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The distribution of *Sphagnum* species along an elevational gradient in the southern Alps (Italy)

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Abstract

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Response curves for 16 species of *Sphagnum* along an elevational gradient were obtained using data from 116 mire sites in South Tyrol (Italy). Most of the species investigated exhibit unimodal curves along the gradient, usually peaking at low elevations. Only three species have bimodal curves. The shape of the curves is mainly determined by the indirect effects climate exerts on the altitudinal distribution of mire types and microhabitats rather than by a direct response of species to climatic factors.

Introduction

The vegetation of peatlands is locally influenced by three main gradients: 1) ombrotrophy to minerotrophy, viz. from areas fed only by precipitation to areas receiving increasing amounts of nutrients from mineral water-table; 2) wet to dry; 3) mire margin to mire expanse (Malmer 1986). On a regional scale, climate plays a major role in determining the distribution of mire plants, among which peat mosses (genus *Sphagnum*) are usually dominant in the bottom layer of bogs and poor fens, with at least some species commonly occurring also in intermediate to rich fens (Moore and Bellamy 1974, Andrus 1986).

Several studies focused on the distribution of *Sphagnum* species along gradients of nutrient availability, water chemistry and soil moisture (Vitt and Slack 1975, Vitt et al. 1975, Damman and Dowhan 1981, Andrus et al. 1983, Glaser et al. 1990). On the other hand, only few studies analysed the performance of *Sphagnum* species along climatic gradients in north-temperate and boreal regions (Gignac and Vitt 1990, Gignac et al. 1991a, Gignac et al. 1991b).

Information about the elevational distribution of *Sphagnum* in the mountains of central Europe can be drawn from ancient floristic papers (Rénauld 1883, Henry 1912). Recently, only Gauthier and Polidori (1988) gave a semi-quantitative illustration of the frequencies of *Sphagnum* along an altitudinal gradient in the Maritime Alps. So far, however, no specific study was devoted to analysing the performance of *Sphagnum* species with altitude and the causal relationships with the underlying climatic and ecological gradients. This study aims at filling such gap by analysing the frequency of *Sphagnum* species collected in a sample of peatlands from the southern Alps.

Study area

The area investigated covers the whole territory of South Tyrol (Südtirol, Alto Adige), administratively corresponding to the Bozen (Bolzano) province, in the southern Alps of Italy. This region has an area of ca. 7500 km², with an altitudinal range between 200 m and 3905 m (Fig. 1). Wetlands, although covering only ca. 0.2% of the territory (Göttlich 1991), are relatively frequent. Mires are mostly concentrated in the montane and subalpine vegetation belts, becoming progressively rarer at higher elevations. Wetlands are also infrequent at low altitudes, due both to unfavourable climate and to heavy alterations brought about by man.

Climate in the study region can be defined as cool-temperate montane with a mean annual temperature of about 6.5°C at 1200 m and a mean annual precipitation ranging from appr. 900 to appr. 1100 mm in the central-eastern sector, and from appr. 600 to appr. 800 mm in the drier western sector (Fliri 1975). Rainfall generally peaks in summer, thus showing a continental regime (Fig. 1).

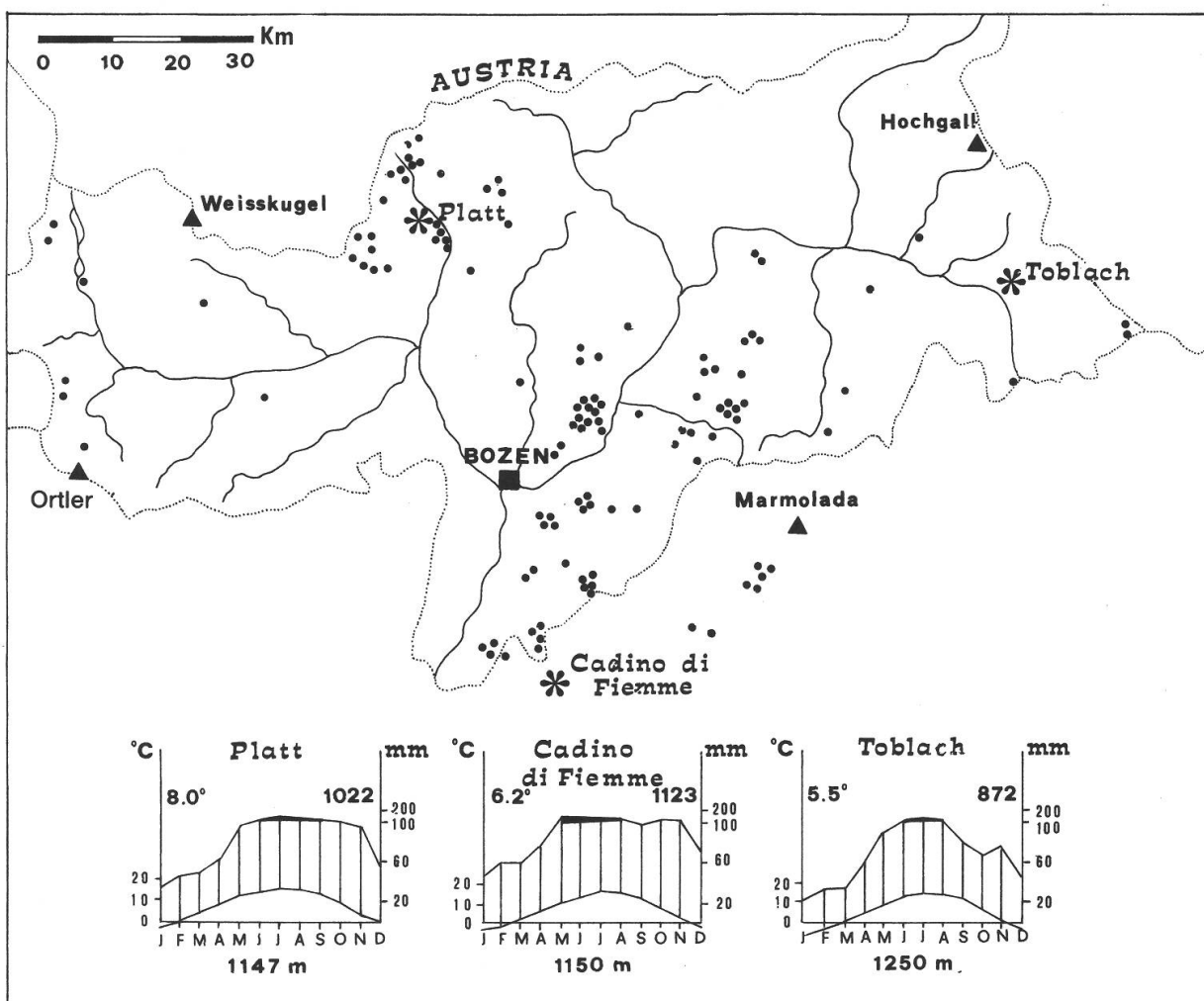


Fig. 1. Geographical distribution of the sampling sites and climatic diagrams at three representative stations.

Material and methods

Samples of *Sphagna* were collected from 116 mire sites. The large majority of these are located within the province of Bozen (Bolzano), only 11 lying in the neighbouring provinces of Trento and Belluno, in close proximity to the administrative border. The geographic location of the study sites is shown in Fig. 1. A detailed list is available on request from the authors.

The mires were visited by different investigators at different times during 1981–1992. The collections of R. Alber, L. Bragazza, R. Gerdol and E. Lochmann were made within a survey of the vegetation of wetlands in the southern Alps. Voucher specimens are deposited in the herbarium of the Botanical Institute of Ferrara University (FER). The collections of B. Wallnöfer were made as part of a project devoted to listing and mapping mires and wetlands in South Tyrol. Voucher specimens are deposited in the private herbarium Wallnöfer (Duplicates in FER).

The mire sites are located between appr. 1100 m and 2400 m. This elevational range was divided into 13 classes, each spanning 100 m. The first two and the last three classes were united due to the low number of sites included (Table 1). The mires investigated can be grouped into the following main types:

- 1) fens: fed by spring water and usually having a flat surface;
- 2) transitional mires: consisting of a mosaic-like pattern of fen areas, *Sphagnum* carpets and wet hollows;
- 3) forested mires: slightly raised above the surrounding terrain and bearing a well-developed tree layer rooting in a *Sphagnum* carpet;
- 4) poor mires: more or less distinctly raised peat bodies with poor, if any, contact to mineral water.

The frequencies of the four mire types in each elevational class are in Table 1. Typic raised bogs do not occur in the study area.

For every *Sphagnum* species found in at least 10% of the sites, the frequency of occurrence in each altitudinal class was calculated. Univariate smoothed curves were drawn along the gradient, after smoothing the observed frequencies by the following formula (Økland 1986):

$$y'_j = 0.25 * y_{j-1} + 0.5 * y_j + 0.25 * y_{j+1}$$

where y'_j is the smoothed frequency in the j -th class, while y_{j-1} , y_j and y_{j+1} are the observed frequencies respectively for the preceding, the j -th and the following class.

For end-points the frequencies were smoothed according to the formula:

$$y'_j = 0.67 * y_j + 0.33 * y_{j\pm 1}$$

where y_j is the calculated frequency in the j -th class and y_{j-1} and y_{j+1} respectively in the preceding and the following ones.

Tab. 1. Altitudinal classes, number of mire sites (total $n = 116$) and percentages of mire types in each class. The latter were calculated on a subsample of 89 sites from which samples were personally collected by the authors.

| Class | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|------------------------|-------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|-------|
| Elevation | <1300 | 1300 1400 | 1400 1500 | 1500 1600 | 1600 1700 | 1700 1800 | 1800 1900 | 1900 2000 | 2000 2100 | >2101 |
| N. of sites | 9 | 12 | 8 | 9 | 7 | 16 | 20 | 10 | 14 | 11 |
| Fens (%) | 17 | 14 | 29 | 33 | 0 | 15 | 40 | 29 | 54 | 70 |
| Transitional mires (%) | 49 | 43 | 29 | 33 | 86 | 62 | 60 | 71 | 46 | 30 |
| Forested mires (%) | 17 | 29 | 29 | 17 | 0 | 0 | 0 | 0 | 0 | 0 |
| Poor mires (%) | 17 | 14 | 13 | 17 | 14 | 23 | 0 | 0 | 0 | 0 |

Nomenclature of *Sphagnum* species follows Frahm and Frey (1987) except for *Sphagnum lescurii* which follows Andrus (1980).

Results

Distribution curves could be drawn for 16 of the 23 species or *Sphagnum* collected in the survey (Fig. 2). A list of the rare species is included in App. 1. Some short comments about the distribution of *Sphagnum* species along the gradient are given below.

Sect. *Sphagnum*

S. palustre shows a strongly positively skewed curve, viz. with modal frequency located in the left half of the gradient, corresponding to low-elevation classes. The curve peaks at 1300–1400 m and gradually decreases towards higher elevations (right-hand side; Fig. 2).

The curve of *S. centrale* is truncated to the left and declines much more irregularly to the right, showing an indistinct secondary peak at 1500–1600 m (Fig. 2).

S. papillosum shows a single-topped, almost symmetric curve (Fig. 2).

S. magellanicum occurs within a broad altitudinal range and has very high frequencies in all of the early classes, rapidly decreasing above 1600–1700 m. The curve is asymmetric and truncated at the left-hand flank (Fig. 2).

Sect. *Acutifolia*

The curve of *S. fuscum* is single-topped, peaking at 1500–1600 m (Fig. 2).

S. capillofolium has high frequencies in all of the first four classes with a rather indistinct peak at 1500–1600 m. The curve declines fairly rapidly above 1600–1700 m, showing a small secondary peak at 1900–2000 m (Fig. 2).

S. rubellum has a two-topped curve with a main peak at 1400–1500 and a secondary peak at 1800–1900 m (Fig. 2).

S. warnstorffii shows a negatively skewed curve, viz. with modal frequency located in the right half of the gradient, corresponding to high-elevation classes. The curve peaks at 1800–1900 m and declines to the left. The last three classes have frequencies close to the mode (Fig. 2).

S. russowii has a single-topped curve, distinctly peaking at 1400–1500 m and showing a small rise in the last two classes (Fig. 2).

S. girgensohnii shows a strongly positively skewed curve, with an only top at 1400–1500 m (Fig. 2).

Sect. *Squarrosa*

S. squarrosus has a distinctly bimodal curve with a main top at 1900–2000 m and a secondary top at 1400–1500 m (Fig. 2).

Sect. *Subsecunda*

S. subsecundum has a positively skewed single-topped curve with a distinct peak at 1500–1600 m (Fig. 2).

S. lescurii has a bimodal response curve with two tops, respectively at 1500–1600 m and at 1800–1900 m (Fig. 2).

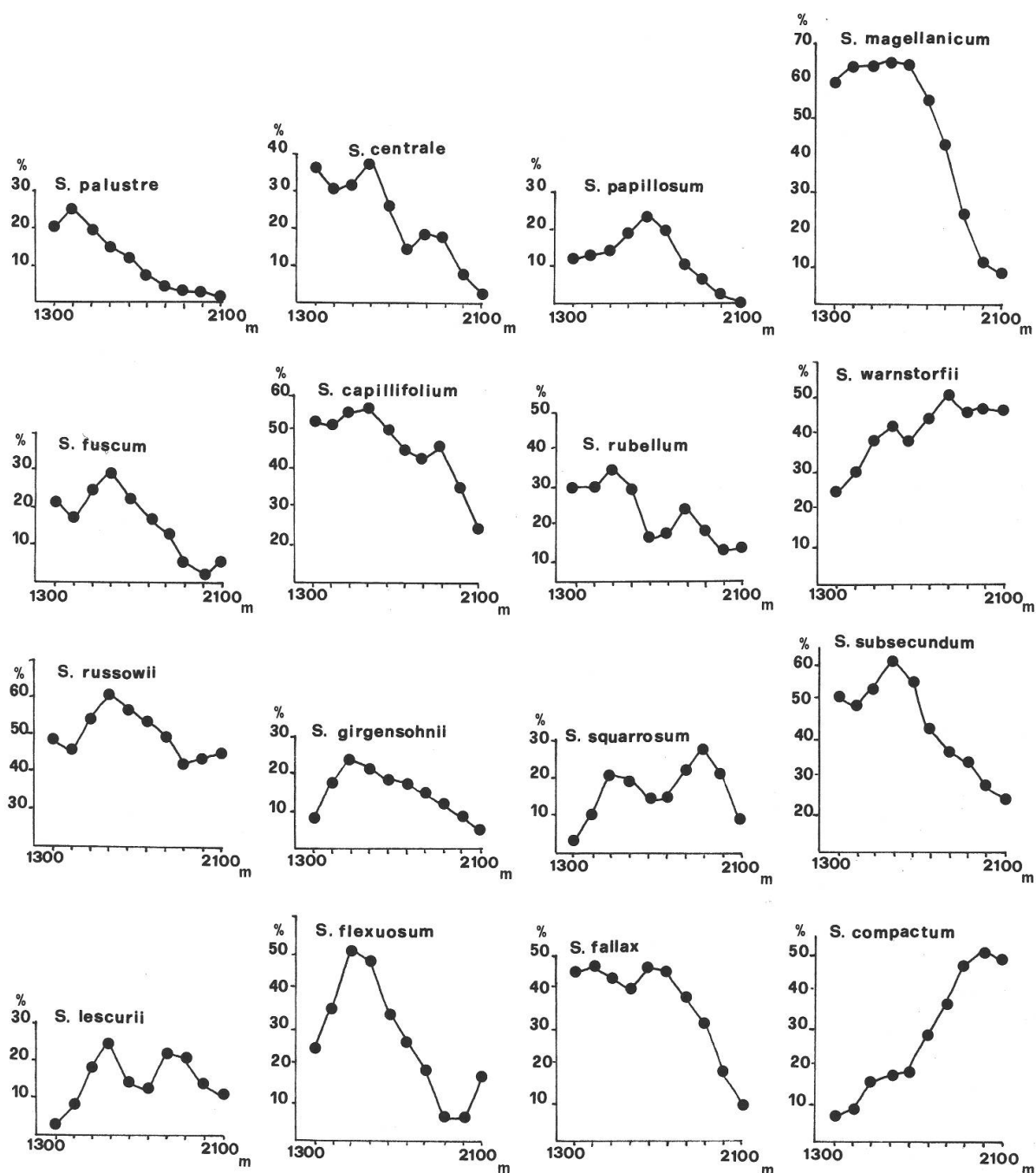


Fig. 2. Distribution curves of *Sphagnum* species along the elevational gradient. Each class spans 100 m (see Table 1).

Sect. *Cuspidata*

S. flexuosum shows a positively skewed, substantially unimodal curve peaking at 1400–1500 m, with a small additional peak in the highest-elevation class (Fig. 2).

The curve of *S. fallax* presents a broad top extending over the first six classes, the frequencies rapidly decreasing above 1700–1800 m. The curve appears truncated at its left-hand side (Fig. 2).

Sect. *Rigida*

S. compactum has a strongly negatively skewed curve, peaking at 2000–2100 m and gradually declining to the left (Fig. 2).

Discussion

Climate varies with altitude in much the same way over the whole area investigated. Using data from Fliri (1975), we estimated a mean gradient in the mean annual temperatures of $-0.64^{\circ}\text{C} \times 100 \text{ m}$ ($r=0.79$, $P<0.001$), thus giving mean values of about 8°C at 1000 m, about 5°C at 1500 m, about 2°C at 2000 m, and about 0°C at 2300. Although precipitation does not increase significantly with altitude ($r=0.08$; $P>0.50$), climate obviously becomes moister as far as elevation increases, due to reduced evapotranspiration.

Climate, besides directly influencing the physiological response of *Sphagna*, also has an indirect effect on the altitudinal distribution of the different species. The development of peat bodies proceeds at very different rates as a result of complex equilibria between radiation and water regime. This results in an uneven frequency of mire types along climatic gradients (Eurola 1962, Moore and Bellamy 1974, Damman 1979) that are, in turn, tightly correlated with elevation. In some cases hydrological and/or hydrochemical microhabitats suitable for a certain species to develop can be found only within a well defined mire type. For instance, forested mires are confined to the montane belt having a relatively dry climate, whereas raised peat bodies rarely develop over 2000 m owing to both low temperature and excessive moisture surplus. Fens, although occurring at all elevations, are relatively enriched at high altitudes for representing the only mire type developing under cool-moist climates (Table 1).

The set of peatlands analysed in this study can be regarded as a representative sample for South Tyrol and adjacent areas, especially as far as their altitudinal distribution is concerned. Nearly half of the about 700 mire sites catalogued in South Tyrol are concentrated between 1500 and 2000 (Göttlich 1991). Only class 5 (1600–1700 m; Table 1) is clearly underrepresented in our sample. Peatlands are less frequent below 1500 m, since most level areas at these elevations correspond to thalwegs subject to a relatively high human pressure. The frequency of peatlands declines again over 2000 m, as a probable effect of climate being too cold and dry for at least some types of mires to develop.

The distribution curves of *Sphagnum* species along the elevational gradient are prevalently unimodal, albeit often skewed or even truncated, only *S. papillosum* showing a fairly symmetric curve. This species is typical of open wet carpets in poor and transitional mires (Daniels and Eddy 1990), which are particularly frequent at mid altitudes.

Most of the skewed curves peak in the lower half of the gradient (Fig. 2). However, the reasons for such a seemingly uniform behaviour may strongly differ among the species. For instance, *S. palustre* is one of the most widespread species in temperate-warm Mediterranean territories (Warnstorf 1911) and becomes rarer to the North (Daniels and Eddy 1990). *S. palustre* can be regarded, therefore, as a relatively thermophilous species.

In contrast, the *Acutifolia* *Sphagna* do not exhibit any preference for climatically favoured areas but are enriched at low elevations owing to an indirect influence climate exerts on other environmental factors. *S. girgensohnii* is typical of forested mires which preferentially develop under a relatively dry climate in the montane belt, gradually disappearing with altitude as far as the moisture surplus increases (Table 1). *S. fuscum*, *S. russowii* and *S. capillifolium* occur in a vast range of peatlands, from poor and

transitional mires to forested mires, being excluded only from fens. As a result, they are relatively enriched at mid-low altitudes (Table 1 and Fig. 2). *S. fuscum* forms high hummocks raised up to 1 m above the water table, where it practically excludes any potential competitor (Gignac 1992). *S. russowii* and *S. capillifolium* have wider niche widths as far as both distance to water table and nutrient availability are concerned. *S. russowii* is particularly abundant in moderately acidic microhabitats relatively rich in cations (Andrus 1986, Gignac and Vitt 1990), whereas *S. capillifolium* prefers oligotrophic sites (Daniels and Eddy 1990). However, both species are frequent in the right half of the gradient (Fig. 2) and probably represent two of the most widespread *Sphagna* at high-elevation mires in the Alps (Gauthier and Polidori 1988).

S. magellanicum and *S. fallax* are major constituents of the vegetation of poor and transitional mires. *S. magellanicum* usually lives on low hummocks and *S. fallax* in wet carpets and hollows (Daniels and Eddy 1990). Accordingly, these species exhibit very high frequencies at low-elevation sites where suitable habitats are particularly abundant. Whereas *S. magellanicum* becomes rare above 1800–1900 m, *S. fallax* remains fairly frequent even well above 2000 m where it actively grows in mesotrophic wet habitats. *S. centrale* has a distribution curve quite similar to that of *S. magellanicum* for growing in comparable microhabitats, although somewhat richer in nutrients with respect to the latter. However, the curve of *S. centrale* declines more irregularly towards the right end of the gradient (Fig. 2).

S. subsecundum occurs in a wide range of minerotrophic habitats, provided not subject to prolonged desiccation (Daniels and Eddy 1990). This explains the shape of its distribution curve exhibiting appreciable frequencies all over the gradient with a rather smooth peak at low elevations (Fig. 2). *S. flexuosum* usually grows in poorer microhabitats than those of *S. subsecundum*, which are relatively enriched at mid-low altitudes. In addition, *S. flexuosum* often forms quaking rafts in high-elevation waterbodies (Gerdol unpublished), and this justifies the small additional peak observed at the right end of the gradient (Fig. 2).

Sphagnum compactum and *S. warnstorffii* are the only species exhibiting negatively skewed unimodal curves, both peaking in the high-elevation classes (Fig. 2). *S. compactum* cannot by any means be regarded as typical of cold territories, for being very common in heathlands of Atlantic Europe (Daniels and Eddy 1990). Owing to its ruderal life strategy, tolerating desiccation and disturbance (Økland 1990), this species is well suited for colonising slowly-growing bare peat in high-elevation carpet mires. By contrast, *S. warnstorffii* is confined to base-rich fens (Daniels and Eddy 1990). Although such fens occur at all elevations in the Alps, they represent the by far most common type of peatlands above treeline (Table 1), thus determining a relative enrichment of *S. warnstorffii* in the higher sector of the gradient.

Bimodal curves were obtained only for a small fraction of the species investigated in this study (3 of 16), including *S. rubellum*, *S. squarrosum* and *S. lescurii* (Fig. 2). *S. rubellum* is a typical species of poor mires at mid-low elevations. The shape of its distribution curve along the gradient presumably is an artifact of sampling due to the low number of sites included in class 5 (Table 1). By contrast, *S. squarrosum* only occurs in eutrophic fens which are proportionally less frequent in the central classes where oligotrophic (viz. poor and transitional) mires are most abundant (Table 1). Finally, the bimodal curve of *S. lescurii* may reflect some intraspecific variability of that species. *S. lescurii* is a still controversial taxon probably including both *S. auriculatum* Schimp. and *S. inundatum* Russ. (Andrus 1980). A number of taxa, formerly regarded as species, such as *S. rufescens* (Nees et Hornsch.) Warnst., *S. obesum* (Wils.) Warnst. and others (Warnstorf 1911) were

distinguished within that group. All of these live in wet habitats, often waterlogged, ranging from moderately oligotrophic to slightly mesotrophic, the former being more frequent at low elevations and the latter at higher elevations. *S. lescurii* s.l. is completely lacking, however, in poor mires and this justifies its lower frequency at mid elevations where nutrient-poor mires are concentrated.

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Appendix 1 – N. of records of rare species of *Sphagnum* in each altitudinal class.

| Class | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|-------------------------|---|---|---|---|---|---|---|---|---|----|
| <i>S. quinquefarium</i> | – | – | – | – | – | 1 | – | – | – | 1 |
| <i>S. subnitens</i> | 2 | 1 | 1 | 1 | 2 | – | – | – | – | – |
| <i>S. teres</i> | 1 | 1 | – | 2 | – | – | 4 | 1 | 1 | – |
| <i>S. contortum</i> | 1 | 1 | 2 | 2 | – | – | 2 | – | – | – |
| <i>S. plathyphyllum</i> | 1 | 0 | 1 | 1 | – | – | 1 | – | – | – |
| <i>S. angustifolium</i> | 1 | 2 | 3 | 2 | – | 2 | 1 | – | – | – |
| <i>S. majus</i> | 1 | 1 | – | 2 | 1 | 2 | – | 1 | 1 | – |

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