Slow Recovery In A Mount Washington, New Hampshire, Alpine Plant Community Four Years After Disturbance

SLOW RECOVERY IN A MOUNT WASHINGTON, NEW HAMPSHIRE, ALPINE PLANT COMMUNITY FOUR YEARS AFTER DISTURBANCE

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ABSTRACT. Four years after a trench was dug through alpine habitat on Mount Washington, New Hampshire, we surveyed vascular plants, bryophytes, and lichens in the disturbed area, analyzing species richness and abundance compared with values in adjacent, undisturbed areas. Plants had begun recolonizing the disturbed area, but species richness and abundance remained far lower than in the undisturbed community. Among vascular plants, graminoids colonized most quickly, and woody species were largely absent. Species with the highest frequency and greatest abundance in the disturbed area also were common and abundant in the undisturbed community. Bryophytes appeared to be colonizing no more quickly than vascular plants. Treeline and elevation exerted separate effects on community structure and recovery. Treeline influenced species richness, abundance, and the rate of recovery of vascular plants, but there was no evidence of an additional effect of elevation either above or below treeline. Treeline also influenced species richness of bryophytes and lichens. In addition, elevation appeared to have a separate effect on their rate of recovery in alpine habitat: species richness of bryophytes and lichens declined with elevation in the disturbed community but not in the undisturbed community. This suggests that elevation has a transient effect on colonization and/or survival, but only above treeline. In general, recovery has occurred more quickly below treeline. This survey establishes baseline information that will be useful in assessing the rate of recovery after future surveys.

Key Words: alpine plants, disturbance recovery, global climate change, vascular plants, bryophytes, lichens, Presidential Range, White Mountain National Forest, succession

Many alpine plant communities are resilient in the sense that the composition of post-disturbance communities can be very similar to that of the pre-disturbance community (Ebersole 2002; Rydgren et

al. 2011; Willard and Marr 1971). However, the process of recovery can take many years (Billings 1973). Researchers observing recovery after disturbances have reported that some species colonize quickly, but the abundance of plants often reaches pre-disturbance levels only after many decades (Brown et al. 2006; Chambers 1993; Curtin 1995; Lloyd et al. 2003; Willard and Marr 1971). Alpine plant communities recover slowly from disturbance, in part because of the short growing season and low temperatures (Chambers 1995; Körner 2003). Cells differentiate and mature more slowly at the low temperatures found at high elevations, so plants grow more slowly and take longer to produce flowers, ripen fruit, and spread vegetatively (Milla et al. 2009). In addition, high mortality of seedlings due to frost-heaving and drought stress retards recovery (Chambers 1995; Ebersole 2002; Marchand and Sproul 1981).

Assemblages of plants growing above treeline vary with elevation, slope, topography, aspect, soil chemistry, and other conditions, and include the constituents of sedge meadow, heath, dwarf shrub, fellfield, snowbank, and other communities. Because of life history and physiological differences among the plants in these assemblages, recovery in alpine communities depends in part on the species occurring in a particular area (Chambers 1995). In addition, the nature of a disturbance influences recovery, which occurs more slowly where surface soils have been removed (e.g., by landslides or mining) than where recreational use or small mammal burrowing has left the often well-developed soils in place (Chambers 1995). Because cold and wind become more severe with increasing elevation, it might also be expected that recovery from disturbance would vary with elevation above treeline.

Here, we investigate colonization by vascular plants, bryophytes, and lichens four years after excavation work done on Mount Washington, New Hampshire. We analyze the effect of treeline and elevation on numbers of species and plant abundance in the disturbed area. We also compare species richness and abundance with values in an adjacent, undisturbed area. The purpose of this research was to record the process of succession after disturbance in the alpine habitat, beginning four years after a major disturbance and continuing with periodic surveys in the future. Although this research is largely descriptive, we did predict that recovery would proceed more quickly at lower elevations than near the summit.

At 1914 m, Mount Washington (44°16′N, 71°18′W) is the highest mountain in the northeastern US. The area of contiguous alpine habitat in the Presidential Range of the White Mountain National Forest (11.3 km^2) is larger than on any other mountain range in the Northeast (Kimball and Weihrauch 2000). The climate in the region is classified as Dfb (cool-summer, humid continental type) in the Köppen-Geiger system (Ward et al. 1938), but summits are classified as ET (tundra climate; Reiners and Lang 1979). Summertime weather is cloudy, wet, and windy (Babrauckas and Schmidlin 1997). During the period from 1935 to 2003, the temperature on the summit ranged from $-14.0 \pm 1.6°$C (mean $\pm$ SE) in the winter to $8.3 \pm 0.8°$C in the summer, and temperatures in Pinkham Notch (the valley to the east of the mountain) ranged from $-8.3 \pm 1.5°$C in the winter to $16.2 \pm 0.7°$C in the summer (Seidel et al. 2009).

During the summer of 2008, a trench was dug along the Cog Railway (a rail line built in 1869) from the bottom of Mount Washington to the summit to permit burial of electric and photo-optic cables (Figure 1). The 90 cm deep trench was dug with an excavator that eliminated plants in an area about 5 m wide as it excavated soil and rocks from the trench, buried the cable, and finally refilled the trench with the soil and rock it had removed. In this process, the earth-moving equipment essentially created a crude road up the mountain, roughly parallel to the rail line and a minimum of 3–8 m from it. We surveyed along this disturbed area for a linear distance of 1800 m in July 2012, from an area just north of the summit (elevation 1853 m) down to an area just above "Jacob's Ladder" (elevation 1457 m), where continued disturbance interferes with recovery. The area where the trench was dug had been somewhat disturbed previously, especially below treeline, where fires had burned trees along the tracks. Decades of maintenance and repairs of the Cog Railway had left debris such as railroad ties beside the rail line, but it was largely confined to the area immediately beside the track. Any railroad debris extending into the area of the trench was removed as the trench was dug, and most of the rest had been removed by 2012. The coal-fired engines used by the Cog Railway before 2009 (by 2102, biodiesel engines were used for all but one of the daily trips) also produced cinders that were evident in the area of the trench and, to a lesser degree, in

Figure 1.   A backhoe was used in the summer of 2008 to dig a trench on Mount Washington, just north of the Cog Railway, to bury an electric cable and a fiber-optic line. The work severely disturbed the plant communities from the bottom of the mountain to the summit, through the alpine habitat, removing all plants and much of the organic soil. A survey was done to assess recovery of the alpine community four years later. (Photo by Kent McFarland)

the undisturbed community; the possible effect of the cinders on the plants is unknown. Digging the trench essentially reset the community, eliminating plants in the disturbed area and allowing succession to begin anew. Soil that had developed was not lost, but it would have been mixed with rock when returned to the trench. Nor was the seedbank lost, but when the trench was refilled some seeds likely were buried too deeply to emerge. Four years after succession began in 2009, we compared species presence and, in some cases, abundance in the disturbed area with the same parameters in the undisturbed community nearby (the ''natural'' community toward which succession would presumably progress).

We sampled at 50 m intervals along two transects, one in the center of the disturbed area and a second 5–8 m to the north (or to the south, in a brief stretch where the disturbed area crossed to the south side of the rail line). Above treeline, there would have been no edge effect from light in the undisturbed community, but the plants

we sampled in the undisturbed area below treeline may have received somewhat more light than plants in areas farther from the disturbance. Aspect through most of this area is west-northwest, although at the lowest elevations it tends to the west-southwest. At each sampling location, we used a 1 m^2 quadrat frame to survey the community, and recorded the presence and abundance (% cover) of all vascular plants and bryophytes. We also recorded the presence (but not abundance) of all lichen species and the proportion of bare rock in each plot. We recorded the latitude, longitude, and elevation of each plot, using a GPS unit (Garmin GPS Map 60, Olathe, KS). Moving downslope, the survey passed through several community types (Sperduto and Cogbill 1999), from sedge meadow near the summit, to sedge-rush-heath meadow, and finally into black spruce-balsam fir krummholz at treeline. Based on plots in the two transects (N = 37 plots in each), we evaluated changes in species richness (number of species per plot) of vascular plants, bryophytes, and lichens, as well as abundance of vascular plants and bryophytes along the elevational gradient in the disturbed area. We then compared the data from the recovering community and the undisturbed community nearby.

Variation in species richness related to the disturbance and elevation was evaluated with ANOVAs, t-tests, and linear regressions. Differences in species richness between disturbed and undisturbed plots were analyzed with paired t-tests. Total cover in each plot was calculated as the sum of individual species' cover values (because species overlapped, cover totals could exceed 100%). Differences in square-root-transformed abundance values were analyzed with paired t-tests. All statistical tests were done in SYSTAT, version 7.0 for Windows (SPSS, Chicago, IL). We collected specimens of bryophytes and lichens that could not be identified in the field and identified them later in the laboratory. These and vouchers for identification of vascular plants, which had been collected previously in the White Mountains (or in two cases, on a mountain in western Maine), were deposited in the George Safford Torrey Herbarium (CONN) at the University of Connecticut. Nomenclature follows Haines (2011) for vascular plants, and the PLANTS database (USDA, NRCS 2013) for bryophytes and lichens.

RESULTS

A total of 20 vascular plant species was present in the disturbed plots, compared with a total of 29 species recorded in undisturbed plots (Table 1). However, most species in the disturbed transect

Table 1. The relative frequency of occurrence of species above and below treeline in undisturbed and disturbed plots (N = 37 for each) in a survey of alpine plants on Mount Washington in 2012. The survey was done to assess community recovery four years after a major disturbance. Transects in the disturbed and undisturbed (control) communities were run from near the summit, down to an elevation of about 1450 m (somewhat below treeline). Voucher specimens (deposited at CONN) are listed below species names, with collection numbers and unique herbarium accession barcode numbers. Because a number of species occurred only in plots above treeline (N = 27) or below treeline (N = 10), frequency values for these plots are shown separately. For each plant category (Vascular plants, Mosses, Liverworts, and Lichens), species are listed in order of frequency—first in undisturbed areas above treeline, followed by undisturbed below tree line (for species that do not occur above treeline), etc. [1]Frequencies for *Polytrichum* and *Polytrichastrum* species are minimum values; they were not identified to species in the field, and samples were not taken in every location, so many were recorded only as "Polytrichaceae."

| | Relative Frequency of Occurrence Above and Below Treeline[1] | | | |
| | Undisturbed | | Disturbed | |
Species and Collection Information	Above	Below	Above	Below
VASCULAR PLANTS	0.89	1.00	0.52	0.80
Carex bigelowii Torr. *ex* Schwein. (*R.S. Capers 2227*, CONN00139484)	0.74	–	0.19	–
Minuartia groenlandica (Retz.) Ostenf. (*R.S. Capers 2238*, CONN00139473)	0.52	–	0.19	–
Juncus trifidus L. (*R.S. Capers 2234*, CONN00139477)	0.41	0.30	0.41	0.70
Vaccinium vitis-idaea L. subsp. *minus* (Lodd.) Hultén (*R.S. Capers 2235*, CONN00139476)	0.30	0.20	–	–
Vaccinium uliginosum L. (*R.S. Capers 2239*, CONN00139472)	0.15	0.30	–	–
Sibbaldiopsis tridentata (Aiton) Rydb. (*R.S. Capers 2240*, CONN00139471)	0.15	0.10	–	0.10
Calamogrostis canadensis (Michx.) P. Beauv. (*R.S. Capers 2185*, CONN00140022)	0.11	–	–	–
Diapensia lapponica L. (*R.S. Capers 2250*, CONN00138332)	0.11	–	–	–
Betula cordifolia Regel (*R.S. Capers 2236*, CONN00139475)	0.07	0.40	–	0.20
Agrostis mertensii Trin. (*R.S. Capers 2184*, CONN00139730)	0.07	–	0.04	–
Abies balsamea (L.) Mill. (*R.S. Capers 1679*, CONN00085644)	0.04	0.90	–	0.20
Rhododendron groenlandicum (Oeder) Kron & Judd (*R.S. Capers 2405*, CONN00155650)	0.04	0.50	–	–

Table 1.   Continued.

Species and Collection Information	Relative Frequency of Occurrence Above and Below Treeline[1]			
	Undisturbed		Disturbed	
	Above	Below	Above	Below
Chamaepericlymenum canadense (L.) Asch. & Graebn. (*R.S. Capers 2215*, CONN00139710)	0.04	0.40	–	0.10
Gaultheria hispidula (L.) Muhl. *ex* Bigelow (*RC 2314*, CONN00139612)	0.04	0.30	–	–
Carex brunescens (Pers.) Poir. (*R.S. Capers 2225*, CONN00139714)	0.04	0.20	–	0.40
Huperzia appressa (Desv.) Á. & D. Löve (*R.S. Capers 1687*, CONN00085663)	0.04	0.10	–	–
Anthoxanthum monticola (Bigelow) Y. Schouten & Veldkamp (*R.S. Capers 2241*, CONN00139470)	0.04	–	–	0.60
Luzula spicata (L.) DC. (*R.S. Capers 2246*, CONN00164350)	0.04	–	–	–
Spinulum annotinum (L.) A. Haines (*R.S. Capers 2194*, CONN00140030)	–	0.40	–	–
Deschampsia flexuosa (L.) Trin. (*R.S. Capers 2288*, CONN00143246)	–	0.30	–	–
Vaccinium cespitosum Michx. (*R.S. Capers 2436*, CONN00164341)	–	0.30	–	0.20
Coptis trifolia (L.) Salisb. (*R.S. Capers 2305*, CONN00139446)	–	0.30	–	–
Maianthemum canadense Desf. (*R.S. Capers 2278*, CONN00141576)	–	0.30	–	–
Empetrum nigrum L. (*R.S. Capers 2237*, CONN00139474)	–	0.20	–	0.10
Vaccinium angustifolium Aiton (*R.S. Capers 2327*, CONN00139598)	–	0.20	–	–
Solidago macrophylla Pursh (*R.S. Capers 2232*, CONN00139479)	–	0.10	–	0.10
Clintonia borealis (Aiton) Raf. (*R.S. Capers 2219*, CONN00139720)	–	0.10	–	–
Phegopteris connectilis (Michx.) Watt (*R.S. Capers 2242*, CONN00139469)	–	0.10	–	–
Sorbus decora (Sarg.) C.K. Schneid. (*R.S. Capers 2221*, CONN00139718)	–	0.10	–	–
Picea sp.	–	–	0.04	–
Carex debilis Michx. (*R.S. Capers 2438*, CONN00164343)	–	–	–	0.10
Festuca filiformis Pourr. (*R.S. Capers 2462*, CONN00166686)	–	–	–	0.10

Table 1.   Continued.

Species and Collection Information	Relative Frequency of Occurrence Above and Below Treeline[1]			
	Undisturbed		Disturbed	
	Above	Below	Above	Below
Festuca ovina L.	–	–	–	0.10
(*R.S. Capers 2461*, CONN00166687)				
Grass No. 7	–	–	–	0.10
Lysimachia borealis (Raf.) U. Manns & Anderb.	–	–	–	0.10
(*R.S. Capers 2213*, CONN00140041)				
Oclemena acuminata (Michx.) Nesom	–	–	–	0.10
(*R.S. Capers 2460*, CONN00166675)				
MOSSES	0.96	1.00	0.41	0.80
Polytrichaceae spp.	0.89	0.70	0.26	0.60
Polytrichum piliferum Hedw.	0.26	0.20	0.19	0.20
(*R.S. Capers & D.W. Taylor 102*, CONN00132955)				
Polytrichum juniperinum Hedw.	0.11	–	0.04	–
(*R.S. Capers & D.W. Taylor 104*, CONN00132943)				
Polytrichum commune Hedw.	0.04	0.30	0.07	0.50
(*R.S. Capers & D.W. Taylor 103*, CONN00132951)				
Polytrichastrum alpinum (Hedw.) G.L. Sm. var. *alpinum*	–	0.30	–	–
(*R.S. Capers & D.W. Taylor 101*, CONN00132953)				
Other mosses				
Andreaea rupestris Hedw.	0.44	0.30	0.15	0.20
(*R.S. Capers & D.W. Taylor 111*, CONN00132944)				
Pogonatum dentatum (Brid.) Brid.	0.26	0.10	0.15	0.50
(*R.S. Capers & D.W. Taylor 113*, CONN00132942)				
Dicranum montanum Hedw.	0.15	0.30	–	–
(*R.S. Capers & D.W. Taylor 105*, CONN00132952)				
Dicranum fuscescens Turner	0.07	0.60	–	–
(*R.S. Capers & D.W. Taylor 106*, CONN00132957)				

Table 1. Continued.

Species and Collection Information	Relative Frequency of Occurrence Above and Below Treeline[1]			
	Undisturbed		Disturbed	
	Above	Below	Above	Below
Pleurozium schreberi (Brid.) Mitt. (*R.S. Capers & D.W. Taylor 107*, CONN00132958)	0.04	0.50	–	–
Pohlia nutans (Hedw.) Lindb. (*R.S. Capers & D.W. Taylor 108*, CONN00132954)	0.04	0.40	–	0.30
Grimmia donniana Sm. (*R.S. Capers & D.W. Taylor 110*, CONN00132945)	0.04	–	–	–
Andreaea rothii Weber & D. Mohr (*R.S. Capers & D.W. Taylor 112*, CONN00132950)	–	0.20	–	–
Brotherella recurvans (Michx.) Fleisch. (*R.S. Capers & D.W. Taylor 114*, CONN00132962)	–	0.20	–	–
Dicranum scoparium Hedw. (*R.S. Capers & D.W. Taylor 109*, CONN00132959)	–	0.20	–	–
Dicranum elongatum Schleich *ex* Schwaegr.	–	0.10	–	–
LIVERWORTS	0.04	0.60	–	–
Gymnomitrion concinnatum (Lightf.) Corda (*R.S. Capers & D.W. Taylor 116*, CONN00132946)	0.04	–	–	–
Ptilidium ciliare (L.) Hampe (*R.S. Capers & D.W. Taylor 117*, CONN00132947)	–	0.50	–	–
Barbilophozia floerkei (F. Weber & D. Mohr) Loeske (*R.S. Capers & D.W. Taylor 119*, CONN00132961)	–	0.20	–	–
Cephalozia bicuspidata (L.) Dumort. (*R.S. Capers & D.W. Taylor 118*, CONN00132960)	–	0.10	–	–
Lophocolea heterophylla (Schrad.) Dumort. (*R.S. Capers & D.W. Taylor 115*, CONN00132956)	–	0.10	–	–
Ptilidium pulcherrrimum (Weber) Vain. (*R.S. Capers & D.W. Taylor 122*, CONN00132965)	–	0.10	–	–

Table 1. Continued.

Species and Collection Information	Relative Frequency of Occurrence Above and Below Treeline[1]			
	Undisturbed		Disturbed	
	Above	Below	Above	Below
LICHENS	0.85	0.60	0.19	0.10
Rhizocarpon geographicum (L.) DC.	0.74	0.40	0.19	0.10
Umbilicaria sp.	0.59	0.20	0.07	0.10
Arctoparmelia centrifuga (L.) Hale	0.41	–	0.11	–
Aspicilia sp.	0.33	0.20	0.15	–
Cetraria laevigata Rass. (*R.S. Capers & D.W. Taylor 121*, CONN00132948)	0.22	0.50	–	–
Stereocaulon sp.	0.15	0.30	0.07	0.10
Cladonia cervicornis (Ach.) Flotow subsp. *verticillata* (Hoffm.) Ahti	–	0.20	–	–
Cladonia gracilis (L.) Willd. subsp. *gracilis* (*R.S. Capers & D.W. Taylor 120*, CONN00132949)	–	0.20	–	–
Cladonia chlorophaea (Flörke *ex* Sommerf.) Spreng.	–	0.10	–	–

occurred only below 1600 m, where krummholz became common and below which the cover of stunted trees was nearly continuous. Only five species established in disturbed plots in the alpine habitat above treeline (compared with 15 extant in the undisturbed plots), two of which were found only once. Among these, only *Juncus trifidus* occurred with higher relative frequency (the proportion of all plots in which a species or functional group occurred) in disturbed than undisturbed plots. In disturbed plots, plants became increasingly sparse with higher elevation, and five of the 10 highest elevation plots in the disturbed transect had no vascular plants at all (compared with one of 10 in the undisturbed transect). Even where plants had colonized, abundance was low (Table 2; Figure 2). With the exception of a single spruce (*Picea* sp.) seedling, the plants colonizing above treeline in the disturbed area were also members of the undisturbed community. Three of the four species most frequently found in disturbed plots (*Carex bigelowii*, *J. trifidus*, and *Minuartia groenlandica*) were also among the four most frequently found species in the undisturbed community.

Table 2.   Mean (± SE) species richness and abundance (percent cover) values in the disturbed alpine plant community are compared with values in the undisturbed community. Separate data are shown for vascular plants, bryophytes, and lichens. Because values differed dramatically above (n = 27) and below (n = 10) treeline, separate analyses were done for the two areas. Abundance values combine the cover values for individual species in each component of the community. For abundance, mean values are shown, but t-tests were conducted with square-root-transformed data, and the t values shown are from those tests. * = $p \leq 0.05$; ** = $p \leq 0.01$; *** = $p \leq 0.001$.

SPECIES RICHNESS

	Below Treeline			Above Treeline		
	Disturbed	Undisturbed	t	Disturbed	Undisturbed	t
Vascular plants	3.3 ± 0.99	6.1 ± 0.69	−2.35*	0.9 ± 0.182	2.9 ± 0.38	−6.00***
Bryophytes	1.6 ± 0.33	4.6 ± 0.50	−4.74**	0.56 ± 0.14	1.96 ± 0.16	−5.54***
Lichens	0.3 ± 0.3	2.1 ± 0.69	−2.25	0.59 ± 0.27	2.44 ± 0.30	−5.13***

ABUNDANCE

	Below Treeline			Above Treeline		
	Disturbed	Undisturbed	t	Disturbed	Undisturbed	t
Vascular plants	6.8 ± 2.36	102.5 ± 14.61	−7.14***	0.8 ± 0.18	50.7 ± 8.50	−5.90***
Bryophytes	15.5 ± 5.00	38.0 ± 9.13	−1.97	1.3 ± 0.47	21.5 ± 3.43	−9.09***

Figure 2. A quadrat (1 meter square) sample in the disturbed alpine community, left, compared with the alpine community in the undisturbed community at the same elevation (1837 m) near the summit of Mount Washington, right. In 2012, four years after a disturbance in the alpine habitat, plants had begun to recolonize, but abundance was far lower than in the undisturbed area.

Six bryophyte species (all mosses, including three in the Polytrichaceae) colonized the disturbed transect (five above tree-line), compared with 21 (15 mosses and six liverworts) extant in the undisturbed transect. Five lichens were recorded in the disturbed transect (compared with nine extant in the undisturbed communi-ty), all above treeline. However, four of these occurred only on rock, and it was impossible to determine if these species colonized after the disturbance or were moved into the area on rocks as the excavation work ended and the area was regraded.

Species richness of vascular plants in disturbed plots was 1.5 ± 0.34 (mean $\pm$ SE), compared with 3.8 ± 0.40 in undisturbed plots (t $= -5.72$, $p < 0.0001$). Abundance of vascular plants also was lower in disturbed plots (Figure 2; 2.5% cover vs. 64.7% overall; t = 10.5, $p < 0.0001$ with square-root transformed data). We identified four species of *Polytrichum* or *Polytrichastrum* moss but we were unable to distinguish these from each other with certainty in the field and did not collect a specimen of each from every site where it was recorded. Thus, we combined them as Polytrichaceae spp. in analyses of species richness, resulting in lower estimates than actually occurred. Richness of both bryophytes and lichens was lower in the disturbed plots than in the undisturbed plots (bryophytes: 0.84 ± 0.157 vs. 2.65 ± 0.246, t $= -7.50$, $p < 0.0001$; lichens: 0.51 ± 0.211 vs. 2.38 ± 0.286, t $= -5.51$, $p < 0.0001$). Mean cover of bryophytes overall was 5.1% $\pm$ 1.71 in disturbed plots compared with 26.0% $\pm$ 3.65 in undisturbed plots (t $= -7.37$, $p < 0.0001$). Relative frequency

values for most species of bryophytes and lichens also were lower in the disturbed transect than in the undisturbed community (Table 1). Polytrichaceae species and *Pogonatum dentatum* were the bryophytes that most frequently colonized the disturbed areas. Five lichens were recorded in the disturbed transect, but only one was a soil-dwelling lichen—a species of *Stereocaulon* that colonized three locations, including two above treeline.

Elevation over the entire distance sampled had a significant negative effect on species richness and abundance of vascular plants and bryophytes. However, when above-treeline and below-treeline plots were analyzed separately, the effect of elevation disappeared or was limited to the alpine area above treeline. Among vascular plants, for instance, linear regression indicated that elevation and disturbance (the latter entered as a categorical variable) each had a highly significant influence on species richness (F = 26.04 for elevation, and F = 24.32 for disturbance, $p < 0.0001$ in both cases), explaining 41% of variation. However, elevation was no longer significant when treeline was entered into the regression, and the best-fit model included only treeline and disturbance (F = 26.23 for disturbance, and F = 33.66 for treeline, $p < 0.0001$ in both cases; $R^2 = 0.458$). When above-treeline and below-treeline species richness were analyzed separately, species richness was lower in disturbed plots than undisturbed plots, both above and below treeline (Table 2), but elevation was not significant in either the disturbed or undisturbed community (below treeline: F = 0, p = 0.99 for disturbed plots, and F = 0.418, p = 0.5363 for undisturbed plots; above treeline: F = 0.738, p = 0.3984 for disturbed plots, and F = 0.665, p = 0.4224 for undisturbed plots; Figure 3). As a result, separate analyses were conducted for above-treeline (N = 27) and below-treeline (N = 10) plots.

Similarly, abundance of vascular plants was significantly influenced by both elevation and disturbance when they were entered in a regression together (F = 87.03, $p < 0.0001$ for disturbance, and F = 4.88, p = 0.0304 for elevation; $R^2 = 0.564$) but, when treeline was entered into the regression, elevation no longer was significant and the best-fit regression model included only treeline and disturbance (F = 14.84, p = 0.0003 for treeline, and F = 98.50, $p < 0.0001$ for disturbance; $R^2 = 0.615$). Abundance of vascular plants was lower in disturbed plots than undisturbed plots both above and below treeline (Table 2), but elevation did not influence abundance within either area (below
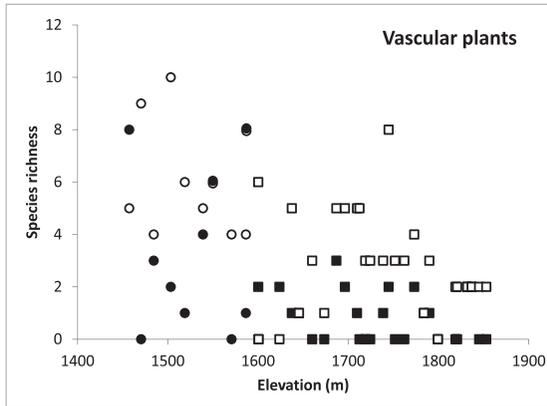
Figure 3.   The species richness of vascular plants in disturbed quadrats (closed symbols) is compared with richness in undisturbed quadrats (open symbols) in high-elevation habitat on Mount Washington. Species richness declined with elevation in both disturbed and undisturbed communities. However, the effect of elevation disappeared when treeline, which occurs at about 1600 m in this area, was taken into account. In both disturbed and undisturbed communities, declines in richness with elevation were not significant in linear regressions when above-treeline quadrats (squares) and below-treeline quadrats (circles) were analyzed separately.

treeline: $F = 0.0037$, $p = 0.95$ for disturbed plots, and $F = 0.7756$, $p = 0.40$ for undisturbed plots; above treeline: $F = 0.8353$, $p = 0.37$ for disturbed plots, and $F = 2.8874$, $p = 0.10$ for undisturbed plots). Above treeline, no vascular plant species in disturbed plots had cover in excess of 1%, compared with a maximum of 100% cover in the undisturbed plots. Below treeline, total cover of vascular plants exceeded 20% only in one disturbed plot, where eight species had established, whereas cover exceeded 100% in several undisturbed plots. Although the frequency of vascular plants in general was low in the disturbed area above treeline, it was especially low for woody species, which occurred in only 3.7% of plots, compared with the undisturbed transect, where woody species appeared in 37% of plots.

When all samples were considered, bryophyte richness declined with elevation in both disturbed and undisturbed transects ($F = 18.92$, $p = 0.0001$, and $F = 31.21$, $p < 0.0001$, respectively), whereas lichen richness was uncorrelated with elevation ($F = 0.36$, $p = 0.5506$ for disturbed transects, and $F = 0.04$, $p = 0.8431$ for undisturbed transects). For both bryophytes and lichens (Figure 4),
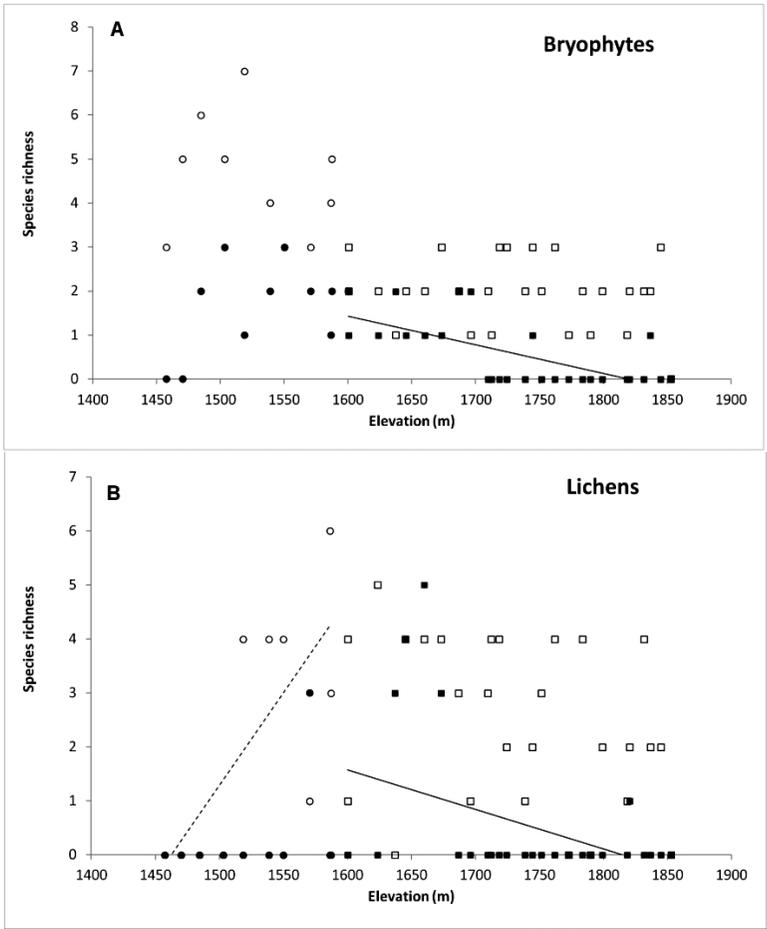
Figure 4.   Species richness of lichens was unrelated to elevation and bryophyte richness declined with elevation in both disturbed and undisturbed communities, but the effect was greatly reduced when treeline was taken into account and subcommunities were analyzed separately. In the undisturbed communities (open symbols) of bryophytes (A) and lichens (B) above treeline (open squares), species richness was not influenced by elevation. However, species richness declined above treeline in both disturbed communities (closed squares and solid lines), suggesting that rates of colonization and/or survival decline with elevation in the alpine habitat. For bryophytes, $S = -0.0065*Elevation + 11.83$, $p = 0.002$, adjusted $R^2 = 0.419$; for lichens, $S = -0.007*Elevation + 13.30$, $p = 0.037$, adjusted $R^2 = 0.129$. Lichen richness below treeline also increased with elevation in the undisturbed community (open circles and broken line), probably because light availability increases in the understory closer to treeline: $S = 0.034*Elevation + 50.13$, $p = 0.018$, adjusted $R^2 = 0.462$.

richness declined with elevation above treeline in the disturbed community (bryophytes: $F = 18.26$, $p = 0.0003$; lichens: $F = 4.85$, $p = 0.0370$) but not in the undisturbed community (bryophytes: $F = 0.11$, $p = 0.7470$; lichens: $F = 2.79$, $p = 0.1074$). Below treeline, elevation was uncorrelated with bryophyte richness in both disturbed and undisturbed communities ($F = 1.54$, $p = 0.2548$, and $F = 0.75$, $p = 0.4166$, respectively). Lichen richness was uncorrelated with elevation below treeline in the disturbed community as well ($F = 0.95$, $p = 0.3589$), but increased with elevation in the undisturbed community ($F = 8.72$, $p = 0.0183$).

Abundance of bryophytes was lower in the disturbed plots, especially above treeline, where no species achieved more than 5% cover. Below treeline, bryophyte cover exceeded 25% in three of 10 plots in the disturbed area, compared to seven of 10 undisturbed plots, where cover reached a maximum of 80% cover. However, below treeline, mean abundance of bryophytes in the disturbed area did not differ significantly from abundance in the undisturbed community (Table 2). Bryophyte abundance (square-root-transformed) declined with elevation in both disturbed and undisturbed transects above treeline ($F = 23.5184$, $p = 0.0001$ for disturbed plots, and $F = 5.1816$, $p = 0.0317$ for undisturbed plots) but not in either transect below treeline ($F = 4.0577$, $p = 0.0787$ for disturbed plots, and $F = 0.0440$, $p = 0.8392$ for undisturbed plots).

DISCUSSION

Four years after a major disturbance, recovery of the alpine plant community had barely begun. Twenty species of vascular plants had colonized in the disturbed area (Table 1), but only five of them occurred in the alpine area above treeline. No vascular plant species had cover greater than 1% in any disturbed plot above treeline, whereas recovery at lower elevations was more advanced. Mosses also had begun colonizing the disturbed area, but fewer than half of the species occurring in the undisturbed community were found in the disturbed area. Moss abundance remained low in the disturbed area of alpine habitat, but mosses had increased in abundance more quickly in the disturbed area below treeline than had vascular plants. Six liverwort species were collected in the undisturbed community, but none had recolonized the disturbed area. Among lichens, five of the nine species occurring in the undisturbed community were recorded in the disturbed area. Mean species

richness was significantly lower in the disturbed plots for all groups (Table 2).

Several studies have shown that, even where alpine plants recolonize soon after a disturbance, vascular plant abundance can remain low for decades to centuries (Ebersole 2002; Rydgren et al. 2011; Sklenář et al. 2010). Total cover of vascular plants in a Montana borrow pit was 25% after 35 years (Chambers 1993). Likewise, 475 years following an eruption of a volcano in Ecuador, plant cover was only 69% (Sklenář et al 2010). However, one study has documented more rapid recovery. Chacón and Cavieres (2008) found total cover of 28% on a south-facing slope and 24% on a northwest-facing slope (compared with 52% and 61%, respectively, in the undisturbed communities) two years after organic soil and vegetation were removed by bulldozers during dam construction in Chilean alpine habitat. Most recovery was apparently due to a persistent seedbank that existed below the organic soil that had been removed (Chacón and Cavieres 2008).

The rate of recovery in alpine habitat depends to a large degree on the severity and duration of disturbance. Willard and Marr (1971) found that lichens in a fellfield could recover to nearly a natural state after only two years if they had been trampled for only one year. On the other hand, a sedge meadow they studied would need more than 100 years to fully recover from 26 years of trampling (Willard and Marr 1971; Willard et al. 2007). The sedge meadow had strong turf that was resistant to disturbance, but once the turf was broken the soil was vulnerable to erosion that left only coarse gravel, where recovery proceeded slowly. A previous study of alpine recovery in the White Mountains found that plants had re-established 12 years after scree walls were built to reduce trampling by hikers, but cover had increased only from 6% to 26% (Doucette and Kimball 1990). The disturbance in the area we studied was more severe, involving the removal of soil, disruption of the seedbank, and trampling by backhoes, not boots, so recovery might be expected to take longer there.

It is difficult to know on the basis of a single year's survey how the recovery rate on Mount Washington will compare with that in other areas. Our study was located on the northwest side of the mountain where prevailing winds are most severe, which may retard recovery by preventing seed germination or reducing seedling survival. Soil in the disturbed area is rocky and the organic soil has been largely removed, which leaves a nutrient-poor substrate in

which newly arrived seeds must establish (Chambers 1995). The
nature of disturbance events also interacts with seed morphology
and life history traits to influence community composition; small
seeds are trapped more easily in fine-grained soils, whereas only
coarse soils can effectively trap large seeds (Chambers 1995). Soil
texture and organic content also affect temperature and water-
holding ability and, thus, influence seedling survival (Chambers
1995; Ebersole 2002). Many alpine plants produce abundant seeds,
but germination often is limited by conditions in the soil (Chacón
and Cavieres 2008; Chambers et al. 1990), and survival of seedlings
in disturbed areas often is low (Chacón and Cavieres 2008;
Chambers 1995; Roach and Marchand 1984), largely as a result
of frost-heaving or drought stress (Forbis 2003). In general, seedling
survival has been found to be more limiting than seed availability
for disturbance recovery in alpine plant communities (Chambers
1993, 1995; Ebersole 2002).

Vascular plant colonization in the disturbed area of Mount
Washington appears to result from seedling establishment, either
from seeds produced nearby or from the seedbank. We looked for
evidence that plants were expanding vegetatively into the disturbed
area, and we did see occasional evidence of this along the sides of
the disturbance, but these plants did not extend into the center of
the disturbance where the sampling was done. Vegetative coloni-
zation appeared to be related to collapse of small embankments,
which permits chunks of turf to slip into the lower, disturbed area.
We also noted that, in a few areas, turf had been thrown into the
disturbed area by railway workers doing maintenance along the
Cog Railway (none occurred in the plots), although the long-term
viability of these plants is questionable.

In general, the species colonizing the disturbed area were those
that were among the most frequent and abundant in the
undisturbed community. The three most successful colonizing
angiosperms in the alpine area were all herbaceous (*Carex bigelowii*,
Juncus trifidus, and *Minuartia groenlandica*), and all were common
in the high alpine areas of the Presidential Range (Antevs 1932;
Bliss 1963). *Juncus* and *Minuartia* are part of an early successional
community often found along trails and in other disturbed areas
(Marchand and Roach 1980; Sardinero 2000). Graminoids such as
J. trifidus and *C. bigelowii*, which have abundant small seeds, often
dominate alpine communities after disturbance, although clonal
plants with fewer but larger seeds frequently come to dominate

later in succession as communities become more similar to their undisturbed counterparts (Chambers 1993; Roxburgh et al. 1988). Only one woody species (a single spruce seedling) had colonized in the disturbed plots above treeline. Among the woody species that were conspicuous by their absence from disturbed plots were *Vaccinium vitis-idaea* subsp. *minus* and *V. uliginosum*, which are frequent and often abundant in alpine areas of the Presidential Range. These species were present in 26% and 15%, respectively, of our above-treeline undisturbed plots. Rydgren et al. (2011) found the same two species rare in, or absent from, communities establishing on five alpine spoil heaps in Norway more than 20 years after abandonment, although both species were common in the surrounding communities. The absence of these shrubs from disturbed areas is likely the result of seed limitation, which also has been found to limit alpine colonization by *Vaccinium myrtillus* (Lindgren et al. 2007).

Among bryophytes, *Polytrichum piliferum*, *P. commune*, and *Pogonatum dentatum* have most readily colonized the disturbed plots above treeline, though abundance values for all remained lower than in the undisturbed community. Few alpine disturbance recovery studies have included bryophytes and lichens, but they often indicate that these groups recover more quickly than vascular plants. Rydgren et al. (2011) found little recovery of bryophytes and lichens six to 20 years after disturbance, but species richness and cover had returned to levels comparable to those of the surrounding communities after 30 years. On the other hand, Ebersole (2002) found that lichen cover generally remained lower in disturbed than in control plots after 30 years. We found no evidence that bryophytes have colonized any more quickly than vascular plants above treeline on Mount Washington. Future research is needed to establish the course of lichen recovery.

We had expected that elevation would affect the rate of recovery and, overall, species richness and abundance did decline with elevation. However, among vascular plants, these declines appear to be the effect of treeline, not elevation itself. We found no evidence that elevation had an additional effect on richness or abundance either above or below treeline. We suspect that the protective cover of trees, even where stunted in the krummholz, provides a more benign environment for seedling establishment and survival, producing greater abundance and species richness below treeline. Despite not affecting vascular plant colonization, elevation did

affect bryophytes and lichens, but only above treeline. Species richness of both bryophytes and lichens declined with elevation in the disturbed community above treeline but not in the undisturbed community (Figure 4). These results suggest that there is a transient effect of elevation—disappearing in mature communities—in which moss and lichen colonization and/or survival rates in alpine habitat decline with elevation. An increase in lichen richness with elevation in the undisturbed community below treeline is likely an effect of increasing light availability in the understory closer to treeline.

In retrospect, it does not seem surprising that treeline influences vascular plants' occurrence more than elevation does. Treeline itself is influenced by elevation but varies greatly—by nearly 600 m in the Presidential Range (Kimball and Weihrauch 2000)—depending primarily on aspect, which determines exposure to the prevailing northwest winds. Winter winds blow snow off the northwest slope of Mount Washington where we conducted our survey (most is deposited in the Alpine Garden and deep ravines east of the summit), leaving plants exposed and unprotected from desiccation and blowing ice, which can erode stem and bud tissue (Harries 1966). Loss of snow cover also can increase soil disturbance as a result of freeze-thaw cycles (Kimball and Weihrauch 2000; Roach and Marchand 1984). Ultimately, these and other abiotic and biotic conditions are what regulate the occurrence of plants, not elevation or treeline (Billings 1974; Billings and Mooney 1968). These conditions interact with each other and affect individual species in ways that are often inferred but are poorly characterized quantitatively. Differences among species' affinities and tolerances produce the distinctive alpine communities, with, for instance, sedge meadows in high-elevation areas on west- or north-facing slopes, and with forb communities dominating wet sites such as snowbanks (Antevs 1932; Sperduto and Kimball 2011). Experimental manipulations would be needed to determine how specific environmental conditions affect colonization and survival of the community we studied.

In the absence of disturbance, alpine communities would be expected to change little over time, and previous studies have assumed that disturbed alpine communities would return eventually to the pre-disturbance condition (Lloyd et al. 2003; Rydgren et al. 2011). However, alpine communities are sensitive to changes in warming, precipitation amount and timing, and nitrogen deposi-

tion, and all of these conditions are now changing in northeastern North America (Galloway et al. 1984; Keim et al. 2003; Trombulak and Wolfson 2004). Under such conditions, disturbance can trigger state changes, in which communities switch quickly from one stable state to a different one (Post et al. 2009; Scheffer et al. 2001). It will be especially important to follow the course of succession in the disturbed area of Mount Washington as a way of assessing whether more widespread changes in alpine community composition should be anticipated with changing environmental conditions. Any such changes are likely to first become apparent where disturbance allows succession to begin again, and future researchers should be alert for evidence of such fundamental shifts in community composition.

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