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A GIS-based survey for the conservation of bryophytes at the landscape scale

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Abstract

Geographical information system (GIS) data on landscape features and land use were collected to predict bryophyte diversity and conservation value in order to determine the factors that favour bryophytes at a large geographical scale and propose the relevant conservation measures. Total species diversity and diversity in species of high conservation value were highly correlated, and the landscape features promoting them were the proportion of military lands, steep slopes, and broadleaf woodland. Military lands seemed to be especially important for the conservation of endangered species highly specialized to open habitats maintained by the appropriate level of disturbance. Woodland cover was also as a key factor for bryophyte diversity but landscape heterogeneity, such as steep slopes with a range of contrasting ecological conditions, was required to reach the highest species numbers. The GISbased approach presented here may help focusing the attention on sites exhibiting the appropriate landscape features in terms of conservation, which is especially relevant in the context of the European network 'Natura 2000' for designating, conserving, and managing the sites of high biological value.

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1. Introduction

A comprehensive approach to conserving species diversity requires data on the geographic distribution, habitat, and abundance of species (Hunter and Webb, 2002). Biologists therefore commonly undertake studies on the biocenoses of a particular region. In this endeavour, they often record the presence of taxa in an array of grid-squares. If such studies provide useful insights on species distribution and abundance at the regional scale, species diversity and distribution patterns are rarely interpreted in the context of major environmental and landscape features. As a consequence, these studies do not allow the identification of the factors that are responsible for floristic differences at the regional level (Bates, 1995). In this context, geographical information systems (GIS) are an increasingly used tool that

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integrates the complex information from different data sets at different geographical scales. In conservation biology, they have been recently applied to examine the impact of a series of factors related to ecological conditions and land use on species diversity and rarity patterns at the landscape scale (Bayliss et al., 2003; Draper et al., 2003; Rouget et al., 2003; Taplin and Lovett, 2003; Vanderpoorten and Engels, 2003).

In a wide array of taxa including bryophytes and other poorly known groups (Hunter and Webb, 2002), such an information is, despite an increasing concern (Hallingback, 2003) and the high relevance of these taxa for conservation and management (Sergio et al., 2000; Zechmeister and Moser, 2001; Zechmeister et al., 2002, 2003; Vanderpoorten et al., 2004a), crucially lacking. As a consequence of the lack of information on species distribution and landscape features potentially hosting a rich bryoflora, important sites for bryophyte conservation may be difficult to identify at the country scale. In particular, certain sites of prime importance for

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bryophyte conservation were not identified as such in a preliminary check-list of the bryophyte 'hot-spots' at the European scale (ECCB, 1995). This is, for example, the case of the Semois river basin, an area hosting 80% of the Belgian bryoflora and about half of its European red-list species within an area only representing 5.7% of the country (Sotiaux and Vanderpoorten, 2004).

As the recording effort can hardly be increased due to the low number of bryologists enrolled in mapping projects, surrogates of bryophyte diversity and conservation value are required to predict areas of potential conservation interest depending on readily available landscape features (Moser et al., 2002). Although it is often assumed that species communities exhibit nestedness, i.e., that rare species are confined to species-rich sites, rare species can also be over-represented in high quality habitats (Berglund and Jonsson, 2003). This is one of the ideas behind the concept of 'mesohabitat' as an appropriate level for a coarse filter approach to prioritizing conservation efforts for mosses by land managers (Vitt and Belland, 1997; Heinlen and Vitt, 2003).

In the present paper, we investigated whether bryophyte communities exhibit nestedness at the landscape scale and determined which landscape features maximise species diversity and conservation value in order to determine the factors that favour bryophytes at a large geographical scale and propose the relevant conservation measures.

2. Methods

2.1. Data sets

The Semois river basin, an area of about 1760 km² at the Belgian–French border, is an exceedingly variable landscape including a range of topographies, soil conditions, and land uses that makes it appropriate for surveying the influence of environmental variation on biocenoses. A set of variables of land use and soil conditions (Table 1) was compiled thanks to a geographical information system, providing the exact cover of each variable in each of the investigated floristic grid-squares. Soil conditions were scored from a digitized version of the map of soil associations at a 1:500,000 scale (Maréchal and Tavernier, 1970). Information of land use was scored from a digital document at a 1:50,000 scale (Walphot-Cicade, 1993).

The Semois river basin was systematically divided into 104 grid-squares of 4×4 km. Bryological inventories of each grid-square were undertaken at least twice during one complete day each. In order to assess species frequency, each individual 4×4 km grid-square was further divided into $16 \ 1 \times 1$ km sub-grid-squares. Presence/absence of each species was recorded as accurately as possible in each sub-grid-square, and the sum of each species occurrences in the 16 sub-grid-squares was used as an estimate of species frequency according to a scale corresponding to 0, 1, 2–10, and >10 occurrences in the 16 sub-grid-squares.

A total of 519 species was recorded, including a subset of 97 species of high conservation value, i.e., 16 species of the European Red List Species (ECCB, 1995) and 81 species of high conservation value at the Belgian scale (Sotiaux and Vanderpoorten, 2004). The nomenclature follows Sotiaux and Vanderpoorten (2001) except for the species distinguished within Schistidium apocarpum (Blom, 1996) and for Sphagnum inundatum, grouped with Sphagnum denticulatum s.l., pending for a critical taxonomic re-evaluation of these taxa applied to the Belgian material. In addition, for practical reasons of identification, Chiloscyphus pallescens was grouped with Chiloscyphus polyanthos s.l. Indeed, although the two species differ in sporophytic characters, the taxonomic value of the gametophytic characters used to distinguish the two species, which are almost always sterile, has been questioned (Paton, 1999). For the same reason, the species of the Hypnum cupressiforme complex were not distinguished.

2.2. Data analysis

Regression techniques were employed to determine which of the investigated landscape features best explain total bryophyte diversity and diversity of species of high conservation value at the landscape scale and measure the predicting power of these variables. Ordinary leastsquares regression (OLS) over-fit the observed data

Table 1

Variables of land use

Soil denomination follows the terminology of the map of soil associations of Belgium at a 1/500,000 scale (Maréchal and Tavernier, 1974), where a B textural horizon refers to an illuvial horizon enriched with silicate clay, as indicated by a higher clay content than the overlying eluvial horizon.

Variables of land use and soil conditions scored in percent cover within each of the 104 investigated grid-squares of the Semois river basin

Total forest, broadleaf woodland, conifer plantation, mixed woodland, permanent meadow, crop field, wasteland, quarries Variables of soil conditions

Sandy to loamy-sandy soils with a B textural horizon, well-drained loamy soils with a B structural horizon, poorly-drained loamy soils with a B structural horizon, clayey soils and stony-loamy soils with a B textural horizon, stony-shaly and stony-slaty loamy soils with a B textural horizon, stony-shaly and sandstony loamy soils with a B textural horizon, pebbly-loamy soils with a B textural horizon, steep slopes (>25%), poorly drained alluvial soils, well-drained alluvial soils

when there are many predictors, that is, tailor the model too much to the current data to the detriment of future predictions. OLS predictors also exhibit large variances and are consequently unstable and sometimes difficult to interpret when the predictors are multicollinear (see, e.g., Vanderpoorten and Palm, 2001, for a review), which was the case for the variables of soil conditions and land use. Partial least-squares regression (PLS) was therefore used to model the relationship between species diversity and landscape features. The number of components to extract was determined by maximizing the cross-validated r^2 . Cross-validation was performed by selecting a maximum of five components with 50 crossvalidation groups. The importance of each predictor was assessed by the product of its coefficient and standard deviation, divided by the standard deviation of the response (i.e., species diversity). Predictors with the lowest importances were removed from the model, as recommended by SCAN (1995). A predictor was removed from the model if its importance was less than 5% of the average importance of all predictors.

In order to determine how landscape conditions determine the patterning of diversity in species of high conservation value, and thus, which landscape features exhibit the highest conservation value, the 97 species were ordinated along linear combinations of the 19 variables of soil conditions and land use. The coefficients of the latter were computed so as to maximise the percent variance of the floristic data explained by redundancy analysis, as implemented by ADE4 (Thioulouse et al., 1997).

3. Results

Among the investigated features of soil conditions and land use, species diversity per grid-square was significantly positively correlated with steep slopes (r = 0.71, p < 0.001), cover in broadleaf trees (r = 0.49, p < 0.001), military lands (r = 0.21, p < 0.05) and negatively with cover in permanent meadows (r = -0.50, p < 0.001) (Fig. 1). The r^2 between species diversity and the variables of land use was maximized at a value of 0.54 by selecting three components including steep slopes (*s*, with an importance of 0.64), military lands (*m*, 0.26), and permanent meadows (*p*, -0.19). Species diversity (\hat{D}) could thus be predicted by the following relationship

$\hat{D} = 146.9 + 0.994s - 0.25p + 0.993m.$

Total species diversity and diversity in species of conservation value were correlated at r = 0.82 (p < 0.001). The r^2 between diversity in species of high conservation value and the variables of land use was maximized at a value of 0.44 by selecting three components including the same landscape features as for total species diversity, i.e., steep slopes (s, with an importance of 0.55), military lands (m, 0.40), and permanent meadows (p, -0.13).

$\hat{D}_c = 2.113 + 0.095s - 0.019p + 0.169m$

The first two axes of the redundancy analysis between the floristic and landscape features data sets accounted for 26.5% of the total floristic variance and 53.9% of the



Fig. 1. Species diversity per grid-square superimposed on a background cover of steep slopes, broadleaf woodland, and permanent meadows that best explains the observed patterns of species diversity at the landscape scale in the Semois river basin.



Fig. 2. Species scores along the first two axes of the redundancy analysis between the floristic and landscape feature data sets. Only the species with a significant correlation coefficient on at least one of these axes are represented.

species-environment relationship. RDA1 was highly correlated with the cover of military lands (r = -0.99, p < 0.001), RDA2 with the cover of steep slopes (r = -0.94, p < 0.001), broadleaf woodland (r = -0.44, p < 0.001)p < 0.001), and permanent meadows (r = 0.35, p < 0.001) 0.001). Species associated to this pattern of landscape features are represented in Fig. 2. Along axis one, species typical for alkaline fens (e.g., Palustriella commutata, Scorpidium scorpioides, Campylium stellatum, and Tomentypnum nitens), wet heaths (e.g., Sphagnum fuscum, Sphagnum molle, Leptodontium flexifolium, Cladopodiella fluitans, Cladopodiella francisci, Nardia geoscyphus, and Mylia anomala), and open, disturbed soils (e.g., Pohlia andalusica, Pohlia drummondii) were identified by a strong negative coordinate. Along axis 2, a large number of rupicolous species formed a wellseparated group at the bottom of the axis.

4. Discussion

4.1. Factors accounting for the observed patterns of diversity at the landscape scale

The high correlation found between total species diversity and diversity in species of high conservation value clearly show that the investigated bryophyte communities exhibited nestedness at the landscape scale. This confirms previous assessment of patterns in bryophyte species diversity and conservation value at a large geographical scale (e.g., Vanderpoorten and Engels, 2003; Vitt et al., 2003).

The factors promoting a high species diversity and capturing a maximum of species of high conservation value at the landscape scale were the proportion of military lands, steep slopes, and broadleaf woodland. The importance of military lands for providing valuable habitats for endangered organisms highly specialized to open landscapes was documented for a series of other organisms (Burton and Williams, 2001; Tazik and Martin, 2002; Wanner and Xylander, 2003). In the investigated area, this was true for a series of species that are restricted to open environments and thus limited to areas with the appropriate level of disturbance. These habitats ranged from sandy tank tracks, where pioneer species of conservation value such as P. andalusica and P. drummondii specifically occurred and successfully dispersed thanks to the massive production of bulbils, to fire-maintained heathlands including large sets of species of high conservation value such as C. fluitans, C. francisci, M. anomala, N. geoscyphus, and S. molle. At the same time, military lands are, by nature, areas of extremely limited access, thus allowing the persistence of fragile habitats such as alkaline fens that have almost vanished everywhere else in Belgium. Such environments are vital for the conservation of a series of species of high conservation value, including Hamatocaulis vernicosus, Meesia triquetra, S. scorpioides, Sphagnum warnstorfii, and T. nitens.

Woodland cover was already identified as a key factor for bryophyte diversity at the landscape scale (Bates, 1995; Vanderpoorten and Engels, 2002, 2003), but cannot account for a very high bryophyte diversity in itself as species richness is quickly saturated in a homogeneous landscape (Vanderpoorten and Engels, 2003). Landscape heterogeneity is required to reach the highest species numbers (Rambo, 2001). This is also true in the Semois river basin, where steep slopes create a range of contrasting ecological conditions. For instance, a total of 147 species, including 2 species of high conservation value, were expected in a flat 16 km² landscape unit (the other explaining variables of the model set to 0), while these numbers reached up to 246 and 12, respectively, when the proportion of steep slopes was set to 100%.

Proportion of spruce plantation did not influence these patterns of bryophyte diversity and conservation value at the landscape scale. This contrasts with previous assessments of the negative impact of conifer plantations on bryophytes (Moe and Botnen, 2000; Vanderpoorten et al., 2004b; but see Humphrey et al., 2002). In the Semois river basin, spruce plantations may locally exhibit a lower diversity than broadleaf woodland and undoubtedly constitute a threat to fragile habitats such as peat bogs. At the landscape scale, however, spruce plantations increase the level of spatial heterogeneity, and hence, species diversity. Spruce plantations indeed provide adequate growth conditions for a set of acidophilous species that are either restricted to them or increase in abundance in this habitat. In terms of diversity, this may globally counterbalance the local negative effect of spruce plantations. In terms of conservation value, it is noteworthy that even species of high interest such as Orthotrichum rogeri, a vulnerable (sensu IUCN) species at the European scale, was found on willow within a large spruce plantation (Sotiaux and Sotiaux, 2002).

4.2. Application to the conservation of bryophytes at the landscape scale

Small habitats of high biological value are often readily identified as key sites for nature conservation and their small size allows their protection as nature reserve. In the Semois river basin, this is for example the case for most of the alkaline fens and peat bogs, which are appropriately managed, even if certain practices favouring the cryptogamic flora could be implemented. For example, the recolonization of wetlands by shrubs is mostly seen as a threat to the vascular flora. For bryophytes, but also for other organisms (Cattin et al., 2003), conversely, shrub patches are essential to the conservation of a specialized flora which can include rare species of high conservation value, such as Rhizomnium pseudopunctatum and Pseudobryum cinclidioides. In many peat bogs, our observations over 20 years show that, in military lands with the appropriate level of disturbance apart, the abundance of a number of pioneer bryophytes of bare peat and wet heathland, e.g., C. francisci and Odontoschisma sphagni, strongly decreased due to the spread of Molinia caerulea and the consequent closing-up of the herb canopy. We propose that removal of the peat layer could be locally practiced. This technique indeed allows the recovery of many pioneer bog species within a few years (Jacquemart et al., 2003).

At the landscape scale, the conservation of species diversity requires a conservation policy involving much bigger areas, all of which cannot acquire a nature reserve status. In the investigated area for instance, a high species diversity per grid-square correlated with extensive steep slopes under broadleaf woodland. To achieve the biodiversity conservation goals in woodland, several authors suggested that vulnerable habitats should be strictly protected while biodiversity-oriented practices should be implemented in production forests (Bentsson et al., 2000; Angelstam and Andersson, 2001). Several countries, including Ireland, Germany, and Sweden, thus implemented a classification system for defining a coherent ecological network made of significant conservation core areas and nature enhancement areas, including: (i) conservation core areas that will be entirely dedicated to nature conservation, either through active management (e.g., traditional practices such as coppicing and wood grazing) or through cessation of logging; (ii) nature enhancement areas that will be dedicated to both nature conservation and wood production, which means that specific management constraints will be applied; (iii) other areas that will be dedicated to wood production and could involve minimal biodiversity-oriented prescriptions. We suggest that such a framework could be adapted in the study area, where conservation core areas could be designated locally to protect the bryophyte assemblages of the highest conservation value. In nature enhancement areas, spruce plantations should be prohibited on steep slopes in favour of coppice woodland and rock climbing, which is an increasing practice, should be forbidden on the outcrops. Areas that would be dedicated to wood production could be designed on the less rich flat hill tops.

5. Conclusion

We showed in this paper that patterns of bryophyte diversity and conservation value can be predicted from landscape features that are readily available from a GIS. In the same way that potential areas for ancient forests can be quickly detected by means of easily accessible landscape features (Stahle and Chaney, 1994), it is possible to designate areas that present the features favouring a high bryophyte diversity. These features may not be the same elsewhere, but the implementation of the approach illustrated here may speed-up the process of selection of habitats of prime importance in terms of conservation. This is especially relevant in the context of the European network 'Natura 2000' for designating, conserving, and managing the sites of high biological value. As the number of biologists, and especially bryologists, involved in biodiversity recording and site assessment, is most often very low with regard to the task, this may help focusing the attention on sites exhibiting the appropriate landscape features for subsequent field investigation.

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