Tropical Bryology 11: 119-127, 1995

Niche Breadth and Overlap of *Sphagnum* Species in Costa Rica

Cyrus B. McQueen

Environmental and Health Sciences Department, Johnson State College, Johnson, VT 05656

Abstract. Niche breadth and overlap values of *Sphagnum* species in Costa Rica are similar to those reported for *Sphagnum*-dominated peatlands in North America. *Sphagnum magellanicum* Brid. and *S. sparsum* Hampe have the broadest niche breadth of the common species in Costa Rica. Although *S. sancto-josephense* Crum & Crosby has a relatively narrow niche breadth, it is one of the most common species along with *S. magellancium* and *S. sparsum* in the *Sphagnum* habitats of Costa Rica. Niche overlap is high among species with the exception of *S. platyphyllum* (Braithw.) Warnst. which is found in habitats that are rich in iron. The pH, conductivity, and concentrations of Ca, Fe, Mg, Mn, Na, K, and P of *Sphagnum* habitats in Costa Rica are similar to those reported for páramo habitats in South America.

Introduction

Calculations of niche breadth and overlap for *Sphagnum* species in North America suggests independent species utilization of the gradients. Vitt and Slack (1975, 1984) found that niche breadths of Ca and pH become narrower from hollow to hummock. The broadest niche breadths appear to be for midhummock species along the height gradient. They concluded that individual species appear to interact independently to different gradients. For these reasons they believed 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, whereas, fugitive species are characterized by strong niche overlap with similar species.

There is some disagreement over the characterization of *Sphagnum* species as being equilibrium species in general. Andrus (1986) felt 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 often characteristic of fugitive species. In contrast, the distribution of *Sphagnum* in peatlands was 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 which was viewed as a relatively long-lived habitat.

Gignac and Vitt (1990) reported that climate and water chemistry gradients are 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. They also found that shade and height relative to the water table have little effect on species distributions except for those species found at either end of the height gradient.

Much less is known of the niche preferences of *Sphagnum* species in Central and South America. I have found that niche breadth and overlap values for *S. magellanicum* Brid., *S. recurvum* P. Beauv., *S. sancto-josephense* Crum & Crosby, and *S. subsecundum* var. *rufescens* (Nees & Hornsch.) Hub. in Ecuador are similar to those reported for *Sphagnum*-dominated peatlands in North America (McQueen 1990). In these peatlands, *S. magellanicum* and *S. sancto-josephense* appear to have the largest niche breadths and they are the most common species in the region. However, this earlier study was limited to four peatlands in southern Ecuador and not all types of habitats in the region were examined. Therefore, it is reasonable to assume that the values reported by McQueen (1990) are truncated compared to the studies in North America.

Several other studies corroborate the niche study in Ecuador. Wolfe and McQueen (1992) reported that *S. magellanicum* and *S. sancto-josephense* are the most common species in the páramo habitats of Costa Rica. Although they did not calculate niche breadth and niche overlap, Wolfe and McQueen believed that their data suggest niche diversification along microhabitat gradients and independent species utilization of the gradients similar to the studies of Vitt and Slack (1984) and McQueen (1990).

Both Cleef (1981) and Sánchez et al. (1989) have described similar niche relationships for *Sphagnum* species in Colombia. Although they did not directly study quantitative niche diversification, they noted that *S. magellanicum* and *S. sancto-josephense* also appear to have relatively broad niches in the páramo habitats of Colombia.

The purpose of the present study was to examine niche diversification of *Sphagnum* species in Costa Rica. A wider range of habitats was examined than in my previous study of Ecuadorian peatlands (McQueen 1990) in order to obtain a more realistic measure of niche breadth and overlap for Neotropical *Sphagnum* species. Costa Rica has a *Sphagnum* flora of at least 20 species of both the Nearctic and Neotropics (McQueen 1995) which is more diverse than the Central American countries to the north or Panama to the south (Crum 1980; Allen 1986, 1994; Griffin 1981). The great bryophyte diversity within Costa Rica has been attributed to its varied ecological habitats (Bowers 1974, Holdridge 1967, Janzen 1983).

Methods and Materials

The sites examined in this study were selected because they are representative of the types of *Sphagnum* habitats in Costa Rica. Only two of the sites can be referred to as peatlands. The largest of these peatlands is located near Kilometer 70 along the Pan American Highway approximately halfway to the summit of Cerro de la Muerte (3,491 m). This peatland is quite large for Central America at more than 40 ha. in size. The peat in this wetland is 25 cm deep in the center. A 5 cm thick deposit of outwash consisting of stones as large as 1 cm in diameter is found directly beneath the peat. Approximately 20 cm of a black clay are found beneath the outwash and below this is a deposit of red clay. *Sphagnum* forms quite extensive carpets in this peatland with hummocks nearly 30 cm high. The most noticeable vascular plants are *Blechnum*, *Vaccinium*, *Carex*, *Juncus*, and *Xyris*. Karlin (1991) has reported *S. sancto-josephense* Crum & Crosby, *S. lescurii* Sull., *S. magellanicum* Brid. and *S. platyphyllum* (Lindb.) Sull. In addition, I found *S. alegrense* Warnst. and *S. sparsum* Hampe. This peatland is probably frequently disturbed by fire since many of the older *Blechnum* trunks show evidence of being burned and many young *Blechnum* plants showed evidence of recent burning in early 1991.

The second peatland is located just outside the entrance to Volcán Poás National Park. This peatland is approximately half the size of the other peatland. *Sphagnum sancto-josephense* is the most common species and forms extensive carpets throughout the peatland. Other species in the peatland include *S. poasense* Crum, *S. magellanicum*, *S. recurvum*, and *S. sparsum*. The dominant vascular plants include *Vaccinium*, *Carex*, *Juncus*, and *Xyris*. There are several water courses that traverse the peatland that are nearly 3 m deep. In some of the drier portions of the peatland where there is little water in the main stream, at least during the dry season of 1991, it was possible to see that the peat deposit was more than 2 m in depth in some places. The substrate beneath the peat is volcanic in origin.

Additional sites examined were on the slopes and summits of Cerro Chirripó (3,819 m) and Cerro de la Muerte (3,491). *Sphagnum* forms small carpets and hummocks in the subalpine paramo forests of both mountains, dominated by forests of *Quercus*, *Arctostaphylos*, and *Lomaria*. On Cerro Chirripó *Sphagnum* becomes common at an elevation of approximately 2,700 m and on Cerro de la Muerte at approximately 3,300 m. Cerro Chirripó differs from Cerro de la Muerte in that it was glaciated during the Pleistocene (Weber 1959). In the páramo of Cerro Chirripó, *Sphagnum* is found primarily around the margins of the numerous moraine lakes near the summit. According to the ranger, the moraine lakes may recede by as much as 5 m during the dry season. Whereas, on Cerro de la Muerte *Sphagnum* is found in the paramo just below the summit. *Sphagnum aureum* McQueen, *S. meridense* (Hampe) C.M., *S. cuspidatum* Hoffm., *S. gomezii* Crum, *S. perichaetiale* Hampe, *S. sparsum*, *S. magellanicum*, and *S. alegrense* are found on both mountains.

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 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 $NB = 1/(nP_{ij}^2)$, 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). Niche overlap was calculated using $O_{jk} = (P_{ij}P_{ik}) / ((P_{ij}^2)(P_{ik}^2))^{1/2}$, 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 3.0-5.2; n = 6; classes, 3.0-3.3, 3.4-3.7, 3.8-4.1, 4.2-4.5, 4.6-4.9, ≥5.0.

Conductivity: range 11.3-93.6 µS/cm; n = 10; classes, 0-10, 11-20, 21-30, 31-40, 41-50, 51-60, 61-70, 71-80, 81-90, ≥91.

Ca: range 0.5-24.8 ppm; n = 10; classes, 0-2.5, 2.6-5.0, 5.1-7.5, 7.6-10.0, 10.1-12.5, 12.6-15.0, 15.1-17.5, 17.6-20.0, 20.1-22.5, ≥22.6.

Fe: range 0.05-176 ppm; n = 10; 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, 8.1-9.0, ≥9.1

Mg: range 0.31-9.97 ppm; n = 10; 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, 7.1-8.0, 8.1-9.0, ≥9.1.

Mn: range 0-3.22 ppm; n = 7; classes, 0-0.5, 0.6-1, 1.1-1.5, 1.6-2.0, 2.1-2.5, 2.6-3.0, ≥3.0.

P: range 0-6.7 ppm; n = 11; classes, 0-0.5, 0.6-1.0, 1.1-1.5, 1.6-2.0, 2.1-2.5, 2.6-3.0, 3.1-3.5, 3.6-4.0, 4.1-4.5, 4.6-5.0, ≥5.1.

K: range 6.0-326 ppm; n = 11; classes, 0-10, 10.1-20, 20.1-30, 30.1-40, 40.1-50, 50.1-60, 60.1-70, 70.1-80, 80.1-90, 90.1-100, ≥100.1.

Na: range 2.1-76.4 ppm; n = 8; classes, 0-10, 11-20, 21-30, 31-40, 41-50, 51-60, 61-70, ≥71.

It was not possible to collect data on all species at these sites because this study was undertaken during the dry season. The species for which no water samples were taken were *S. cuspidatum*, *S. gomezii*, *S. lescurii*, *S. meridense*, *S. perichaetiale*, *S. poasense*, and *S. recurvum*. Some species appear to survive with little ground water near the plants. Height above the water table and shade were not measured due to time constraints on my time spent in the country and limitations in carrying equipment in the field.

Results

The pH, corrected conductivity, and elemental concentrations of the surface water collected around the species examined, with a few exceptions, exhibit little variation (Table 1). The greatest differences are for Fe and K. The surface water around *Sphagnum platyphyllum* was about 100 times higher in Fe than for any other species. *Sphagnum alegrense* was also found in sites that had relatively higher concentrations of Fe than the other species. The concentration of K around *S. aureum* was almost double that of the other species examined. These three species are associated with the highest conductivity levels.

Niche breadth was variable among species (Table 2). The species fall into three groups based on mean niche breadth. *Sphagnum sparsum* and *S. magellanicum* have the broadest mean niche breadths, *S. alegrense* and *S. aureum* form a second group with similar mean niche breadths, and *S. platyphyllum* and *S. sancto-josephense* have the lowest mean niche breadths. The narrowest niche breadth for nearly all species is Fe. This is primarily due to the skewness of the data with *S. platyphyllum*.

Niche overlap among species is high (Table 3). The greatest overlap among species is for Ca and the lowest for Fe and Mn. Mean niche overlaps between each pair of species are shown in Table 4. The majority of the overlap values are greater than 0.70. In general there is a high degree of overlap among all the species with the exception of *S. platyphyllum*.

Discussion

The parameters measured for the two large peatlands are very similar to the peatlands examined by McQueen (1990). The low pH values for these two Costa Rican peatlands is no doubt due to seasonal variation of the dry season. I examined these peatlands near the end of the dry season when water levels in the páramo and most other habitats are low. Wolfe and McQueen (1992) reported that the Cerro de la Muerte peatland is most similar to the *Xyris-Sphagnum* bog type described by Cleef (1981). These peatlands occur in northwestern South America between 3300 and 3700 m in the upper subpáramo and lower grass páramo. Cleef described the soils as clayey to black peat with a pH range of 4.6-5.3. The bare peat in some portions of this peatland was dark brown to black. Some of the areas with black peat were very wet and soggy similar to portions of quaking mats in North America. *Sphagnum magellanicum* and *S. sancto-josephense* are the most common species in this peatland which corresponds to Cleef's description of this type of peatland. One major difference is that this Costa Rican peatland had at least six *Sphagnum* species, whereas, Cleef only reported *S. magellanicum*, *S. sancto-josephense*, and *S. cuspidatum* for these types of peatlands in Colombia.

The Volcan Poás peatland corresponds to the *Xyris acutifolia* bog of Cleef (1981) which he considered as a subtype of the *Xyris-Sphagnum* bog. These peatlands are described by Cleef as forming on gentle slopes (3°-5°), with a peaty clay depth of more than 120 cm, and a pH of about 5.0. These peatlands also include species of *Vaccinium* and *Isoetes*. The low pH of this peatland may be attributed to the season because herbarium specimens that I collected in December 1988 from this peatland [*S. sancto-josephense*: *McQueen 4060*, *4061*, *4062*, *4067*, *4074* (NY)] indicate that the pH ranged from 4.5 to 6.25. *Sphagnum magellanicum* and *S. sancto-josephense* are the most common species in this peatland in addition

Table 1. Mean values of environmental parameters measured for Sphagnum species from Costa Rica. 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	Mg	Fe	Mn	Na	K	P
S. alegrense	3.9	51.5	6.5	3.5	8.1	0.9	46.8	79.3	2.5
	(0.4)	(19.5)	(5.4)	(2.4)	(0.6)	(0.5)	(19.5)	(26.3)	(1.4)
S. aureum	3.4	63.3	7.5	3.2	0.4	1.5	30.6	132.5	3.2
	(0.3)	(17.3)	(6.3)	(2.6)	(0.1)	(0.9)	(11.3)	(27.9)	(1.8)
S. magellanicum	4.3	41.3	7.8	2.9	0.9	0.9	24.6	71.2	1.8
	(0.7)	(24.5)	(6.2)	(2.6)	(0.2)	(0.3)	(20.0)	(40.7)	(1.5)
S. platyphyllum	4.0	54.6	7.9	4.9	100.5	1.2	30.5	61.6	1.6
	(0.6)	(26.7)	(0.2)	(0.1)	(75.5)	(0.2)	(3.9)	(33.4)	(0.5)
S. sancto-josephense	3.5	42.1	3.9	2.7	0.9	0.3	30.3	70.2	1.6
	(0.5)	(18.7)	(4.2)	(3.1)	(0.1)	(0.3)	(24.3)	(31.7)	(1.4)
S. sparsum	4.1	44.9	5.6	2.6	1.2	1.0	24.9	82.0	1.7
	(0.6)	(25.4)	(4.0)	(2.0)	(0.7)	(0.5)	(17.3)	(42.0)	(1.2)

Table 2. Niche breadth of *Sphagnum* species for nine microhabitats in Costa Rica.

Species	pH	K_{corr}	Ca	Mg	Fe	Mn	Na	K	P	Mean
S. alegrense	0.51	0.34	0.20	0.20	0.18	0.43	0.39	0.05	0.26	0.28
S. aureum	0.40	0.26	0.28	0.26	0.10	0.34	0.30	0.22	0.27	0.27
S. magellan.	0.53	0.68	0.50	0.38	0.14	0.34	0.55	0.59	0.45	0.46
S. platyphyll.	0.17	0.21	0.10	0.10	0.10	0.14	0.23	0.17	0.16	0.15
S. sancto-josephense	0.33	0.21	0.13	0.13	0.10	0.18	0.16	0.22	0.22	0.19
S. sparsum	0.56	0.64	0.44	0.46	0.12	0.64	0.49	0.31	0.62	0.48
Mean	0.42	0.39	0.28	0.26	0.12	0.35	0.35	0.26	0.33	

Table 3. Mean niche overlap of *Sphagnum alegrense*, *S. aureum*, *S. magellanicum*, *S. platyphyllum*, *S. sancto-josephense*, and *S. sparsum* for pH, K_{corr}, Ca, Mg, Fe, Mn, Na, K, and P in Costa Rica.

Microhabitat	Mean	SD
pH	0.70	0.35
K_{corr}	0.64	0.35
Ca	0.78	0.33
Mg	0.70	0.39
Fe	0.59	0.48
Mn	0.59	0.40
Na	0.70	0.35
K	0.60	0.33
P	0.75	0.34

Table 4. Mean niche overlap values of *S. alegrense* (ale), *S. aureum* (aur), *S. magellanicum* (mag), *S. platyphyllum* (pla), *S. sancto-josephense* (san), and *S. sparsum* (spa) for pH, K_{corr}, Ca, Mg, Fe, Mn, Na, and P.

	ale	aur	mag	pla	san	spa
ale	-	0.72	0.61	0.22	0.84	0.70
aur		-	0.71	0.33	0.87	0.78
mag			-	0.81	0.80	0.81
pla				-	0.44	0.68
san					-	0.78
spa						-

to *S. poasense, S. recurvum*, and *S. sparsum*. Cleef only reported *S. magellanicum*, *S. sancto-josephense*, and *S. cuspidatum* for similar peatlands in Colombia.

Sphagnum sparsum is by far one of the most common species found in Costa Rica. The results of this study confirm that this species has a broad niche and it is frequently found in association with many other species of *Sphagnum*. Crum (1990b) reported that this is one of the most commonly collected species in the mountains of northern South America. It is common above 2000 m above tree line in moist, montane forests in Mexico and more commonly in páramo habitats to the south.

Sphagnum magellanicum is confirmed by the studies of Vitt and Slack (1984), McQueen (1990), and the present study to have a broad niche breadth compared to most species. In each study, this species has the second highest niche breadth. This is not surprising since *S. magellanicum* has a cosmopolitan distribution (Crum 1984).

Sphagnum sancto-josephense is one of the most common species in the páramo of Central and South America. In Ecuador, I found this species to have the broadest niche breadth (McQueen 1990), whereas in the present study it was found to have one of the lowest niche breadths compared to other species. The differences in niche breadth in these studies may be due to the inclusion of more diverse kinds of *Sphagnum* habitats in the present study. *Sphagnum sancto-josephense* may have a broad niche breadth within peatlands, but narrow when all *Sphagnum* habitats are included. Based on my own field experience, *S. sancto-josephense* and *S. magellanicum* are the most common species in the larger peatlands of Costa Rica and Ecuador. These two species are also the most common species found in the páramo habitats throughout the Andes that I have examined at least south to Bolivia. Ecologically, *S. sancto-josephense* is very similar to *S. angustifolium* C. Jens. in North America which has a broad distribution in the Northern Hemisphere. *Sphagnum angustifolium* is also very common in open, poor to medium fen peatlands (Andrus 1980), but it is also widespread in poor to medium-wooded coniferous fens and cedar swamps.

Sphagnum alegrense superficially resembles *S. magellanicum*, but it differs in micromorphology and in its range. Crum (1990a) reported it from Brazil, Venezuela, Guadeloupe, Dominica, and possibly Panama. There is very little information on its habitat. McQueen (1989) found it on wet seeps on Cerrro de la Muerte with *S. magellanicum*, *S. meridense*, *S. perichaetiale*, and *S. sparsum*. The results of this study indicate that the niche breadth of *S. alegrense* is less than that of *S. magellanicum*, a species with which it is closely related. *Sphagnum alegrense* also has one of the lowest overlap values with other species examined in this study. This species is usually found in damp, shaded seeps above 2500 m in Costa Rica forming small carpets or hummocks to 0.5 m in height. *Sphagnum alegrense* is most often associated with *S. sancto-josephense* and *S. aureum*.

Sphagnum platyphyllum was first reported in Costa Rica by Karlin (1991). It has a disjunct pattern of distribution throughout most of its range. The nearest populations outside of Costa Rica are in the southwestern United States, but Karlin believed that is probably occurs at other high elevation habitats in Central America. The site at which it is found on Cerro de la Muerte is typical of the intermediate fens and minerotrophic habitats in which it occurs in North America (Andrus 1980, Crum 1984).

Sphagnum aureum was first described by McQueen (1989). The plants form tightly compact hummocks at the bases stands of bamboo, small cushions on the edges of eroding stream banks, and as an infrequent species in the larger, more diverse *Sphagnum* habitats of Cerro de la Muerte and Cerro Chirripó. Although closely related to *S. magellanicum*, it is more frequently found in association with *S. alegrense*, *S. sancto-josephense*, and *S. sparsum*.

In general, the niche values for *Sphagnum* species in the Neotropics are very similar to those in the Nearctic. The results of the present study and those of Vitt and Slack (1984) and McQueen (1991) suggests independent utilization of different microgradients. The greater similarity of the Costa Rican niche values to the niche values of *Sphagnum* species in North America than to the niche values reported for South America may be accounted for by diversity. Of the 20 *Sphagnum* species reported by McQueen (1995) for Costa

Rica, 10 of the species are found in North America. The rest of the species are more common to Central and South America, primarily in the Andes. Costa Rica has been described as a filter bridge (Simpson 1965, Marshall et al. 1982, Janzen 1983) where terrestrial organisms from the Nearарctic and Neotropics mix. My own experience in the northern Andes south to Bolivia suggests that there are fewer species in the páramo and cloud forest habitats than in Costa Rica. Therefore, I would expect the species in the Andes to have greater niche values than the more diverse habitats further north.

Literature cited

Allen, B. 1986. The Genus *Sphagnum* in Panama. Evansia 3: 46-48.

Allen, B. 1994. Moss Flora of Central America. Part 1 *Sphagnaceae-Calymperaceae*. Missouri Botanical Garden. St. Louis, Missouri.

Andrus, R. E. 1980. *Sphagnaceae* of New York State. New York State Museum Bulletin 422. Albany, New York.

Andrus, R.E. 1986. Some aspects of *Sphagnum* ecology. Canadian Journal of Botany. 64: 416-426.

Bowers, F. D. 1974. The mosses reported from Costa Rica. The Bryologist 77: 150-171.

Cleef, A. M. 1981. The vegetation of the paramos of the Colombian Cordillera Oriental. Dissertations Botanicae 61: 320 pp. J. Cramer. Vaduz.

Crum, H.A. 1981. 1980. A guide to the identification of Mexican Sphagna. Contributions of the University of Michigan Herbarium 14: 25-52.

Crum, H.A. 1984. Sphagnopsida. *Sphagnaceae*. North AmericanFlora, II, 11. New York Botanical Garden, Bronx, New York.

Crum, H.A. 1990a. Comments on *Sphagnum* sect. Sphagnum in South America. Contributions of the University of Michigan Herbarium 17: 71-81.

Crum, H.A. . 1990b. A new look at *Sphagnum* sect. Acutifolia in South America. Contributions of the University of Michigan Herbarium 17: 83-91.

Daubenmire, R. F. 1959. A canopy-coverage method of vegetation analysis. Northwest Scientist 33: 43-64.

Gignac, L. D. & D. H. Vitt. 1990. Habitat limitations of *Sphagnum* along climatic, chemical, and physical gradients in mires of western Canada. The Bryologist 93: 7-22.

Griffin, D. 1981. El genero *Sphagnum* en los Andes de Columbia. Cryptogamie, Bryologie, Lichenologie 2: 201-211.

Holdridge, L. R. 1967. Life zone ecology. Tropical Science Center. San Jose, Costa Rica.

Janzen, D. H. 1983. Costa Rican natural history. The University of Chicago Press. Chicago, Illinois.

Karlin, E. F. 1991. Notes on *Sphagnum* in Costa Rica: A major range extension for *Sphagnum platyphyllum*. The Bryologist 94: 51-52.

Levins, R. 1968. Evolution in changing environments: Some theoretical explorations. Princeton University Press, Princeton, New Jersey.

Marshall, L. G., S. D. Webb, J. J. Sepkoski Jr., and D. M. Raup 1982. Mammalian evolution and the great American interchange. Science 251: 1351-1357.

McQueen, C. B. 1989. *Sphagnum aureum*, a new species from Costa Rica. The Bryologist 92: 405-406.

McQueen, C. B. 1990. Niche breadth and overlap of four species of *Sphagnum* in Southern Ecuador. The Bryologist 94: 39-43.

McQueen, C. B. 1995. The genus *Sphagnum* in Costa Rica. Brenesia 38(in press).

Pianka, E. R. 1974. Niche overlap and diffuse competition. Proceedings of the National Academy of Sciences 71: 2141-2145.

Pianka, E. R. . 1978. Evolutionary ecology. Harper and Row, Publishers. New York.

Sánchez, R., O. Rangel, & J. Aguirre. 1989. Estudios ecológico en la Cordillera Oriental IV: Aspectos sinecológicos de la brioflora de los depositos turbosos paramunos de los alrededores de Bogotá. Caldasia 16: 41-57.

Simpson, G. G. 1965. The geography of evolution. Hilton Press. Philadelphia.

Sjörs, H. 1950. On the relation between vegetation and electrolytes in North Swedish mire waters. Oikos 2: 241-258.

Slack, N. G. 1982. Bryophytes in relation to ecological niche theory. Journal of the Hattori Botanical 52: 199-217.

Vitt, D.H. & N.G. Slack. 1975. An analysis of the vegetation of *Sphagnum*-dominated kettle-hole bogs in relation to environmental gradients. Canadian Journal of Botany 53:332-359.

Vitt, D.H. & N.G. Slack. 1984. Niche diversification of *Sphagnum* relative to environmental factors in northern Minnesota peatlands. Canadian Journal of Botany 62: 1409-1430.

Weber, H. 1959. Los páramos de Costa Rica y su concatenación fitogeográfica con los Andes Suramericanos. Instituto Geográfico de Costa Rica. San José, Costa Rica.

Wolfe, J. & C. B. McQueen. 1992. Biogeochemistry of six species of *Sphagnum* in Costa Rica. Tropical Bryology 5: 73-77.