

# BRYOPHYTE DISPERSAL INFERRED FROM COLONIZATION OF AN INTRODUCED SUBSTRATUM ON WHITEFACE MOUNTAIN, NEW YORK<sup>1</sup>

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A long-standing debate in bryophyte biogeography concerns the frequency of long-distance spore dispersal. The diversity of bryophytes on mortared rock walls along the Veterans Memorial Highway on Whiteface Mountain, New York, USA, was studied to document the recruitment of species over the 65 years since the highway was constructed. The highway is situated in the Adirondack Mountains, a relatively unpopulated region with a largely acidic flora. The introduction of mortar has increased the bryophyte diversity by 50% above that of native lithic substrata on the mountain. The composition of the native and mortar floras differed greatly, suggesting that the walls were not colonized by locally abundant ruderal species. Many of the species sampled on the walls are typically found only in lower elevation forested sites, distant (~5 km or more) from the highway, and not on anthropogenic calcium carbonate. These results suggest that a bryophyte community consisting of common and uncommon species assembled from distant sites at the rate of at least one species per year in the last 65 years. These data provide the ecological context for experimental and phylogeographic studies and suggest that some bryophytes may be capable of routine dispersal over distances of at least 5 km.

**Key words:** Adirondack Mountains; bryophyte; calcicole; calcium carbonate substrata; long-distance dispersal; ruderal.

The area of distribution of a species is the product of its ecological niche and its unique evolutionary history. The relative contributions of ecological and historical factors in governing where a particular species occurs are mediated by the ability of individuals to migrate among suitable sites, usually over short distances. Species with highly disjunct distributions have generated controversy, however, because long-distance migration is thought to be rare (Nathan, 2001). Recent theoretical work on seed dispersal challenges these assumptions (Nathan et al., 2002), and several empirical studies suggest that long-distance dispersal of spores may be more common than previously appreciated (James et al., 2001; Skotnicki et al., 2001; Liepelt et al., 2002; McDaniel and Shaw, 2003). Such migration events may have important consequences for the evolutionary trajectory of species. Although theoretical metapopulation studies are well advanced, empirical estimates of central parameters, such as rates of migration and colonization, are lacking (Husband and Barrett, 1996). An understanding of migration is also essential for predicting how organisms will respond to changing habitat structure and climate and therefore is critical for shaping approaches to the conservation of genetic diversity.

The present study concerns the dispersal ability of bryophytes (mosses and liverworts). Although the predominant means of dispersal on a local scale may be by gametophyte

fragments (Miller and Ambrose, 1976; During, 1997; McDaniel and Miller, 2000) or specialized asexual reproductive structures (e.g., Kimmerer, 1994), most long-distance dispersal is presumably accomplished by spores (Mogensen, 1981; Bremer and Ott, 1990; Miles and Longton, 1992). Studies of spore dispersal typically address either the mechanics of potential dispersal or use floristic or genetic tools to examine realized dispersal. Crum (2001), reviewing studies of dispersal potential, concluded that spore dispersal distances are leptokurtically distributed. Consistent with some spores traveling long distances, van Zanten (1978) found a strong positive correlation between spore longevity and size of distributional area.

Floristic studies of oceanic islands and recently deglaciated regions confirm that some successful migrants colonize new regions over the course of hundreds to millions of years. Phylogeographic studies indicate that the population structure among disjunct populations of some bryophytes is inconsistent with historical tectonic patterns, suggesting dispersal (McDaniel and Shaw, 2003; Shaw et al., 2003). For example, genetic study of so-called “copper-mosses” revealed striking cases of limited genetic structure among rare and intercontinentally disjunct species (Shaw, 1995, 2000; Shaw and Schneider, 1995). Similarly, genetic data suggest a recent dispersal of spores of *Campylopus pyriformis* (Schultz) Brid. across Antarctica (Skotnicki et al., 2001). Patterns of nucleotide variation in multiple nuclear genes from the cosmopolitan moss *Ceratodon purpureus* (Hedw.) Brid. suggest ongoing intercontinental dispersal (S. D. McDaniel and A. J. Shaw, Duke University). While powerful, the chronological resolution of such studies is limited by the mutation rate of molecular markers, typically single nucleotide substitutions over millions of years. Thus, the frequency of migration on an ecological time scale remains unknown.

An exceptional set of circumstances in the Adirondack Mountains of northern New York, USA, created by the introduction of an exotic substratum, allowed us to examine realized dispersal in bryophytes on an ecological time scale. A fundamental ecological division among bryophytes is between

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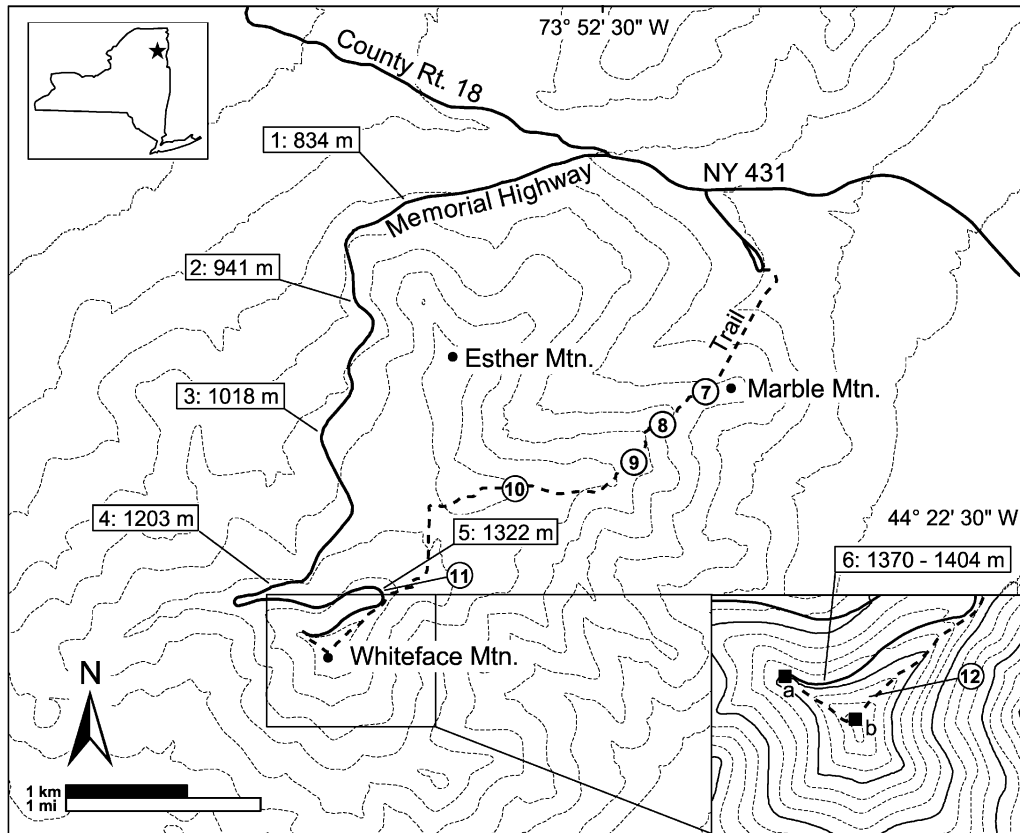


Fig. 1. Whiteface Mountain area, northern New York, USA, showing Veterans Memorial Highway, Marble Mountain Trail, and sample locations. Inset shows location of Castle (a) and summit building (b).

species of acidic sites (calcifuges) and species characteristic of substrata containing calcium and/or magnesium carbonate (calcicoles) (Bates, 2000). The higher Adirondack Mountains are characterized by boreal vegetation dominated by red-spruce-balsam-fir forest (Whitehead and Jackson, 1990) and anorthosite and gneiss bedrock that has zero to trace amounts of carbonate minerals and acidic soil. Base-rich rocks are rare and occur only in valleys where Grenville marble and associated calcareous rocks are exposed or sometimes also as camptonite dikes of limited occurrence in the higher terrain (Miller, 1919; Jaffe and Jaffe, 1986). Such outcrops are generally small and are very rare in the alpine region. The bryophyte flora, therefore, consists largely of calcifuge species (Peck, 1899; Slack, 1976, 1977).

Between 1931 and 1935, the Veterans Memorial Highway was constructed on Whiteface Mountain, terminating at 1400 m just below the 1489 m summit (Fig. 1). Mortar, a rich source of calcium carbonate, was used to build various structures from native bedrock, thereby providing extensive, previously unavailable habitat for calcicole bryophytes. Here we document the recruitment of such species on mortar in the ~65 years since the highway was constructed.

We studied the diversity (species richness) of bryophytes on mortar along the Veterans Memorial Highway to answer two questions: (1) are species found on mortar locally abundant ruderal species, indicating limited dispersal from nearby stations (<1 km) or calcicole specialists immigrating from distant (>5 km) outcrops of calcareous rock; and (2) are species on mortar homogeneously distributed, or are they structured along

an altitudinal gradient, suggesting an additional degree of ecological specialization?

## MATERIALS AND METHODS

**Study site**—Whiteface Mountain (44°21'56.7" N, 73°54'10.9" W; summit altitude 1489 m) and five adjacent lesser peaks (Esther, Little Whiteface, Lookout, and Marble Mountains; Baldwin Hill) form an isolated massif, 29 km north of Mt. Marcy (the highest Adirondack mountain summit [1628 m]) and other high peaks near it. Mean summer temperatures on Whiteface are 11°C (summit) and 18°C (603 m); annual precipitation (mean 97 cm at 603 m) is evenly distributed throughout the year. Cool, wet summers and cold, snowy winters are characteristic of the region.

Below about 650 m, the forest vegetation of Whiteface Mountain contains northern hardwoods (*Acer saccharum* Marsh., *Betula alleghaniensis* Britton, *Fagus grandifolia* Ehrh.). Upslope, these are replaced by conifers, *Abies balsamea* (L.) Mill. and *Picea rubens* Sarg., with *Betula papyrifera* Marsh. in admixture. Above about 1100 m, *A. balsamea* is found in almost pure stands, and higher still on the mountain, this tree forms krummholz, which occurs nearly to the alpine summit cone among heaths, boulders, and bedrock ledges. In certain areas, the spatial distribution of the vegetation deviates from the expected zonation according to aspect, site history (e.g., logging, fires, blow-downs), prevailing wind direction (mostly from the west or northwest), depth to bedrock, and other factors, including tree mortality from acidic deposition.

Settlement of Wilmington, New York (310 m altitude, 7.5 km east-northeast of Whiteface summit), the nearest village, began in 1800, but the population across the northern Adirondacks remained very small until 1840 (Watson, 1869). Early land use on Whiteface Mountain was restricted to logging, and no evidence of 19th-century concrete construction has been found. Logging in the early 1800s appears to have been restricted to lower slopes. Forests

TABLE 1. Bryophyte study sites, Veterans Memorial Highway, Whiteface Mountain, New York, USA.

| Site no. | Wall no. | Plot area (m <sup>2</sup> ) | Elevation (m) | Exposure   | Distance from toll house (m) | Pointing* | Vegetation  |
|----------|----------|-----------------------------|---------------|------------|------------------------------|-----------|---|
| 1        | W1       | 45                          | 834           | N facing   | 1288                         | o, n      | <i>Betula papyrifera</i> – <i>Abies balsamea</i> – <i>Picea rubens</i> forest |
| 2        | W4       | 95                          | 941           | NW facing  | 1974                         | o, m, n   | same  |
| 3        | W7       | 47                          | 1068          | NW facing  | 3406                         | o, m, n   | <i>A. balsamea</i> – <i>P. rubens</i> forest                                  |
| 4        | W8       | 81                          | 1203          | NNW facing | 5977                         | o, m      | <i>A. balsamea</i> – <i>B. papyrifera</i> forest                              |
| 5        | W11      | 241                         | 1322          | NE facing  | 7793                         | o, m, n   | same  |
| 6        | W12      | 69                          | 1395          | N facing   | 7921                         | o, m, n   | <i>A. balsamea</i> forest   |

Note: \* o = old, n = new, m = intermediate age.

higher up the mountain were not harvested until the 1890s and early 1900s, when much of this area was cut over (D. Wolfe, Atmospheric Sciences Research Center, State University of New York at Albany, personal communication). A downhill ski area existed from 1948 to 1960 on the north slope of Marble Mountain, ~4 km northeast of Whiteface summit. Tourists were drawn to Lake Placid village (Town of North Elba), 11 km southwest of the summit, starting in about 1850, and a trail up nearby Whiteface existed as early as 1859 (Waterman and Waterman, 1989).

The bedrock geology of Whiteface Mountain is well known (Miller, 1919; Crosby, 1966, 1971; Fisher et al., 1970). Much of the northern and eastern portions of the mountain consist of meta-anorthosite gneiss, whereas southern and southwestern parts beginning just south of the summit are meta-syenite gneiss. The summit rock is meta-gabbroic anorthosite gneiss (Crosby, 1971). All of these rocks are devoid of carbonates, although they contain minerals such as plagioclase that during the characteristically slow dissolution these resistant rocks release calcium and other cations. Only bedrock comprising the lowest sample of a series taken from fresh outcrop faces along the highway between 826 and 1265 m by Crosby (1966) contained calcite, a calcium carbonate mineral, the presence of which presumably reflected the characteristic low elevation occurrence of marble of the Grenville series. In contrast, large noncontinuous areas of marble and other carbonate-containing rocks occur in lowlands 5–10 km or more from the mountain (Fisher et al., 1970).

The Veterans Memorial Highway (VMH) climbs approximately 1036 m in about 8 km from the tollhouse to the summit buildings along the north- and northwest-facing sides of the mountain (Fig. 1). Construction began in 1931, and the Highway opened to the public in July 1935. The roadbed was blasted out of bedrock, and the fragments were used as fill and in the construction of retaining walls, road and trailside guardrails, summit buildings, and other stonework. Mortar was employed above grade to build these structures, and dry stone construction without mortar was also used extensively. Approximately 65 yr had lapsed between the start of highway building (and the introduction of calcium carbonate mortar) and our field research.

**Sampling strategy**—During the summers of 1997 and 1998, we established study sites (sample plots) at six guardrail walls along the VMH, each separated by approximately 100 m elevation (0.5–2.5 km by road), where we exhaustively sampled all moss and liverwort species (Fig. 1). Distances from the tollhouse and general condition of studied mortared guardrail walls along the highway are reported in Table 1. We performed a total inventory of all species on the walls and structures, as well as in adjacent areas likely to have elevated levels of calcium carbonate leached from the mortar. For comparative purposes, we established six plots, each at a similar elevation to a site along the VMH, on the Marble Mountain Trail (MMT) (named for its color rather than its rock type) up the northeast slope of Whiteface Mountain (Fig. 1, Table 2). At each site, we identified an area consisting largely of rock surface from which to obtain bryophytes and established a 10 m diameter (~80 m<sup>2</sup>) circular plot to reflect the approximate area of wall surface samples along the VMH. We collected or noted examples of all bryophytes on rock substrata in the circles. Areas sampled were largely treeless but surrounded by forest communities of differing density (Table 2). Within each transect, the study sites varied in canopy composition, solar irradiance, moisture availability, and rock surface quality.

Voucher specimens for all except the most common species in both the

VMH and MMT samples were collected and deposited in the New York State Museum Bryophyte Herbarium. Collections of species not recognized in the field were identified in the laboratory where fertility and sexuality were also established. Nomenclature for hepatics largely follows Stotler and Crandall-Stotler (1977) and for most of the mosses, Anderson et al. (1990). Species were classified as calcicoles on the basis of information in Crum and Anderson (1981), supplemented by our experience with the bryoflora of eastern North America.

**Statistical analyses**—To test whether species composition on mortared rock walls differed from that of native rock in the forest, we conducted a  $\chi^2$  contingency test to determine whether species were homogeneously distributed between the two transects. Because we collected presence–absence data for each species in each of the 12 sites, we removed species occurring in fewer than three sites to gain the statistical power to test this hypothesis. To visualize the difference in species composition between the two transects, we performed a principal components analysis (PCA) of species composition in all plots using the software PCOrd (MJM Software Design, Gleneden Beach, Oregon, USA). To test whether the introduction of mortar resulted in an increase in diversity across the VMH sample, we conducted a one-tailed *t* test for unequal variances between the mean number of species in each site for the VMH and MMT.

To examine differences in distributional patterns among liverworts, mosses of native rock, and mosses on mortar, we plotted frequency spectra for these three classes of species (i.e., the number of species in a given number of sites, up to the maximum number of sites in which the species were found). We used a one-tailed *t* test to determine whether mosses of native rock occurred in fewer sites than did mortar mosses. We used linear regression to evaluate the relationship between site elevation and number of species for hepatics and mosses in both transects, as well as to test whether sample area influenced species richness.

## RESULTS

A total of 122 species were found in the two transects, comprising 23 hepatics and 99 mosses (Table 3). Four hepatics were found only on the VMH transect: *Lophozia excisa* at a low elevation site and *Cephaloziella* sp., *Marchantia alpestris*, and *Pellia epiphylla*, all near the summit. Two hepatics, *Barbilophozia kunzeana* and *Ptilidium ciliare*, were found on both transects, exclusively in the highest elevation site along the VMH. A total of 17 hepatics were found only along MMT. Among mosses, 56 species were found only on the VMH transect, and 25 species were found only along the MMT. A total of 18 mosses was common to both transects. *Andreaea rupestris* and *Ptilium crista-castrensis* overlapped only at the lowest elevations, while *Dicranella heteromalla*, *Dicranum fuscescens*, *Pogonatum dentatum*, *Polytrichum strictum*, *Racomitrium fasciculare*, *R. macrocarpon*, and *Sphagnum russowii* overlapped only in the alpine zone. Other overlapping species (*Hylocomium splendens*, *Oncophorus wahlenbergii*, *Paraleucobryum longifolium*, *Polytrichastrum alpinum*, *Polytrichum*

TABLE 2. Bryophyte study sites, Marble Mountain Trail, Whiteface Mountain, New York, USA. All plots were 10 m (80 m<sup>2</sup>) in diameter.

| Plot no. | Elevation (m) | Exposure     | Rock area (%) near site and surface type | Vegetation   |
|----------|---------------|--------------|--|--|
| 1        | 834           | N facing     | 20, boulders                             | open forest: <i>Picea rubens</i> , <i>Betula papyrifera</i>                          |
| 2        | 941           | S facing     | 60, bedrock pavement, gravel, sand       | very open forest: <i>P. rubens</i> , <i>B. papyrifera</i> , <i>Abies balsamea</i>    |
| 3        | 1068          | E facing     | 15, bedrock ledge                        | dense forest: <i>P. rubens</i> , <i>B. papyrifera</i> , <i>A. balsamea</i>           |
| 4        | 1203          | E facing     | 60, bedrock ledge                        | dense forest: <i>A. balsamea</i> , <i>Sorbus americana</i>                           |
| 5        | 1322          | S facing     | 75, boulders                             | dense forest: <i>A. balsamea</i> , <i>B. papyrifera</i>                              |
| 6        | 1440          | N, NE facing | 80, bedrock pavement, boulders           | open alpine or shaded by krummholz: <i>A. balsamea</i> , <i>Vaccinium uliginosum</i> |

*commune*, *P. juniperinum*, *P. piliferum*, *Pohlia nutans*, and *Sanionia uncinata*) showed no detectable elevational pattern to their overlap.

We found considerable variation in species richness among sites in both transects (Fig. 2). The highest elevation VMH wall yielded five hepatic species, but most VMH sites contained none. The highest elevation MMT site contained more hepatic species as well, but no clear elevation trend was evident over the transect as a whole ( $r^2 = 0.02$ ). For example, the second highest site contained one hepatic species, while the summit sample contained 10. In contrast to the situation in liverworts, the VMH moss sample was consistently richer than the MMT sample (Fig. 3), comprising an average of 24 species per site, as opposed to 15 on the MMT ( $t = 1.92$ ,  $P = 0.056$ ). However, this relationship was driven by the large number of species in VMH6, and the variance in species number for the VMH sample was very large compared to that for the MMT sample (153 and 4.27, respectively). Higher elevation sites contained more moss species, but neither this difference nor any relationship between diversity and elevation were significant for either the VMH or MMT samples. No relationship was evident between species richness and either wall area in the VMH samples or rock areas sampled along MMT (Fig. 2;  $r^2 = 0.03$  and  $r^2 = 0.06$ , respectively).

The qualitative difference between species composition of VMH and MMT samples is evident by comparing the most common species in both. *Schistidium dupretii*, *Tortella tortuosa*, *Barbula unguiculata*, *Ceratodon purpureus*, *Campylopus chrysophyllum*, *Encalypta procerca*, *Polytrichum piliferum*, *Bryoerythrophyllum recurvirostre*, *Bryum argenteum*, *Brachythecium rutabulum*, *Bryum lisae* var. *cuspidatum*, and *Orthotrichum anomalum* were found in four or more sites along the VMH, while *Andreaea rupestris*, *Dicranum fuscescens*, *D. scoparium*, *Pleurozium schreberi*, *Pohlia nutans*, *Scapania nemorea*, *Brotherella recurvans*, *Paraleucobryum longifolium*, and *Plagiothecium laetum* were at four or more sites along the MMT. The 43 species occurring more than twice in our sample were not homogeneously distributed between the two transects (Table 3;  $\chi^2 = 62.0$ ,  $df = 42$ ,  $P < 0.02$ ). The PCA (Fig. 4) shows a graphical depiction of the difference among sites in the two samples. The first three axes of the PCA explained 26.7, 17.2, and 10.9%, respectively, of the variance in the species distribution matrix. All MMT plots group together and are clearly differentiated from all VMH sites. Site six of VMH is distant from all sites in both transects, and indeed it contained more species (53) than any other site.

We took two approaches to examine the homogeneity of the distribution of species found on mortar substratum. First, we examined the frequency spectra (number of species occurring in a given number of sites) for liverworts, mosses on native bedrock, and mosses on mortar in the total sample (Fig. 5). Among liverworts and mosses of native bedrock, more than half (57 and 56%, respectively) were observed in a single plot (i.e., there were more rare species), and the number of species found in more sites dropped precipitously as the number of sites increased. Mortar mosses showed a different pattern. Only 38% were found in a single site, but 31% were found in four or more sites, compared to 9 and 19% for liverworts and native mosses, respectively. Accordingly, the mean number of species occurrences of mortar mosses was consistently higher than that for mosses of native bedrock (Fig. 6,  $t = 1.60$ ;  $P = 0.056$ ).

## DISCUSSION

The introduction of calcium carbonate as mortar in walls and other structures built on Whiteface Mountain, where carbonate bedrock is otherwise largely unknown, has dramatically increased bryophyte richness far above that of any other alpine peak in the Adirondacks. For example, Mount Marcy and Algonquin Peak in the MacIntyre Range, mountains of similar size and habitat diversity to Whiteface but without introduced mortar, respectively, have 82 and 72 species of mosses and liverworts above 1067 m (3500 ft) (data available at the Web site <http://www.nysm.nysed.gov/research/biology/bryopaleo.html>). In contrast, we found 122 species of mosses and liverworts above 1067 m in our survey of Whiteface Mountain. The higher number of species on Whiteface is a direct result of the calcicoles established there. Our sample from mortared walls along VMH contained nearly two times more species than the native rock sites. However, while the number of moss species showed a remarkable increase, hepatic diversity was largely unaffected by the introduction of mortar along the highway. This may be not because of a lack of response to the introduction of calcium carbonate, but rather that liverworts favor habitats wetter than roadside walls. We found more liverwort species in some higher elevation samples where cloud moisture accumulates with greater frequency on rock surfaces and plants than at lower altitudes, but our sampling was insufficient to test this association.

The flora of walls along the VMH is very different from that of native lithic bryophyte communities. The complete lack of overlap between the 10 most common species in the VMH and MMT transects clearly indicates that the mortar has not been colonized by common weedy species from the native forest. For example, although *Andreaea rupestris* is present in all but one MMT plot, it is found in only one site along the VMH. Accordingly, most of the species most often sampled along the VMH were rare or not found along the Marble Mountain Trail ( $P < 0.02$ ), and we could reject a homogeneous distribution of species between the two transects. Although we were only able to test this difference for the species occurring in more than two sites, our test is biased conservatively. Undoubtedly, many rare species have a substratum preference (e.g., *Brachythecium turgidum*, *Didymodon rigidulus*, *Distichum capillaceum*, *Ditrichum flexicaule*, *Grimmia anodon*, *Gymnostomum aeruginosum*, *Orthotrichum anomalum*; see Crum and Anderson, 1981), but our sampling was designed to compare the overall floras of native and introduced substrata.

The bryophyte flora of the Adirondack region, particularly that of calcium-carbonate-containing rock outcrops, is sufficiently well studied to permit us to make inferences regarding the dispersal abilities of some of the bryophytes we found on mortar along the VMH. All of the calcicole bryophyte species along the VMH are either unknown or very rare species in the high altitude flora of the Adirondacks. Although all of them are recorded from lowland areas where Grenville calcareous rock is exposed or in the region surrounding the Adirondacks, the Whiteface stations are the highest recorded ones in New York State for several of the species. Detailed geologic mapping of Whiteface Mountain by Miller (1919) revealed only two small areas of possible marble-containing rock on the western and southern flanks of the mountain, both below an altitude of 730 m. These areas were not relocated, and therefore it is not known whether they support calcicole bryo-

phytes. Together, the significant difference between the native lithic flora and that found on mortar and the rarity of suitable calcium carbonate outcrops on the mountain, either anthropogenic or native, indicate that calcicoles in the VMH sample have immigrated from distant (~5 km or greater) stations.

While we interpret these data as evidence of natural dispersal, the highway itself presents an avenue for anthropogenic dispersal. Our observations show that the highway has served as a dispersal route for species of other plant groups, for example, mountain alder (*Alnus crispa* (Ait.) Pursh). It was originally restricted along the VMH to tree line but now is found along the highway at lower elevations in the balsam fir and red spruce–balsam fir zones. In contrast, oxeye daisy (*Leucanthemum vulgare* Lam.), a roadside weed, is present well into the balsam fir zone along VMH as a result of migration or transport upward from the lowland. Some bryophyte range expansions are linked to human activity, such as the introduction of *Campylopus introflexus* (Hedw.) Brid. and *Orthodontium lineare* Schwaegr. from the temperate Southern Hemisphere to the UK and Europe in the early 20th century (Söderström, 1992), and *Psuedoscleropodium purum* (Limpr.) Fleisch. in Broth. in the United States (Miller and Trigoboff, 2001). We do not believe this to be the case with the VMH flora. While some of the mortar mosses are ruderal species common on anthropogenically disturbed substrata (e.g., *Bryum argenteum* Hedw., *Ceratodon purpureus*), a majority of the species are more typically found on native calcareous rock or soil. Some of them, *Brachythecium turgidum*, *Didymodon rigidulus*, *Distichum capillaceum*, *Ditrichum flexicaule*, and *Myurella julacea*, are rare or absent from native lowland calcium carbonate outcrops in the region and are unknown in local anthropogenically altered habitats.

The VMH was the first large-scale introduction of mortar to the mountain, and completion of the highway in 1935 provides a reasonable benchmark for the introduction of calcium carbonate substratum. Although a concrete foundation was built near the summit in 1919 (Curth, 1987) to anchor a fire tower (since removed), we found in 1998 no bryophytes on what remained of the concrete, and thus it is not possible to evaluate the role of this small island of exotic substratum in immigration to the mountain. To reach the species richness we found in our sample, moss immigrants must have established on mortar in the alpine–subalpine zone at a rate of a least one species per year since completion of the highway. This may be an underestimation because we know little about the chronology of species arrival, and many of the walls show evidence of recent pointing (replacement of decaying mortar; Table 1) that may have resulted in species loss. This is a remarkable rate considering that many of the Whiteface mortar mosses produce sporophytes infrequently and that many of the nearest sites for the species are marble or carbonate-containing outcrops in low elevation forests that are sheltered from dispersing winds by topography and vegetation. This suggests that in at least some calcicole mosses selection may favor spores capable of surviving conditions encountered during long-distance dispersal.

A growing body of evidence suggests that mosses may be more vagile than has been previously appreciated. In experiments involving samples of *Atrichum undulatum* (Hedw.) P. Beauv. and *Bryum argenteum* Hedw., Miles and Longton (1992) estimated that 85–95% of the spore mass was dispersed more than 2 m from the parent sporophyte. Bremer and Ott (1990), in a study of land reclaimed from the sea in the Neth-

TABLE 3. Species of liverworts and mosses in study plots on Whiteface Mountain, New York, USA. VMH = Veterans Memorial Highway; MMT = Marble Mountain Trail. Plots from the same altitudes but different transects are organized in pairs. Mosses preceded by an asterisk were found at least once on mortar; those with two asterisks exhibit a pronounced calcicole tendency. Figure 1 shows the location of the plots on Whiteface Mountain.

| Plot No.   | VMH<br>1 | MMT<br>1 | VMH<br>2 | MMT<br>2 | VMH<br>3 | MMT<br>3 | VMH<br>4 | MMT<br>4 | VMH<br>5 | MMT<br>5 | VMH<br>6 | MMT<br>6 |
|--|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|
| <b>Liverworts</b>  |          |          |          |          |          |          |          |          |          |          |          |          |
| <i>Anastrophyllum michauxii</i> (Web.) Buch ex Evans                       |          |          |          |          |          |          |          |          |          |          |          | •        |
| <i>A. minutum</i> (Schreb.) Schust.  |          |          |          |          |          |          |          | •        |          |          |          | •        |
| <i>Barbilophozia attenuata</i> (Mart.) Loeske                              |          | •        |          |          |          |          |          | •        |          |          |          | •        |
| <i>B. kunzeana</i> (Hüb.) Gams   |          |          |          |          |          | •        |          |          |          |          | •        | •        |
| <i>Bazzania trilobata</i> (L.) S. Gray                                     |          |          |          |          |          | •        |          |          |          |          |          |          |
| <i>Blepharostoma trichophyllum</i> (L.) Dum.                               |          |          |          |          |          |          |          | •        |          |          |          |          |
| <i>Cephaloziella</i> sp.   |          |          |          |          |          |          |          |          |          |          | •        |          |
| <i>Diplophyllum apiculatum</i> (Evans) Steph.                              |          |          |          |          |          |          |          | •        |          |          |          |          |
| <i>Gymnocolea inflata</i> (Huds.) Dum.                                     |          |          |          | •        |          |          |          |          |          |          |          | •        |
| <i>Jamesoniella autumnalis</i> (DC.) Steph.                                |          | •        |          |          |          | •        |          |          |          |          |          |          |
| <i>Lepidozia reptans</i> (L.) Dum.   |          |          |          |          |          |          |          | •        |          |          |          |          |
| <i>Lophocolea heterophylla</i> (Schrad.) Dum.                              |          | •        |          |          |          |          |          |          |          |          |          |          |
| <i>Lophozia bicrenata</i> (Schmid. ex Hoffm.) Dum.                         |          |          |          | •        |          |          |          |          |          |          |          |          |
| <i>L. excisa</i> (Dicks.) Dum.   | •        |          |          |          |          |          |          |          |          |          |          |          |
| <i>L. guttulata</i> (Lindb. & H. Arnell) Evans                             |          |          |          |          |          | •        |          |          |          |          |          |          |
| <i>L. sudetica</i> (Nees) Grolle   |          |          |          |          |          |          |          |          |          |          |          | •        |
| <i>L. ventricosa</i> (Dicks.) Dum.   |          |          |          |          |          | •        |          | •        |          |          |          | •        |
| <i>Marchantia alpestris</i> (Nees) Burgeff                                 |          |          |          |          |          |          |          |          |          |          | •        |          |
| <i>Marsupella emarginata</i> (Ehrh.) Dum.                                  |          |          |          |          |          |          |          |          |          |          |          | •        |
| <i>Pellia epiphylla</i> (L.) Corda   |          |          |          |          |          |          |          |          |          |          | •        |          |
| <i>Ptilidium ciliare</i> (L.) Hampe  |          | •        |          |          |          | •        |          |          |          |          | •        | •        |
| <i>P. pulcherrimum</i> (Web.) Hampe  |          | •        |          | •        |          |          |          |          |          | •        |          |          |
| <i>Scapania nemorea</i> (L.) Grolle  |          | •        |          | •        |          | •        |          |          |          |          |          | •        |
| <b>Mosses</b>  |          |          |          |          |          |          |          |          |          |          |          |          |
| * <i>Amblystegium serpens</i> (Hedw.) Schimp. in B.S.G.                    |          |          |          |          | •        |          | •        |          |          |          |          | •        |
| * <i>A. varium</i> (Hedw.) Lindb.  |          |          |          | •        |          |          |          |          |          |          |          | •        |
| <i>Andreaea rupestris</i> Hedw.  | •        | •        |          | •        |          |          |          | •        |          | •        |          | •        |
| <i>Arctoa fulvella</i> (Dicks.) Bruch & Schimp. in B.S.G.                  |          |          |          |          |          |          |          |          |          |          |          | •        |
| <i>Aulacomnium palustre</i> (Hedw.) Schwaeagr.                             |          |          |          | •        |          |          |          |          |          |          |          |          |
| ** <i>Barbula convoluta</i> Hedw.  | •        |          | •        |          |          |          |          |          |          |          |          | •        |
| ** <i>B. unguiculata</i> Hedw.   |          |          | •        |          | •        |          | •        |          | •        |          |          | •        |
| * <i>Blindia acuta</i> (Hedw.) Bruch & Schimp. in B.S.G.                   |          |          |          |          |          |          |          |          |          |          |          | •        |
| * <i>Brachythecium campestre</i> (C. Müll.) Schimp. in B.S.G.              |          |          |          |          |          |          |          |          |          |          |          | •        |
| * <i>B. erythrorrhizon</i> Schimp. in B.S.G.                               | •        |          |          |          |          |          |          |          |          |          |          |          |
| * <i>B. oxycladon</i> (Brid.) Jaeg.  |          |          |          |          |          |          |          |          |          |          |          | •        |
| * <i>B. populeum</i> (Hedw.) Schimp. in B.S.G.                             |          |          |          |          |          |          |          | •        |          |          |          |          |
| * <i>B. reflexum</i> (Starke in Web. & Mohr) Schimp. in B.S.G.             | •        |          |          |          |          |          |          |          |          |          |          |          |
| * <i>B. rotabulum</i> (Hedw.) Schimp. in B.S.G.                            | •        |          |          |          |          |          |          |          |          |          |          | •        |
| * <i>B. salebrosum</i> (Web. & Mohr) Schimp. in B.S.G.                     | •        |          |          |          |          |          |          |          |          |          |          |          |
| ** <i>B. turgidum</i> (Hartm.) Kindb.                                      |          |          |          |          |          |          |          |          |          |          |          | •        |
| * <i>B. velutinum</i> (Hedw.) Schimp. in B.S.G.                            | •        |          | •        |          |          |          |          |          |          |          |          |          |
| <i>Brotherella recurvans</i> (Michx.) Fleisch.                             |          | •        |          |          |          | •        |          | •        |          | •        |          |          |
| ** <i>Bryoerythrophyllum recurvirostre</i> (Hedw.) Chen                    | •        |          |          |          |          |          |          | •        |          | •        |          | •        |
| * <i>Bryum argenteum</i> Hedw.   | •        |          | •        |          | •        |          |          |          | •        |          |          |          |
| * <i>B. caespiticium</i> Hedw.   | •        |          |          |          |          |          |          |          |          |          |          |          |
| * <i>B. lisae</i> var. <i>cuspidatum</i> (Bruch & Schimp. in B.S.G.) Marg. | •        |          | •        |          |          |          |          |          | •        |          |          | •        |
| <i>B. sp.</i>  |          |          |          |          |          |          |          |          | •        |          |          | •        |
| <i>Callierygon stramineum</i> (Brid.) Kindb.                               |          |          |          |          |          |          |          |          |          |          |          | •        |
| ** <i>Campylium chrysophyllum</i> (Brid.) J. Lange                         | •        |          | •        |          |          |          |          | •        |          | •        |          | •        |
| * <i>C. hispidulum</i> (Brid.) Mitt.                                       |          |          |          |          |          |          |          |          |          |          |          | •        |
| * <i>C. polygamum</i> (Schimp. in B.S.G.) C. Jens.                         |          |          |          |          |          |          |          |          |          |          |          | •        |
| * <i>Ceratodon purpureus</i> (Hedw.) Brid.                                 | •        |          | •        |          | •        |          |          |          | •        |          |          | •        |
| <i>Cynodontium tenellum</i> (Bruch & Schimp. in B.S.G.) Limpr.             |          |          |          |          |          |          |          |          |          |          |          | •        |
| * <i>Dicranella heteromalla</i> (Hedw.) Schimp.                            |          |          |          | •        |          | •        |          |          |          |          | •        | •        |
| <i>Dicranum bonjeanii</i> De Not. in Lisa                                  |          |          |          | •        |          |          |          |          |          |          |          |          |
| * <i>D. fuscescens</i> Turn.   |          |          |          | •        |          | •        |          | •        |          | •        | •        | •        |
| <i>D. montanum</i> Hedw.   |          | •        |          |          |          |          |          |          |          | •        |          |          |
| <i>D. polysetum</i> Sw.  |          |          |          |          |          | •        |          |          |          |          |          |          |
| <i>D. scoparium</i> Hedw.  |          | •        |          | •        |          | •        |          | •        |          | •        |          |          |
| ** <i>Didymodon rigidulus</i> Hedw.  |          |          |          |          |          |          |          | •        |          | •        |          | •        |

TABLE 3. Continued.

| Plot No.  | VMH<br>1 | MMT<br>1 | VMH<br>2 | MMT<br>2 | VMH<br>3 | MMT<br>3 | VMH<br>4 | MMT<br>4 | VMH<br>5 | MMT<br>5 | VMH<br>6 | MMT<br>6 |
|---|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|
| ** <i>Distichium capillaceum</i> (Hedw.) Bruch & Schimp. in B.S.G.    |          |          |          |          |          |          |          |          | •        |          | •        |          |
| ** <i>Ditrichum flexicaule</i> (Schwaeger.) Hampe                     |          |          |          |          |          |          | •        |          |          |          |          |          |
| <i>D. pusillum</i> (Hedw.) Hampe                                      |          |          |          | •        |          |          |          |          |          |          |          |          |
| ** <i>Encalypta procera</i> Bruch                                     | •        |          |          |          | •        |          | •        |          | •        |          | •        |          |
| * <i>Fissidens dubius</i> P. Beauv.                                   | •        |          |          |          |          |          |          |          |          |          |          |          |
| ** <i>Grimmia anodon</i> Bruch & Schimp. in B.S.G.                    |          |          |          |          | •        |          |          |          |          |          |          |          |
| * <i>G. donniana</i> Sm.  |          |          |          | •        |          |          |          |          | •        |          | •        |          |
| ** <i>Gymnostomum aeruginosum</i> Sm.                                 |          |          |          |          |          |          |          |          |          |          | •        | •        |
| <i>Hedwigia ciliata</i> (Hedw.) P. Beauv.                             |          |          |          |          |          |          |          |          |          |          | •        | •        |
| <i>Herzogiella striatella</i> (Brid.) Iwats.                          |          |          |          |          |          | •        |          |          |          |          |          |          |
| ** <i>Hygroamblystegium tenax</i> (Hedw.) Jenn.                       |          |          |          |          |          |          |          |          |          |          | •        |          |
| <i>Hylocomiastrum umbratum</i> (Hedw.) Fleisch. in Broth.             |          | •        |          |          |          |          |          |          |          |          |          |          |
| * <i>Hylocomium splendens</i> (Hedw.) Schimp. in B.S.G.               |          |          |          |          |          | •        |          |          |          |          | •        |          |
| <i>Hypnum curvifolium</i> Hedw.                                       |          |          |          |          |          | •        |          |          |          |          |          |          |
| <i>H. imponens</i> Hedw.  |          |          |          |          |          |          |          | •        |          |          |          |          |
| <i>H. pallescens</i> (Hedw.) P. Beauv.                                |          | •        |          |          |          |          |          |          |          | •        |          |          |
| <i>Isopterygiopsis muelleriana</i> (Schimp.) Iwats.                   |          |          |          |          |          |          |          | •        |          |          |          |          |
| * <i>Mnium spinulosum</i> Bruch & Schimp. in B.S.G.                   |          |          |          |          |          |          |          |          |          |          | •        |          |
| ** <i>Myurella julacea</i> (Schwaegr.) Schimp. in B.S.G.              |          |          |          |          |          |          |          |          | •        |          | •        |          |
| <i>Oncophorus wahlenbergii</i> Brid.                                  |          | •        |          |          |          |          | •        |          |          | •        |          |          |
| ** <i>Orthotrichum anomalum</i> Hedw.                                 | •        |          | •        |          |          |          | •        |          | •        |          |          |          |
| * <i>Paraleucobryum longifolium</i> (Hedw.) Loeske                    | •        | •        |          |          |          |          | •        | •        |          | •        |          | •        |
| * <i>Philonotis fontana</i> (Hedw.) Brid.                             |          |          |          |          |          |          |          |          |          |          | •        |          |
| <i>Plagiomnium ciliare</i> (C. Müll.) T. Kop.                         | •        |          |          |          |          |          |          |          |          |          | •        |          |
| * <i>P. cuspidatum</i> (Hedw.) T. Kop.                                | •        |          |          |          |          |          |          |          |          |          | •        |          |
| * <i>P. medium</i> (Bruch & Schimp. in B.S.G.) T. Kop.                |          |          |          |          |          |          |          |          |          |          | •        |          |
| <i>Plagiothecium laetum</i> Schimp. in B.S.G.                         |          | •        |          |          |          |          |          | •        |          | •        |          | •        |
| <i>Pleurozium schreberi</i> (Brid.) Mitt.                             |          | •        |          | •        |          | •        |          | •        |          | •        |          |          |
| <i>Pogonatum dentatum</i> (Brid.) Brid.                               |          |          |          |          |          |          |          |          |          |          |          | •        |
| * <i>P. urnigerum</i> (Hedw.) P. Beauv.                               |          |          |          |          | •        |          | •        |          | •        |          |          |          |
| <i>Pohlia cruda</i> (Hedw.) Lindb.                                    |          |          |          |          |          |          |          |          |          |          | •        |          |
| <i>P. nutans</i> (Hedw.) Lindb.                                       |          |          |          | •        | •        | •        | •        | •        |          | •        |          | •        |
| * <i>P. prolifera</i> (Kindb. ex Breidl.) Lindb. ex Arnell            |          |          |          |          |          |          |          |          |          |          | •        |          |
| * <i>P. wahlenbergii</i> (Web. & Mohr) Andrews                        |          |          |          |          |          |          |          |          |          |          | •        |          |
| <i>P. sp.</i>   |          |          |          |          |          |          |          |          |          | •        |          |          |
| <i>Polytrichastrum alpinum</i> (Hedw.) G. L. Sm.                      |          |          |          |          |          |          | •        | •        |          |          | •        |          |
| <i>Polytrichum commune</i> Hedw.                                      |          |          |          | •        |          | •        |          |          |          |          | •        |          |
| * <i>P. juniperinum</i> Hedw.   | •        |          |          | •        |          |          | •        |          |          | •        |          |          |
| <i>P. pallidisetum</i> Funck  |          |          |          |          |          |          |          | •        |          | •        |          | •        |
| * <i>P. piliferum</i> Hedw.   |          |          | •        | •        | •        |          | •        |          | •        |          | •        |          |
| <i>P. strictum</i> Brid.  |          |          |          |          |          |          |          |          |          |          | •        | •        |
| <i>Pseudotaxiphyllum elegans</i> (Brid.) Iwats.                       |          |          |          |          |          | •        |          |          |          |          |          |          |
| <i>Ptilium crista-castrensis</i> (Hedw.) De Not.                      | •        | •        |          |          |          |          |          |          |          |          |          |          |
| <i>Racomitrium fasciculare</i> (Hedw.) Brid.                          |          |          |          | •        |          |          |          |          |          |          | •        | •        |
| <i>R. heterostichum</i> (Hedw.) Brid.                                 |          |          |          |          |          |          |          |          |          | •        |          |          |
| <i>R. microcarpon</i> (Hedw.) Brid.                                   |          | •        |          | •        |          |          | •        |          |          |          | •        | •        |
| * <i>Sanionia uncinata</i> (Hedw.) Loeske                             | •        |          | •        | •        |          |          |          |          |          | •        | •        | •        |
| ** <i>Schistidium apocarpum</i> subsp. <i>canadense</i> (Dupret) Blom | •        |          |          |          |          |          |          |          |          |          | •        | •        |
| ** <i>S. boreale</i> Poelt  |          |          |          |          |          |          |          |          |          |          | •        | •        |
| ** <i>S. dupretii</i> (Ther.) W. A. Weber                             | •        |          | •        |          | •        |          | •        |          | •        |          | •        |          |
| ** <i>S. papillosum</i> Culm.   |          |          | •        |          | •        |          |          |          |          |          | •        |          |
| ** <i>S. poeltii</i> Blom   |          |          |          |          |          |          |          |          | •        |          |          |          |
| ** <i>S. pulchrum</i> Blom  |          |          |          |          | •        |          |          |          |          |          |          |          |
| * <i>S. sp. nov.</i> , fide Blom                                      |          |          |          |          | •        |          |          |          | •        |          | •        |          |
| * <i>S. sp.</i>   | •        |          |          |          |          |          |          |          |          |          |          |          |
| <i>Sphagnum capillifolium</i> (Ehrh.) Hedw.                           |          |          |          |          |          | •        |          |          |          |          |          |          |
| <i>S. girgensohnii</i> Russ.  |          |          |          |          |          |          |          |          |          |          | •        |          |
| <i>S. russowii</i> Warnst.  |          |          |          |          |          |          |          |          |          |          | •        | •        |
| <i>Tetraphis pellucida</i> Hedw.                                      |          |          |          |          |          | •        |          | •        |          | •        |          |          |
| * <i>Timmia megapolitana</i> Hedw.                                    | •        |          |          |          |          |          |          |          |          |          |          |          |
| ** <i>Tortella tortuosa</i> (Hedw.) Limpr.                            | •        |          | •        |          | •        |          | •        |          | •        |          | •        |          |
| ** <i>Tortula ruralis</i> (Hedw.) Gaertn. et al.                      |          |          | •        |          |          |          | •        |          | •        |          |          |          |
| <i>Warnstorfia fluitans</i> (Hedw.) Loeske                            |          |          |          |          |          |          |          |          |          | •        |          | •        |

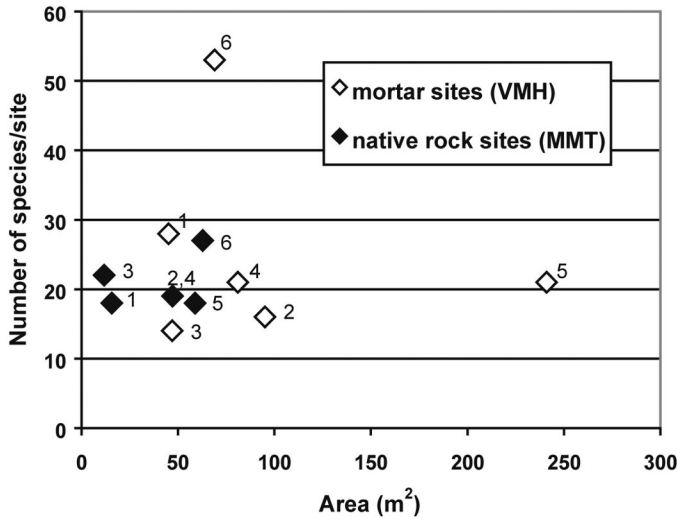


Fig. 2. Scatter diagram of bryophyte species richness and native rock (MMT) and mortared wall (VMH) sample plots on Whiteface Mountain, New York, USA. Numbers are plot designations (see Tables 1 and 2).

erlands, concluded that moss establishment for some species had occurred from sources tens of kilometers distant and for others over 100 km. Moreover, the spore germination studies of van Zanten (1978) show that species with broad distributions often have spores tolerant of long storage and temperature extremes. We believe that our floristic data add an ecological context to the pattern illustrated by van Zanten (1978). That is, the correlation between distributional area and spore tolerance may be underlain by additional habitat correlates such as substratum availability. Furthermore, the Whiteface data provide long-term estimates of dispersal distance and migration rates—critical metapopulation parameters for which reliable empirical estimates are lacking in plants in general (Husband and Barrett, 1996).

The distributional patterns of calcicole and native rock mosses differed in our Whiteface transects. Mosses on mortar were, on average, at more sites along the VMH than mosses on native rock along the MMT ( $P = 0.056$ ). In additional sampling on and around concrete structures on the summit cone, we found 40 species, considerably more than the 27 found at the highest MMT site. Four occurred on native bedrock and had not been previously encountered (the liverwort *Tritomania quinquedentata* (Huds.) Buch and the mosses *Funaria hygrometrica* Hedw., *Pohlia annotina* (Hedw.) Lindb., and *Rhytidium rugosum* (Hedw.) Kindb.), while 21 were calcicoles represented one or more times in samples along the VMH. Inclusion of these data in our analyses indicates that additional sampling would result in increasingly significant differences in distribution between calcicole and non-calcicole mosses, both in average species richness and species frequency spectra. Even within our paired samples, more than half of the mosses on native rock were present at only one site, while nearly a third of all calcicoles were found at four or more sites (Fig. 5). This pattern, in addition to the inferences regarding dispersal distances of several kilometers, suggests that some of the calcicoles in our sample adopt a more ruderal strategy than mosses typical of native rock in the Adirondack forest. Our data did not allow us to detect any ecological correlates of species composition in either the VMH or MMT samples. We found no detectable elevational trend in diversity in either

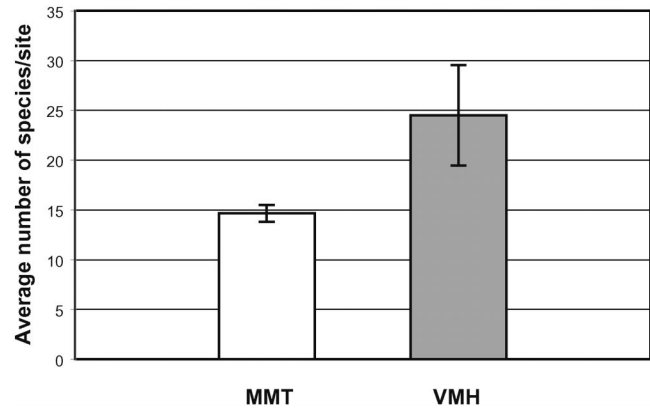


Fig. 3. Average number of bryophyte species/site along the Marble Mountain Trail (MMT) and Veterans Memorial Highway (VMH), with standard error ( $t = 1.92$ ,  $P = 0.056$ ).

transect, although this may be a result of considerable habitat variation overwhelming any subtle trend. Undoubtedly, other habitat features, such as moisture, irradiance, or substratum chemistry, pattern the species over a landscape. However, our data suggest that substratum availability rather than ability to migrate among suitable sites is more likely to limit the species range of calcicoles.

While our approach to studying the diversity of bryophytes on mortar walls along VMH was explicitly quantitative, it was impractical to incorporate species abundances into our sampling. Our sampling strategy enabled us to find many rare species that we might not have in random samples and by estimating abundances. However, preliminary abundance data we collected showed some additional patterns that may relate to dispersal and establishment. In 24 populations of the mosses *Barbula convoluta* and *B. unguiculata*, we found female : male plant ratios of 5 : 1 and 11 : 3 in accordance with numerous studies that have demonstrated similar female-biased sex ratios (Bowker et al., 2000; Stark et al., 2001). However, we cannot rule out chance for the ratios we obtained and the 1 : 1 ratio that is expected in dioicous mosses with potential or known sex chromosomes (Fritsch, 1982), such as these species of

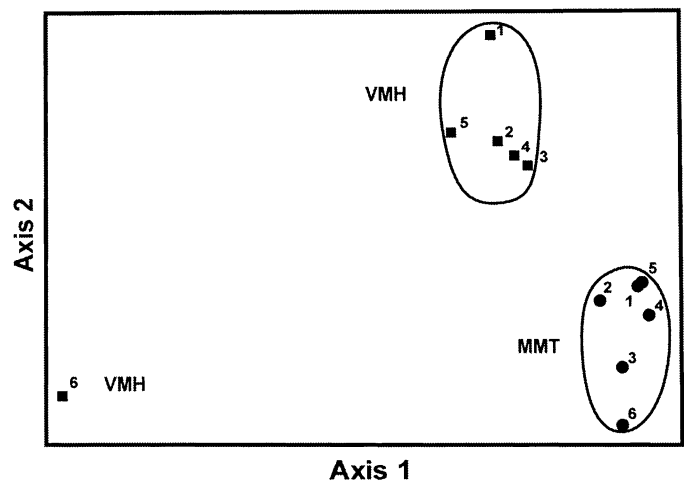


Fig. 4. Principal components analysis of bryophyte species composition at study sites along the Marble Mountain Trail (MMT 1–6) and the Veterans Memorial Highway (VMH 1–6), Whiteface Mountain, New York, USA.

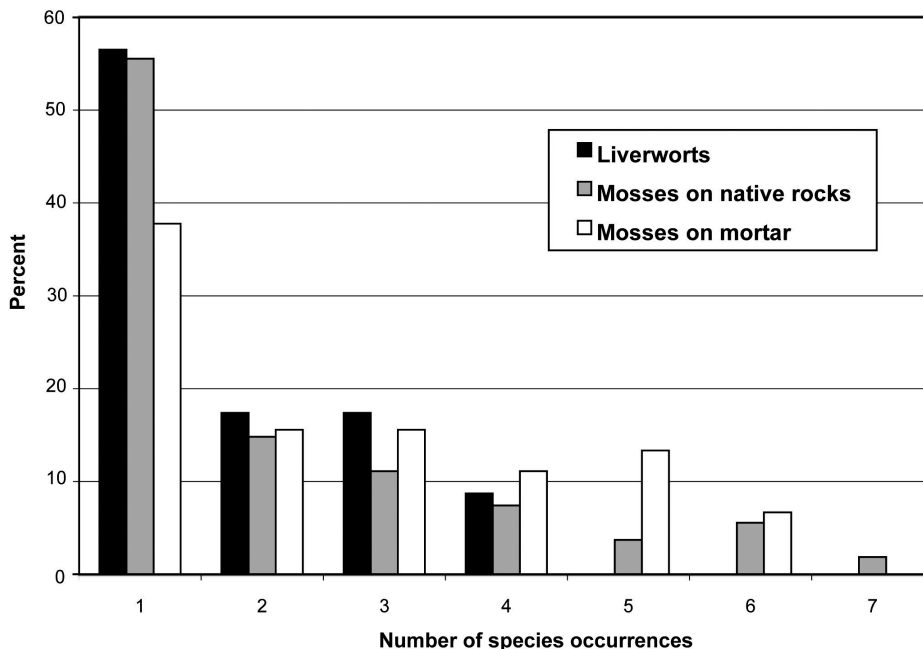


Fig. 5. Percentages of liverworts, mosses on native rock, and mosses on mortar that occurred in from one to seven sample plots. No species was in more than seven plots.

*Barbula*. Unbalanced sex ratios may reflect sexual dimorphism in dispersal or spore germination ability and may be most pronounced immediately following the creation of new habitat, for example, mortar emplacement along the VMH.

Taken as a whole, the floristic data from Whiteface Mountain complement phylogeographic studies of more restricted numbers of species and infraspecific taxa across broader regions. A community consisting of both common and rare bryophytes has dispersed a minimum of 5 km, but potentially much farther, and subsequently established within the 65 years following introduction of calcium-carbonate-rich habitat along the VMH. For species with narrow ecological niches and suitable sites separated by many kilometers, such as mosses with strong substratum preference, selection may favor individuals with highly dispersible spores. Genetic data from two species found in our VMH samples (*Bryum argenteum*, T. Hedderston, Bolus Herbarium, University of Cape Town; *Ceratodon pur-*

*pureus*, S. F. McDaniel and A. J. Shaw, Duke University) reveal little large-scale population structure, suggesting frequent long-distance dispersal. Mosses may be highly heterogeneous in their dispersal capabilities for reasons related to habitat, spore longevity and drought tolerance, sexual condition, or sporophyte production. If any of these factors can be shown to predominate, this will be an important step toward understanding patterns of speciation and diversification in mosses.

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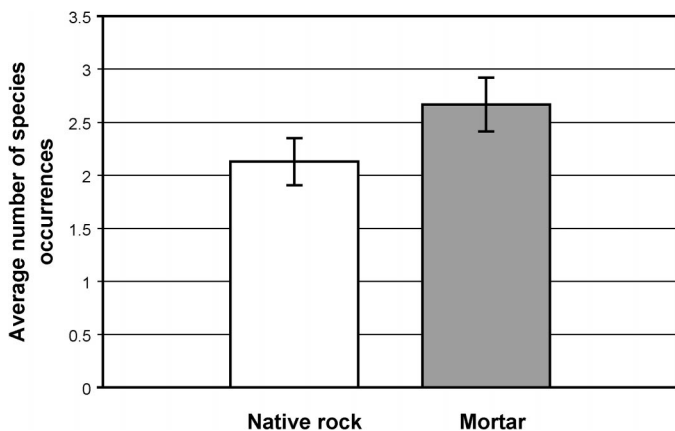


Fig. 6. Average number of occurrences of mosses on native rock and mosses on mortar, with standard error ( $t = 1.60$ ,  $P = 0.056$ ).

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