

*Original research***Successional trends of some epiphytic bryophytes in Mediterranean Basin****Tülay EZER^{1,*}**, **Mevlüt ALATAŞ²**, **Nevzat BATAN³**¹Niğde Ömer Halisdemir University, Faculty of Science, Biology Department, 51100 Niğde, TURKEY²Munzur University, Engineering Faculty, Department of Bioengineering, 62000, Tunceli, TURKEY³Karadeniz Technical University, Maçka Vocational School, 61750, Trabzon, TURKEY*Corresponding author, e-mail: tuezer@gmail.com; tezer@ohu.edu.tr

Abstract: Bryophytes are pioneer plants of different substrate types such as soil, rock and tree. Colonisation of epiphytic bryophytes on tree trunk is mainly determined by ecological factors of environment. Environmental drought is one of the most important abiotic factors affecting the distribution on epiphytic habitats of species in particular. In addition, phorophyte type, tree exposure, height, tree age, tree canopy and forest stand type as well as climatic conditions were the most important ecological factors influencing bryophyte colonisation along trunk surfaces and epiphytic bryophyte succession. The present study is focused on successional trends of epiphytic bryophytes in Mediterranean Basin. And, also it reveals the relationship between successional trends and the life forms and the life strategies of the epiphytic bryophytes. Thus, this study aims to fill this gap by adding more new information to this field.

Keywords: Epiphytes, Liverworts, Mosses, Succession

Citing: Ezer, T., Alataş, M., & Batan, N., 2019. Successional trends of some epiphytic bryophytes in Mediterranean Basin. *Acta Biologica Turcica*, 32(4): 181-193.

Introduction

Succession include all of the vegetational changes which occur in the same habitat over a certain period of time. The gradual development of the succession can be observed quickly and easily in the first stages, but, approach towards the climax stage, the evolution of the stages is slower due to competition of the species. In the vegetation, progressive succession occurs with increasing structural complexity and species richness. On the contrary, regressive or retrogressive succession occurs with structural degradation resulting from the deterioration of habitat conditions (humidity, heat, light etc.) and the decrease of species richness (Akman et al., 2004).

Primary succession, a type of succession, occurs on previously unvegetated area and the development time varies depending on habitat conditions. While, with the effect of ecological factors, changes occurring in vegetation along with the environment are defined as "allogeneic succession", the succession formed by

changing the environment of the vegetation itself is called the "autogenous succession" (Tansley, 1920). Secondary succession occurs on previously vegetated landscapes with the caused by a partial destroying in the ecosystem, such as overgrazing, cutting, or fire. The regeneration of vegetation depends on whether these external effects continue.

The aim of the present study was to reveal the relationship between life forms and life strategies of epiphytic bryophytes and colonization stages on epiphytic habitat and successional tendencies.

General features of bryophytes

Evolutionally, bryophytes, more complex than algae and fungi, more primitive than ferns and flowering plants, are the largest second group of terrestrial plants. The group including three divisions as hornworts, liverworts and mosses. Bryophytes have been surveyed in three classes under the classical Bryophyta division until the last

molecular phylogeny studies. In addition to the morphological characters, studies on rRNA sequences and chloroplast genes with low variability revealed that these three classes should be handled in three divisions under Bryobiotina subkingdom. These divisions consist of

Marchantiophyta (liverworts, about 5,000 species), Anthocerotophyta (hornworts, about 150 species), and Bryophyta (mosses, about 13,000 species) (Glime, 2009; Goffinet and Shaw, 2009) (Fig. 1).



Figure 1. a. Marchantiophyta (*Marchantia polymorpha* L. subsp. *ruderalis* Bischl. & Boisselier), b. Anthocerotophyta (*Anthoceros agrestis* Paton), c. Bryophyta (*Encalypta vulgaris* Hedw.) (original)

Bryophytes have a wide distribution in all the climates of the world where there is enough moisture to survive, from the tropical regions to subarctic and subantarctic regions. Although bryophytes are known as terrestrial plants, they can also be found at the edges of water, and sometimes completely submerged in water. Some species of mosses can also be found at the seaside, but none of the bryophytes live in the seas. They have a wide distribution in areas with more humid climates, shady areas and fresh water (Fig. 2). In addition, they can survive on extreme conditions such as arid environments with very little soil and moisture. Bryophytes can be found in various habitats such as tree bark, bare rock surfaces where many plants can not survive (Schofield, 2001).

The mosses are morphologically divided into two large groups as acrocarpous and pleurocarpous (Fig. 3). In acrocarpous mosses, the gametophyte is perpendicular on substratum, while sporophyte is located at the tip of gametophyte or main branches. In the pleurocarpous mosses, gametophyte usually develops parallel to the substrate and have secondary stems or side branches. Sporophyte is located perpendicular to the gametophyte on small bud-like lateral branches on the main stem or branches. Some species such as *Cryphaea* and *Fontinalis* are cladocarpous and gametangia are located on short side branches (Smith, 2004).



Figure 2. Habitats of bryophytes (original)

Bryophytes grow in various habitats. Some of these habitats; terricolous (on soil), epilithic (on rocks), epiphytic (on plants), corticolous (on tree trunks and barks), epiphyllous (on leaves) epixilous (on fallen dead or dying trees) (Fig. 4). In this development, gametophyte's ecological requirements play an important role.

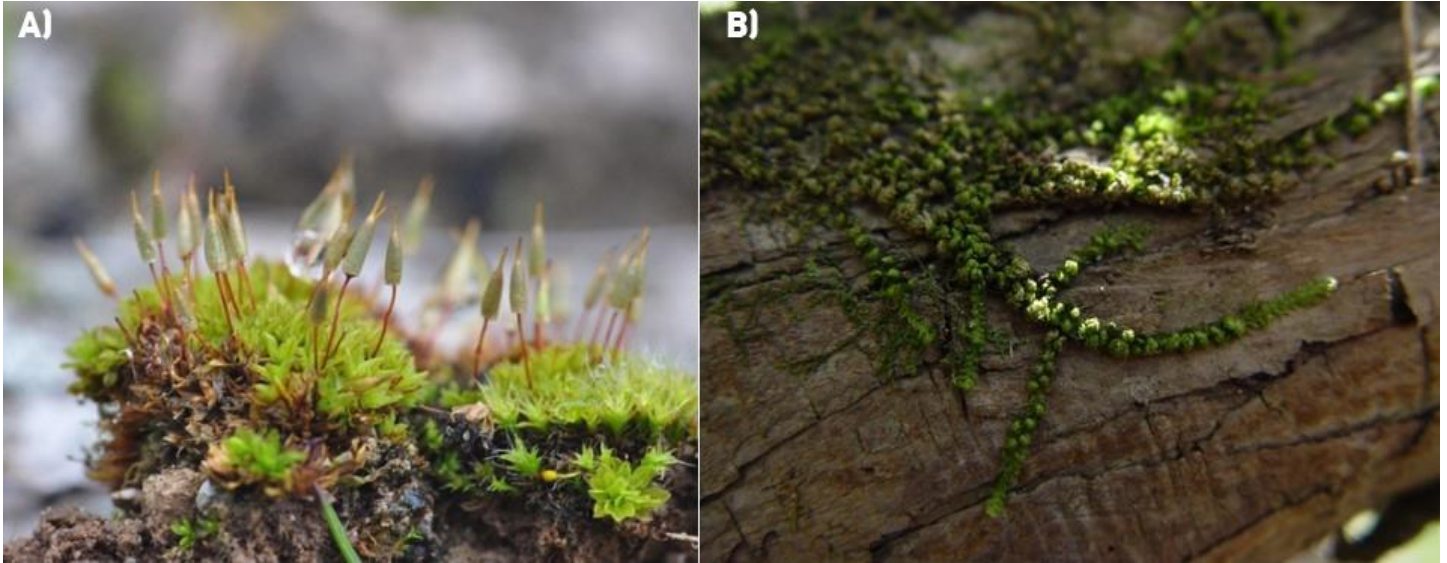


Figure 3. a. Acrocarpous moss (*Encalypta vulgaris* Hedw.), b. Pleurocarpous moss (*Leptodon smithii* (Hedw.) F. Weber & D. Mohr) (original)



Epiphytic moss

Epixilous moss

Figure 4. Epiphytic and epixilous mosses (original)

Bryophytes have their own ecological preferences. These ecological features are mainly characterized by the humidity, the acidity, and the light conditions of the habitats. According to habitat acidity; bryophytes are named as the acidophiles (in the $\text{pH} < 5.7$), sub-neutrophils (in the $\text{pH} 5.7-7$), and basophils (in the $\text{pH} > 7$). According to the humidity conditions of the habitat; bryophytes are named as the hygrophytes, mesophytes, and xerophytes. Some bryophytes are also referred to as hydrophytes that have adapted to floods. Rheophytic bryophytes grow

submerged in a part of the year, but that are emergent at other times. According to light requirements; while bryophytes that grow in open habitats or in part in shady habitats are named as photophytic, bryophytes that have adapted to shade habitats are named as sciophytes (Dierßen, 2001). Smith classified epiphytic bryophytes as either *obligate* and *facultative* (Smith, 1982). While obligate epiphytes are most frequently found on epiphytic habitats, facultative epiphytes are also commonly found

on other substrata such as soil or rocks (Shaw and Goffinet, 2000).

Life forms and life strategies of bryophytes

The life form is described by Mägdefrau (1982) as the habit of a plant in harmony with its life conditions. The life strategy is described by Stearns (1976) as a system of co-evolved adaptive traits of life history tactic of a species or population (During, 1979). The adaptive traits of bryophytes are based on the life forms, life strategies, and eco-morphological adaptations. The results of numerous studies showed that bryophyte communities are characterized by life forms and life strategies of species (Kürschner, 1994; Frey and Kürschner, 1995; Bates, 1998; Kürschner and Parolly, 1999; Kürschner et al., 1998; Kürschner, 1999; 2004; Sabovljevic, 2004; Kürschner et al., 2006; Guidice and Bonanno, 2010). The life forms and the life strategies show the strong correlation with ecological conditions such as light regime, intensity of drought periods, humidity and perfectly match the ecological site conditions provided by the habitat. They also give evidence to co-evolved mechanisms of habitat maintenance, species dispersal abilities, establishment of species and communities, and environmental demands (Kürschner et al., 1998).

The life forms of bryophytes were classified by Mägdefrau (1982) as ten main groups. These; annuals (An), cushions (Cu), dendroids (De), fans (Fa), mats (Ma), pendant (Pe), short turfs (sT), tall turfs (tT), tails (Ta), and wefts (We). The solitary plants (So) category, which is typical for arid habitats, was added to these life forms by Frey and Kürschner (1991). Finally, in a total, 17 life form has been categorized by Hill et al. (2007) (Fig. 5).

The type of life strategy is determined mainly based on reproduction and dispersal strategies. The life strategy of species also reflects the habitat conditions and provides information about the establishment and re-establishment

of species, populations, and communities (Puglisi et al., 2016). The life strategies of bryophytes were classified by During (1979) as six main categories. These; fugitives (K), annual shuttle species (Pe), colonists (B), short-lived shuttle species (Pk), perennial shuttle species (P), and perennial stayers (A). The geophytic (G) life strategy was added to these life strategies by Frey and Kürschner (1991) as seventh one category. Colonists, perennial shuttle species, and perennial stayers subdivided depending on the sexual and asexual reproduction effort (Kürschner and Parolly, 1999; Kürschner, 2004; Puglisi et al., 2012) (Fig. 6).

Epiphytic bryophytes

Epiphytes are organisms that grow on dead external tissues of a plant without take food and nutrients from live tissues (Barkman, 1958). Epiphytic bryophytes are significant component of many forest ecosystems. The development of epiphytic bryophytes generally depends on preservation status of natural forests, humidity, microclimatic changes, and the regeneration periods of the bark (Smith, 1982; Bates, 1993; Moe and Botnen, 2000). Among them, environmental drought particularly is one of the factors that affect the distribution of epiphytic bryophyte species (Mazimpaka and Lara, 1995). To date, many studies on correlations between epiphytic bryophyte community composition and their phorophyte characteristics have been conducted in Mediterranean Basin (Burgaz et al., 1994; Lara and Mazimpaka, 1998; Draper et al., 2005; Mazimpaka et al., 2009; 2010; Medina et al., 2015; Calleja et al., 2016; Ezer, 2017). These studies showed that phorophyte-type, tree bark characteristics, tree age, diameter at breast height (DBH), exposure of tree stems, forest stand type, and tree canopy as well as climatic conditions were the most important variables influencing bryophyte colonisation on epiphytic habitats and successional stages in Mediterranean areas.

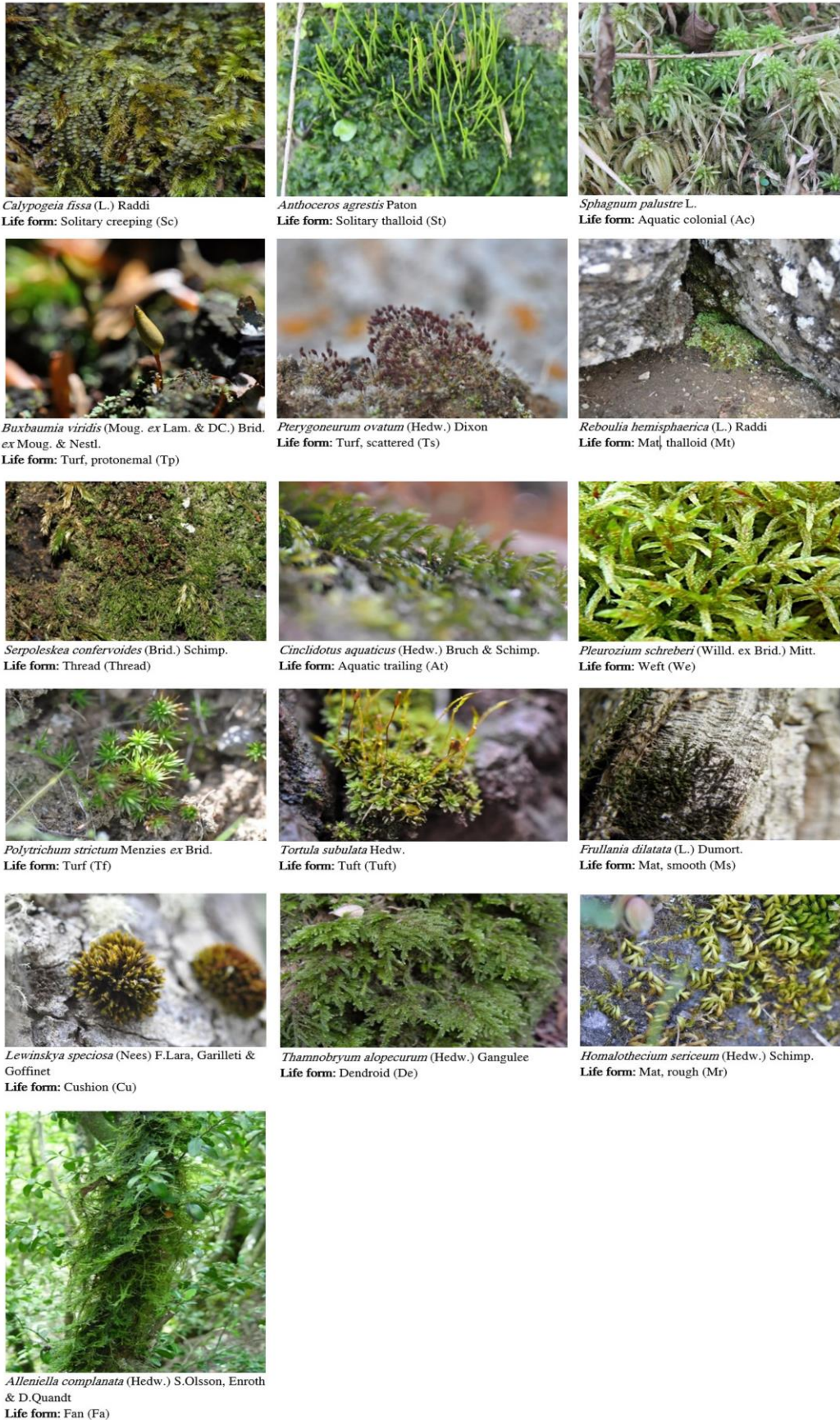


Figure 5. The life forms of some bryophytes



Funaria hygrometrica Hedw. (original)
Life strategy: Fugitives (K)



Entosthodon fascicularis (Hedw.) Müll.
Hal. (original)
Life strategy: Annual Shuttle Species (Pe)



Syntrichia ruralis (Hedw.) F.Weber &
D.Mohr (original)
Life strategy: Pauciennial colonists
(Ba)



Pterygoneurum ovatum (Hedw.) Dixon
(original)
Life strategy: Short Lived Shuttle
Species (Pk)



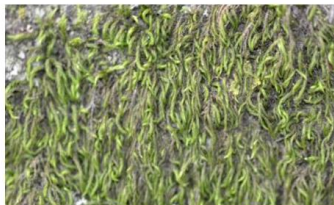
Syntrichia laevipila Brid. (original)
Life strategy: Perennial stayers with
high sexual and asexual reproductive
effort (Av, g)



Homalothecium sericeum (Hedw.)
Schijmp. (original)
Life strategy: Perennial stayers with
moderately or low sexual and asexual



Lewinskya affinis (Schrad. ex Brid.)
F.Lara, Garilleti & Goffinet (original)
Life strategy: Perennial stayers with
high sexual reproductive effort (Ag)



Pterigynandrum filiforme Hedw.
(original)
Life strategy: Perennial stayers with high
asexual reproductive effort (Av)



Bryum argenteum Hedw. (original)
Life strategy: Colonists with high sexual
and asexual reproductive effort (Bv, g)



Frullania dilatata (L.) Dumort.
(original)
Life strategy: Perennial shuttle species
with high sexual reproductive effort
(Pg)



Leucodon sciuroides (Hedw.) Schwägr.
(original)
Life strategy: Perennial shuttle species
with high asexual reproductive effort
(Pv)

Figure 6. The life strategies of some bryophytes

Epiphytic bryophytes are generally more common in angiosperm forests than in gymnosperm forests. Angiosperm forests, consisting of deciduous trees provide suitable epiphytic habitats for bryophytes. In other words, when the leaves of the tree are fallen in winter, the water coming from the rains directly penetrates surface of the trunk, and in the summer, the shadow of the leaves on the tree creates a suitable environment for bryophytes that need absolute moisture. Environmental differences affecting to the epiphytic habitats are seasonally

increasing in deciduous angiosperm forests (Fig. 7). Tree bark pH is another important factor for epiphytic bryophyte colonisation and spatial distribution (Barkman, 1958; Weibull, 2001; Znotina, 2003). Bark pH values show a great variation among phorophyte-type and coniferous trees have a lower pH than deciduous trees (Smith, 1982; Putna and Mežaka, 2014). This variance is determined by the pollutants in the atmosphere together with the soil structure around the tree (Ezer, 2008).



Angiosperm-forest-(original)α



Gymnosperm-forest-(original)α

Figure 7. Bryophytes of angiosperm and gymnosperm forests

The shape and size of the canopy of these forests increase the diversity of the ecological factors on different parts of the tree such as the trunk, base, and branch. For example, epiphytic bryophytes, living on the branches and the forest-canopy are in general more desiccation-tolerance than those living on the lower base (Proctor et al., 2007). Because they are exposed to more insolation. Again, the bark structure at the canopy and branches shows distinct differences from the bark structure at the lower base. The variety of such ecological factors brings together the floristic diversity within the epiphytic bryophytes (Schofield, 2001; Ezer, 2008). Suitable habitats for epiphytes include; nutrient-rich tree bases, cracks and surfaces of tree bark, irregular surfaces in the branches, and collapses on the branch. These microhabitats formed on the trunk varies primarily along

the height of the tree and according to the phorophyte species. Insolation, soil and nutrient status in microhabitats provide colonisation and continuity for epiphytic bryophytes on the tree trunk. Epiphytic bryophytes are usually found together with lichens as pioneers, which provide a suitable environment for establishment on the tree trunk. But, sometimes the colonies formed by lichens entering the competition with bryophytes and prevent the development of bryophytes, especially in arid conditions (Schofield, 2001).

Successional Trends

The floristic composition and spatial distribution of epiphytic bryophyte communities on tree trunks primarily change as the tree ages because of the growth of the tree and accompanying changes in bark characteristics and

microhabitat properties (Studlar, 1982). Namely, as the tree matures, the bark undergoes changes affecting rugosity, peeling, hardness, water retention, dust accumulation and chemical properties. Therefore, the change in the bark of the tree also changes the microclimate of the epiphytic habitat (Lara and Mazimpaka, 1998). The results of several studies on the succession of epiphytic bryophyte communities showed that changes of the floristic composition of epiphytic bryophytes and spatial patterns in the per successional stages are closely related to tree diameter, tree age, and modifications of bark characteristics. Phorophyte-type and microclimate of epiphytic habitats are also relevant determinants of epiphytic bryophyte diversity. Older and larger trees maintain more diverse assemblages than younger ones where specific bark characteristics have not yet developed, with many associated species (Barkman, 1958; Studlar, 1982). Therefore, successional trends of epiphytic bryophytes are fairly complex due to changes in the host tree and positive and negative interactions themselves within the epiphytic bryophyte communities (Lara and Mazimpaka, 1998; Mazimpaka et al., 2010; Ódor et al., 2013; Bargali et al., 2014; Ezer, 2017). In the per successional stages, the epiphytic bryophyte community composition, vertical (tree height) and horizontal (tree diameter) distribution patterns change progressively together with phorophyte growth.

Successional trends on young trees

Several studies (Burgaz et al., 1994; Lara and Mazimpaka, 1998; Draper et al., 2005; Mazimpaka et al., 2009; 2010; Medina et al., 2015; Calleja et al., 2016; Ezer, 2017) on succession of epiphytic bryophytes indicated that young trees (*Quercus faginea* Lam., *Q. ilex* L., *Q. pyrenaica* Willd., *Q. cerris* L., *Fagus sylvatica* L., *Cedrus libani* A. Rich., *Prunus lusitanica* L., *Platanus orientalis* L.) are colonized by pioneer species such as *Lewinskya striata*, *Pulviger a lyellii*, *Lewinskya affinis*, *L. rupestris*, and *Hypnum cupressiforme* in general. *Pterigynandrum filiforme*, *Palamocladium euchloron*, *Homalothecium sericeum*, *Alleniella complanata*, and *Leucodon sciuroides* are also grows on the young trees as primary colonisers. In addition, early colonizers *Frullania dilatata* and *Porella platyphylla* are abundantly found on the base zones of young *P. orientalis*, *F. sylvatica*, *Q. pyrenaica*, *Q. ilex* and *Prunus lusitanica* trees. The acrocarpous mosses such as *Tortella tortuosa* and *Syntrichia ruraliformis* and

the pleurocarpous mosses such as *Eurhynchium striatum*, *E. angustirete* and *Brachythecium albicans*, are very scarcely found the lower bases on young *P. orientalis* and *Cedrus libani* trees. Mats are the most dominant life form at the basal zones of young trees. Tufts, represented by *T. tortuosa*, *S. ruraliformis*, *Tortula subulata*, *Ptychostomum capillare* and Wefts, represented by pleurocarpic mosses, such as *Amblystegium serpens*, *Eurhynchium striatum*, *E. angustirete* and *Oxyrrhynchium hians* are also frequently seen on basal zone of young trees.

Pulviger a lyellii, *Lewinskya speciosa*, *Orthotrichum diaphanum*, *Habrodon perpusillus*, *Porella platyphylla*, *Frullania dilatata*, *Radula complanata*, *Homalothecium sericeum*, *Anomodon viticulosus*, and the customary epiphyte *Leucodon sciuroides* are frequently occurred on middle zones of young *Prunus lusitanica*, *P. orientalis*, *Q. ilex*, *Q. cerris*, *Q. pyrenaica*, *F. sylvatica* and *Cedrus libani* trees. Mats and cushion life forms are wide-spread in this part.

Leucodon sciuroides, *Habrodon perpusillus*, *Frullania dilatata*, *Pulviger a lyellii*, *Lewinskya speciosa*, *Lewinskya striata* are relatively abundant, customary epiphyte *Zygodon rupestris* and *Leptodon smithii* as final colonist are the most dominant on upper parts of young *Q. ilex*, *Q. pyrenaica*, *F. sylvatica* and *Prunus lusitanica* trees. Mat and cushion-type life forms are wide-spread (Lara and Mazimpaka, 1998; Mazimpaka et al., 2010; Ezer, 2017) (Fig. 8).

Perennial shuttle species such as *Lewinskya striata*, *Frullania dilatata*, and *Leucodon sciuroides* are appearing in early successional stages on young trees. Especially, robust pleurocarpous moss *Leucodon sciuroides*, perennial shuttle species with high asexual reproductive effort (Pv), is one of the first colonizer in the epiphytic habitats. The barks of the young trees not suitable for growth of bryophytes because of it's acidic, low moisture content, and smooth texture. Therefore, establishment and growth of propagules of some of the pioneer species can be limited (Bargali et al., 2014). But, perennial stayers with high asexual reproductive effort (Av) such as *Pulviger a lyellii* and *Pterigynandrum filiforme* are also colonized by extensive clonal growth on a new epiphytic habitat.

Successional trends on middle-aged trees

Most of the bark surface of young trees is free of bryophytes and only a small portion is covered by

cushion-type mosses. But, on middle-aged trees, bryophyte cover increases due to communities which are dominated by *Orthotrichum* members. Middle-aged trees are also colonized by secondary colonists. *Orthotrichum*

stramineum undergoes increase, while tail mosses *Leucodon sciuroides* and *Pterigynandrum filiforme* become the most dominant in mature communities (Lara and Mazimpaka, 1998).

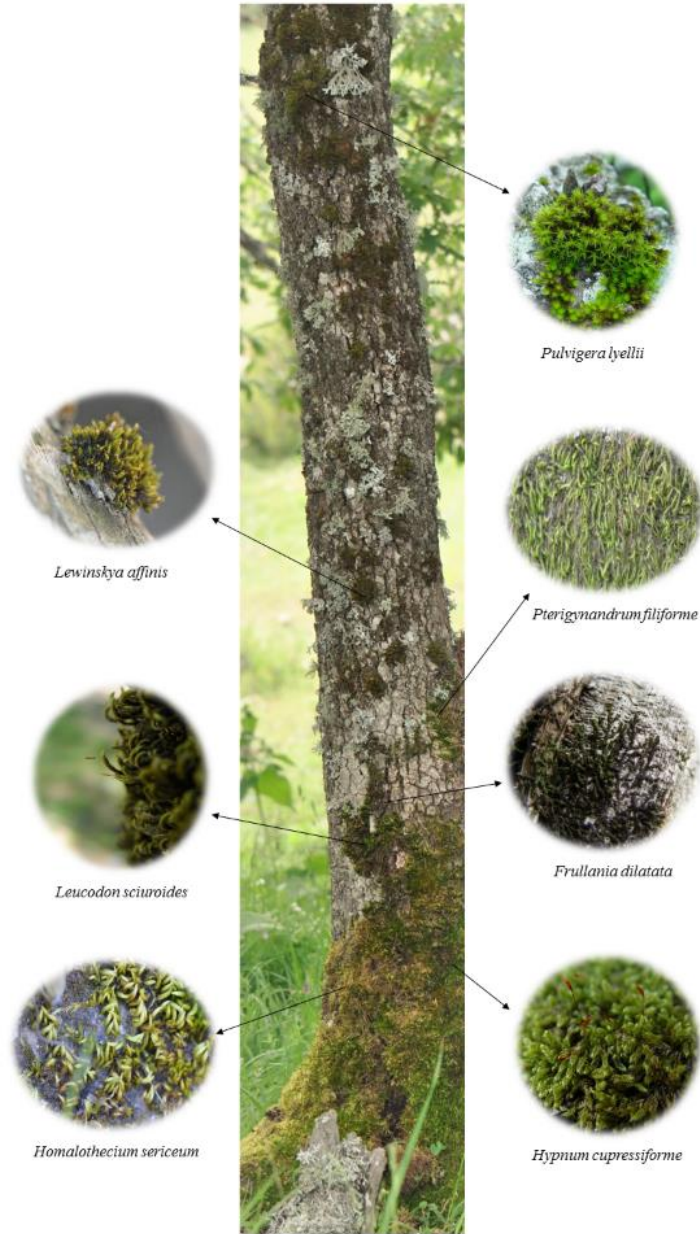


Figure 8. Successional trends of some epiphytic bryophytes on a young *Q. cerris* tree (original)

Pterigynandrum filiforme and *Hypnum cupressiforme*, *Pulviger a lyellii*, *Lewinskya striata*, *Lewinskya affinis*, and *L. rupestris* are most dominant pioneer species on basal parts of middle-aged *Cedrus libani*, *P. orientalis*, *Q. cerris*, *Q. ilex*, *Q. pyrenaica*, *Prunus lusitanica* and *F. sylvatica* trees again. Moreover, these pioneer species are increase their frequency and cover on middle-aged trees.

The liverworts *Frullania dilatata*, *Porella platyphylla* and *Radula complanata* are occurred sporadically. Both of mat and weft life forms are also dominant on the lower base of middle-aged trees.

Pulviger a lyellii, *Habrodon perpusillus*, *Leucodon sciuroides*, *Homalothecium sericeum*, *Porella platyphylla*, and *Frullania dilatata* are the frequent and common on

middle zones of middle-aged trees. In this zone, the predominant life form is mats.

On middle-aged *Cedrus libani*, *P. orientalis*, *Q. cerris*, *Q. ilex*, *Q. pyrenaica*, *Prunus lusitanica* and *F. sylvatica* trees, *Pulviger a lyellii*, *Habrodon perpusillus*, *Leptodon smithii*, and *Frullania dilatata* are frequently grow on the top zones. *Leucodon sciuroides* and *Lewinskya speciosa* are also common on this part. But *Lewinskya striata* is very

scarce. Mat and cushion life forms are most dominant on upper part of middle-aged trees (Fig. 9).

Perennial shuttle species (P) and perennial stayers (A) are the most dominant life strategies on middle-aged trees. Habitat maintenance on middle-aged trees is mainly the result of strongly colonisation of the inhabitants which are growing with unisexual propagules such as *Leucodon sciuroides*, *Pterigynandrum filiforme*, and *Pulviger a lyellii* (Kürschner et al., 2006).



Figure 9. Successional trends of some epiphytic bryophytes on a middle-aged *Q. cerris* tree (original)

Successional trends on aged trees

While the frequency and cover of primary colonists such as *Pulviger a lyellii*, *Lewinskya affinis*, and *Hypnum cupressiforme* on young trees are increasing on middle-aged trees, their colonizations gradually decline on aged trees (*Cedrus libani*, *P. orientalis*, *Q. cerris*, *Q. ilex*, *Q. pyrenaica*, *Prunus lusitanica* and *F. sylvatica*). Even, some species such as *Lewinskya rupestris* and *Brachytheciastrum velutinum* disappear on aged trees. At the same time, *Pterigynandrum filiforme* and *Leucodon sciuroides* which are early colonizers are becoming co-

dominant on aged *Q. pyrenaica* trees (Lara and Mazimpaka, 1998). Perennial stayer *Homalothecium sericeum* is conspicuously dominant species on aged trees. Final colonists (e.g. *Zygodon rupestris*, *Leptodon smithii*, *Antitrichia californica*, *Ptychostomum pallens* and *Syntrichia virescens*) are gradually appear on aged *Cedrus libani*, *P. orientalis*, *Q. pyrenaica* and *Q. cerris* trees, whereas *Porella platyphylla*, *Syntrichia princeps* and *Syntrichia laevipila* declines and *Radula complanata* disappears. Mat life form and perennial stayer strategy become dominant as the tree ages (Fig. 10).



Figure 10. Successional trends of some epiphytic bryophytes on an aged *Q. cerris* tree (original)

Conclusions

Finally, colonization on trunks of epiphytic communities in the early successional stage begins with desiccation tolerant small cushions of Orthotrichaceae members which are sparsely established on these young trees. As the tree ages, frequency and cover of the pioneer species increase, and new cushion and tail-shaped mosses appear. The epiphytic bryophyte communities in the middle and advanced successional stages of succession toward to climax are dominated by mat and tail type bryophytes and robust pleurocarpous mosses that facultatively colonise, whereas cushion-type mosses decline.

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