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Research Article

The diversity and ecology of epiphytic lichens in "Evolution Canyon" II, Lower Nahal Keziv, Upper Western Galilee, Israel

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Abstract: Different populations of epiphytic lichens were studied in a microsite in Lower Nahal Keziv, Western Upper Galilee, Israel, which is designated as an "Evolution Canyon" (EC) II. In all, 24 lichen species from 5 orders, 11 families, and 17 genera were registered, about one third of them (7 species) for the first time in Israel. Species richness was higher on the warmer, drier, climatically more fluctuating and biotically more heterogeneous south-facing slope (SFS). Most lichens of EC II were mesophytic and photo-indifferent species; however, humid and shaded habitats of the north-facing slope (NFS) and valley bottom (VB) were characterised by a dominance of moderately photophytic species and a high frequency of hygrophytic species, while dry and sun-exposed habitats of the SFS were characterised by a dominance of very photophytic and xerophytic species. In all, 6 environmental variables were evaluated at the research site. Canonical correspondence analysis (CCA) was used to determine the influence of these ecological variables on lichen diversity and morpho-anatomic characteristics of the lichens in EC II.

Key words: Epiphytic lichens, species diversity, ecology, biogeography, reproductive strategy, canonical correspondence analysis

Introduction

The study of biodiversity in different ecosystems is of great importance to the conservation of all life forms (Wilson, 1992; Hawksworth, 1995; Prance, 1995) and demands an understanding of all organisms, their biology, evolution, and ecology, as well as the biogeography of particular groups and species. One of the most interesting and intriguing aspects of biodiversity investigation is the study of the effect of microscale environmental variability on biodiversity patterns. Microsite ecological contrasts are excellent critical tests for evaluating biodiversity evolution across all organizational levels, from genes to biota (Nevo, 2001). The Institute of Evolution, University of Haifa established microscale tests within the framework of the long-term biodiversity "Evolution Canyon" model research program (Nevo, 1995; 1997; 2001; 2006). Four "Evolution Canyons" (EC I-IV) in different climatic regions of Israel were chosen. Among the 4 chosen research sites, the most complete and successful investigations of the influence of variability of environment and stress on

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the biodiversity of different groups of organisms were made in "Evolution Canyon" I. The investigations showed that inter- and intraslope microclimatic differences were the major causes of inter- and intraslope biotic divergence (Nevo, 1997; Nevo et al., 1999; Pavlíček et al., 2003).

The subject of the present study was the epiphytic lichen vegetation in "Evolution Canyon" II (EC II), located in the Lower Nahal Keziv, Upper Western Galilee. We examined the lichen diversity of oak trees (*Quercus calliprinos* Webb) on opposite slopes and in the valley at the bottom of the canyon. The following characteristics of local lichen biotas were studied: species richness, systematic diversity, biogeographical elements, frequency and distribution of lichen species, morphological and anatomical characteristics, reproductive strategy, and ecological peculiarities. The influence of 6 ecological variables on lichen diversity, distribution of biogeographic groups, and lichen morpho-anatomic characteristics were also analysed.

Materials and Methods

Site Description

EC II (Figure 1) is located within the Nahal Keziv Nature Reserve in Western Upper Galilee (33°02′ N, 35°11′ E) in the northern part of Israel. EC II is a Plio-Pleistocene erosion canyon cut into the Upper Cenomanian limestone (Geological Maps of Israel, 1998). The climate in the region is Mediterranean, with warm dry summers (mean temperature of the hottest months—July-August—is 22-27 °C) and humid winters (mean temperature of the coldest months—January-February—is 6-12 °C). Mean annual rainfall is about 700 mm (Atlas of Israel, 1985). EC II consists of 2 opposite slopes—south-facing (SFS) and north-facing (NFS)—that slope 20-40° and 30-40°, respectively. These slopes are separated by only 50 m at the bottom and 350 m at the top, but display substantial physical and biotic contrasts due to about 600% more solar radiation on the SFS than on the NFS (Finkel et al., 2002). The SFS is, therefore, warmer, drier, microclimatically more fluctuating, and less predictable than the NFS.

The plant communities vary remarkably between the slopes (Finkel et al., 2001). The SFS changes from

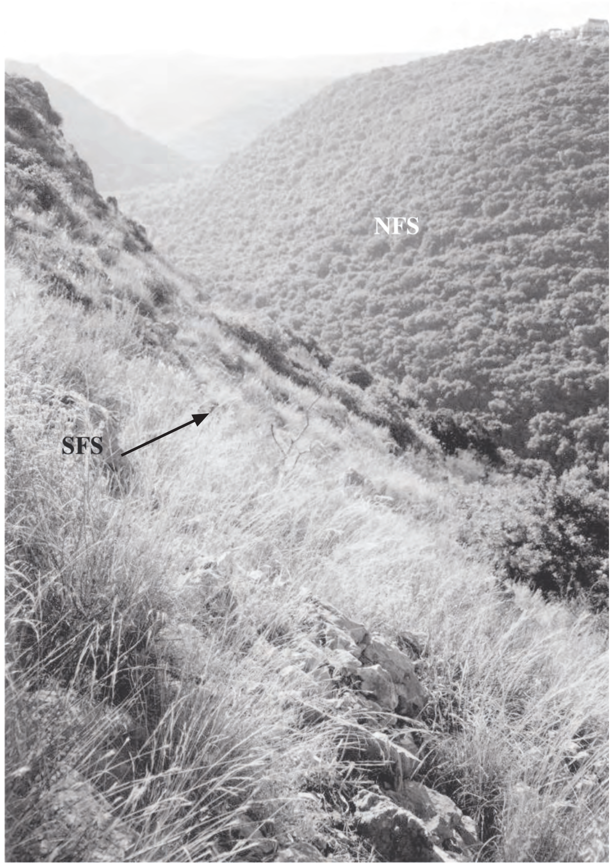

Figure 1. EC II microsite in Lower Nahal Keziv, Upper Western Galilee. Note the plant formation on opposite slopes: dense forest on the cool, humid NFS, and the garrigue on the warm, xeric SFS.

Calicotome villosa (Poir.) Link. and *Salvia fruticosa* Mill. garrigue at the bottom to a dry, Mediterranean, savanoid, open park forest of *Ceratonia siliqua* L.-*Pistacia lentiscus* L. association at the top, with plant cover increasing by almost 70% downslope. In contrast, the NFS is covered 100% by homogeneous dense forest of *Acer obtusifolium* Sibth. & Sm. and *Laurus nobilis* L. The summer-dry riverbed at the valley bottom (VB) is covered by a dense *Quercus calliprinos* plant community.

Sampling

The EC II canyon has 7 sampling stations: 3 on each slope at altitudes of 140, 170, and 200 m a.s.l. (stations 1, 2, 3 on the SFS, and stations 7, 5, 6 on the NFS from top to bottom, respectively), and 1 on the VB at 110 m a.s.l. (station 4). As a lush, dense forest covers the NSF, all 3 stations on this slope (NFS-5, NFS-6, and NFS-7) represent rather homogeneous, shaded, humid habitats. In contrast, the SFS represents a spatiotemporal "broader niche" (Van Valen, 1965), and has more microhabitat patches and subdivisions than the NFS. The 2 upper stations on this slope (SFS-1 and SFS-2) are in xeric and sunny habitats. The lower station of this slope (SFS-3) is in a mesic habitat with diffuse light (i.e. half-shaded). The ecological conditions of the VB are between those of the NFS and those of the lower station of the SFS.

Fieldwork was conducted between 2005 and 2007. Twelve oak trees (*Quercus calliprinos*) were randomly chosen at each station, excluding stations 1 and 2. We found only 3 trees at station 1 and only 6 trees at station 2. Thus, in total, 69 trees were examined. All lichen species were recorded on the trunks of the selected trees up to a height of 1.6 m. The lichen specimens were collected from these trees for precise identification in the laboratory. Bark samples (up to 3 mm thick) were collected from the same trees to measure pH.

Bark and soil temperatures and soil moisture

Three environmental variables (soil and tree bark temperatures, and soil moisture) that could be expected to characterise the microclimatic conditions were measured at each sampling station. Soil and tree bark temperatures were measured 4 times during July 2007. Soil temperature was recorded with an E.T.I. 2001 thermometer (E.T.I. LTD, Sussex, UK). Tree bark surface temperature was measured with a Micron infrared thermometer (model M102HTL). To determine soil moisture content, soil samples were collected twice during July 2007. Soil moisture was determined as $(c - g)100/g$, where c is wet weight of the soil, and g is the dry weight (dried at 105 °C for 24 h).

Determination of bark pH

Bark samples were cleared of lichens, dried at 25 °C for 2 weeks, and then ground in a mill. The ground bark samples (2.0 g) were shaken for 8 h in 50 mL of de-ionised water. pH was determined directly in the solution using a digital pH meter (HANNA HI 9813-0) with a glass electrode.

Identification of the collected material

The lichen specimens were identified at the Laboratory of Lichenology at the Institute of Evolution, University of Haifa (Israel), the Laboratory of Lichenology & Bryology at Komarov Botanical Institute (St. Petersburg, Russia), and the Institute for Plant Sciences of Karl-Franzens University (Graz, Austria), according to standard methods. The following references were used to identify the specimens: Clauzade & Roux, 1985; Mayrhofer, 1987; Golubkova, 1988; Purvis et al., 1992; Egea & Torrente, 1993; Etayo, 1993; Wirth, 1995; Tretiach & Hafellner, 1998; Boqueras, 2000; Zedda, 2000; 2002; Temina et al., 2005. TLC (thin layer chromatography) analysis was carried out on sterile lichens, following Culberson & Kristinsson (1970), Culberson (1972), Culberson & Johnson (1982), and White & James (1985). Herbarium specimens were deposited at the herbarium of the Institute of Evolution, University of Haifa (HAI, Israel). Duplicates were deposited at the herbarium of lichens of the Komarov Botanical Institute (LE, Russia).

Data analysis

Canonical correspondence analysis (CCA) with CANOCO for Windows v.4.5 (ter Braak, 1987, 1990) was used to clarify the relationship between environmental variables and the abundance of lichen species, as well as to determine the influence of ecological variables on the morpho-anatomic characteristics of the lichens and on the distribution of biogeographic groups. Analysis was performed on the basis of 4 environmental factors: soil moisture, soil temperature, tree bark pH, and tree bark temperature (Table 1). To the available parameters we added 3 variables: the number of species at each sampling station, exposition, and light conditions. Habitat light conditions were visually rated on a scale of 1 (totally shaded, poorly lit) to 4 (sun-exposed, very well lit). The term "exposition" denotes the location in the canyon (NFS = 1, VB = 2, SFS = 3).

Results and Discussion

Species diversity (Table 2)

The comparatively small sample area (7000 m²) in EC II had high species richness of epiphytic lichen biota, containing 24 out of the 82 (29%) epiphytic species known for the territory of Israel (Temina et al., 2005). The species belong to 5 orders, 11 families, and 17 genera. Primary species diversity is presented

Table 1. The values of environmental variables at the EC II sampling stations.

	Stations						
	SFS-1	SFS-2	SFS-3	VB-4	NFS-5	NFS-6	NFS-7
Soil temperature (°C)	35.11	34.34	31.9	30.08	25.47	27.93	28.02
Soil moisture content (%)	8.81	9.18	9.22	9.53	9.995	9.77	9.53
pH of tree bark	5.9	5.1	5.6	5.9	6.0	6.0	5.7
Tree bark temperature (°C)	34.75	32.5	30.6	29.85	28.9	29.0	28.95
Total number of species	2	8	20	14	9	12	10
Exposition	3	3	3	2	1	1	1
Light conditions	4	3.5	2.5	2	1	1	1.5

Table 2. The distribution of lichen species at the EC II sampling stations.

Species	Species code	Stations						
		SFS-1	SFS-2	SFS-3	VB-4	NFS-5	NFS-6	NFS-7
		Commonness-rarity status*						
Bacidina phacodes (Körb.) Vězda	BAPHA	-	-	c	vc	vc	vc	vc
Bactrospora patellarioides (Nyl.) Almq. var. *patellarioides*	BAPAT	-	-	r	vr	r	r	r
Biatoridium delitescens (Arnold) Hafellner	BIADE	-	r	rc	r	vr	vr	r
Caloplaca cerina (Hedw.) Th. Fr.	CALOC	-	r	vr	-	-	-	-
Caloplaca obscurella (Körb.) Th. Fr.	CALOO	-	-	vr	-	-	-	-
Catillaria praedicta Tretiach & Hafellner **	CATIP	-	vr	-	-	-	-	-
Dirina ceratoniae (Ach.) Fr.	DIRIC	-	-	c	vr	-	-	-
Hyperphyscia adglutinata (Flörke) H. Mayrhofer & Poelt	HYPAD	-	-	r	vr	-	-	-
Lecania naegelii (Hepp) Diederich & Van den Boom	LENAE	-	-	rc	c	-	-	-
Lecanora argentata (Ach.) Malme	LEARG	-	-	-	-	r	vr	rc
Lecanora glabrata (Ach.) Malme **	LEGLA	-	-	rc	r	vr	r	rc
Lecanora leuckertiana Zedda **	LELEU	-	-	-	-	-	-	vr
Lecanora subintricata (Nyl.) Th. Fr. **	LESUB	-	-	vr	vr	-	-	-
Lecidella elaeochroma (Ach.) M. Choisy	LECEL	-	-	vr	-	-	-	-
Lecidella euphorea (Flörke) Hertel	LECEU	-	-	r	-	-	-	-
Leptogium tenuissimum (Dicks.) Körb.	LEPTE	-	vr	r	r	-	vr	-
Opegrapha varia Pers. **	OPEVA	r	vr	vr	r	rc	rc	r
Physcia biziana (A. Massal.) Zahlbr.	PHYBI	-	-	vr	vr	-	-	-
Physcia tenella (Scop.) DC.	PHYTE	-	-	vr	-	-	vr	-
Ramalina lacera (With.) J.R. Laundon	RAMAL	-	-	-	-	-	vr	-
Strigula affinis (A. Massal.) R.C. Harris **	STRIA	-	vr	rc	-	-	-	-
Strigula mediterranea Etayo **	STRIM	-	-	-	rc	r	r	rc
Thelenella hassei (Zahlbr.) H. Mayrhofer	THEHA	rc	r	r	c	vc	c	rc
Xanthoria parietina (L.) Th. Fr.	XANPA	-	r	c	c	r	rc	rc

vr: Very rare; r: rare; rc: rather common; c: common; vc: very common. **Species new to Israel.

in the orders *Lecanorales* (14 species), in the families *Lecanoraceae* (6 species), *Physciaceae* (3 species), and *Teloschistaceae* (3 species), and in the genera *Lecanora* (4 species). Most of the lichens observed in EC II are species common in the Mediterranean region of Israel. They have worldwide distribution and occur on all or almost all continents; however, 29% of the lichens observed in EC II are rare in Israel and the rest of the world. Among the lichens we observed, 7 taxa are first records for Israel. The new species observed in Upper Galilee—the region with the most thoroughly studied lichen biota (Temina et al., 2004)—provided evidence that lichen diversity in Israel has yet to be sufficiently investigated.

Opegrapha varia, *Thelenella hassei*, *Biatoridium delitescens*, and *Xanthoria parietina* were the most widespread lichens, and *Bacidina phacodes* was the most abundant species at the research site. *Caloplaca cerina, C. obscurella, Catillaria praedicta, Hyperphyscia adglutinata*, *Lecanora leuckertiana, L. subintricata, Lecidella elaeochroma, L. euphorea, Physcia biziana, P. tenella,* and *Ramalina lacera* are rare species in EC II (only 1-3 specimens each were found). Among the studied lichens, there were several very remarkable species. *Thelenella hassei* is a very rare species, registered only in California (Mayrhofer, 1987) and in the Sharon Plain in Israel (Galun & Mukhtar, 1996). EC II is the third locality of this lichen in the world. In EC II it was observed both in humid and shaded, and dry and sunny habitats. Nonetheless, its occurrence was optimal on subneutral, anitrophic bark in rather humid and shaded conditions. *Catillaria praedicta* and *Lecanora leuckertiana* are recently described rare Mediterranean species (Tretiach & Hafellner, 1998; Zedda, 2000). *Lecanora subintricata* is a rare circumboreal-montane lichen (Nimis, 1993). It is interesting to note that although common in EC II, *Thelenella hassei* and *Biatoridium delitescens* are rare in the world.

The recorded EC II lichen vegetation on the canyon's opposite slopes developed under contrasting environmental conditions. The structure of lichen biota in these localities reflects this environmental contrast. In all, 20 and 13 lichen species were observed on the SFS and NFS, respectively, and 14 species at the VB. Three species occurred only on the NFS, 6 species only on the SFS, and 8 species at all 3 localities (NFS, SFS, and VB). Species diversity on the SFS increased downslope. By contrast, species diversity on the NFS increased upslope. Thus, the lichen biota on the south-facing, xeric, and ecologically more varied slope demonstrated significantly greater diversity than on the north-facing, humid, and ecologically homogeneous slope and at the VB. Our data also confirm the substantially higher number of vascular plant, soil micro-fungi, and beetle species on the SFS, as compared with the NFS, reported by other researchers (Finkel et al., 2001; 2002; Grishkan et al., 2003).

Biogeographic elements (Table 3, Figure 2)

The lichens observed in EC II belong to 5 biogeographic elements, following Zedda (2002): temperate, northern temperate, southern temperate, sub-oceanic, and Mediterranean. Most lichens in EC II (58%) belong to the temperate element. The sub-oceanic element accounts for 21% and the Mediterranean element accounts for 13% of the observed lichens. The northern temperate and southern temperate elements were represented by 4% each. The frequency of sub-oceanic species was higher, and the frequency of temperate species was lower on the more humid and cool NFS and VB than on the warmer SFS. The same tendency was noted by Zedda (2002), who observed increases in the number of sub-oceanic species in the epiphytic lichen communities as habitat humidity increased.

Growth forms and photobionts (Table 3, Figure 2)

Crustose species dominated (75%) the lichen biota in EC II. Foliose lichens were represented by 4 species (17%), and fruticose and squamulose lichens by 1 species each (4%). The distribution of the different growth forms varied by location in EC II. The frequency of crustose lichens was higher on the xeric SFS than on the humid NFS and at the mesic VB. The only fruticose species (*Ramalina lacera*) registered in EC II was found on the NFS. Thus, on the more humid NFS, lichen growth forms were more diverse than on the drier SFS and at the VB.

The great majority of all lichen species in the world have green algae as their photobionts, and only 10% of them contain cyanobacterial photobionts

Table 3. Lichen species collected in EC II and their morpho-anatomical, ecological, and biogeographical characteristics.

Species	Morpho-anatomical characteristics						Ecological peculiarities					Biog
	Grf	Ph	Rs	Fc	As	Az	Li	Mo	Eu	pH (L)	pH (O)	
Bacidina phacodes	Cr	Ch	S	Br	Tm	40-60 × 3-3.8	2	1	1	4.1-7.0	4.6-6.7	Suboc
Bactrospora patellarioides var. *patellarioides*	Cr	Tr	S	Bl	Tm	70-95 × 3-4	2-4	1	1-2	3.3- 5.6	5.4-6.4	Suboc
Biatoridium delitescens	Cr	Ch	S	Oth	Sp	4-4.5	3-4	1	1	5.7-7.0	4.8-6.4	Temp
Caloplaca cerina	Cr	Ch	S	Or	Pl	12-15 × 6-8	2-4	2-3	2-3	5.7-7.5	4.9-5.9	Temp
Caloplaca obscurella	Cr	Ch	S; As	Br	Pl	13 × 7	3	2	2-3	5.7-7.0	6.1-6.2	Temp
Catillaria praedicta	Cr	Ch	S	Bl	Os	5-8 × 2-2.5	2-4	1	2	4.9-7.5	4.6-4.9	Med
Dirina ceratoniae	Cr	Tr	S	Bl	Tm	24-32 × 4.8-6	1-3	1	2-3	5.7-7.5	4.6-6.1	Suboc
Hyperphyscia adglutinata	Fol	Ch	As	-	-	-	3-4	2-3	2-4	5.7-7.5	4.6-6.1	Temp
Lecania naegelii	Cr	Ch	S	Oth	Tm	13-28 × 4-5	3	2	2-3	4.9-7.0	4.6-6.7	Temp
Lecanora argentata	Cr	Ch	S	Br	Sp	11-14 × 6-8	2-3	2	1	4.9-7.0	4.6-6.7	Temp
Lecanora glabrata	Cr	Ch	S	Br	Sp	12-16 × 5-8	2	2	1-2	5.7-7.0	4.7-6.4	Temp
Lecanora leuckertiana	Cr	Ch	As	-	-	-	2-3	1	1	4.9-5.6	5.2	Med
Lecanora subintricata	Cr	Ch	S	Br	Sp	9-11 × 2.5-3	1-3	2	1	3.3-5.6	4.7-5.8	Ntemp
Lecidella elaeochroma	Cr	Ch	S	Bl	Sp	10-14 × 6-7	1-4	1-3	1-4	4.1-7.5	4.7	Temp
Lecidella euphorea	Cr	Ch	S	Bl	Sp	11-16 × 6-7	1-3	1-3	1-3	4.1-7.5	5.4-6.1	Temp
Leptogium tenuissimum	Sq	Cyan	S	Br	Mr	24-35 × 9-12	1-3	1-2	1-2	5.7-7.5	5.5-6.5	Temp
Opegrapha varia	Cr	Tr	S	Bl	Tm	21-35 × 6.5-8	1-2	1-2	1-2	4.9-7.0	5.0-6.4	Temp
Physcia biziana	Fol	Ch	S	Bl	Os	15-18 × 6-8	3-4	2-3	3-4	5.7-7.0	5.3-6.2	Stemp
Physcia tenella	Fol	Ch	As	-	-	-	3-4	2-3	2-4	4.9-7.5	4.6	Temp
Ramalina lacera	Fr	Ch	As	-	-	-	3-4	1	2	4.9-7.0	4.9	Suboc
Strigula affinis	Cr	Tr	S	Bl	Tm	16-20 × 5-6	2-3	2	2	5.7-7.0	4.6-5.9	Temp
Strigula mediterranea	Cr	Tr	S	Bl	Os	24-29 × 4.5-5	2	1-2	1-2	4.9-7.0	5.0-6.6	Suboc
Thelenella hassei	Cr	Ch	S	Bl	Mr	25-40 × 10-17	-	-	-	-	5.0-6.7	Med
Xanthoria parietina	Fol	Ch	S	Or	Pl	12-16 × 5-9	2-4	2-3	2-4	4.9-8.5	4.6-6.7	Temp

Morpho-anatomical characteristics.
Grf: Growth forms; Cr: crustose; Sq: squamulose; Fol: foliose; Fr: fruticose; **Ph**; Photobiont: Ch: green, other that *Trentepohlia*; Tr: *Trentepohlia*; Cyan: cyanobacteria. **Rs**: Reproductive strategy: S: sexual; As: asexual, by soredia. **Fc**: Fruit colour: Br: brown; Bl: black; Or: orange; Oth: others. **As**: Ascospore septation: Sp: simple (unicellular and non-septate) ascospores; Pl: polarilocular ascospores; Os: 1-septate ascospores; Tm: transversely septate, multicellular ascospores; Mr: muriform ascospores. **Az**: Ascospore sizes (µm).
Ecological peculiarities:
Li: Light; 1: skiophytic species; 2: moderately photophytic species; 3: rather photophytic species; 4: very photophytic species. **Mo**: Moisture: 1: hygrophytic species; 2: mesophytic species; 3: xerophytic species. **Eu**: Eutrophication: 1: anitrophytic species; 2: moderately nitrophytic species; 3: rather nitrophytic species; 4: very nitrophytic species. **pH(L)**: pH values of substrates: literature data (Wirth, 1995; Nimis & Martellos, 2008). **pH(O)**: Our measurements of pH bark in EC II.
Biog: **Biogeographic elements:**
Suboc: sub-oceanic: Temp: temperate; Ntemp: northern temperate; Stemp: southern temperate; Med: Mediterranean.

(Rikkinen, 1995; Friedl & Büdel, 1996). Green algae from the genera *Trebouxia* and *Trentepohlia* are the most frequent photobionts. Among them, trebouxioid photobionts occupy the lead position, especially in cold and temperate regions. Trentepohlian photobionts are dependent on warm-humid conditions (Friedl & Büdel, 1996) and are the most common lichen symbionts in tropical and subtropical regions (Rikkinen, 1995; Friedl & Büdel, 1996).

In the lichen biota of EC II, 75% of lichens had green algae as photobionts, 21% had *Trentepohlia*, and 4% were cyanobacteria. The occurrence of these photobionts in different populations in EC II varied. Lichens with trentepohlian photobionts were more frequent on the more humid NFS and VB than on the drier SFS. Similarly, a higher frequency of lichens with *Trentepohlia* in humid habitats in comparison with the frequency of lichens with *Trentepohlia* in arid

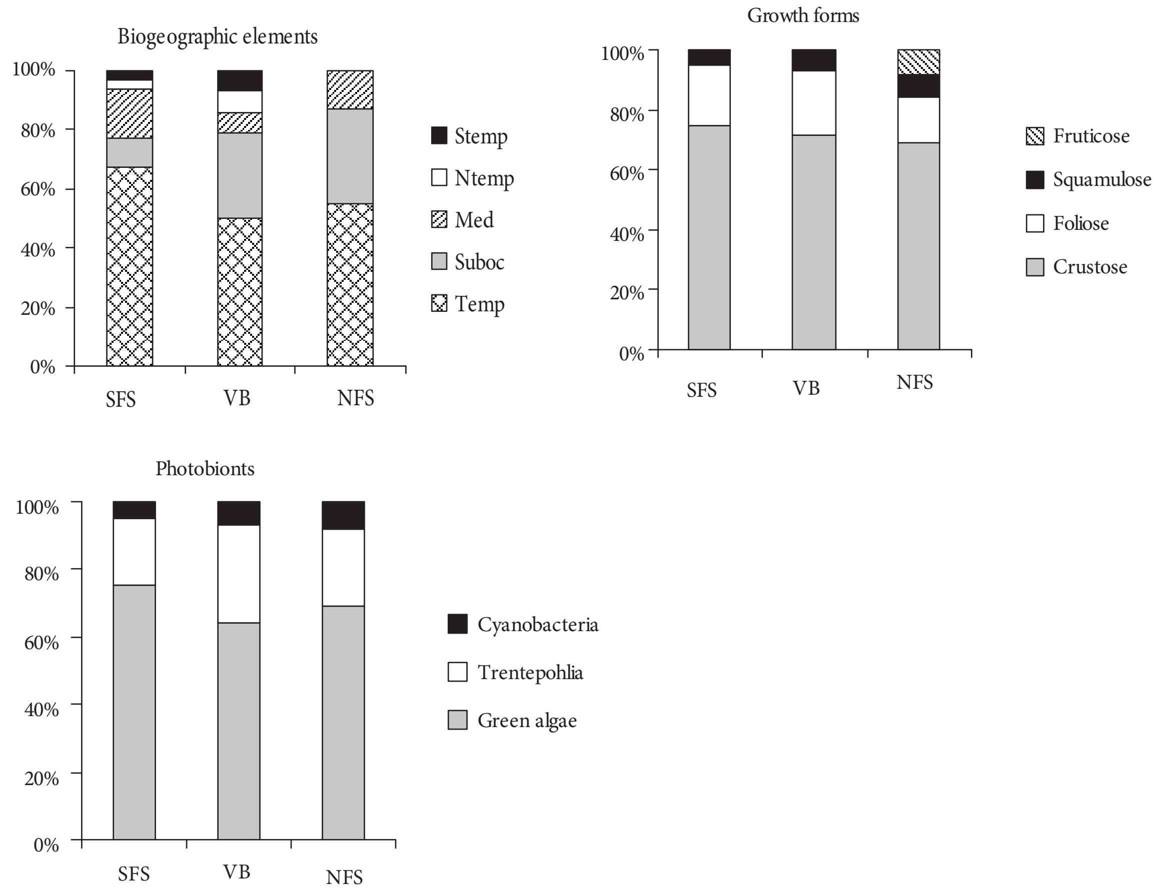

Figure 2. Biogeographic elements, growth forms, and photobionts of lichens on the slopes and VB of EC II (for abbreviations, see footnote to Table 3).

habitats was also observed in oak forests of Sardinia (Zedda, 2002).

Reproductive strategy (Table 3, Figure 3)

The majority of lichens in EC II (83%) have a sexual reproductive strategy. Lichens with asexual reproduction account for 17% of the total. Analysis of the distribution of species with different reproductive strategies in various EC II populations showed that the frequency of sexual species was higher and that the frequency of asexual species was lower on the more stressful SFS than on the milder NFS. Similar results were obtained for soil micro-fungi in EC II (Grishkan et al., 2003). The proportion of sexual ascomycetes was higher on the SFS in comparison with the proportion of sexual ascomycetes on the NFS.

Among the sexual lichens in EC II, most species have black or brown fruits. The black-fruit lichens dominated on the more sun-exposed SFS and VB, while brown-fruit lichens dominated on the shaded NFS. In all, 65% of sexual lichens in EC II produced small (4-16 × 2-8 µm), simple, or 1-septate ascospores, and 35% produced large (24-90 × 3-17 µm) multi-septate, or muriform ascospores. Lichens with small, simple, or 1-septate ascospores prevailed on the xeric SFS, while lichens with large multi-septate or muriform ascospores dominated on the humid NFS and mesic VB.

Ecology of studied lichen species (Table 3, Figure 4)

The ecological peculiarities of the lichen species are given in Table 3 and Figure 4, based on the

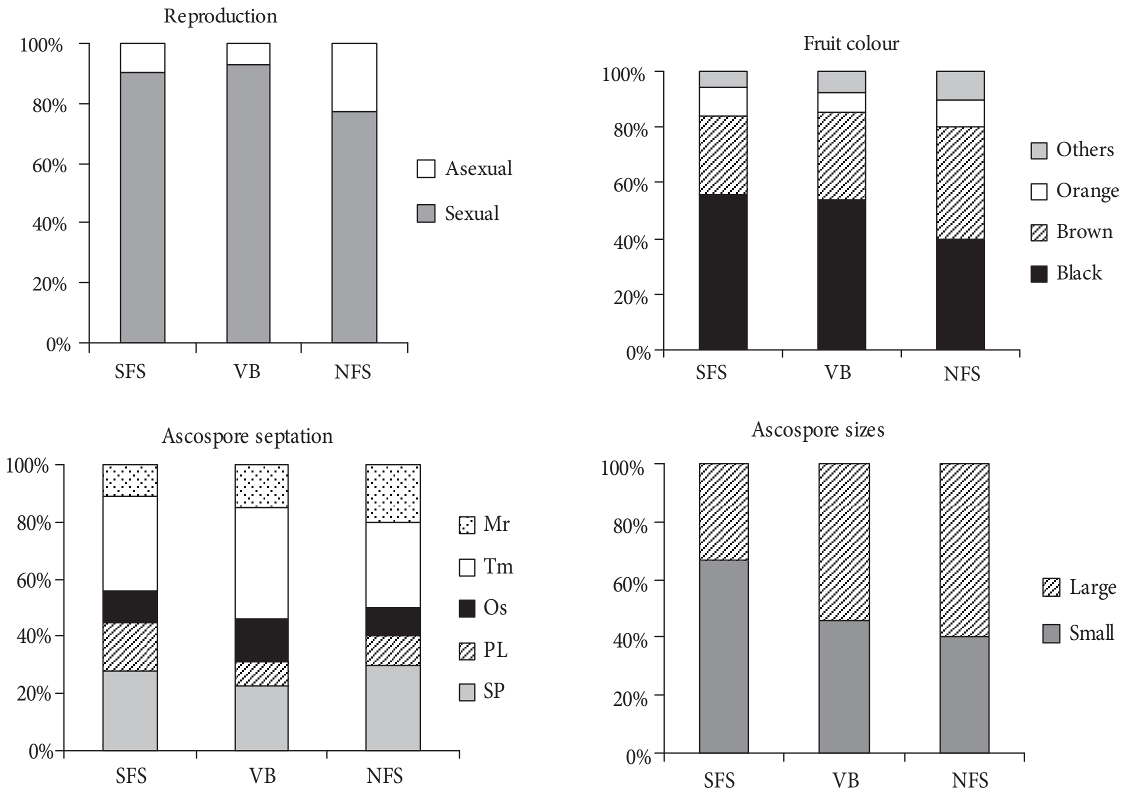

Figure 3. Lichen species with different reproductive strategies on the slopes and VB of EC II (for abbreviations, see footnote to Table 3).

publications of Purvis et al. (1992), Egea and Torrente (1993), Etayo (1993), Nimis (1993), Wirth (1995), Tretiach & Hafellner (1998), and Zedda (2002).

a) Relationship to solar radiation and moisture conditions

In EC II 46% of the lichens were mesophytic, 25% were hygrophytic, 21% were xerophytic, and 8% were indifferent to moisture conditions. The frequency of hygrophytic and mesophytic species was lower, and the frequency of xerophytic species was higher on the dry SFS in comparison with the frequencies on the humid NFS and mesic VB.

In EC II 42% of the lichens were photo-indifferent, 33% were photophytic, and 25% of the species preferred half-shaded habitats. The shaded habitats of the NFS and VB are characterised by a dominance of moderately photophytic species, while the sun-exposed and half-shaded habitats of the SFS are characterised by a dominance of very photophytic and photo-indifferent species.

b) Relationship to pH-value and eutrophication of bark

The pH values of oak bark in the research site ranged from 4.6 to 6.7. Most trees had sub-neutral bark (pH 5.7-7.0); therefore, it was not surprising that the majority of lichens in EC II (42%) were subneutrophytic species that prefer sub-neutral substrates. Acidophytic lichens accounted for 37% of the observed lichens and 21% of the lichen biota were indifferent to the pH of bark in EC II. Subneutrophytic species dominated on the SFS and VB (50% in each locality). The NFS was characterised by the dominance of acidophytic species (62%).

According to Loppi and De Dominicis (1996), the eutrophication of substrates includes the deposition of dust and nitrogen compounds. Numerous lichenological studies have shown that lichen species tolerance to the eutrophication of substrates is variable. Many species grow exclusively on nutrient-poor substrates, whereas others occur on substrates

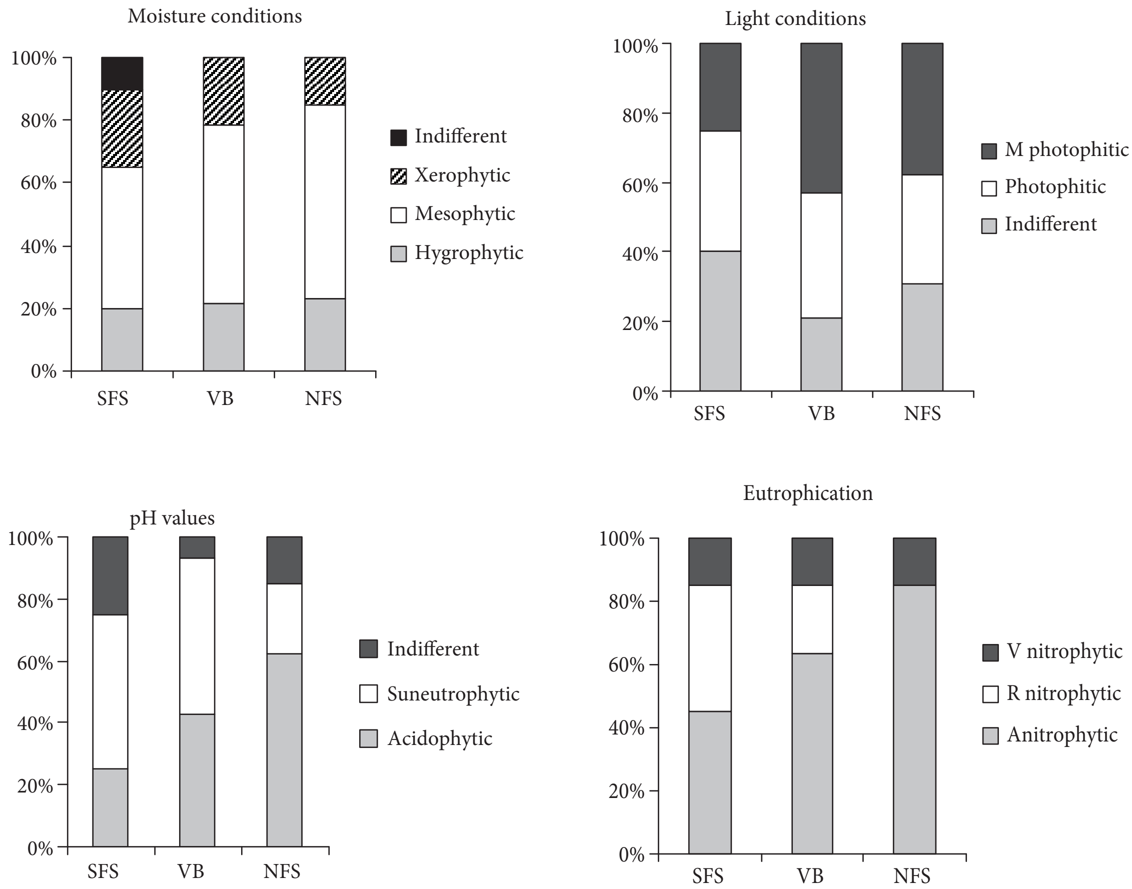

Figure 4. Lichen species with different ecological peculiarities on the slopes and VB of EC II (for abbreviations, see footnote to Table 3).

with weak eutrophication. Some species are rather resistant to high levels of eutrophication or even prefer to live on strongly eutrophicated substrates. Many researchers also reported that agriculture and grazing have increased the eutrophication of lichen substrates, resulting in an increase in the number of nitrophytic species in lichen communities (De Bakker, 1989; Ruoss et al., 1991; Purvis et al., 1992; Benfield, 1994, Loppi & De Dominicis, 1996; Fos, 1998; Loppi et al., 1998; Pirintsos et al., 1998; Ruoss, 1999).

In the present study the epiphytic lichen biota was analysed based on the ecological indices of eutrophication developed by Nimis (1993), Wirth (1995), and Zedda (2002). All lichen species observed in EC II were divided into the following 3 groups: group 1: (anitrophytic or moderately nitrophytic) species growing on mineral-poor to moderately nutrient-rich bark, without eutrophication; group 2: (rather nitrophytic) species growing on nutrient-rich bark with weak eutrophication; group 3: (very nitrophytic) species growing on nutrient-enriched bark, often with an accumulation of dust or moderate manuring. Most lichens in EC II (54%) belong to group 1, 33% of the species belong to group 2, and 13% of species belong to group 3. The predominance in EC II of group 1 lichens is not surprising because the research site represents a natural area that has developed for a long time without disturbance by human activity. Our results are in agreement with the findings of Zedda (2002), who observed high frequencies of anitrophytic and moderately nitrophytic lichens in well-preserved oak forests in Sardinia. This researcher also observed that the frequency of very nitrophytic species increased as human disturbance to forest vegetation increased.

The occurrence of these groups in different localities in EC II was analysed and showed that anitrophytic or moderately nitrophytic species (group 1) occurred more frequently on the NFS and VB than on the SFS, while rather nitrophytic species (group 2) occurred more frequently on the SFS than at the other localities. This might have been due a higher accumulation of wind-blown dust in the more open habitats of the SFS in comparison with the closed forest canopy habitats of the VB and NFS.

Effects of environmental variables on species diversity

The biplot obtained using CCA (Figure 5) represents the ordination of species in relation to the combination of the different environmental variables. Environmental variables are represented by arrows; the maximal value for each variable is located at the arrow head. According to ter Braak (1987), species projected near the centre of the biplot may have their optima in this area and are generalists: “they are not related to the first 2 axes”. Thus, species that are linked to high parameter levels are indicators for this parameter, while species that have strong reactions to any slight change in the selected parameter are biosensors for the selected parameter. The analysis of EC II lichen data with CCA shows that the environmental variables that influence species diversity were divided into 2 main groups (Figure 5). The first group includes the light and temperature conditions of the habitats, and the second group includes the moisture conditions of habitats and tree bark pH values. The distribution of *Biatoridium delitescens, Caloplaca cerina, Catillaria praedicta, Leptogium tenuissimum*, and *Strigula affinis* was positively correlated with the first group of variables, while the distribution of *Bacidina phacodes, Bactrospora patellariosdes, Lecanora glabrata,* and *Strigula mediterranea* was positively correlated with the second group of factors. The other species did not have significant relationships with the 2 groups of variables. *Caloplaca cerina*, *Catillaria praedicta* and *Strigula affinis* can be used as indicators of the first group of variables (light and temperature conditions of habitats). Based on this analysis we didn’t identify any species that could serve as biosensors of the analyzed variables. The group of species (*Dirina ceratoniae, Hyperphyscia adglutinata, Lecania naegelii, Lecanora subintricata*, and *Physcia biziana*) located in the lower left quadrant of the biplot is connected with the species richness in the community. We concluded that these species prefer to grow in multispecies communities.

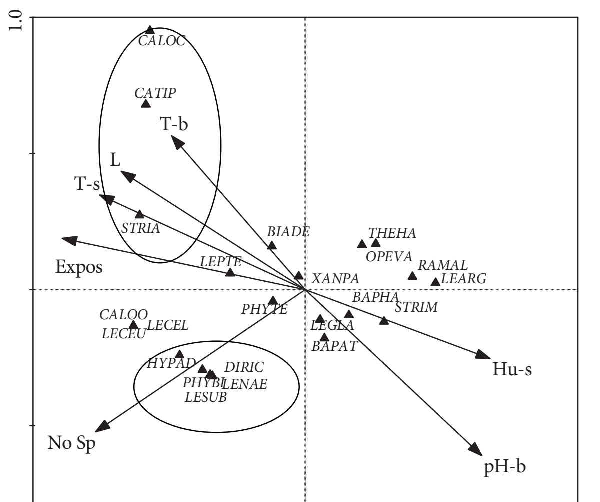

Figure 5. CCA ordination of the lichen species and environmental variables in EC II.
Abbreviations for environmental variables:
Expos: exposition (location in the canyon: NFS, VB, SFS); Hu-s; soil moisture; L: light conditions of habitats; No Sp: number of species in each sampling station; pH-b: pH of tree bark; T-b: temperature of tree bark; T-s: soil temperature. Species codes are given in Table 2.

Effects of environmental variables on biogeographic elements and morpho-anatomic characteristics of lichens

Analysis of the biogeographic elements with CCA revealed that the distribution of temperate species was correlated with light and temperature conditions, while the distribution of sub-oceanic species was correlated with the moisture conditions of habitats and tree bark pH values (Figure 6).

Figure 7 shows the relationship between environmental variables and the morpho-anatomic characteristics of the lichens in EC II. Among the lichen characteristics, only some were connected with the studied environmental variables. According to our analysis, the distribution of fruticose lichens was correlated with the moisture conditions of habitats

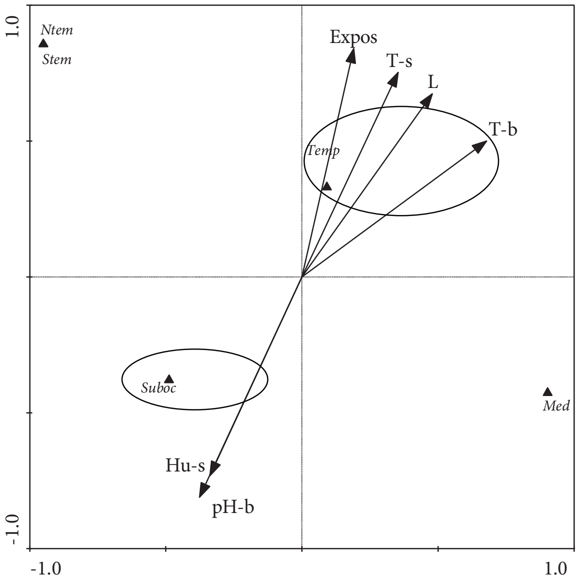

Figure 6. CCA ordination of the biogeographic elements and environmental variables in EC II.
Abbreviations for environmental variables:
Expos: exposition (location in the canyon: NFS, VB, SFS); Hu-s: soil moisture; L: light conditions of habitats;, pH-b: pH of tree bark; T-b: temperature of tree bark; T-s: soil temperature.
Abbreviations for biogeographic elements:
Suboc: sub-oceanic; Temp: temperate; Ntemp: northern temperate; Stemp: southern temperate; Med: Mediterranean.

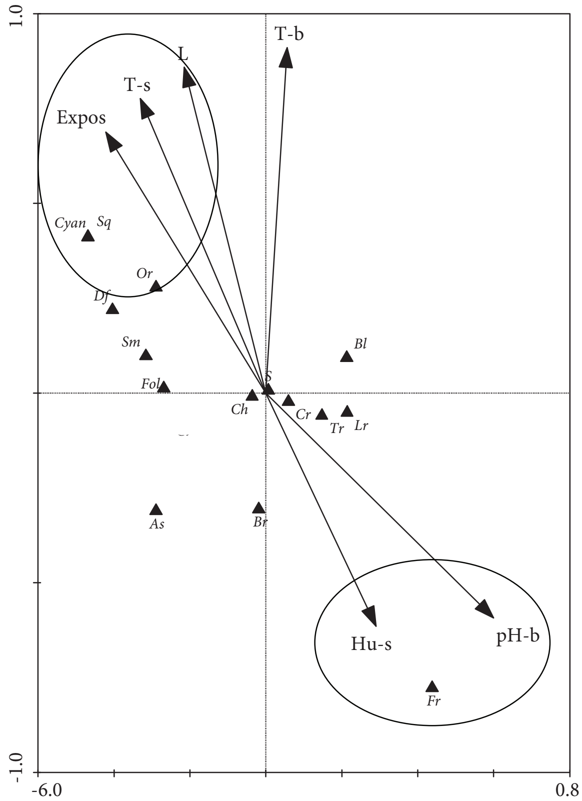

Figure 7. CCA ordination of the morpho-anatomic characteristics of lichens and environmental variables in EC II.
Abbreviations for environmental variables:
Expos: exposition (location in the canyon: NFS, VB, SFS); Hu-s: soil moisture; L: light conditions of habitats: pH-b: pH of tree bark; T-b: temperature of tree bark; T-s: soil temperature;
Abbreviations for morpho-anatomic characteristics:
Cr: crustose species; Sq: squamulose species; Fol: foliose species; Fr: fruticose species; Ch: green photobionts; Tr: trentepohlial photobionts; Cyan: cyanobacterial photobionts; S: sexual reproduction; As: asexual reproduction; Br: brown fruits: Bl: black fruits; Or: orange fruits; Df: fruits of other colours; Lr; large ascospores, small ascospores.

and tree bark pH values. The light and temperature conditions of habitats were correlated with the distribution of squamulose lichens, lichens with cyanobacterial photobionts, and lichens with orange apothecia.

Conclusions

Our study shows that EC II in Lower Nahal Keziv, Upper Western Galilee is a unique environment rich in epiphytic lichen vegetation, including many interesting and rare species. The analysis of the distribution of lichen species on the opposite slopes of the canyon and on the VB revealed that the lichen biota of these localities differed in many parameters (species richness, biogeographical elements, reproductive strategy, morphological, anatomical, and ecological peculiarities) due to the different microclimatic and biotic conditions of these localities.

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