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The effects of environmental variation on bryophytes at a regional scale

Alain Vanderpoorten and Patrick Engels

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The distribution of bryophytes in central Belgium was investigated using species grid-mapping superimposed on a series of maps which included information on soil conditions and land use. Our objectives were to assess the influence of environmental variation on the bryoflora at a regional scale, to examine how bryophytes respond to environmental variation, and to assess the extent to which species ecological and life-history traits determine the accuracy of the predictability of species occurrence in order to provide comprehensive lists of species based on environmental conditions. The first two axes of a correspondence analysis (CA) of the floristic data explained 14.6% of the total χ^2. CA1 was significantly correlated with loamy-sandy soils on a sand layer ($r = -0.74$, $p < 0.001$), forest cover ($r = -0.80$, $p < 0.001$), loamy soils ($r = 0.79$, $p < 0.001$), and agricultural fields cover ($r = 0.61$, $p < 0.001$). CA2 had a low but significant correlation coefficient with pebbly soils cover ($r = 0.38$, $p < 0.001$). The probability of occurrence of 59% of the investigated species could be significantly predicted by logistic regression from the sets of environmental variables. About 55% of the species exhibited an increasing probability of occurrence with increasing forest cover and loamy-sandy soils cover, 1% with agricultural fields and loamy soils cover, and 3% with pebbly soils cover. The predictability of species occurrence varied as a function of four life-history traits (minimum spore size, life expectancy, type of gametophyte and papillose leaf cell walls) and three ecological traits (indicator values of light, temperature and soil acidity). The most predictable species, including a number of leafy liverworts, were characteristic for acidic, fresh and shaded conditions and displayed a strong preference for forest habitats. Taxa with limited predictability included epiphytes and mosses characteristic of pebbly soils due to the ability of these species to efficiently disperse and adapt to various ecological conditions. Species for which the distribution range could not successfully be predicted were either ubiquitous, characteristic for ephemeral habitats, or highly successful in a very common habitat.

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The recognition of correlations between distribution patterns and environmental factors is a vital starting point in testing hypotheses about causes and effects of biotic interactions, historical factors, immediate physiological requirements, and reproductive characteristics of plants (Bates 1995a). Understanding the causes of observed distribution patterns of organisms can constitute a tool for managing and conserving biota effectively (Begon et al. 1990), reconstructing environmental changes in the past, or predicting changes in future species distributions given likely environmental changes (Birks et al. 1998). Modelling present species ranges has benefited, in recent years, from the increasing availability of geographical information systems for simultaneously examining patterns of environmental factors with species distributions (Debinski et al. 1999, Skov

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2000, Guisan and Theurillat 2000, Lenton et al. 2000, Pearce et al. 2001). Although predicting distribution ranges of higher plants has been stimulated by an increasing concern for global climatic change (Huntley et al. 1989, 1995, Hill 1991, Hogg 1994, Iverson and Prasad 1998, Hall et al. 1998, Iverson et al. 1999), it has rarely been done for overlooked taxa like bryophytes (Hill and Dominguez Lozano 1994, Nilsen et al. 1999, Gignac et al. 2000, Gignac 2001) owing to the difficulty in compiling precise data on environmental factors and species distributions at the same scale. Moreover, in comparison with animals and vascular plants, the distributions of bryophytes are imperfectly known and simple mapping of presence or absence of species is still lacking for most countries (Bates et al. 1997).

Using a geographical information system to superimpose a series of maps including information on species distribution, soil conditions and land use, we examine in this paper 1) which environmental factors control the distribution of bryophytes at a regional scale, 2) how the species respond to these environmental factors, and 3) the extent to which species ecological and life-history traits correlate with environmental variation and determine the accuracy of the predictability of species occurrence in order to provide comprehensive lists of species depending on environmental conditions.

Methods

Study area

Walloon Brabant, one of the ten 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⟩). In its western part, the area 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, have determined the choice of a land use oriented to forestry. In the eastern part conversely, the province is made up of low plateaus covered by pure fertile loam favoring intensive agriculture. Hence, there is a strong correlation between soil conditions and land use (Fig. 1).

Data sets

Bryophyte variables

325 bryophyte species were recorded in the course of bryological inventories of the province of Walloon Brabant (Sotiaux and Vanderpoorten 2001a, nomenclature after Sotiaux and Vanderpoorten 2001b). The species occurrence was recorded in 87 squares of the Belgian-Luxembourgian Floristical Institute (IFBL) 4 × 4 km grid. Each square was visited for ca 1 d at least twice a year in order to record the annual or sporadically present species (e.g. *Microbryum* spp., *Tortula* spp., *Fissidens exilis*, *Ephemerum* spp., *Acaulon*, *Dicranella schreberiana*) avoiding periods of drought or frost. Material of rare and/or taxonomically problematic species (e.g., *Plagiothecium*, *Orthotrichum*) was systematically gathered and kept in the private herbaria of the authors.

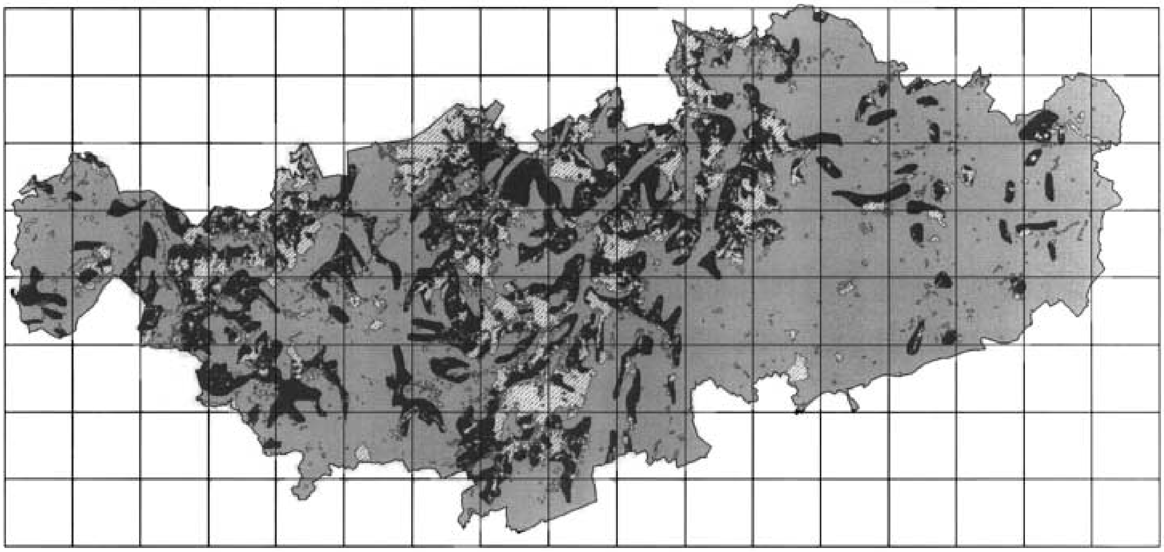

Fig. 1. Simplified map of soil conditions and land use in the study area. Loamy soils appear in light grey, sandy soils in dull grey, and forest stands in hatched.

Table 1. Soil conditions in the study area (classification after Maréchal and Tavernier 1970).

loamy-sandy or loamy soils on clayey-sandy layer
loamy soils with B textural layer (normal association)
loamy soils with B spotted layer
loamy soils with B textural layer (moderately humid association)
loamy soils with B patchy layer
humid alluvial soils without layers
pebbly-loamy soils with B structural or textural layer containing chalk or silexite
pebbly-loamy soils with B structural or textural layer containing schist or limestone
sandy-loamy or loamy soils on sand
pebbly-loamy soils with B structural or textural layer containing schist and sandstone
sandy-loamy or loamy soils on clay
loamy soils with B textural layer (moderately dry association)
loamy soils with B textural layer (dry association)
loamy soils with B textural layer (humid association)

The following ecological and life-history traits were scored on each species included in the analyses based on a review of the literature (Smith 1978, Düll 1992, During 1992, Paton 1999): 1) type of gametophyte and mode of growth (leafy liverwort, thalloid liverwort and hornwort, acrocarpous moss, pleurocarpous moss); 2) minimum spore size (in μm); 3) sexuality (dioicous/monoicous); 4) asexual reproduction (production of specialized diaspores, not including gametophyte fragments); 5) life expectancy (ephemeral or annual/perennial); 6) growth form (chamaephyte, epiphyte, hemicryptophyte); 7) papillose leaf cell walls; and 8) ecology: light, temperature, moisture, phytogeographical range, and acidity index as scored by Düll (1992) but adapted to the present data (for example, *Homalothecium sericeum* and *Neckera complanata* never occur on trees in the study area).

Environmental variables

Environmental variables included data on soils (Table 1), vegetation, and land use (Table 2). Soil data were scored from a digitized version of the map of soil associations at a 1:500 000 scale (Maréchal and Tavernier 1970). Information concerning land use was scored from a digital document (Anon. 1993). Thanks to the facilities of a geographical information system, these data were superimposed on the IFBL grid used for species recording. The cover of each association of soil or type of land use was calculated in each grid-square. These variables were analyzed individually and cumulatively in the analyses. For example, broadleaf trees, conifers, and total forest cover in each grid-square were employed as explanatory variables.

Data analysis

After removal of the species occurring in either $< 10\%$ or all the investigated squares, the matrix of 87 sites and 155 species was submitted to a correspondence analysis (CA) in order to study the segregation of the species along the main floristic axes. After graphic examination of the relationship between the variables, these gradients were correlated with the environmental variables and a set of environmental factors significantly correlated with the floristic gradients was selected.

Species response curves along the selected environmental variables were determined by logistic regression to obtain a prediction of the probability of occurrence p of a species given one or a combination of environmental factors x_I from the matrix of observation (1)/non-observation (0) of the species in the investigated grid-squares. Two models, fitting a monotonic and a unimodal response curve, were tested. These models employed a sigmoid curve: $p = \exp(b_0 + b_1x)/[1 + (b_0 + b_1x)]$ or a Gaussian logit curve: $p = \exp(b_0 + b_1x + b_2x^2)/[1 + (b_0 + b_1x + b_2x^2)]$ (ter Braak and Looman 1986). Employing these two models and their logarithmic expression, a logistic regression using backward variable selection with a significance level of 0.05 for staying in the model was computed for each species. The fit of each model was measured by the correct classification rate (CCR), which is potentially more informative than a goodness-of-fit statistic (Ryan 1997). The CCR is calculated by dividing the predictor into classes and comparing the predicted and observed relative frequencies of occurrence of a species in each class of the predictor and is expressed as a percent value. For

Table 2. Variables of land use.

1. Forest cover
   1.1. broad-leaf trees
   1.2. conifers (planted)
   1.3. mixed broad-leaf and conifer forests
2. Agricultural fields
   2.1. permanent meadow
   2.2. agricultural fields
3. Towns
   3.1. green areas
   3.2. continuously populated area
   3.3. discontinuously populated area
4. Miscellaneous
   4.1. wastelands
   4.2. industrial areas
   4.3. quarries
   4.4. water bodies, canals and rivers

each species, the CCR was used as the criterion for selecting the model best fitting the data.

In order to investigate the relationships among habitat conditions, species life-history and ecological traits, and species predictability, we ranked the species depending on their CCR and examined the significance of the Spearman's correlation coefficient between the species ranks and their traits. The relationship between the species life-history and ecological traits and the main environmental gradients was investigated by studying the correlation between the CA axes (i.e., the species scores) and the species traits.

Results

Effects of environmental variation on species distribution

The first two CA axes explain 10.7 and 4.5% of the total χ^2, respectively. CA1 and CA2 are the only ordination axes significantly correlated with the environmental variables. On CA1, loamy-sandy soils on a sand layer ($r = -0.74$, $p < 0.001$) and forest cover ($r = -0.80$, $p < 0.001$) (inter-correlated at $r = 0.74$, $p < 0.001$), have a negative correlation coefficient, whereas loamy soils ($r = 0.79$, $p < 0.001$) and crop cover ($r = 0.61$, $p < 0.001$) (inter-correlated at $r = 0.63$, $p < 0.001$) are positively correlated with the axis. On CA2, loamy soils with limestone pebbles have a low but significant ($r = -0.38$, $p < 0.001$) correlation coefficient.

Two sets of species segregate along CA1: a set of species with negative coordinates characteristic for sandy-loamy soils and important forest cover, and a set of species characteristic for loamy soils and important crop cover. Along CA2, a set of species with a tendency to occur on loamy soils with limestone pebbles occupies the extreme bottom of the axis (Fig. 2).

Species response curves

Forest, agricultural fields, sandy-loamy soils, loamy soils, and loamy soils with limestone pebbles cover were used as explaining variables in logistic regressions for predicting the species probabilities of occurrence. The probability of occurrence of 59% of the investigated species could be significantly predicted from the sets of environmental variables (Table 3). Although certain b_2 coefficients associated with the squared term in the equations linking the species probability of occurrence with the environmental factors were sometimes significant, comparison of the CCR obtained with the monotonic and unimodal models never suggested that the latter dramatically improved the fit on the data.

The accuracy of these predictions was variable, with CCR's ranging between 50 and 96.1% (Table 3). Eighty-six (56%) species exhibited an increasing probability of occurrence with increasing forest cover and loamy-sandy soils cover (Figs 3a, 4). One percent of the investigated species had an increasing probability of occurrence with agricultural fields and loamy soils cover (Figs 3b, 4), and 3% with pebbly soils cover (Figs 3c, 5).

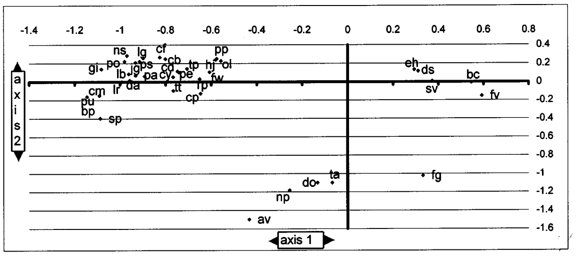

Fig. 2. Species coordinates on the first two CA axes. Only the species whose partial contribution to the inertia of the axis exceeds 1% are represented. av = *Anomodon viticulosus*, bc = *Bryum caespiticium*, bp = *Bartramia pomiformis*, cb = *Cephalozia bicuspidata*, cd = *Cephaloziella divaricata*, cf = *Calypogeia fissa*, cm = *C. muelleriana*, cp = *Chiloscyphus polyanthos*, cy = *Campylopus pyriformis*, da = *Diplophyllum albicans*, ds = *Dicranella staphylina*, do = *Didymodon sinuosus*, eh = *Eurhynchium hians*, fg = *Fissidens gracilifolius*, fv = *Fissidens viridulus*, fw = *Fossombronia wondraczeckii*, gi = *Gymnocolea inflata*, hj = *Hypnum jutlandicum*, jg = *Jungermannia gracillima*, lb = *Lophozia bicrenata*, lg = *Leucobryum glaucum*, lr = *Lepidozia reptans*, np = *Neckera complanata*, ns = *Nardia scalaris*, ol = *Orthodontium lineare*, pa = *Plagiochila asplenioides*, pe = *Pellia epiphylla*, po = *Pogonatum aloides*, pp = *Polytrichum piliferum*, ps = *Pleurozium schreberi*, pu = *Plagiothecium undulatum*, rp = *Rhizomnium punctatum*, sp = *Sphagnum palustre*, sv = *Syntrichia virescens*, ta = *Thamnobryum alopecurum*, tp = *Tetraphis pellucida*, tt = *Thuidium tamariscinum*.

Relationships between species predictability, species ecological and life-history traits, and environmental variation

Species predictability, as assessed by ranking the species CCR's, is correlated with four life-history traits – minimum spore size ($p < 0.05$), type of gametophyte ($p < 0.01$), papillose leaf cell walls ($p < 0.01$) and life expectancy ($p < 0.05$) and three ecological traits – indicator values of light ($p < 0.01$), temperature ($p < 0.01$) and soil acidity ($p < 0.001$). Examination of the CCR's indicate that the most predictable species are characteristic for the grid-squares with the highest forest covers, with CCR's ranging between 61.7 and 96.1%. Species characteristic for loamy and agricultural landscapes and pebbly loamy soils are less predictable, with CCR's ranging between 64.8 and 78.3 and 50.9 and 42.2%, respectively. The gradient of forest and sandy soil cover (CA1) correlates with increasing species requirements for acidic, fresh and shaded conditions and change in gametophyte type, including the decrease in therophyte

Table 3. Ranking of the predictability of the species occurrence from the sets of environmental variables by logistic regression and species whose occurrence could not be significantly predicted from the investigated variables.

	CCR
Forest and sandy soils cover	
Diplophyllum albicans	96.1
Campylopus flexuosus	96.0
Nardia scalaris	95.3
Cephalozia bicuspidata	94.9
Cephaloziella divaricata	93.0
Pleurozium schreberi	93.0
Calypogeia muelleriana	92.9
Calypogeia fissa	92.6
Leucobryum glaucum	92.2
Orthodontium lineare	91.0
Sphagnum palustre	90.6
Gymnocolea inflata	90.5
Hypnum jutlandicum	89.5
Mnium hornum	88.9
Tetraphis pellucida	87.9
Pseudotaxiphyllum elegans	87.9
Bartramia pomiformis	86.5
Plagiothecium undulatum	86.4
Dicranum tauricum	86.0
Lophozia bicrenata	85.2
Metzgeria furcata	85.0
Campylopus pyriformis	84.8
Lepidozia reptans	84.4
Thuidium tamariscinum	80.9
Dicranum montanum	80.5
Dicranum scoparium	80.5
Campylopus introflexus	80.0
Jungermannia gracillima	79.7
Chiloscyphys polyanthos	79.3
Dicranella rufescens	79.1
Cryphaea heteromalla	78.0
Scleropodium purum	77.8
Plagiothecium curvifolium	77.6
Mnium stellare	77.2
Pohlia wahlenbergii	76.5
Conocephalum conicum	75.8
Eurhynchium schleicheri	75.7
Bryoerythrophyllum recurvirostrum	75.2
Fossombronia wondraczeckii	74.9
Isothecium myosuroides	74.7
Plagiochila asplenioides	74.5
Orthotrichum pallens	74.4
Pseudephemerum nitidum	74.2
Eurhynchium striatum	74.2
Encalypta streptocarpa	74.0
Orthotrichum pulchellum	73.8
Polytrichum juniperinum	73.7
Plagiothecium nemorale	73.6
Lophocolea bidentata	73.6
Platygyrium repens	73.3
Brachythecium rivulare	73.3
Pohlia nutans	73.0
Plagiomnium rostratum	72.3
Plagiothecium cavifolium	72.3
Herzogiella seligeri	72.3
Polytrichum formosum	72.1
Frullania dilatata	71.7
Aphanorhegma patens	71.0
Polytrichum piliferum	70.4
Zygodon viridissimus	70.3
Didymodon luridus	70.2
Pylaisia polyantha	69.8
Rhynchostegium murale	69.5
Plagiothecium laetum	69.5
Isothecium alopecuroides	69.1
Didymodon rigidulus	68.2
Fissidens crassipes	68.2
Pohlia lutescens	68.0
Plagiomnium affine	67.9
Brachythecium salebrosum	67.9
Cratoneuron filicinum	67.6
Homalia trichomanoides	67.4
Neckera complanata	67.3
Leskea polycarpa	66.8
Orthotrichum lyellii	66.5
Orthotrichum obtusifolium	66.5
Orthotrichum stramineum	66.1
Platyhypnidium riparioides	65.4
Orthotrichum pumilum	65.0
Pellia epiphylla	63.8
Pellia endiviifolia	63.8
Physcomitrium pyriforme	63.1
Radula complanata	63.0
Orthotrichum striatum	62.8
Amblystegium tenax	62.4
Orthotrichum tenellum	61.7
Agricultural fields and loamy soils cover	
Fissidens viridulus	78.3
Bryum caespiticium	64.8
Pebbly loamy soils	
Anomodon viticulosus	54.2
Pohlia wahlenbergii	53.6
Rhnychostegiella tenella	51.7
Mnium stellare	50.9
Thamnobryum alopecurum	50.9
Uncorrelated species distribution	
Aloina aloides	
Aneura pinguis	
Anthoceros agrestis	
Aulacomnium androgynum	
Brachythecium albicans	
Brachythecium populeum	
Brachythecium velutinum	
Bryum barnesii	
Bryum bicolor	
Bryum gemmiferum	
Bryum rubens	
Bryum ruderale	
Bryum subapiculatum	
Cirriphyllum piliferum	
Dicranella schreberiana	
Dicranella staphylina	
Dicranella varia	
Dicranoweisia cirrata	
Didymodon fallax	
Didymodon sinuosus	
Didymodon tophaceus	
Didymodon vinealis	
Ditrichum cylindricum	
Ephemerum serratum	
Eurhynchium crassinervium	
Eurhynchium pumilum	
Fissidens gracilifolius	
Fissidens incurvus	
Fissidens taxifolius	
Gyroweisia tenuis	
Homalothecium lutescens	
Homalothecium sericeum	
Leptobryum pyriforme	
Leptodictyum riparium	
Lunularia cruciata	
Marchantia polymorpha	

Table 3 (Continued).

	CCR
Marchantia polymorpha	
Mnium marginatum	
Orthotrichum cupulatum	
Pellia neesiana	
Phaeoceros carolinianus	
Plagiomnium undulatum	
Plagiothecium denticulatum	
Pleuridium subulatum	
Pogonatum aloides	
Pohlia melanodon	
Pseudocrossidium revolutum	
Rhizomnium punctatum	
Riccia bifurca	
Riccia glauca	
Riccia sorocarpa	
Sphaerocarpos texanus	
Syntrichia intermedia	
Syntrichia laevipila	
Syntrichia papillosa	
Syntrichia ruraliformis	
Syntrichia ruralis	
Syntrichia virescens	
Tortula subulata	
Tortula truncata	
Ulota bruchii	
Ulota crispa	
Weissia controversa	

and acrocarp number and the decrease in species with papillose leaf cell walls (Table 4). The gradient of pebbly loamy soils (CA2) correlates with increasing species requirements for non-acidic soils and a tendency to possess papillose leaf cell walls.

Discussion

Effects of environmental variation on bryophyte distribution

Soil conditions, especially loam, sand, and pebble content, and forest cover were the best predictors of species distribution. The prime importance of these factors for explaining species distribution and richness at a regional scale was already emphasized by Bates (1995a, b). More precise relationships between soil condition and changes in floristic assemblages were not detected. This lack of resolution might be due to the scale of the grid-square, each unit including heterogeneous habitat conditions and different species assemblages. Indeed, because weakly competitive bryophytes react to topographic variation on scales < 0.25 m^2, Økland (1994) suggested a sample plot size of 0.01 m^2 for identification of the major gradients in cryptogamic vegetation. Hence, the present analyses permit only broad-scale investigation of the bryophyte-environment relationships.

Eighty-six species exhibited an increasing probability of occurrence with increasing forest cover and loamy-sandy soils cover. Species response curves were mostly monotonic, as could be expected along rather short ecological gradients at a regional scale (Jongman et al. 1987). This list of species is difficult to compare in the context of quasi-absence of quantitative data on terricolous bryophytes (Robinson et al. 1989) but includes a series of species, such as *Plagiothecium* spp., *Dicranum* spp., *Scleropodium purum*, *Herzogiella seligeri*, commonly qualified as "forest bryophytes" from field observations and mapping (Hill et al. 1991–1994, Bates 1995b, Hebrard and Loisel 2001). The list also includes a few species, such as *Encalypta streptocarpa* and *Bryoerythrophyllum recurvirostre*, with no particular forest requirements but which mostly occur in the study area on non-acidic sand outcrops. Surprisingly, few of the species highly associated with large forest stands in this study were listed as indicators for woodlands in previous assessments based on field experience by Rose

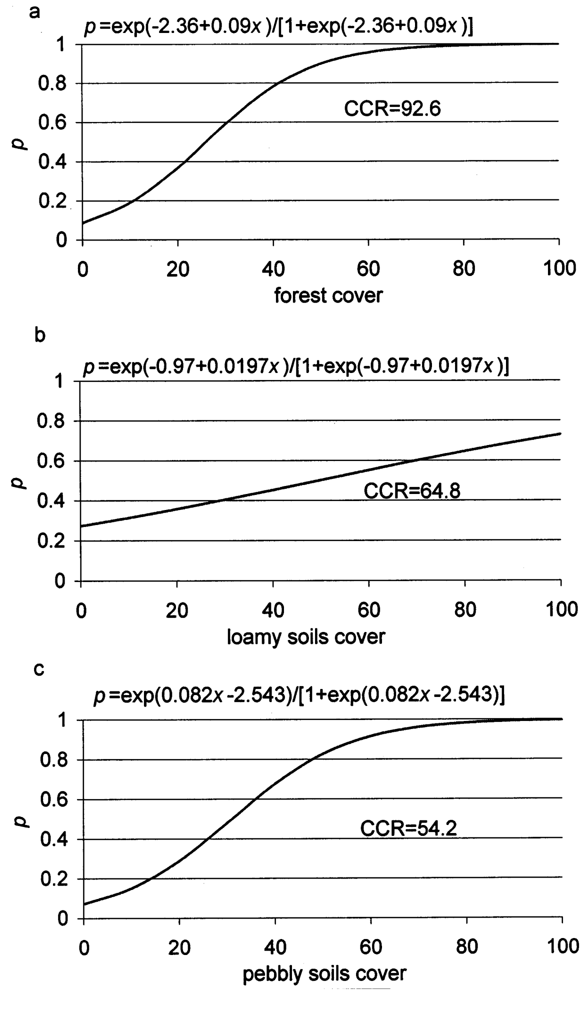

Fig. 3. Response curve of selected species fitted by logit regression. a: response curve of *Calypogeia fissa* as a function of forest cover; b: response curve of *Bryum caespiticium* as a function of loamy soils cover; c: response curve of *Anomodon viticulosus* as a function of pebbly soil cover.

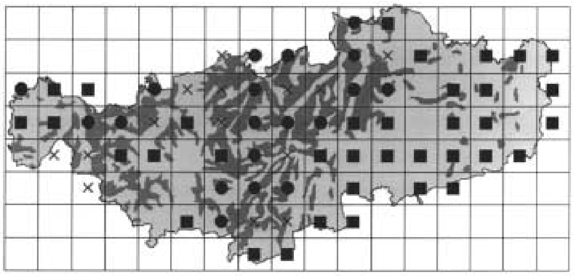

Fig. 4. Distribution of *Calypogeia fissa* and *Bryum caespiticium*, two species with contrasting responses to soil conditions, in the 87 investigated grid-squares superimposed on sandy (in dull grey) and loamy (light grey) soils. Plain circles represent the occurrences of *Calypogeia fissa*, squares represent the occurrences of *Bryum caespiticium*, and crosses represent the co-occurrences of both species in the same grid-square.

(1992) and Trass et al. (1999). Conversely, no species listed by Rose (1992) as "only found in ancient, little-disturbed woodlands", such as *Brachythecium populeum*, *Herzogiella seligeri*, *Mnium stellare*, and *Orthotrichum stramineum*, or listed as "commonly found in ancient woodland but not confined to it", such as *Radula complanata*, *Anomodon viticulosus*, *Eurhynchium pumilum*, *Homalia trichomanoides*, *Homalothecium sericeum*, *Thamnobryum alopecurum*, could be successfully predicted from forest cover. In the study area, indeed, *Anomodon viticulosus*, *Brachythecium populeum*, *Mnium stellare*, and *Thamnobryum alopecurum* are able to colonize man-made habitats such as concrete walls not necessarily located in forested areas. Such geographical differences in species niche have already been pointed out by Shaw (1985) and Vanderpoorten and Durwael (1999). They might be due to different inter-correlations between the environmental variables or among the species (competition) in the study areas. Further formal and more fine-scale analyses on the relationships between forest cover and species distribution are thus needed to define and classify forest bryophytes.

The five species whose occurrence could be significantly predicted from pebbly soils cover were all neutrophilous to calciphilous mosses (pH ranging between 6 and 9, Düll 1992) of rocks or pebbles (Smith 1978). The natural habitats of these species have been largely destroyed but some of them were able to colonize man-made habitats such as concrete. For example, *Anomodon viticulosus*, a species naturally occurring in the area on shaded calcareous rocks or calcareous pebbly forest soils, was found many times in diverse ecological conditions on adequate man-made habitats. As a consequence, the correlation between these species and their natural potential habitat was fairly low.

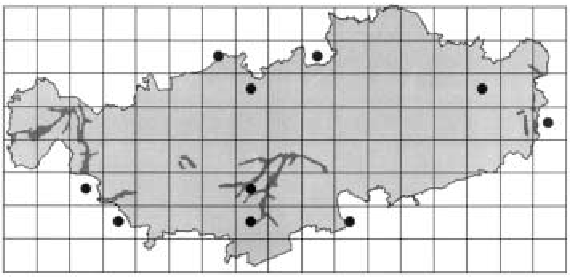

Fig. 5. Distribution of *Anomodon viticulosus* in the 87 investigated grid-squares superimposed on pebbly soils (in dull grey).

Table 4. Significant correlation coefficients between the first two CA axes and the species life history and ecological traits. *, **, ***, NS: $p<0.05$, $p<0.01$, $p<0.001$, and $p>0.05$, respectively.

Character	CA1	CA2
Light	0.29**	0.25
Temperature	0.30**	NS
Acidity index	0.53***	−0.54***
Life expectancy	0.19*	NS
Papillose leaf cell walls	0.20*	−0.42***
Asexual reproduction	NS	0.21*
Type of gametophyte (leafy liverwort)	−0.45***	NS
Type of gametophyte (acrocarp)	0.20*	NS

Relationships between species predictability, species ecological and life-history traits, and environmental variation

The accuracy of the fitted response curves varied depending on species ecological and life-history traits. The most predictable species, including a number of leafy liverworts, were characteristic for fresh, acidic and shaded conditions and displayed a strong preference for forest habitats. Typical forest species, sensitive to drought, are confined to a forest mesoclimate (Laaka 1992, Frisvoll and Prest 1997, Loppi et al. 1999). Such conditions exist only in the largest forest stands. Small, scattered stands are mostly made of contact zones and include species with more photophytic, nitrophytic, and xerophytic requirements (Hebrard and Loisel 2001). The relationship between the indicator value for acidity and the occurrence in forests was probably partly due to the existence of numerous acidic habitats in forests, such as decaying wood, but also due to the correlation between forest cover and sandy, mostly acidic soils in the study area.

The distribution range of another set of species including *Bryum caespiticium*, *Fissidens taxifolius*, *Pellia epiphylla*, *Campylopus introflexus*, *Polytrichum juniperinum* and a number of epiphytes (e.g., *Orthotrichum* spp. and *Ulota* spp.) could also be predicted from forest cover and soil condition, but with a lower accuracy, with CCR's ranging between 0.60 and 0.80. These species had indeed a tendency for given habitat and soil conditions but were not restricted to them. In particular, acidophytic species such as *Campylopus introflexus*, *Polytrichum juniperinum*, *P. formosum*, and *P. piliferum*, usually characteristic of acidic grasslands or forests (Smith 1978, Hill et al. 1991–1994, Düll 1992), were sometimes found in the middle of large, loamy areas at the top of old brick walls. These species possess large, perennial gametophytes but display a strong ability to disperse to suitable microhabitats in otherwise largely hostile grid squares. The dispersal ability relies on features including the production of a vast number of very small spores and the development of dispersal features such as the presence of a well-developed peristome (Hedderson and Longton 1995). Substrate properties may thus have a greater influence on the distribution of such species than space-related factors such as dispersal ability in areas where suitable habitats, although patchily distributed, are separated by rather small distances (Heegaard and Hangelbroek 1999). This holds especially true for epiphytes, which must spread from old to young trees to persist in an area as their hosts eventually die, and efficiently disperse by means of to the production of abundant sporophytes and/or gemmae (Bates et al. 1997). Comparative examination of previous distribution maps by Schumacker (1985) with those of the present study (Fig. 6) suggest that epiphytes are spreading in the study area. Similar evidence of increase has been reported in other European countries including Great Britain (Jones 1991, Adams and Preston 1992, Bates 1995b), Scandinavia (Virtanen and Wahlberg 2000), and The Netherlands (Siebel et al. 2000, Koopman and Weeda 2001). The causes of such a spread are unclear, but the most common hypothesis is a decline in SO_2 (Bates et al. 1997). Another possible explanation for the increase of bryophyte epiphytes is the spread of nitrophytic bryophyte-rich phorophytes such as elder favored by the increase in surface of agricultural wastelands encouraged by recent EEC directives and in agricultural nutrient inputs (Vannerom 1999). Indeed, most of the epiphytes were found in sites with a good light exposure, mostly on isolated trees with eutrophic bark, such as the oldest specimens of *Sambucus nigra*. The spread of epiphytes on common, well-illuminated phorophytes explains their low sensitivity to factors of soil conditions and land use and explains why, as opposed to former studies (Schumacker 1985, Rose 1992, Hazell et al. 1998), these species could hardly be used as indicators of ancient forests.

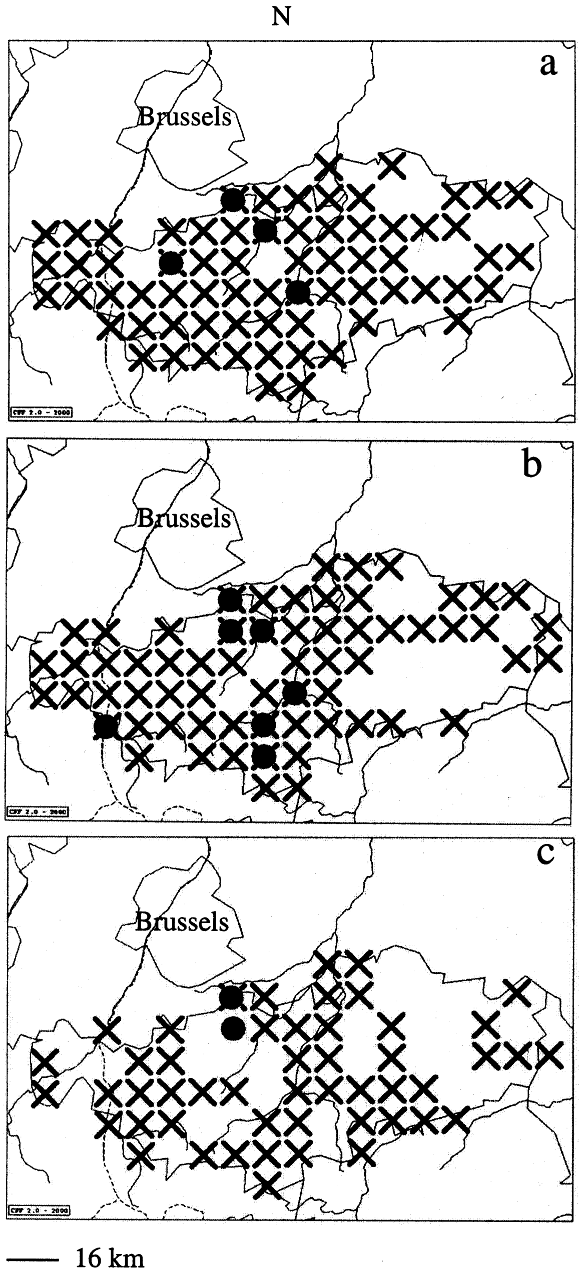

Fig. 6. Distribution of the three epiphytic liverworts *Frullania dilatata* (a), *Metzgeria furcata* (b), and *Radula complanata* (c) in the study area before (plain circles, data from Schumacker 1985) and after 1985 (crosses, present data).

Species for which the distribution range could not successfully be predicted were either ubiquitous, characteristic for ephemeral habitats or highly successful in a very common habitat. Species of ephemeral habitats such as bare soils include a number of therophytes producing large spores (e.g., *Riccia* and *Sphaerocarpos*) persisting in the diaspore bank and germinating when disturbance creates suitable growth condition again (Jonsson 1993). There was therefore a negative relationship between predictability of occurrence, life expectancy and spore size. Highly successful bryophytes in common habitats included a few common and generalist pleurocarp species (e.g., *Eurhynchium* spp., *Brachythecium* spp.) displaying, among the bryophytes, the most competitive features (Grime et al. 1990) and dominating the moss layer in permanent meadows. Ubiquitous species (e.g., *Barbula* spp., *Didymodon* spp., *Tortula muralis*), conversely, were characterized by perennial gametophytes adapted to drought and producing small to very small spores in vast numbers allowing efficient dispersal (Grime et al. 1990, Hedderson and Longton 1995). Such species were thus abundant in disturbed habitats including wastelands, urban, and industrial areas.

Conclusion

Combining information on soil condition, land use and species distribution and inferring probabilistic models of occurrence using logistic regression, as proposed by Hill (1991), enabled us to predict the occurrence of 59% of the investigated species. About 25 bryophyte species intolerant to drought were faithful indicators of forest cover and their occurrence could be predicted from forest cover with a probability higher than 80%. Sixty-four other species also had a preference for forest habitats but were not restricted to them because of efficient dispersal mechanisms and a greater tolerance to drought. Two species were characteristic of open, loamy spots and five of calcareous pebbles. This approach, limited in the present study by the size of the study area, is currently being tentatively developed at a national scale in order to determine the environmental conditions controlling the occurrence of the most interesting species assemblages deserving protection and targeted management of their habitat.

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