanised fungi, dominant or frequently occurring in the majority of studied endolichenic communities, possess such adaptive traits, as melanins contribute to fungal cell resistance against various kinds of stresses (e.g. Grishkan 2011 and references therein; Treseder et Lennon 2015).

On the SFS of Nahal Oren, high air temperatures and UV radiation are added to the above environmental conditions, especially in summer. Probably because of that, melanised fungi with large, multi-celled and thick-walled spores represented the core of endolichenic communities on this slope. Therefore, the communities inhabiting *Caloplaca aurantia* on the SFS were similar to those isolated from the lichens covering basaltic and chalk rocks in Upper Galilee and cobbles at Nahal Boker, central Negev Desert (Grishkan et Temina 2019, 2023). The multicellular spore morphology can also be considered an important feature of microfungal communities in their adaptation to severe environmental conditions, which has been shown on the example of desert soil mycobiota (e.g. Grishkan 2019b). Additionally, the prevailing species from the genus *Alternaria*, as well as the frequently occurring *Stemphylium botryosum* and *Cladosporium cladosporioides* are known to be endophytes (e.g. Xiong et al. 2013, Cosoveanu et Cabrera 2018) and phylloplane-inhabiting species (Ellis et Ellis 1997). The latter group can cope with substantial variations in temperature and water content of the external environment.

Contrary to the SFS endolichenic communities, melanised fungi were comparatively abundant in the NFS lichen thalli only in summer. In the winter, *Clonostachys rosea* dominated or co-dominated the NFS endolichenic communities in the lower part of the slope. This species is known for its fast growth over other fungi in culture (Domsch et al. 2007) and the ability to produce secondary metabolites with antibacterial and antifungal activity (Sun et al. 2020). *Clonostachys rosea* was abundantly isolated from the soil of the NFS (Grishkan 2019a) and from the soil of a nearby forest burned in a fire (Grishkan 2016). It is likely that the dominance of *C. rosea* decreased the species richness of the corresponding NFS endolichenic communities in the winter (Tab. 3).

The frequent and abundant occurrence of *Fusarium* spp. in the NFS endolichenic communities in the summer is also worth mentioning. Based on the

morphology of the dominant *Fusarium* species – aggregation of conidia in slimy structures and chlamydospore production – these species can be considered drought-resistant, which was experimentally demonstrated (Jorge-Silva et al. 1989). Fusaria were abundantly present in the soils of south-oriented sun-exposed localities of the canyons in the northern part of Israel (Grishkan et al. 2000, 2003).

Spatial and seasonal variations in species richness and isolate densities of the endolichenic communities at Nahal Oren were not significantly expressed, except for the communities from *Caloplaca aurantia* containing 1.1–1.7 times higher isolate densities on the SFS in both seasons. This pattern differed from that revealed in desert canyon Nahal Boker, where species richness and isolate densities of the endolichenic communities were higher on the NFS with a comparatively favourable microclimate. Moreover, communities from most lichen species contained the smallest number of species and CFUs in the climatically most severe summer period (Grishkan et Temina 2023).

Notably, the lowest number of endolichenic fungal species and especially the lowest isolate densities in the summer characterised the communities from *Collema cristatum* with a cyanobacterial photobiont. This is likely associated either with the production of secondary metabolites, which can inhibit the development of fungi in *Collema* thalli (Torres et al. 2004, Temina et al. 2010), or with the water regime inside the thalli. It is known that cyanolichens need liquid water (mainly rain) for their metabolic activity, whereas chlorolichens can use vapour from humid air in addition to rainwater (Lange et al. 1986, 1993). In the absence of rain in summer, the thalli of cyanolichens often remain dry for a long period, while the thalli of chlorolichens can rehydrate due to their ability to absorb moisture from the air. Thus, in the dry season, the dry black thalli of *Collema cristatum* would represent a more unfavourable substrate for the development of endolichenic fungi than the wetter thalli of chlorolichens.

The cluster analysis revealed a closer relationship between endolichenic and rock-surface microfungal communities on the SFS than on the NFS. This seems to be associated with the more severe environmental conditions on the SFS, which lead to the dominance of melanised fungi with multicellular spores both in the lichen thalli and on the rock surface. On the NFS, at the same time, while melanised fungi prevailed in the rock-inhabiting communities, lichen thalli served as shelter for certain common soil fungi such as *Clonostachys rosea* and *Fusarium* spp. Other common genera in the soil of Nahal Oren are *Penicillium* and *Aspergillus*, which constituted rare components of the studied endolichenic communities, just as in the communities isolated from lichens covering basaltic and chalk rocks in Upper Galilee (Grishkan et Temina 2019). *Penicillium* and *Aspergillus* species were considered to be unspecifically associated with lichens as ubiquitous contaminants, which can be isolated from lichen thalli after insuffi-

cient surface sterilisation (Suryanarayanan et al. 2005, Muggia et Grube 2018). Nevertheless, we cannot fully exclude the possibility of these fungi entering lichen thalli and surviving there in low quantities, as the presence of *Penicillium* and *Aspergillus* species was reported in several studies dealing with endolichenic and endophytic fungal communities (e.g. Peršoh et Rambold 2012, Cosoveanu et Cabrera 2018, Oh et al. 2020, Santiago et al. 2021).

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