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Reprint of: Patterns and drivers of species composition of epiphytic bryophytes and lichens in managed temperate forests ☆

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ABSTRACT

Epiphytic bryophytes and lichens are an important component of the endangered forest biota in temperate forests, their diversity and composition patterns being regulated by tree, stand and landscape scale factors. The aim of this study is to improve ecological understanding of such factors in managed coniferous–deciduous mixed forests of Hungary in the context of forest management. In particular, this study investigate the effect of tree species composition, stand structure (tree size distribution, shrub layer and dead wood), microclimate (light, temperature and air humidity), landscape and historical factors on the stand level and tree level composition of epiphytic bryophytes and lichens. The relationships were explored by multivariate methods (redundancy analysis, canonical correspondence analysis and variation partitioning) and indicator species analysis. Tree species is among the most important driver of species composition in both organism groups. For bryophytes, the continuity of forest microclimate and the presence of shrub layer are also important, while lichen assemblages are influenced by light availability. Landscape and historical variables were less influential than stand scale factors. On the basis of our results, the main strategy of management focusing on epiphyte diversity conservation should include: (1) the maintenance of tree species diversity in mixed stands; (2) increasing the proportion of deciduous trees (mainly oaks and hornbeam); (3) the maintenance of large trees within the stands; (4) the presence of shrub and regeneration layer; (5) the creation of heterogeneous light conditions.

1. Introduction

Epiphytic bryophytes and lichens comprise a considerable part of the forest biota in the temperate and boreal zone (Barkman, 1958; Ellis, 2012; Smith, 1982). In moist boreal coniferous forests they play an important role in ecosystem processes, influencing water balance and nutrient accumulation (McCune, 1993; Pike, 1978; Pypker et al., 2006a,b). In deciduous and mixed forests their biomass is smaller, but they largely contribute to forest biodiversity (Coppins and Coppins, 2005; Slack, 1977).

Their diversity and composition patterns are regulated by tree, stand and landscape scale factors (Barkman, 1958; Bartels and Chen, 2012; Ellis, 2012; Hauck, 2011; Marini et al., 2011; Nascimbene et al., 2012). Many studies focused on tree level patterns have emphasized that different tree species in the same locality maintain diverse epiphytic assemblages (Mezaka et al., 2012; Slack, 1976; Szövényi et al., 2004) as an effect of different chemical–physical features of the bark (Bates and Brown, 1981; Fritz and Heilmann-Clausen 2010; Gustafsson and Eriksson, 1995). Tree size and age are also relevant determinants of epiphyte diversity; larger and older trees maintain more diverse assemblages than younger ones, with many associated species (Fritz et al., 2008a; Lie et al., 2009; Nascimbene et al., 2009a). This phenomenon has a complex explanation: big trees provide larger colonization surface (area effect), and old trees ensure longer time for the establishment and growth of local populations, also providing higher microhabitat diversity.

Abbreviations: CCA, canonical correspondence analysis; DBH, diameter at breast height; DCA, detrended correspondence analysis; ISA, indicator species analysis; RDA, Redundancy Analysis; SD, standard deviation.

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On a tree, a clear vertical zonation of epiphytes is observed, which appears in the vertical distribution of different growth forms, and functional traits (Fritz, 2009; McCune, 1993). This is influenced mainly by microclimatic factors as light availability and air humidity (Hosokawa and Odani, 1957; Peck et al., 1995).

At the stand scale, the importance of tree species diversity in driving epiphytic assemblages reflects the host preferences of many epiphytes (Mezaka et al., 2012; Palmer, 1986). However, at this spatial scale also microclimatic factors (light, air humidity and temperature), and structural elements modifying microclimate (canopy openness, shrub layer and vertical structure of the canopy) are very influential for epiphytes (Király et al., 2013; Song et al., 2012). Moreover, old-growth unmanaged stands maintain more diverse epiphytic communities than managed forests (Lesica et al., 1991), providing higher microhabitat and substrate diversity (e.g. higher tree species richness, tree size heterogeneity and presence of veteran trees, quantity and quality of dead wood). The continuity of the forest stands and the available substrates is determinant for many dispersal limited species (Fritz et al., 2008b; Rose, 1992).

At the landscape scale, many epiphytic species are regulated by metapopulation dynamics (Johansson et al., 2012; Löbel et al., 2006; Snäll et al., 2003). The mortality of the local populations is regulated mainly by deterministic factors, as the cessation of the host trees, while the colonization of new areas is influenced by stochastic factors (Löbel et al., 2006; Roberge et al., 2011). The landscape scale distribution of many epiphyte species is limited by their dispersal ability, especially for asexual species with high substrate specificity (Johansson et al., 2012; Löbel and Rydin, 2009), particularly where potential microhabitats have very isolated distributions across the landscape. These species are very sensitive to past and recent habitat fragmentation, and the longevity of the available substrates (Snäll et al., 2004).

Tree, stand and landscape scale factors are considerably modified by human activities which have made cryptogamic epiphytes a threatened group in temperate forests (Paillet et al., 2010). Supported by historical and archeobotanical evidences, 30–80% of these species disappeared from the Atlantic region of Europe before the 18th century (Rose, 1992; Ellis et al., 2011). Recent land use, especially forest management (including timber production and conservation purposes), has considerable influence on survival and local population size of these organisms (Nascimbene et al., 2013a). For this reason, it is necessary to explore the most important regulating factors acting at different spatial scales across regions. While the effect of host species is relatively widely studied for epiphytes there is a lack of information concerning the effect microclimate and stand structure that in our study are accounted for with a set of directly measured variables. The separation of stand level and tree level composition and the comparison of the effects of environmental constraints between epiphytic bryophytes and lichens are also novel to this study.

This study aimed to investigate the effect of potentially relevant factors in determining the bryophyte and lichen diversity of coniferous-deciduous mixed forests in Hungary. In particular, it will explore the effect of tree species composition, stand structure (tree size distribution, shrub layer and dead wood), microclimate (light, temperature and air humidity), and landscape and historical factors on the stand level composition of epiphytic bryophytes and lichens. A similar analysis was also conducted at the tree level, assessing the effect of tree species, tree size and light conditions on epiphytic assemblages on individual trees. Preferences of individual epiphyte species to different tree species were also tested. This study is closely related to Király et al. (2013), which investigated species richness patterns of epiphytes utilising the same dataset.

2. Materials and methods

2.1. Study area

The study area is located in Őrség National Park (N 46°51′–55′ and W 16°07′–23′), West Hungary (Fig. 1). The elevation is 250–350 m, the mean annual temperature is 9.0–9.5 °C and the precipitation is 700–800 mm (Dövényi, 2010). The bedrock consists of alluviated gravel and loess, the most common soil types are pseudogleyic and lessivage brown forest soils, which are nutrient poor and slightly acidic (pH of the 0–30 cm layer is 4.0–4.8, Bidló pers. comm.).

The study area is dominated by beech (*Fagus sylvatica* L.), sessile and pedunculate oak (*Quercus petraea* L. and *Quercus robur* L.), hornbeam (*Carpinus betulus* L.), Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.), forming monodominant and mixed stands as well. The proportion of different subordinate tree species (*Betula pendula* Roth., *Populus tremula* L., *Castanea sativa* Mill., *Prunus avium* L., etc.) is relatively high (Tímár et al., 2002). The main forest habitat types of the region are sessile oak-hornbeam woodlands (Hungarian habitat code: K2), acidofrequent beech woodlands (Hungarian habitat code: K7a), and acidofrequent mixed coniferous forests (Hungarian habitat code: N13) (Bölöni et al., 2008).

Most of the original forests of the region were cut in the middle ages and in the regrown secondary forest the proportion of pioneer tree species (such as *P. sylvestris* and *B. pendula*) and the cover of acidofrequent herbs, bryophytes and lichens increased (Gyöngyössy, 2008; Tímár et al., 2002). Today, the mixed forests with natural tree species composition are increasingly managed harmonizing timber production and conservation purposes. In private forests, stem selection is applied by local farmers without real management planning, while state forests are managed by shelterwood silvicultural systems with a rotation period of 70–110 years (Tímár et al., 2002).

2.2. Data collection

Thirty-five 2–10 ha sized stands were selected by stratified random sampling from the database of the Hungarian National Forest Service (Fig. 1). In all studied stands the age of the dominant trees was between 70 and 110 years. The topography was more or less flat and the top-soil was not influenced by ground-water. The forest stand compartments of the database were grouped according to tree species combination types and the studied plots (5–10 per type) were randomly selected within the groups. In this way the sample represented the main tree species combinations of the region, including a continuous gradient in the proportion of the main tree species. The distance between selected stands was a minimum of 500 m.

Within each stand, a 40 m × 40 m plot was established for stand structure measurements. For each tree with DBH larger than 5 cm geographical position, circumference, species identity, height, height of crown base, and crown projection were recorded. Average diameter and length of logs thicker than 5 cm diameter and longer than 0.5 m were also recorded as well as density of sapling species (tree or shrub individuals taller than 0.5 m and thinner than 5 cm DBH). Relative light conditions (percentage of above canopy total light) were modelled by the tRAYci model (Brunner, 1998) using the position, size and canopy data of the trees (see details in Tinya et al., 2009). For stand level conditions, light values were predicted in 36 systematically arranged points at 1.3 m height using a grid of 5 m intervals. For tree level analyses, relative light values were predicted in the position of each individual tree. Air humidity and temperature were measured in the middle of the