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Patterns of bryophyte diversity and rarity at a regional scale

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Abstract. Information on bryophyte diversity and rarity were combined with information on soil conditions and land use for Walloon Brabant (central Belgium, 1091 km^2) in order to investigate which landscape features sustain the most rare and diverse species assemblages. Presence–absence of 325 bryophyte species was recorded in 87 grid-squares of 4×4 km. Species diversity was significantly correlated with forest cover ($r = 0.71$, $P < 0.001$), sandy soils ($r = 0.61$, $P < 0.001$), loamy soils, ($r = -0.68$, $P < 0.001$), and agricultural fields ($r = -0.49$, $P < 0.001$). The most diverse grid-squares possessed up to 182 species and were characterized by at least 10% forest cover and the presence of unique micro-habitats. Grid-squares with forest cover reaching at least 10% but lacking unique micro-habitats contained between 90 and 130 species. Below 10% forest cover, diversity ranged between 55 and 110 species per grid-square. However, even the least diverse cultivated areas included a significant amount of the regionally rare species. A number of the latter are characteristic in other areas for specific primary habitats lacking in Walloon Brabant but display an unexpected ability to disperse throughout hostile areas and colonize secondary habitats. The tendency of such species to occur in man-made habitats decreased our ability to predict species richness and rarity from landscape features and soil conditions.

Introduction

Interest in biodiversity and conservation biology is rapidly increasing, including concern for lower plants (Hedenäs and Söderström 1992; European Committee for the Conservation of Bryophytes 1995; Hallingbäck and Hodgetts 2000; Tan and Pocs 2000; Kautz and Gradstein 2001; Sabovljevic et al. 2001). However, there are never the resources nor the expertise to survey the total biodiversity of an area. As a result, taxonomically difficult groups such as bryophytes and lichens are rarely included (Pharo et al. 1999). Vascular plants, which are comparatively easily surveyed and constitute the bulk of the primary producer biomass, are therefore often used as a surrogate for total biodiversity in conservation evaluation (Pharo et al. 2000). However, the most diverse sites in terms of vascular plant numbers do not always correspond to the richest sites for cryptogams (Cox and Larson 1993; Prendergast et al. 1993; Prendergast 1997; Pharo et al. 1999). Hence, further analysis is required to identify the ecological conditions that control diversity and rarity patterns of bryophytes. Species occurrence has been well documented for some regions, but there are few studies that summarize and synthesize the relations between bryophyte diversity and landscape features at a regional scale (Fensham and Streimann 1997; Vitt and Belland 1997).

Predicting species diversity from environmental conditions and describing priority areas for conservation have benefited, in the last few years, from the increasing availability of geographic information systems to combine information on species richness and habitat conditions (Swindel et al. 1991; Bojorqueztaquia et al. 1995; O'Brien 1998; Cowley et al. 2000; Lenton et al. 2000). In a previous paper (Vanderpoorten and Engels 2002), we combined information on environmental conditions and species distribution to investigate which environmental factors correlate with the distribution of bryophytes at a regional scale and how the species respond to these environmental factors, in order to provide comprehensive lists of species grouped by environmental conditions. The scope of the present study was to (1) examine whether soil conditions and landscape features control bryophyte diversity and rarity at a regional scale, (2) determine which landscape features sustain the highest levels of diversity and rare species number, and (3) propose regional predictive models of bryophyte diversity and rarity.

Methods

Study area

Walloon Brabant, one of the 10 Belgian provinces, was selected for this study because of the availability of a recent species mapping and of precise information on soil conditions and land use. With 347 423 inhabitants (1/1/1999) on 1091 km^2, the population density in the province is one of the highest in the country (http://www.pixelsbw.com/cartes/belgique.htm). As a consequence, natural habitats are patchy and of fairly reduced size. The western part of the province is hilly, with an altitude ranging between 30 and 170 m. The soils, mostly loamy-sandy with pure loam layers at the top of the hills, make this area best suited for forestry. In the eastern part, conversely, the province is made up of low plateaus covered by pure fertile loam, favoring intensive agriculture. Rock outcrops are restricted to a few areas. They consist of primary schist in the deepest valleys where the tertiary and quaternary sand and loamy layers were eroded, and of chalk in a few places restricted to the most eastern part of the area.

Data sets

Our data include information on species distribution and environmental conditions. Species information consists of presence–absence data for 325 bryophyte species recorded in 87 squares of the Belgian–Luxembourgian Floristical Institute (IFBL) 4 $\times$ 4 km grid (Sotiaux and VanderPoorten 2001a; nomenclature after Sotiaux and VanderPoorten 2001b). A scale of species rarity was built based on species frequencies. Following a national reference of species rarity (Schumacker 1985), species occurring in less than 10% of the grid-squares were considered as rare. The species inventory was completed by examination of material cited in the literature (see Sotiaux and Vanderpoorten (2001a) for a review) at the herbaria BR and LGHF.

Environmental variables include data on soil conditions, vegetation, and land use. Soil conditions were classified by texture and humidity in 14 categories, ranging from humid alluvial soils to dry sandy–loamy or loamy soils on sand. Soil data were scored from a digitized version of the map of soil associations at a 1/500000 scale (Maréchal and Tavernier 1970). Information concerning vegetation and land use was scored from a digital document (Walphot-Cicade 1993) and included different variables such as forest cover (deciduous, coniferous or mix), habitat density, and a number of landscape features such as wastelands, industrial areas and quarries (see Vanderpoorten and Engels 2002 for details).

Data analysis

Using the facilities of a geographical information system, environmental data were superimposed on the IFBL grid used for species recording. After graphic examination of the relationships among variables, a predictive model of species diversity and number of rare species as a function of environmental factors was computed by least-squares regression using backward variable selection with a significance level for staying in the model of 0.05. The validity of these models was tested by cross-validation.

Results

In total, 325 bryophyte species were recorded. Twenty-seven additional previously recorded species (8% of the total number of species currently present), for which we checked the identity in the investigated herbaria, were not seen in the course of this study. Species diversity varied between 55 and 182 species per grid-square, with a median of 91 species.

Regionally rare species (i.e., species occurring in less than 10% of the 87 grid-squares) accounted for 44% of the total number of species in the area (Figure 1). There was a strong correlation between species diversity and number of rare species per grid-square ($r = 0.80$, $P < 0.001$) (Figure 2).

Species diversity was significantly correlated with forest cover ($r = 0.71$, $P < 0.001$), cover of sandy–loamy soils on sand ($r = 0.61$, $P < 0.001$), loamy soils ($r = -0.68$, $P < 0.001$), and agricultural fields ($r = -0.49$, $P < 0.001$) (Figures 3 and 4). The number of rare species in each grid-square had fairly low, although significant, correlation coefficients with forest cover ($r = 0.46$, $P < 0.001$) (Figure 5), pebbly soils ($r = 0.48$, $P < 0.001$), and water surface ($r = 0.54$, $P < 0.001$).

Examination of the patterns of diversity and rarity shows that the grid-squares possessing the highest diversity also contain the maximum numbers of rare species (labels a–g in Figure 2). These grid-squares were characterized by at least 10%

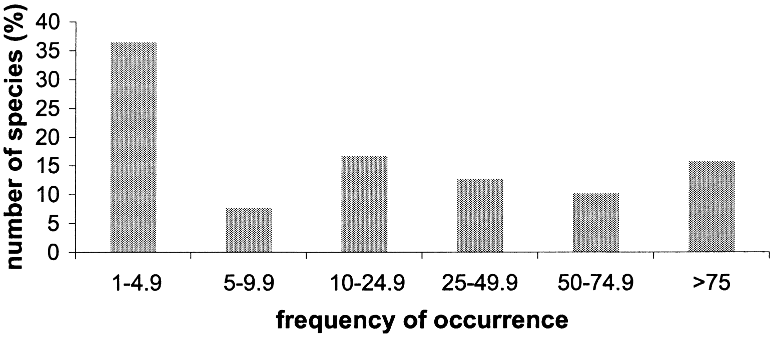

Figure 1. Distribution of frequency of the 325 bryophyte species recorded in 87 4 × 4 km grid-squares in Walloon Brabant.

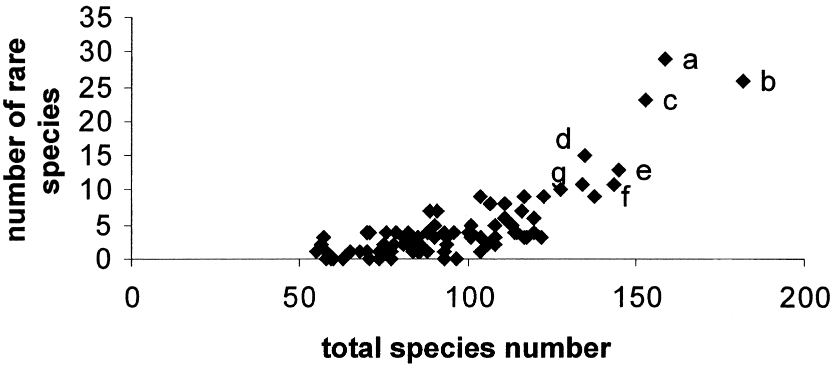

Figure 2. Total number of bryophyte species as a function of number of rare species (i.e., occurring in less then 10% of the investigated grid-squares) in the 87 4 × 4 km grid-squares of Walloon Brabant. Labels a–g identify the most diverse grid-squares including the highest numbers of rare species.

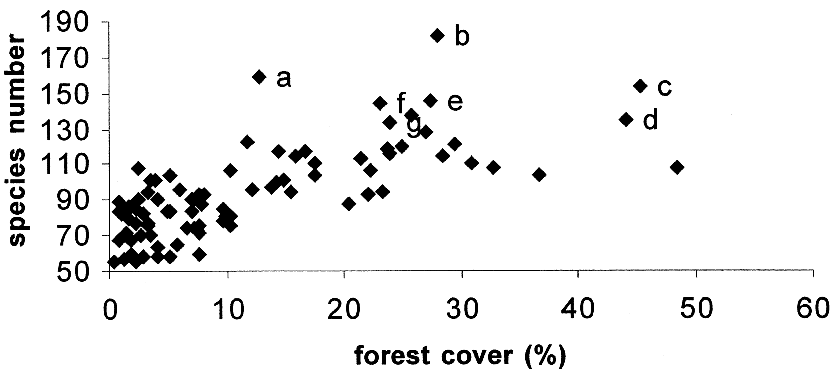

Figure 3. Number of bryophyte species as a function of forest cover in the 87 4 × 4 km grid-squares of Walloon Brabant. Labels a–g identify the most diverse grid-squares including the highest numbers of rare species.

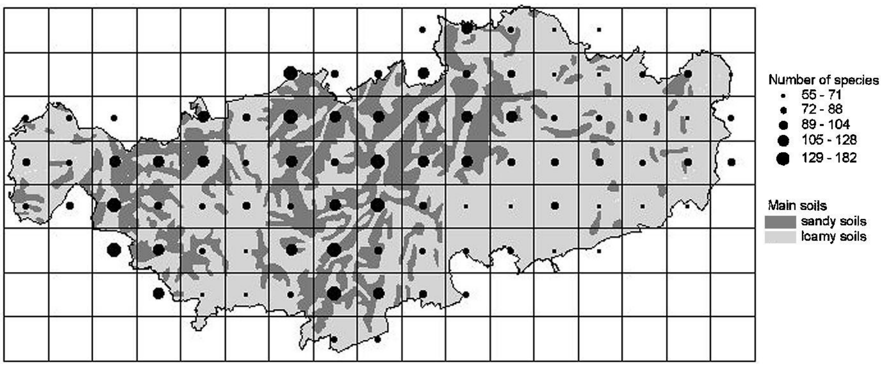

Figure 4. Distribution of species diversity (number of species per 4 × 4 km grid-square) superimposed on soil conditions in the 87 4 × 4 km grid-squares of Walloon Brabant.

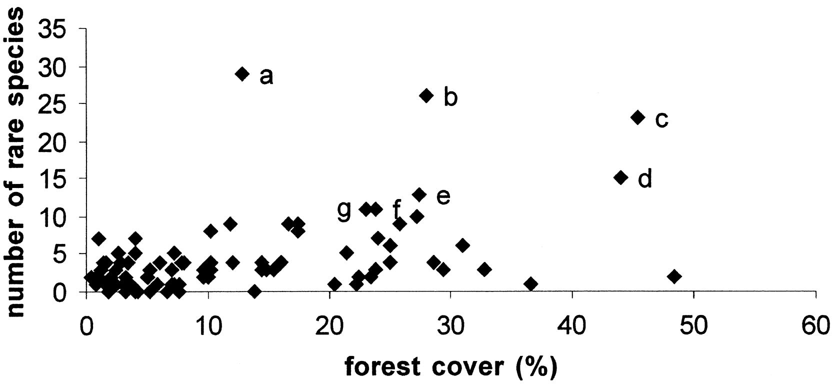

Figure 5. Number of rare species as a function of forest cover in the 87 4 × 4 km grid-squares of Walloon Brabant. Labels a–g identify the most diverse grid-squares including the highest numbers of rare species.

forest cover (Figures 3 and 5) and the presence of rare or unique micro-habitat conditions such as local rock outcrops that were not included in our set of environmental variables on the regional landscape. Grid-squares with a forest cover reaching at least 10% but lacking unique micro-habitats contained between 90 and 130 species (Figure 3). The grid-squares with the lowest diversity were those with less than 10% forest cover, where diversity ranges between 55 and 110 species per 16 km^2. However, grid-squares with forest cover below 10% may contain rather large numbers of regionally rare species (Figure 5).

Forest cover and related edaphic factors could be used as predictors of species richness in a model with a cross-validated multiple correlation coefficient of 0.73:

$$\text{Species number/grid-square} = 103.16 - 0.32(\text{cover of loamy soils}) + 1.05(\text{forest cover})$$

The use of these factors as estimators of rare species numbers resulted in a model with a much lower cross-validated multiple correlation coefficient of 0.51:

Number of rare species/grid-square = 1.874 + 0.212(cover of pebbly soils) + 3.650(water surface)

Discussion

Species diversity was significantly correlated with increasing forest, loamy–sandy and pebbly soil covers, and decreasing loamy soils and agricultural fields. Slightly less than 10% of the total bryoflora was restricted to forest stands and about 25% had an increasing probability of occurrence with forest cover (Vanderpoorten and Engels 2002). This coincides with previous assessments of the role of forest cover on bryophyte diversity (Hebrard and Loisel 1994, 2001; Bates 1995). Species diversity increased with forest cover until reaching a value of about 25% from which diversity did not exceed 130 species per 16 km^2. Unique micro-habitat conditions, containing an associated specialized bryoflora, were necessary to reach higher diversity values. Examination of literature records (see Sotiaux and Vanderpoorten 2001a for details) and herbarium material also tends to indicate that disappearance or degradation of unique habitats, such as alkaline fens and wet heaths, has already led to a decrease in diversity and a loss of specialized species. These results confirm the importance of habitat heterogeneity including rare micro-habitats hosting a specialized bryoflora for the diversity of a regional bryoflora (Jonsson and Esseen 1990; Lampolahti and Syrjaven 1992; Vitt and Belland 1997; Bergamini et al. 2001; Rambo 2001).

Agricultural fields on loamy soils, conversely, had a negative influence on bryophyte diversity, and only two species, *Fissidens taxifolius* and *Bryum caespiticium*, had an increasing probability of occurrence with these factors (Vanderpoorten and Engels 2002). Species richness in agricultural landscapes depends on cropland farming practices and land-use intensity. The bryophyte community of cultivated fields, characterized by a number of thallose liverworts and hornworts, reaches a maximum of diversity in untreated stubble-fields (Bisang 1998; Bisang et al. 1998; Zechmeister and Moser 2001). In the study area, our observations suggest that species of *Anthoceros*, *Phaeoceros*, *Riccia*, and *Sphaerocarpos*, previously designated as fairly frequent (Vanden Berghen 1985), are localized in restricted areas and are decreasing, probably due to year-round crop production and the abusive use of fertilizers (Sotiaux and Vanderpoorten 2001a).

However, even the least diverse cultivated areas included a significant number of regionally rare species. Certain of them, such as *Tortula vahliana*, are of interest at the European scale (European Committee for the Conservation of Bryophytes 1995). A number of these species are, in other areas, characteristic for specific primary habitats lacking in Walloon Brabant, but display an unexpected ability to disperse throughout hostile areas and colonize secondary habitats. For example, *Distichium capillaceum*, a species rare in Belgium where it is confined to slightly calcareous rocks in the mountainous phytogeographical district ‘Ardennais’ (Sotiaux and Sotiaux 1998), was found in large quantity on bricks of a railway bridge in the study area. *Syntrichia latifolia*, a species primarily occurring on tree bases and roots in the flood zone of riverbanks and pool margins, and *Brachythecium plumosum*, a species primarily occurring on rocks or tree roots subject to submergence in fast-flowing streams of mountain areas (Dierssen 2001), were found on dry gravel or concrete far from a river. *Riccia cavernosa*, a species of dried ponds (Schumacker 1985), was found several times in pavement cracks with weeds including *B. argenteum*, *B. dichotomum*, and *Funaria hygrometrica*. All of these species were found fruiting, except for *S. latifolia*, which produces abundant asexual leaf gemmae. The tendency of such species to disperse and occur in man-made habitats decreased our ability to predict species richness and rarity from landscape features and soil conditions.

Conclusions

Bryophyte diversity was significantly correlated with forest cover and reached a maximum in forest grid-squares including unique micro-habitats hosting a rare bryoflora. The least diverse grid-squares were those with less than 10% forest cover. Intensively cultivated areas taken together, however, contained a large number of the regionally rare species. The occurrence of rare species in such areas at least partly relies on the ability of a number of them to disperse throughout apparently hostile areas and to survive in unexpected secondary habitats. Determining rare species ecology and assessing the causes of their rarity thus remains a challenge, due to the low availability of information on their physiological requirements (Cleavitt 2001) and the difficulty of compiling precise information on their scattered habitats.

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