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Succession of epiphytic bryophytes in *Cedrus libani* forest on the Meydan Plateau (Aladağ)

Tülay EZER*, Recep KARA
Biology Department, Faculty of Science, Niğde University, 51100 Niğde, Turkey

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Abstract: The succession of epiphytic bryophytes was investigated in *Cedrus libani* A.Rich. forest on the Meydan Plateau (Aladağ). A total of 19 taxa (16 mosses, 3 liverworts) were recorded in 90 sampling relevés, 4 dm^2 each. Index of ecological significance (IES) was used to evaluate the ecological importance of the taxa in epiphytic habitats on tree trunks. Additionally, the epiphytic bryophyte succession of the cedar forest was analysed using multivariate classification techniques (TWINSPAN and DECORANA). The multivariate analysis results showed that the epiphytic bryophyte communities were divided into 2 main groups and 5 different subgroups associated with successional gradient. Moreover, habitat affinities of the taxa and their life forms were evaluated along a gradient of height and the gradient of age of the host tree. *Tortella tortuosa*, *Syntrichia ruraliformis*, and *Bryum capillare* were only found on young trees, *Zygodon rupestris* only on middle-aged trees, and *Pterigynandrum filiforme* on aged trees.

Key words: Epiphytic succession, bryophytes, multivariate analysis, *Cedrus libani*, Turkey

1. Introduction

Turkey is geographically located on the border between Europe and Asia and, as a result, it contains diverse habitats and ecosystems. Phytogeographically, it is composed of 3 regions: the Euro-Siberian region, the Irano-Turanian region, and the Mediterranean region, which forms the southern part of Turkey. These phytogeographical regions have provided Turkey with rich floral diversity. The eastern Mediterranean region contains a number of different biotopes, including evergreen coniferous forests. *Cedrus libani* A.Rich. (also known as the Lebanon cedar) is a species of cedar native to the mountains of the Mediterranean region, and presently found primarily in the Taurus mountain range of Asia Minor, Turkey. In the Taurus Mountains, *Cedrus libani* generally occur between 800 and 2100 m elevation, but small populations can be found at lower (500–600 m) and higher (2400 m) elevations (Boydak, 2003). Pure cedar forests are widespread between 1000 and 1400 m elevation within the study site (Meydan Plateau).

Although vascular plants, including ferns, in Turkey have been thoroughly investigated, ecological studies of bryophytes are still insufficient, especially those of epiphytic bryophytes. Epiphytic bryophytes are an important component of forest ecology. Due to their poikilohydric character, bryophytes are sensitive to microclimatological changes, particularly changes in environmental moisture and dryness (Studlar, 1982; Moe & Botnen, 2000; Mazimpaka et al., 2009). Several studies of epiphytic bryophyte communities have been conducted in Mediterranean areas (Burgaz et al., 1994; Lara & Mazimpaka, 1998; Draper et al., 2003, 2005; Mazimpaka et al., 2009; Medina et al., 2010). Results of these studies showed that successful colonisation of bryophytes in epiphytic habitats is strongly influenced by ecological factors (biotic and abiotic). These factors include substrates, host species, bark chemicals, and physical properties.

Additionally, studies on epiphytic bryophytes and lichens have been carried out recently in Turkey (Çobanoğlu & Sevgi, 2009; Ezer et al., 2009, 2010; Oran & Oztürk, 2012). These studies showed that host species, exposure on tree stems, tree age, height, forest spatial pattern, and canopy cover affect the vertical distribution of bryophytes along trunk surfaces. The present study investigated successional trends among epiphytic bryophytes using the index of ecological significance (IES) to evaluate the ecological importance of epiphytic bryophytes on the trunks of *C. libani*. This study also aimed to increase knowledge about the succession of epiphytic bryophytes in coniferous forests in Turkey through the use of multivariate techniques (TWINSPAN and DECORANA).

* Correspondence: tuezer@gmail.com

2. Materials and methods

2.1 Study area

The Meydan Plateau (Aladağ) is situated in Adana Province in the eastern Mediterranean region and is located in the south-eastern portion of Aladağlar National Park, one of the largest national parks in Turkey (Figure 1). One of the most important sections of Aladağlar National Park is the Pos forests. The study site, within the Pos forests, has a semi-arid Mediterranean climate type. The annual average precipitation is 703 mm, and the average annual temperature is 13.6 °C. The study site primarily contains serpentine, limestone, and sedimentary rocks, and has red Mediterranean soil.

The study site is a mosaic of deciduous and coniferous formations dominated by *Quercus cerris* L., *Q. pubescens* Willd., *Q. petrea* (Matt.) Liebl., *Fraxinus excelsior* L., *Juniperus oxycedrus* L., *J. foetidissima* Wild., *J. excelsa* M.Bieb., *Cedrus libani* A.Rich., *Abies cilicica* (Ant. et Kotschy) Carr., *Pinus nigra* Arn., and *P. brutia* Ten. (Yurdakulol, 1981; Tüfekçi et al., 2002).

2.2. Vegetation sampling

The specimens were collected from the trunks of cedar trees located on the Meydan Plateau during excursions in 2011. In order to eliminate floral variation caused by different bark substrates (Moe & Botnen, 2000), only one sporophyte species, *C. libani*, was investigated. Four locations in the old-growth forest were selected, each of which contained *C. libani* trees of different diameters, between 1000 and 1500 m a.s.l. (Table 1). A total of 30 cedar trees were sampled. Only cedar trees near the centre of the forest were sampled to avoid the edge effect. *C. libani* trees were assigned to 3 age classes based on trunk diameter at breast height (dbh): young (dbh 25–35 cm, 30 samples), middle-aged (dbh 70–80 cm, 24 samples), and aged trees (dbh 80–130 cm, 36 samples).

From each tree, bryophytes were collected from 20 × 20 cm quadrats, which were randomly chosen from 3 zones: basal zone (0–40 cm above the ground), middle zone (40–120 cm), and top zone (120–180 cm), as per Moe and Botnen (2000). Epiphytic bryophytes from the branches were not included in the present study. A total of 90 sampling relevés were taken from the basal zone (30 samples), middle zone (30 samples), and top zone (30 samples). The percentage cover of each epiphytic bryophyte species was estimated. In addition, before the removal of each sample, ecological and statistical data were recorded for each quadrat.

Epiphytic bryophyte taxa found in the study site were classified as specified by Hill et al. (2006) for mosses, and by Ros et al. (2007) for liverworts (Table 2). Species affinity for the epiphytic habitats was quantified based on Mazimpaka and Lara (1995) and Draper et al. (2003). Life forms were classified as specified by Magdefrau (1982). Specimens are stored in the herbarium of Niğde University.

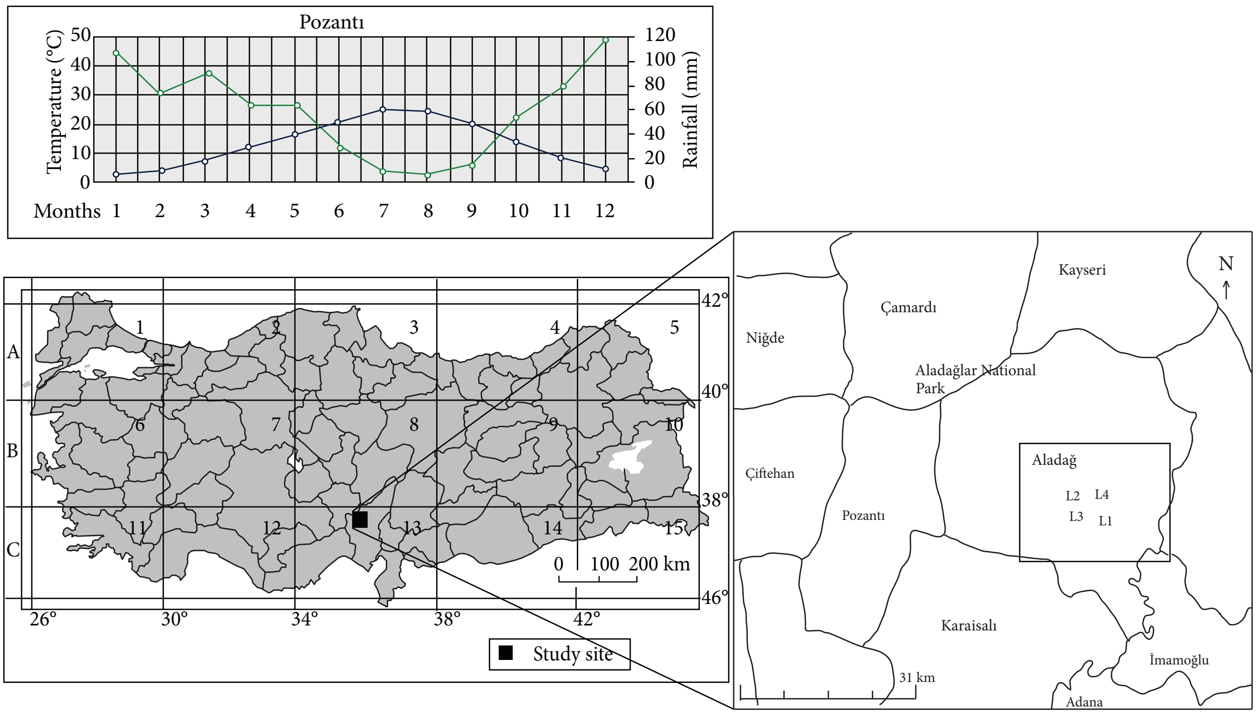

Figure 1. Topographic map of the study site and a climatic diagram of Pozantı.

Table 1. The list of localities.

Localities	GPS Coordinates	Altitude (m)
L1	37°29′41.48″N, 35°21′51.06″E	1185
L2	37°29′30.09″N, 35°22′28.14″E	1340
L3	37°29′06.26″N, 35°21′35.36″E	1280
L4	37°28′49.85″N, 35°22′45.76″E	1470

Table 2. List of epiphytic bryophyte taxa found in the study site, their families, and life form types, and affinity for epiphytic habitats.

Taxa	Family	Life form	Affinity for epiphytic habitats
MOSSES			
Tortella tortuosa (Hedw.) Limpr.	Pottiaceae	short turf	Preferentially not corticolous
Syntrichia ruraliformis (Besch.) Delogne	Pottiaceae	short turf	Preferentially not corticolous
Tortula subulata Hedw.	Pottiaceae	short turf	Preferentially not corticolous
Orthotrichum lyellii Hook. & Taylor	Orthotrichaceae	cushion	Customary epiphyte
Orthotrichum speciosum Nees	Orthotrichaceae	cushion	Customary epiphyte
Orthotrichum striatum Hedw.	Orthotrichaceae	cushion	Customary epiphyte
Zygodon rupestris Schimp. ex Lorentz	Orthotrichaceae	cushion	Customary epiphyte
Bryum capillare Hedw.	Bryaceae	short turf	Indifferent
Brachytheciastrum velutinum (Hedw.) Ignatov & Huttunen	Brachytheciaceae	mat	Indifferent
Homalothecium lutescens (Hedw.) H.Rob	Brachytheciaceae	mat	Indifferent
Homalothecium sericeum (Hedw.) Schimp.	Brachytheciaceae	mat	Indifferent
Hypnum cupressiforme Hedw.	Hypnaceae	mat	Indifferent
Habrodon perpusillus (De Not.) Lindb.	Pterygynandraceae	mat	Customary epiphyte
Pterigynandrum filiforme Hedw.	Pterygynandraceae	tail	Cortico-saxicolous
Leucodon sciuroides (Hedw.) Schwaegr.	Leucodontaceae	tail	Customary epiphyte
Leptodon smithii (Hedw.) F. Weber & D. Mohr	Leptodontaceae	fan	Cortico-saxicolous
LIVERWORTS			
Frullania dilatata (L.) Dum.	Frullaniaceae	mat	Customary epiphyte
Porella platyphylla (L.) Pfeiff.	Porellaceae	mat	Cortico-saxicolous
Radula complanata (L.) Dum.	Radulaceae	mat	Customary epiphyte

2.3. Data analysis

The relative frequency was estimated using the index of ecological significance (IES) (Lara & Mazimpaka, 1998; Albertos et al., 2001), whose mathematical expression is as follows:

IES = F (1 + C).

F (relative frequency) is equal to 100 x/n, and **C** (mean cover) is equal to $\sum c_i /x$, where **x** represents the number of samples containing the species, **n** the total number of samples, and $\mathbf{c_i}$ the cover class attributed to the species in each sample. In the index, cover and frequency, which are the 2 abundance parameters, are combined to best reflect any changes in species abundance (Albertos et al., 2001). Cover classes were classified according to the following scale:

0.5 (<1%); 1 (1%–5%); 2 (6%–25%); 3 (26%–50%); 4 (51%–75%); 5 (>75%).

The values of the IES were combined in frequency classes as follows: very scarce (<25), scarce (26–50), moderately abundant (51–100), abundant (101–200), and dominant (>200). Additionally, multivariate ordination and classification techniques (TWINSPAN and Detrended Correspondence Analysis (DCA)) were based on the IES classes of abundance as pseudospecies (Hill, 1979). Ordination and classification were performed using CAP (Community Analysis Package-III) software (Seaby et al., 2004).

3. Results

A total of 19 epiphytic bryophyte species (16 mosses and 3 liverworts) were recorded on 30 cedar trees at the study site. The identified species belonged to 11 families and 16 genera. In addition, 6 different life forms and 4 habitat affinity classes were determined (Table 2). Orthotrichaceae (4 species) was the most represented family, and the genus *Orthotrichum* was the most important ecologically, both in number of species and abundance (Table 3). Mats were the most common life form due to the pleurocarpic

Table 3. IES values of the taxa on the young, middle-aged, and aged trees

Taxa	Young trees (dbh 25–35 cm)			Middle-aged trees (dbh 70–80 cm)			Aged trees (dbh 80–130 cm)		
	Lower base	Middle zone	Top zone	Lower base	Middle zone	Top zone	Lower base	Middle zone	Top zone
MOSSES									
Tortella tortuosa	20	-	-	38	-	-	17	-	-
Syntrichia ruraliformis	20	-	-	-	-	-	-	-	-
Tortula subulata	40	-	-	25	-	-	-	-	-
Orthotrichum lyellii	30	170	180	25	237	287	17	195	291
Orthotrichum speciosum	-	90	169	25	100	125	-	140	192
Orthotrichum striatum	-	-	20	-	-	25	-	33	100
Zygodon rupestris	-	-	-	25	-	-	-	-	-
Bryum capillare	60	-	-	-	-	-	-	-	-
Brachythecium velutinum	90	-	-	113	-	-	58	-	-
Homalothecium lutescens	-	-	-	75	-	-	200	-	-
Homalothecium sericeum	240	30	-	113	50	-	233	33	-
Hypnum cupressiforme	180	-	-	200	-	-	175	-	-
Habrodon perpusillus	70	350	270	100	287	300	92	300	300
Pterigynandrum filiforme	-	-	-	-	-	-	17	-	-
Leucodon sciuroides	-	-	30	125	275	113	-	183	50
Leptodon smithii	-	20	50	-	38	-	17	17	25
LIVERWORTS									
Frullania dilatata	239	340	350	225	263	325	108	333	341
Porella platyphylla	40	-	-	-	-	-	-	-	25
Radula complanata	100	100	80	125	87	63	108	17	25

mosses and liverwort species, while fan life forms were the least common (Table 2). According to species affinity for epiphytic habitats, customary epiphytes (8 taxa) were the most common at the study site. Indifferent taxa, such as *Bryum capillare*, *Brachytheciastrum velutinum*, *Homalothecium lutescens*, *H. sericeum*, and *Hypnum cupressiforme* were also abundant and had species affinity to epiphytic habitats. The number of preferentially noncorticolous taxa was equal to the number of cortico-saxicolous species (Table 2).

The distribution of epiphytic bryophytes on cedar trees was investigated with respect to: (1) host tree diameter at breast height (lower base, middle zone, top zone) and (2) age of the host tree (young, middle aged, aged) (Table 3).

3.1. Lower base

A total of 12 bryophyte taxa were found at the base of young trees. Among these taxa, *Homalothecium sericeum* was the most frequent and abundant with the highest IES value (240). *Frullania dilatata*, a liverwort species, was abundant on the base zone and also had a high IES value (239). *Tortella tortuosa* and *Syntrichia ruraliformis* were less frequent and very scarce (IES value of <25) (Table 3). Mat life forms were the most dominant with 58.3% at the base of young trees. Short turfs were also highly represented by *T. tortuosa*, *S. ruraliformis*, *Tortula subulata*, and *Bryum capillare* (33.3%). According to the analysis of species affinity for epiphytic habitats, the percentage of indifferent species was equal to that of customary epiphytes (33.3%). Thirteen bryophytes were collected from middle-aged cedar trees. *F. dilatata* was the most dominant, with the highest IES value (225), whereas *T. subulata*, *Orthotrichum lyellii*, *O. speciosum*, and *Zygodon rupestris* were very scarce and had the lowest IES values (25) (Table 3). Mat life forms (53.8%) were still the most dominant on the lower base of middle-aged trees. Customary epiphytes were also dominant on the lower base. Eleven bryophyte species were found on the lower base of aged trees. *H. sericeum* (233) was the dominant and most abundant species, with the highest IES value (Table 3). *T. tortuosa*, *O. lyellii*, *Pterigynandrum filiforme*, and *Leptodon smithii* were less frequent and very scarce, with lower IES values (17). Mats were the most dominant again, with 63.6%. Customary epiphytes and indifferent species had equal values (36.3%). *T. tortuosa*, *S. ruraliformis*, *T. subulata*, *Z. rupestris*, *B. capillare*, *Brachytheciastrum velutinum*, *Homalothecium lutescens*, *H. sericeum*, *Hypnum cupressiforme*, and *Pterigynandrum filiforme* only occurred in the basal zone (Table 3).

3.2. Middle zone

Seven bryophyte species were found on the middle zone of young trees. Among these taxa, *Habrodon perpusillus* (350) and *Frullania dilatata* (340) were the most frequent and dominant (Table 3). Mats (57.1%) and customary epiphytes (71.4%) were dominant on the middle zone of young *C. libani* trees. The middle zone of the middle-aged trees contained 8 species. Among them, *Orthorichum lyellii* (237), *H. perpusillus* (287), *Leucodon sciuroides* (275), and *F. dilatata* (263) were the most frequent and the most common (Table 3). In this zone, the predominant life forms with the highest species affinities were mats (50%) and customary epiphytes (75%). A total of 9 bryophyte species were determined from aged cedar trees. As with the young trees, *H. perpusillus* (300) and *F. dilatata* (333) were the most frequent and the most dominant (Table 3). Mats (44.4%) were still the most dominant, followed by cushions (33.3%), tails (11.1%), and fans (11.1%). In the middle zone of aged trees, 66.6% of the species were customary epiphytes.

3.3. Top zone

A total of 9 species were found in the top zone of young, middle aged, and aged trees. In this zone of young trees, according to the frequency classes, *Habrodon perpusillus* (270) and *Frullania dilatata* (350) were the most dominant. *Orthotrichum lyellii* and *O. speciosum* were the most abundant, with relatively high IES values, whereas *O. striatum* (20) was very scarce, with the lowest IES value (Table 3). On middle aged trees, *O. lyellii*, *H. perpusillus*, and *F. dilatata* were the most dominant and the most frequent species in the top zone, while *Leucodon sciuroides* and *O. speciosum* were the most abundant species. *O. striatum* (25) was very scarce again. As with the young trees, *H. perpusillus* (300) and *F. dilatata* (341) were again the most dominant in this zone of aged trees. However, this time *O. lyellii* (291) was also a dominant species on aged trees. Cushion (37.5%) and mat (42.8%) life forms were predominant on both young and middle aged trees, but, on aged trees, mats (44.4%) were the most frequent and cushions the second-most frequent (33.3%). With regard to habitat affinity, customary epiphyte species were the most common in the top zone of all tree age classes. The middle zone and top zone contained no exclusive species.

3.4. TWINSPAN classification

According to TWINSPAN analysis, the epiphytic bryophyte communities were divided into 2 main groups and 5 different subgroups associated with the successional gradient (Figure 2). The first main group (group A) was composed of lower base communities. Group A was characterised by abundant *Hypnum cupressiforme*, abundant *Homalothecium lutescens*, and moderately abundant *Brachytheciastrum velutinum* (Figure 2). These species were only found on the bases of the tree trunks. The second main group (group B) was composed of middle zone and top zone epiphytic communities. Group B was characterised by abundant and dominant *Orthotrichum lyellii*, abundant *O. speciosum*, and abundant *Leucodon sciuroides*.

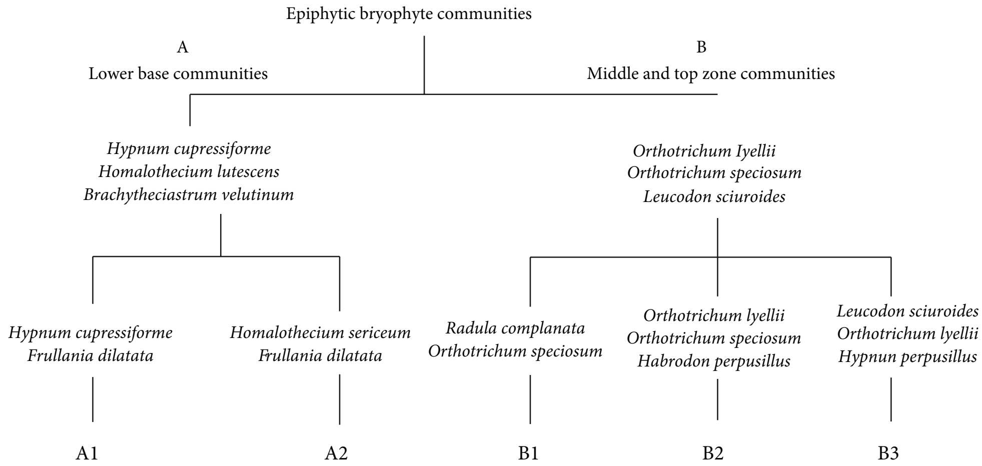

Figure 2. The epiphytic communities identified by multivariate analysis (TWINSPAN).

The 5 different subgroups were A1, A2, B1, B2, and B3. The A1 subgroup was characterised by *H. cupressiforme*, which only occurred on the lower base, and the dominant liverwort taxon *F. dilatata*. The A2 subgroup was characterised by *H. sericeum*, which was the most dominant on the lower base, and *F. dilatata*. The B1 subgroup was characterised by *Radula complanata* and *O. speciosum*. The B2 subgroup was characterised by *O. lyellii*, *O. speciosum*, and *Habrodon perpusillus*, and, finally, the B3 subgroup was characterised by *L. sciuroides*, *O. lyellii*, and the dominant *H. perpusillus* (Figure 2).

Group A was characterised by lower base communities. The A1 subgroup community (*Hypnum cupressiforme* and *Frullania dilatata*) was only found on the lower base of, primarily, young trees. The community was represented in 13 relevés, with *H. cupressiforme* as the dominant species. The A1 subgroup was co-dominated by liverwort taxa, such as *F. dilatata* and *R. complanata*. Another pleurocarpic species, *H. lutescens*, also appeared frequently. The life form of the dominant species in this community was mat.

The A2 subgroup community (*Homalothecium sericeum* and *Frullania dilatata*) was represented by 8 relevés and was also mainly found on the lower base, where more moisture is available compared to the middle and top zones. This community was also found in the basal zones of young and older trees. *Homalothecium sericeum* was the dominant species, and *Frullania dilatata* was co-dominant. The mat life form was still the most dominant, but short turfs also appeared in this community.

Group B was characterised by middle and top zone communities. The B1 subgroup community (*Radula complanata* and *Orthotrichum speciosum*) comprised 12 relevés including mostly meso-xerophytic species. The B1 community, which was common on older trees, was basically dominated by *R. complanata* in the middle zone and by the cushion-type species *O. speciosum* in the upper zone. Within the community, *F. dilatata*, *L. sciuroides*, *H. perpusillus*, *Leptodon smithii*, and *O. lyellii* were also found. The mat life form was dominant, and the cushion life form was co-dominant. With regard to habitat affinity, customary epiphytes were dominant.

The B2 subgroup community (*Orthotrichum lyellii*, *O. speciosum*, and *Habrodon perpusillus*), which was the most common in the study site, was described by 42 relevés. This subgroup was mostly located in the top zone of middle aged trees, but was also found on aged trees. The community was characterised by acrocarpous mosses (*O. lyellii* and *O. speciosum*) and the pleurocarpous moss *H. perpusillus*. In addition, xerophytic *F. dilatata* and *L. sciuroides* were also constant. The cushion life form and customary epiphyte taxa were also dominant within the community.

The B3 subgroup community (*Leucodon sciuroides*, *Orthotrichum lyellii*, and *Habrodon perpusillus*) was represented by 15 relevés and mainly found in the middle zone of middle aged trees. The community was dominated by acrocarpous cushion moss (*O. lyellii*) and pleurocarpous mosses (*L. sciuroides* and *H. perpusillus*). *O. speciosum* and *Leptodon smithii* were also moderately common. *F. dilatata* was constant in this community. With regard to life forms, mats, cushions, and tails were co-dominant, and customary epiphytes were the most common within the community.

Finally, the physiognomy of tree base communities (group A) at the study site was determined by the pleurocarpous mosses *H. cupressiforme* and *Homalothecium sericeum*, while that of the trunk communities (group B) was determined by the acrocarpous mosses *Orthotrichum* spp. and pleurocarpous *L. sciuroides*. In addition, *F. dilatata* was constant on both trunks and tree bases.

3.5. Ordination of epiphytic communities

The Detrended Correspondence Analysis (DECORANA) ordination of the 90 samples on axis 1 and axis 2 is shown in Figure 3. Figure 3 also shows the distribution of the 5 TWINSPAN-based epiphytic communities. Here, axis 1 is related to the height gradient of the host tree. Axis 2 is related to the age gradient of the host tree.

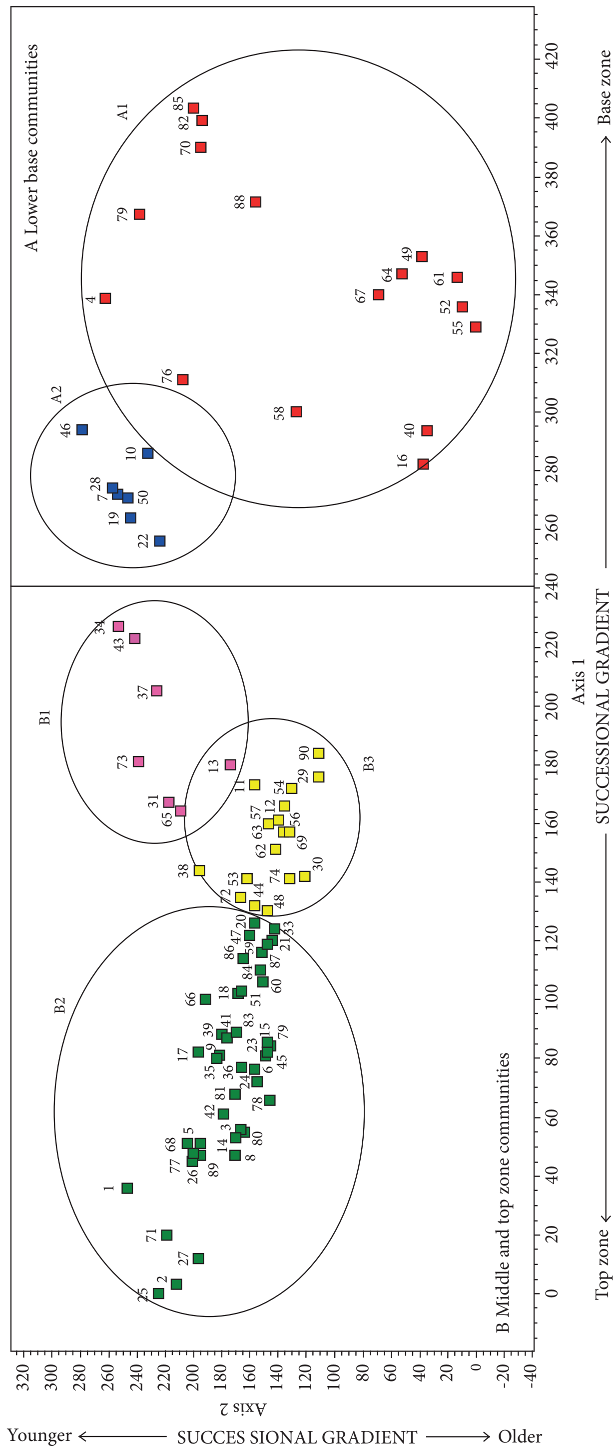

Figure 3. Correspondence analysis (DCA) ordination diagram showing the position of 90 samples of the epiphytic communities based on 5 TWINSPAN groups.

4. Discussion

The lower base of cedar trees is the zone richest in species, containing 16 out of a total of 19 species. Among them, pleurocarpous species, especially mats, were most dominant and most abundant on the lower base (7 species). The basal substratum provides very good shelter for numerous taxa when compared with the other zones. Bases are usually more humid than middle and top zones due to soil influence, the accumulation of rain water, the major capacity of basal bark for water retention, and a low evapotranspiration rate (Mazimpaka et al., 2009). Consequently, bases offer a higher diversity of biotic and abiotic factors compared with other zones (Ezer et al., 2009). That diversity allows for the highest colonisation at the tree base, and may also explain the high diversity and richness of bryoflora, life forms, and habitat affinities. In the Mediterranean climates, deciduous forests offer more suitable conditions for epiphytic bryophytes than coniferous forests (Ezer at al., 2009). Accordingly, many of the acrocarpous mosses, which were mostly mesophytic and xerophytic taxa, were found on the base of *C. libani* trees, such as *Tortella tortuosa*, *Syntrichia ruraliformis*, *Bryum capillare*, and *Tortula subulata*, which are short turf life forms, and *Orthotrichum lyellii* and *Zygodon rupestris*, which are cushion life forms.

Bryophyte species diversity and percentage cover were low in the middle and top zones. Similar results were observed in other studies such as Hébrard (1987), Lara and Mazimpaka (1998), and Ezer et al. (2009). During the summer in the Mediterranean area, the upper zones of the cedar trees are periodically exposed to summer desiccation, which can have an abrasive effect on the epiphytic bryophytes (Moe & Botnen, 2000). As a result, xero-tolerant photophilous *Orthotrichum* spp. are most abundant in the middle and top zones. On young cedar trees, the epiphytic communities of the middle and top zones were dominated by *Orthotrichum* species (*O. lyellii*, *O. speciosum*, and *O. striatum*), by *Habrodon perpusillus* and *Radula complanata* with high vegetative reproduction, and by the xerophytic liverwort *Frullania dilatata* and the xero-mesophytic moss *Leptodon smithii.* While mature trees have more roughly or deeply cracked bark, young trees, with low diameter, have smooth bark. As a result, acrocarpous mosses such as *Orthotrichum* and hepatics such as *Frullania* are often pioneer species in the top zone of young trees (Studlar, 1982). However, on middle and aged trees, xerophytic (mostly cushion-type taxa) and mesophytic species (mostly mats and tails) dominate the top zone. All *Orthotrichum* species (*H. perpusillus*, *L. sciuroides*, *R. complanata*, and *F. dilatata*) are constant species with high IES values in both the middle and top zones. However, some species, such as *T. tortuosa*, *S. ruraliformis*, *B. capillare*, *T. subulata*, and *H. cupressiforme*, disappear before the middle and top zones.

Many authors have stated that the succession of epiphytic bryophytes is complex due to changes in community. Changes in the host tree may be the primary cause of epiphytic succession, while positive and negative interactions among epiphytic bryophytes are also important (Yarranton, 1972; Studlar, 1982; Lara & Mazimpaka, 1998).

Finally, cushion forms of customary epiphytic photophilous mosses (*Orthotrichum* spp.) are found on the upper parts of the trunk, while the lower parts of the trunk appear covered with indifferent mats of pleurocarpic mosses, such as *Homalothecium* spp. and *Hypnum cupressiforme*, revealing a wetness gradient along the trunk related to stem diameter. A microclimatic gradient develops at progressively higher levels on the tree as the moisture level decreases and the light intensity increases, leading to the observed distribution of cushion-form mosses (Studlar, 1982).

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