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Niche Diversification of *Sphagnum* in Bolivia

Cyrus B. McQueen

Environmental and Health Sciences Department, Johnson State College, Johnson, Vermont

05656, USA

Abstract. Niche breadth values of *Sphagnum* species in the páramo and cloud forests of Bolivia are similar to those reported for *Sphagnum*-dominated peatlands in North America, but niche overlap values are higher for *Sphagnum* species in Bolivia. The pH, conductivity, and concentrations of Ca, Mg, Na, K, and P suggest that *Sphagnum* habitats in Bolivia are ombrotrophic in nature. *Sphagnum* is limited to small, scattered carpets in the páramo and cloud forests of the Bolivian Andes between 1800 and 4200 m. Common species found in these habitats include *S. alegrense* Warnst., *S. boliviae* Warnst., *S. cuspidatum* Ehrh., *S. magellanicum* Brid., *S. oxyphyllum* Warnst., *S. recurvum* P. Beauv., *S. sancto-josephense* Crum & Crosby, and *S. sparsum* Hampe.

The purpose of this study was to examine the niche breadth and overlap of *Sphagnum* species in Bolivia. Based on examination of herbarium specimens and field observations in Bolivia, *Sphagnum* species are found between elevations of 1800 and 4200 m. As in other regions of Central and South America, the majority of species are found in the páramo and cloud forests of the Andes (McQueen 1991, 1995). Preliminary field observations in Bolivia suggested that *Sphagnum* does not form extensive mats or peatlands such as those found in the northern Andes; however, species diversity in *Sphagnum* habitats of Bolivia appear to be greater. It is not uncommon to observe more than eight species at a site in Bolivia unlike Ecuador and Costa Rica where habitats typically have five or fewer species. These preliminary observations led me to hypothesize that the niche dimensions of *Sphagnum* species in Bolivia would be different from those examined in the northern Andes and Central America.

Vitt and Slack (1984) reported that niche breadth and overlap for *Sphagnum* species in North America suggest independent species utilization of the gradients. They concluded that individual species appear to react independently to different gradients. For these reasons they concluded that species of *Sphagnum* are largely equilibrium species as opposed to fugitive species. Slack (1982) suggested that equilibrium species have well-defined niches distinct from close competitors. Conversely, fugitive species are characterized by strong niche overlap with similar species.

Niche values for *Sphagnum* species in the northern Andes and Central America are similar to those reported for peatlands in North America. McQueen (1995) reported that niche values for species in Costa Rica were more similar to those of North America than those of South America. This may be due to a greater diversity of species in the northern Andes and Central America. Higher niche values were reported by McQueen (1991) for *Sphagnum* in Ecuador than in North America. This was attributed to the low species diversity of the peatlands examined. McQueen (1995) suggests that species farther south in the Andes would have greater niche values than in the more species rich and diverse habitats farther to the north.

There is disagreement over the characterization of *Sphagnum* species as generally equilibrium species. Andrus (1986) feels that this is probably more appropriate for species in well-developed and slowly evolving peatlands. Andrus noted that periodic drought and fire are common phenomena in northern peatlands. Such disturbances create short-lived habitats that are characteristicly occupied by fugitive species. In contrast, the distribution of *Sphagnum* in peatlands is envisioned by Slack (1982) as a function of colonizing ability and competitive interactions since the last disturbance event, with the establishment of *Sphagnum* as a short phase compared to growth of the *Sphagnum* in an established peatland that is viewed as a relatively long-lived habitat.

Gignac and Vitt (1990) report that climate and water chemistry gradients are two of the most important factors limiting the distribution of individual *Sphagnum* species in northwestern North America. Some species are restricted by climate to oceanic or continental habitats, some are restricted only by surface water and have broad distributions, and nearly all species are limited to habitats that have low cationic concentrations and conductivities. Shade and height relative to the water table appear to have little effect on species distributions except for those species found at either end of the height gradient.

METHODS AND MATERIALS

The sites examined in this study are representative of the types of *Sphagnum* habitats in Bolivia. Páramo and cloud forest sites were examined at Chuspipata (2800-2950 m, Department of La Paz, Nor Yungas Province), Unduavi (2200 m, Department of La Paz, Sud Yungas Province), Alalay (1800-2200 m, Department of Cochabamba, Arani Province), Yungas de Espirita (2400-2800 m, Department of Cochabamba, Chare Province), Cerro Uchumani (2300-2420 m, Department of Cochabamba, Nor Yungas Province), and Sorato (2000-2600 m, Province of La Paz, Nor Yungas Province).

Quadrats, 25 x 25 cm, were placed randomly along a transect through each site. The number of quadrats used depended on the area of the site. Cover values were estimated using Daubenmire's (1959) canopy method as employed by Vitt and Slack (1984). Voucher specimens are in the University of Vermont herbarium (VT) and the New York Botanical Garden (NY).

Water samples were taken from surface water in each quadrat and kept cool until analyzed. The pH and conductivity (K_{corr}), corrected for H^+ concentration (Sjörs 1950), were taken at a temperature of 20°C within 24 hours. The samples were kept frozen until analyzed for Ca, Fe, Mg, Mn, P, K, and Na by atomic adsorption spectrophotometry. The range of variation in the samples of Fe (0.05 - 0.44 mg/l) and Mn (0.01 - 0.88 mg/l) was small so these were not used for the determination of niche breadth and overlap.

The abundance of each species was calculated using the prominence value index $PV = CF^{1/2}$, where C = mean percentage of cover and F = the absolute frequency. Niche breadth and overlap were calculated using these values. Niche breadth was calculated as $NB = 1/(\Sigma_n P_{ij}^2)$, where P_{ij} is the proportion of abundance of species i in microhabitat state j per total abundance of species i in all microhabitat states and n is the number of microhabitat classes used in the analysis (Levins 1968, Colwell & Futuyma 1971). Niche overlap was calculated using $O_{jk} = (\Sigma P_{ij}P_{ik})/((\Sigma P_{ij}^2)(\Sigma P_{ik}^2))^{1/2}$, where P_{ij} and P_{ik} are the proportions of the ith microhabitat classes utilized by the jth and kth species (Pianka 1974, 1978).

The microhabitat parameters were divided into classes as follows:

pH: range 4.5-6.7; n = 6; classes, 4.5-4.8, 4.9-5.2, 5.3-5.6, 5.7-6.0, 6.1-6.4, 6.5-6.7.

Conductivity: range 10.0-70.0 µmohs/cm; n = 7; classes, 0-10, 11-20, 21-30, 31-40, 41-50, 51-60, 61-70.

Ca: range 0.03-8.12 ppm; n = 8; classes, 0-1.0, 1.1-2.0, 2.1-3.0, 3.1-4.0, 4.1-5.0, 5.1-6.0, 6.1-7.0, 7.1-8.12.

Mg: range 0.02-4.96 ppm; n = 5; classes, 0-1.0, 1.1-2.0, 2.1-3.0, 3.1-4.0, 4.1-5.0.

P: range 0-5.9 ppm; n = 6; classes, 0-1.0, 1.1-2.0, 2.1-3.0, 3.1-4.0, 4.1-5.0, 5.1-6.0.

K: range 0.04-60.8 ppm; n = 6; classes, 0-10, 10.1-20, 20.1-30, 30.1-40, 40.1-50, >50.1.

Na: range 0.0-23.5 ppm; n = 8; classes, 0-2.9, 3.0-5.9, 6.0-8.9, 9.0-11.9, 12.0-14.9, 15.0-17.9, 18.0-20.9, >21.0.

Height above the water table and shade were not measured due to time constraints and limitations in carrying equipment in the field.

RESULTS

Eight species were common to nearly all the sites examined (Table 1). *Sphagnum boliviae* Warnst., *S. cuspidatum* Ehrh., and *S. recurvum* P. Beauv. were restricted to sites with permanent pools of water. *Sphagnum oxyphyllum* Warnst., *S. sancto-josephense* Crum & Crosby, and *S. sparsum* Hampe occurred singly in small carpets, usually less than 1 m in diameter, or intermixed in larger carpets. *Sphagnum alegrense* Warnst. and *S. magellanicum* Brid. were found in carpets to 10 m in diameter. Both of these species also formed extensive carpets on west-facing vertical cliff faces above 2200 m.

The mean values of the parameters for the species suggest that there is little variation in the surface water of the sites examined (Table 1). *Sphagnum cuspidatum*, a species that was found either submerged or floating in water, was found in sites with the highest conductivity and the lowest pH and cation concentrations. *Sphagnum boliviae*, *S. sancto-josephense*, and *S. recurvum*, species that were typically found at the edge of pools, have similar values of the parameters measured. *Sphagnum alegrense*, *S. magellanicum*, *S. oxyphyllum*, and *S. sparsum* were most common in habitats that were situated above any pools of water and have higher pH and cation concentrations and a lower conductivity than the more nearly aquatic species.

The species fall more or less into two or three groups based on mean niche breadth (Table 2). *Sphagnum sparsum* has the broadest niche breadth, followed by *S. magellanicum* and *S. alegrense*. *Sphagnum oxyphyllum*, *S. recurvum*, and *S. sancto-josephense* form a second group with similar mean niche breadths. *Sphagnum boliviae* and *S. cuspidatum*, the two aquatic species, have the lowest mean niche breadths. Narrow niche breadths are common for Ca, Na, and P. The broadest niche breadths occur for K, pH, and conductivity.

The species exhibit independent utilization of the microhabitat gradients. Niche breadth values for pH, conductivity, and K gradients were similar for *S. alegrense*, *S. magellanicum*, and *S. sparsum*. These species had the broadest niche breadths. *Sphagnum sancto-josephense* had higher niche breadth values for pH and Ca than did *S. magellanicum*, but the other niche breadth values of the former species were lower. *Sphagnum recurvum* had a higher niche breadth for conductivity than did *S. alegrense*, but its other niche breadth values were consistently lower. The two aquatic species, *S. boliviae* and *S. cuspidatum*, had the most similar niche breadth values, but *S. boliviae* growing above the surface of the water had slightly higher niche breadth values for conductivity, K, and Na.

Niche overlap for the parameters measured is high (Table 3). The greatest overlap among species is for Ca and Mg, with a mean overlap value of 1.0. Three parameters (K, Na, and P) have mean overlap values greater than 0.80. The lowest niche overlap values were for pH and conductivity.

The mean overlap among all species is high (Table 4). Fifteen of the species comparisons have mean niche overlap values equal to or greater than 0.90. The lowest mean niche overlap is between *S. cuspidatum* and *S. oxyphyllum*. *Sphagnum boliviae* has relatively low mean niche overlap values with *S. oxyphyllum* and *S. sparsum*,

Table 1. Mean values of environmental parameters measured for *Sphagnum* species from Bolivia. Ion concentrations are in ppm, conductivity in µS/cm, and n is the number of samples. Standard deviations are in parentheses.

Species	pH	K_{corr}	Ca	K	Mg	Na	P
S. alegrense	5.08	24.0	1.83	11.58	1.45	3.0	3.55
(n = 14)	(0.54)	(26.08)	(5.4)	(2.4)	(0.27)	(0.87)	(2.78)
S. boliviae	4.75	35.0	1.37	7.65	1.21	2.25	0.70
(n = 12)	(0.07)	(7.07)	(0.48)	(6.0)	(0.27)	(2.23)	(0.28)
S. cuspidatum	4.5	70.0	1.29	0.40	0.18	0.01	0.00
(n = 10)	(0.3)	(15.2)	(0.23)	(0.21	(0.13)	(0.0)	(0.00)
S. magellanicum	5.41	21.1	1.72	19.14	1.48	2.81	1.49
(n = 19)	(0.34)	(11.67)	(0.92)	(14.18)	(0.55)	(1.6)	(0.64)
S. oxyphyllum	5.5	15.0	1.44	18.8	1.3	4.4	1.90
(n = 12)	(0.4)	(7.27)	(0.39)	(7.63)	(0.19)	(1.68)	(0.7)
S. recurvum	4.9	43.33	1.52	17.0	1.32	1.83	0.83
(n = 13)	(0.59)	(25.17)	(0.39)	(11.25)	(0.24)	(1.78)	(0.60)
S. sancto-josephense	5.16	34.0	1.44	6.5	1.26	1.72	0.90
(n = 15)	(0.59)	(20.74)	(0.48)	(3.85)	(0.24)	(1.45)	(0.60)
S. sparsum	5.68	30.0	3.82	29.6	3.11	9.8	2.25
(n = 17)	(0.92)	(27.08)	(3.9)	(23.8)	(2.27)	(9.7)	(1.15)

Table 3. Mean niche overlap of *Sphagnum alegrense*, *S. boliviae*, *S. cuspidatum*, *S. magellanicum*, *S. oxyphyllum*, *S. recurvum*, *S. sancto-josephense*, and *S. sparsum* for pH, K_{corr}, Ca, K, Mg, Na, and P in Bolivia.

Microhabitat	Mean	SD
pH	0.66	0.42
K_{corr}	0.74	0.40
Ca	1.0	0.0
K	0.85	0.23
Mg	1.0	0.0
Na	0.91	0.16
P	0.83	0.32

but high values with the other species.

DISCUSSION

The values of the environmental parameters measured in this study suggest that the *Sphagnum* habitats examined are ombrotrophic (for example, K_{corr} <70 µS/cm) in nature, yet there was little or no peat accumulation under the living portions of the plants. In Bolivia, *Sphagnum* grows directly on the bedrock or on non-organic soils. The values of pH, K, Ca, Na, and Mg are similar to those reported by Lewis (1981) and Stallard and Edmond (1981) for cation composition of precipitation in the northern Andes of South

Table 2. Niche breadth of *Sphagnum* species for seven microhabitats in Bolivia.

Species	pH	K_{corr}	Ca	K	Mg	Na	P	Mean
S. alegrense	0.56	0.26	0.25	0.46	0.20	0.25	0.34	0.33
S. boliviae	0.17	0.22	0.13	0.26	0.20	0.19	0.17	0.19
S. cuspidatum	0.17	0.14	0.13	0.17	0.20	0.13	0.17	0.16
S. magellanicum	0.32	0.38	0.16	0.66	0.26	0.27	0.37	0.37
S. oxyphyllum	0.17	0.24	0.13	0.28	0.20	0.21	0.28	0.22
S. recurvum	0.24	0.32	0.13	0.34	0.20	0.18	0.21	0.23
S. sancto-josephense	0.34	0.28	0.22	0.29	0.20	0.22	0.20	0.25
S. sparsum	0.53	0.39	0.37	0.53	0.58	0.18	0.28	0.41
Mean	0.31	0.28	0.19	0.37	0.26	0.20	0.25	

Table 4. Mean niche overlap values of *Sphagnum alegrense* (ale), *S. boliviae* (bol), *S. cuspidatum* (cus), *S. magellanicum* (mag), *S. oxyphyllum* (oxy), *S. recurvum* (rec), *S. sancto-josephense* (san), and *S. sparsum* (spa) for pH, K_{corr}, Ca, K, Mg, Na, and P.

	ale	bol	cus	mag	oxy	rec	san	spa
ale	-							
bol	0.79	-						
cus	1.0	0.86	-					
mag	0.91	0.97	0.71	-				
oxy	0.99	0.57	0.43	0.90	-			
rec	0.79	0.98	1.0	0.87	0.95	-		
san	0.69	0.99	0.71	0.76	1.0	0.98	-	
spa	0.91	0.64	1.0	0.82	0.97	0.76	0.94	-

America. The mean pH of precipitation in the Andes is 5.67 and ion concentrations of Ca, Mg, K, and Na range between 0.04 and 2.2 mg/l. The lowest pH that was recorded from the sites studied in Bolivia was 4.5, with the majority of the pH values (62%) greater than 4.9. These values are similar to the pH of *Sphagnum*-dominated peatlands in Ecuador and Colombia. McQueen (1991) reported a pH range of 4.0 to 6.4 for the *Sphagnum*-dominated páramo habitats of in Ecuador and Cleef (1981) gave a pH range of 4.6 to 5.3 for similar habitats in Colombia. *Sphagnum* habitats in Costa Rica are more acidic with a pH range of 3.0-5.2 (McQueen 1989, 1995).

The occupation by *Sphagnum* species of the parameters examined in this study in Bolivia differs from that in other regions that have been examined. In Bolivia K has the broadest gradient, followed by pH, K_{corr}, Mg, P, Na, and Ca (Table 2). In Ecuador K likewise has the broadest gradient, followed by Mg, pH, P, Fe, Mn, Ca, Na, and K_{corr} (McQueen 1991). The broadest niche in Costa Rica is for pH, followed by K_{corr}, Mn, Na, P, Ca, Mg, and Fe (McQueen 1995). In North America Vitt and Slack (1984) found that Ca had the broadest gradient followed by height above the water table, K_{corr}, Mg, shade, pH, K, and Na.

The niche overlap among species in Bolivia is similar to the values reported by McQueen (1991) for species in Ecuador. Ninety percent niche overlap values for *Sphagnum* species in Ecuador were greater than 0.80. The mean niche overlap for all species in Bolivia is 0.83. These values are higher than those reported by McQueen (1995) for species in Costa Rica that have a mean niche overlap of 0.63. These comparisons are meaningful since the resources examined and the number of classes for the parameters were the same with the exception of Fe and Mn that were not used for the study of species in Bolivia.

A comparison of niche overlap of Central and South American species to North American species is difficult because not all of the same resources nor the same number of classes for the parameters were used in published reports of *Sphagnum* niche. Vitt and Slack (1984) do not give a total mean overlap for all of the 13 species they studied in North America, but the mean niche overlap values that they do report are less than 0.50.

The mean overlap of all the pairwise overlaps has been used by Pianka (1986) to determine the most important gradient. Gradients with low mean niche overlap values separate species niches more than gradients with high mean overlap values. Using this approach, pH and K_{corr} (Table 3) are the most important variables examined in this study in segregating species niches. The mean niche overlap values from Ecuador are all very high, but Fe and Na (mean = 0.87) were the lowest values. In Costa Rica, McQueen (1995) found that Fe and Mn had the most important gradients of those that were examined (mean = 0.59). In the midwestern United States, Vitt and Slack (1984) found pH to have the lowest mean niche overlap among species. Gignac (1992), in a regional study of bryophyte niche in western Canada, found that climate (based upon 30-year means of precipitation) is the most important factor in affecting *Sphagnum* niches and overshadows locally important gradients such as surface water chemistry. The habitat for *Sphagnum* in Central and South America, restricted as it is to high elevation cloud forests and páramo ecosystems, is more limited than in North America so that locally important gradients such as water chemistry are important.

The differences in the niche breadth and overlap values and the occupation of the various gradients examined in North, Central, and South America suggest that *Sphagnum* species may not be strictly equilibrium species as characterized by Vitt and Slack (1984). Slack (1982) believed that equilibrium species should have well-defined niches distinct from close competitors, whereas fugitive species are characterized by strong niche overlap with other species. The present study seems to confirm Andrus' (1986) view that the characterization of *Sphagnum* as equilibrium species may be appropriate for only well-developed and slowly evolving peatlands of North America, but it should not be a general rule in other regions. The reports by Vitt and Slack (1984), Gignac and Vitt (1990), and Gignac (1992) suggest that *Sphagnum* species in the peatlands of North America have well-defined niches and low niche overlap. The *Sphagnum* habitats of Bolivia are not conducive to the formation of well-developed peatlands with deep peat deposits. The high niche overlap values suggest that in Bolivia, the species are better characterized as fugitive species.

The range of niche breadth values of *Sphagnum* species in the páramo and cloud forests of Bolivia are similar to those of previous studies. Vitt and Slack (1984) reported a range of niche breadth values for 13 North American species of 0.20 to 0.39. These values are similar to those reported in this study (Table 2). Comparisions of niche dimensions among species from North, Central, and South America are complicated because few of the species are common to the regions studied. In addition, the parameters examined in each region are somewhat different, the number of classes used for each parameter are not uniform, and the studies were carried out during a small fraction of the growing season. Permanent plot studies such as those conducted by Rydin (1993) would provide better estimates of niche parameters and this approach would permit more meaningful comparisions of *Sphagnum* niche on a continental scale. In spite of these limitations, niche studies, including this one, at least provide a hint of the niche dimensions of *Sphagnum* species.

Sphagnum magellanicum is the only species for which a direct comparison is possible in North, Central, and South America since it is the only one that was examined in all niche studies of the hemisphere. Vitt and Slack reported a mean niche breadth for this species as 0.37 which is identical to the value reported in this study (Table 2). Gignac (1992) found this species to have the highest niche breadth (0.42) of any of the *Sphagnum* species he studied in western Canada. McQueen (1991, 1995) reported higher values for this species in Ecuador (0.45) and Costa Rica (0.46). In the North, Central, and South American studies previously cited, *S. magellanicum* has the second highest niche breadth for all species examined.

Sphagnum sancto-josephense is the only species, except for *S. magellanicum*, that was common to the studies of niche in Central and South America. The mean niche breadth of this species is variable. McQueen (1991) found this species to have the highest mean niche breadth in Ecuador (0.59) and the lowest mean niche breadth (0.19) in Costa Rica (McQueen 1995). The variable niche breadth values of this species may be a function of its range. Costa Rica, the type locality for the species (Crum & Crosby 1974), is the northernmost site for this species (McQueen 1992, Sharp et al. 1994). Cleef (1981) and Sanchez et al. (1989) report that the species is common in the páramo of Colombia. Bolivia may represent the southern limit of the range of this species. A search for specimens of this species in several herbaria (NY, MO, VT) seems to confirm this idea.

Sphagnum sparsum has the broadest niche breadth of any species examined in Central and South America. McQueen (1995) found this species to have the highest niche breadth of *Sphagnum* species examined in Costa Rica. The mean niche breadth reported for this species in Costa Rica (0.48) is very similar to the values determined for it in Bolivia (Table 2). Crum (1990b) described this as a common species in the páramo between elevations of 2250 and 3900 m in the Andes from Bolivia to Costa Rica with sporadic occurrences in Mexico. It is one of the most common *Sphagnum* species in Costa Rica (McQueen 1995) and likewise the most common species found at the sites examined in Bolivia.

Sphagnum alegrense is the only other species for which published niche data are available. The mean niche breadth of 0.33 reported in this study is similar to the value determined by McQueen (1995) for it in Costa Rica (0.28). This species has been reported from Brazil (type locality), Venezuela, Guadeloupe, and Dominica by Crum (1990a), from Panama by Allen (1986), and Costa Rica by McQueen (1989, 1992, 1995).

Sphagnum cuspidatum and *S. recurvum* are cosmopolitan species like *S. magellanicum* and they are widespread throughout the northern and southern hemispheres (Crum 1984). This is the first study of the niche of these species. Their low niche breadth values are to be expected since these species are restricted to aquatic or near-aquatic *Sphagnum* habitats throughout their ranges with few other species occupying this habitat.

There is very little information available for *S. oxyphyllum* and *S. boliviae*. Crum (1990b) reported that *S. oxyphyllum* is found in the southern and Amazonian regions of Brazil, as well as Guyana, Venezuela, and Colombia with an altitudinal range of 430 to 2700 m. Herbarium label information indicates that it is found in moist forests and meadows on wet rocks and banks of soil near streams and waterfalls. These descriptions fit the cloud forest habitat where it is found in Bolivia. This species was not collected in any of the páramo sites in Bolivia.

Much less is known of *S. boliviae*. This species, endemic to Bolivia, has been reported from altitudes of 1600 to 3000 m (Crum 1990c). It is virtually identical to the cosmopolitan species *S. lescurii* Sull. (= *S. subsecundum* var. *rufescens* (Nees & Hornsch.) Hüb.) which is found throughout the northern and southern hemispheres. If it is synonomous with the latter taxon then it may be compared to the niche breadth reported by McQueen (1991) for *S. subsecundum* var. *rufescens* from Ecuador. In Ecuador this taxon has a mean niche breadth of 0.40 and it is restricted to *Sphagnum*-dominated peatlands in the páramo. The Bolivian habitat for this species is on the margins of small, permanent pools of water with *S. cuspidatum* in the páramo surrounded by small carpets of *S. magellanicum*, *S. recurvum*, and *S. sancto-josephense*. However, the taxonomic status of *S. boliviae* needs to be reevaluated before any meaningful niche comparisons can be made with other Section *Subsecunda* taxa.

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