COLONIZATION OF VOLCANIC DESERTS FROM PRODUCTIVE PATCHES[1]

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Dense vegetation can augment landscape biodiversity, promote recovery of surrounding ecosystems, and facilitate colonization. However, dispersal limits affect vegetation structure early in succession to a degree that is not widely appreciated. We studied two contrasting densely vegetated habitats located on Mount St. Helens to explore their effects on surrounding vegetation. We sampled refugia and adjacent barrens and compared them to a study conducted 5 yr earlier. We sampled isolated wetlands and their surroundings. Species richness, total cover, cover of most dispersal types, the information statistic (H'), and the complement of Simpson's Index (D) were negatively correlated with distance from the refugia up to 32 m. Compared to 1997, the 2002 transects had higher cover, and adjacent samples were more similar to one another. Dominance had shifted from wind-dispersed species to more persistent species with less effective dispersal mechanisms. The pattern of these results demonstrated that refugia were a major, but indirect source of recruitment for many species. The influence of wetlands on surrounding vegetation recovery was even more spatially localized. This study demonstrates that dispersal from surviving and rapidly recovered vegetation has been overemphasized as a mechanism for vegetation recovery. The effects of dense vegetation did not extend beyond 32 m in our studies, and local effects appear to diminish over time.

Key words: community assembly; dispersal; Mount St. Helens; primary succession; refugia; vegetation dynamics; volcano.

Since catastrophic disturbances may miss remnants of pre-existing vegetation (i.e., refugia), primary succession may be influenced by the proximity of potential colonizers (Walker and del Moral, 2003). In this paper we assess how refugia accelerated primary succession and compare them to effects of newly formed wetlands on Mount St. Helens, a volcano in northwestern USA.

Landscape ecologists emphasize that surviving vegetation can sustain biodiversity (Turner and Corlett, 1996). Existing vegetation often survives disturbances, may accelerate recovery (Rundgren and Ingolfsson, 1999; Poulin et al., 1999), or at least promote colonization (Brunet and von Oheimb, 1998). Therefore, learning how rich resource patches affect recovery of vegetation informs our understanding of community development. Studies of the assembly of plant communities often describe cases where dispersal limits affect species composition (Primack & Miao, 1992; Kochy and Rydin, 1997; Erikkson, 2000; Zobel et al., 2000; Costa et al., 2003; Foster and Tilman, 2003; Wehncke et al., 2003). However, the degree to which distance from propagule sources affects species composition remains poorly understood. Colonization requires dispersal and establishment. Dispersal abilities vary, so isolation from propagule sources can shape early community composition and create gradients of richness and cover (Borgegärd, 1990; Stöcklin and Bäumler, 1996; del Moral et al., in press). Plants with light, windborne seeds often dominate early succession (Prach and Pyšek, 1999), especially on volcanoes (del Moral and Grishin, 1999). However, survival of these species

is low, while poorly dispersed, large-seeded species establish well (Wood and del Moral, 1987, 1988).

Here we explore the effects of two contrasting habitats on Mount St. Helens. Refugia permitted the survival of forest understory species in soil due to steep northeast-facing slopes and a deep snow pack (Fuller and del Moral, 2003). However, refugia did not contribute relict species to the adjacent vegetation. Instead, refugia provided habitats for newly invading species to establish dense populations from which to expand. Fuller and del Moral (2003) also found that expansion from refugia on Mount St. Helens resulted in major changes in dispersal spectra over short distances. They predicted that sites near refugia would become more similar to distant sites over time. We also explored dispersal spectra near small, isolated wetlands formed soon after the eruption on pyroclastic materials north of the crater (del Moral, 1999b) to determine if there is a more general effect of dense vegetation on the surroundings.

This study searches for patterns associated with biologically rich patches represented by refugia and wetlands. By looking at the spatial effects of different types of dense vegetation we hope to better understand the mechanisms driving vegetation change.

METHODS

Study sites—Refugia—We sampled a subset of refugia described by Fuller and del Moral (2003). Further descriptions of this area are in Wood and del Moral (1988), del Moral (1999a) and del Moral and Jones (2002). We examined refugia centered at 46°13′40″ N, 122°09′10″ W, and all refugia were within 1 km of each other. Individual transects extended uphill from refugia edges starting at 1 m from a refugium and extending to 128 m. The surface was pumice deposited during the 1980 eruption. Sample points were adjusted if necessary to avoid any rills. Pumice has weathered to form a sandy substrate beneath the gravelly surface that forms a mulch. While nutrient poor the soil retains moisture. No pre-eruption soil was exposed near the transects and soils were homogeneous (Fuller, 1999).

Wetlands—The 16 sampled wetlands were within a 1-km² area south of Spirit Lake (between 46°15′34″ N, 122°09′42″ W and 46°15′00″ N,

TABLE 1. Characteristics of refugia and wetlands and the design of sampling. Core refers to the best-developed vegetation, either within the refugium or in the wetland. Refugia soil data from Fuller (1999); wetland soil data from del Moral (1999b).

Characteristic	Refugia	Wetlands
Number	Sites: 17; transects: 32	Sites: 16; transects: 36
Elevation range	1280–1325 m	1050–1100 m
Transect gradient	gentle, extending uphill, exposed	gentle, several directions
Transect length	128 m	32 m
Core sample method	4 m² per refugium (68 m²)	2 m² per transect (72 m²)
Transect sample unit	4 m²	1 m²
Sample locations	2, 4, 8, 12, 16, 24, 32, 64, 128 m	1, 2, 3, 4, 8, 12, 16, 32 m
Core topography	steep slope	depression
Core soil organic %	residual forest soil; 2.3%	newly formed; 2.6%
Core soil pH	4.6	5.3

122°09′45″ W). These wetlands formed in depressions on pyroclastic material (del Moral et al., 1995; Titus et al., 1999; del Moral, 1999b). They are supported by snow that collects in depressions and by upwelling seeps. Transects were established on homogeneous surfaces that have experienced wind erosion since 1980 to form a coarse surface. Subsurface materials were much finer than that of transects above refugia. Transects extended to 32 m.

Comparison—Many characteristics of refugia, wetlands, and their transects were similar (Table 1), but these patches differed in significant ways. Wetlands were about 250 m lower in elevation. Refugia contain old soil on steep slopes, while wetlands formed shortly after the 1980 eruption in depressions. Transects above refugia sample pumice that has decomposed, while those extending from wetlands occur on eroded pyroclastic materials. Wetland soils were similar in organic content, but higher in pH than the refugia soils.

Sampling—The edge of a refugium is defined by where pre-eruption organic soil could not be found 15 cm below the pumice. This usually coincided with where the slope became gentle. All vegetation data were obtained by estimating cover in 1-m² quadrats. In 1997, transects were 20 m belts of contiguous 1-m² quadrats, while isolated barrens were sampled in five 20 × 20 m plots that were over 100 m from any refugium. Here, 20 1-m² quadrats were sampled at random. For the present study, the transect quadrats were pooled to facilitate comparisons with the 2002 data as follows: sample A, centered at 2 m (0–4 m); sample B, centered at 7 m (5–9 m), sample C, centered at 12 m (10–14 m), and sample D, centered at 17 m (15–19 m). This method provided physical separation between the samples. For similarity comparisons, five composite samples in each barren plot were formed by selecting four quadrats at random. Thus, in 1997, there were 25 distant samples. In 2002, 17 refugia were sampled with four 1-m² quadrats, located randomly within each. We established 32 transects that extended uphill. Each sample was a 2 × 2 m quadrat centered at 2, 4, 8, 12, 16, 24, 32, 64, and 128 m, with cover determined separately in each 1-m² portion of the quadrat.

Those 2002 samples centered at 2, 8, 12, and 16 m were used for comparison with the 1997 transects. Two most distant sites sampled in 2002, 64 and 128 m, were used for comparison with the 1997 barren sites.

Each wetland was sampled using two or three transects that included two quadrats 1 m inside the wetland and 1-m² samples starting at 1, 2, 3, 4, 8, 12, 16, and 32 m. The edge was determined using lack of saturation at the surface and rarity of obligate wetland species. Species nomenclature is that found in the Integrated Taxonomic Information System (ITIS; http://www.itis.usda.gov).

Data summary—Structure—The number of species (richness), their percent cover, and two measures of vegetation structure were calculated for each sample unit and for pooled data (e.g., all samples at 2 m from a refugium). We used the complement of Simpson's dominance index [$D = (1 - \Sigma p_i^2)$], which varies from 0 to 1. It is insensitive to small samples and rare species. The Shannon Index ($H' = -\Sigma p_i \ln p_i$) balances the number of species and their relative abundances. In both cases, p_i is the proportion of the cover represented by a species. These measures were calculated using PC-ORD (McCune and Mefford, 1999).

Floristic similarity—The floristic relationship between two samples was quantified using percent similarity [$PS_{ij} = 200\Sigma \min (X_{ik}, X_{jk})/\Sigma(X_{ik} + X_{jk})$, where there are k species, X is percent cover, and min is the lower value (Kovach, 1998)]. Similarity among samples of a year was calculated from 4-m² plots ($N = 37$ in 1997; $N = 32$ in 2002).

Dispersal types—Fuller and del Moral (2003) divided species by their likely dominant dispersal vector. We modified this classification by considering spore-producing species separately. We added species found in wetlands to form additional categories (Table 2).

TABLE 2. Dispersal categories and exemplar species. A list of species encountered on study sites from Mount St. Helens can be found at: http://protist.biology.washington.edu/delmoral/Mastertaxonomy2003.

| Dispersal Type	Structures	Examples (N = number of species in category)
Parachute–Seeds ($N = 14$)	Pappus, hairs	Upland: Asteraceae, *Chamerion angustifolium*, *Salix commutata*
		Wetland: *Salix* spp., *Typha angustifolia*, *Epilobium* spp., *Petasites frigida*
Parachute–Spores ($N = 15$)	Miniscule	Upland: *Polytrichum juniperinum*, *Racomitrium canescens*, *Athyrium distentifolium*
		Wetland: *Equisetum* spp., *Bryum* spp., *Philonotis fontana*
Glider ($N = 6$)	Membranes	Upland: *Carex mertensii*, *Cistanthe umbellate*, conifers
Tumbler ($N = 10$)	Long awns, fragile shoots	Wetland: *Calamagrostis* spp., *Scirpus* spp.
Birds ($N = 13$)	Fleshy fruits	Upland: *Fragaria virginiana*, *Ribes* spp., *Rubus* spp., *Vaccinium* spp.
Other ($N = 36$)	Various	Refugia ($N = 14$): *Aruncus dioica*, *Carex spectabilis*, *Castilleja miniata*, *Lupinus latifolius*, Liliaceae
		Pioneer ($N = 11$): Many *Carex* spp., *Juncus mertensianus*, *J. parryi*, *Luetkea pectinata*, *Lupinus lepidus*, *Luzula parviflora*
		Wetland ($N = 11$): *Cinna latifolia*, *Juncus* spp., *Mimulus lewisii*
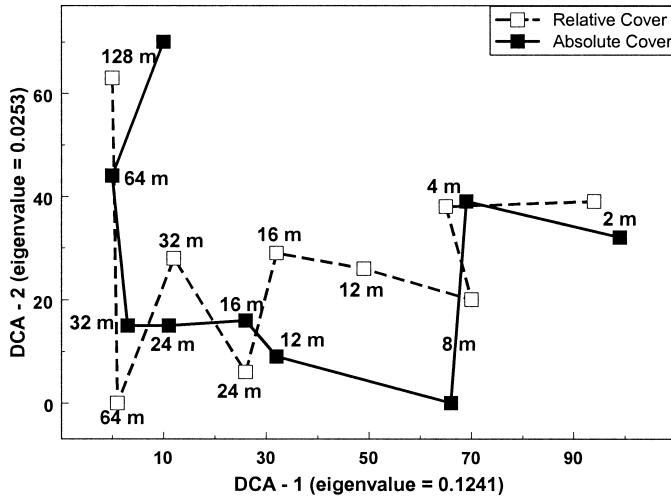
Fig. 1. Pattern of samples along transects from refugia calculated from relative and absolute cover using DCA. Each sample was derived from the mean cover of species in 32 transects. Variation is expressed by eigenvalues in the analysis of absolute cover.

Floristic ordinations—Detrended correspondence analysis (DCA; McCune and Grace, 2002) was used to determine floristic distance between samples. Nonmetric multidimensional scaling (NMS) was used to determine the number of effective dimensions. Both were applied to transect data to explore the extent to which refugia and wetlands influence their surroundings. All ordinations were conducted using PC-ORD (McCune and Mefford, 1999).

Statistical analyses—One-way analysis of variance (ANOVA) and the conservative Bonferroni test of differences among the means were used to detect differences among structural parameters along distance gradients. Regressions of structural measures with distance were calculated where appropriate, and the slopes and intercepts of individual regressions were compared. All statistical procedures were conducted using Statistix (Analytical Software, 2001). Graphs were prepared with Axum 7 (Mathsoft, 2001).

RESULTS

Refugia—*Ordination of transects*—NMS showed that the data could be expressed in just two dimensions. DCA was used to explore community patterns because variation of species distributions along the transects was well within the tolerance of this method and the axes are scaled in floristic units. DCA revealed a consistent pattern of species change along the first axis up to 32 m, whether absolute or relative cover data were used (Fig. 1). The correlation between distance from 1 to 32 m and DCA-1 on each surface was significant ($r^2 = 0.76$; $P < 0.0001$). More distant samples (64 m and 128 m) were separated on the second dimension. Samples near refugia included typical refuge species (e.g., *Lupinus latifolius*, *Rubus* spp., *Alnus viridus*, and *Castilleja miniata*), while more distant samples were dominated by species adapted to pumice, such as *Penstemon cardwellii*, *Carex mertensii*, *Juncus parryi*, *Agrostis scabra*, and *Lupinus lepidus*.

Similarity patterns—The floristic similarity between adjacent samples along transects were estimated. Data from 1997 and 2002 were then compared to determine whether species had expanded from the refugia. If so, then a pair of adjacent samples should be more similar to one another in 2002 than they were in 1997. Similarity between near and distant samples should have increased during this interval.

TABLE 3. Contrasting (A) percent similarity between adjacent samples of transects and (B) between samples near the refugia and more distant samples.

| A) Year | Percent similarity[1] | | | |
	A vs. B	B vs. C	B vs. D	C vs. D
1997 ($N = 32$)	43.0	40.8	33.7	38.5
2002 ($N = 32$)	36.2	53.0[a]	44.0[a]	49.4[a]
B) Year	A vs. Distance	B vs. Distance	C vs. Distance	D vs. Distance
1997, 100 m	15.7	18.4	17.1	18.2
2002, 64 m	20.4[a]	27.3[b]	32.9[c]	38.7[c]
2002, 128 m	19.8	29.1[c]	32.8[c]	31.8[c]

[1] Small superscripts indicate significant differences between 1997 and 2002 determined by *t* tests: [a] $P < 0.05$; [b] $P < 0.001$; [c] $P < 0.0001$.
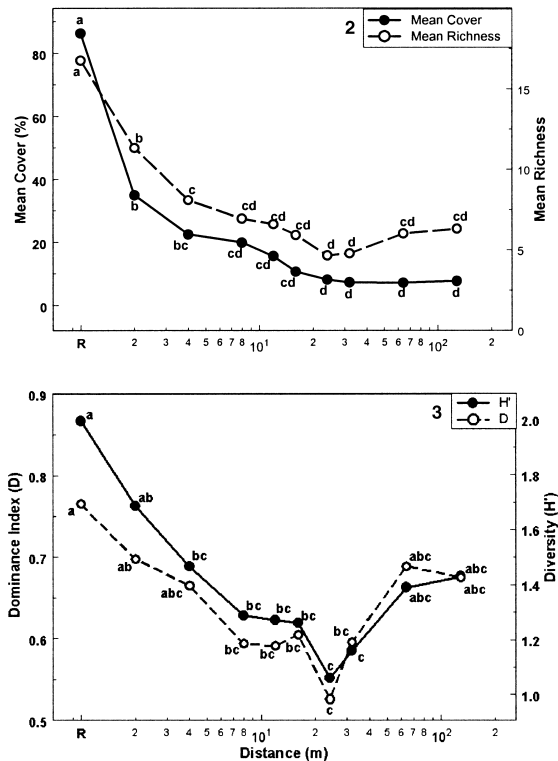
Percent similarity (PS) among sample pairs of each transect was calculated from 4-m^2 samples (see Methods). The rectangles sampled in 1997 show more variation than did the quadrats of 2002. Therefore, the similarity among adjacent samples was higher than had the sampling been conducted with 4-m^2 quadrats. The distance between each sample in 1997 was 1 m, while in 2002 it was either 2 or 4 m. This also reduced the similarity between 2002 samples.

In both 1997 and 2002, individual transects reflected the floristic gradient described by ordinations. PS between the nearest samples (A and B) did not differ between years, though the higher value in 1997 may be due to the sampling artifacts, to greater richness, or to more uncommon species in 2002. The 2002 PS comparisons between B and C and B and D, and C to D were more similar than those comparisons in 1997.

Nearby samples were all compared to distant ones. Similarities of samples A-1997 through D-1997 to the barrens ranged from 15 to 19%. In 2002, the comparison of samples A-2002 to D-2002 to the 64-m and to the 128-m samples ranged from 20 to 39%. The 2002 PS were significantly higher than the 1997 PS (*t-test*) except in one comparison to the 2 m distance (Table 3). Species better adapted to life on the barrens, particularly those with larger seeds in the tumbler and barren other group, were becoming more widely distributed. These species included *Agrostis* spp., *Penstemon cardwellii*, *Luetkea pectinata*, *Lupinus lepidus*, and *Saxifraga ferruginea*, species that were common in barren sites in 1997.

Transect structure—Both species richness and total plant cover declined significantly with distance (Fig. 2), but the refugium effect on cover and richness does not extend beyond 16 m because more distant plots have similar cover and richness. The logarithm of distance predicted the cover percentage well ($P < 0.0001$, $r^2 = 0.56$). Slightly higher cover at 64 and 128 m compared to 32 m lowered the power of this regression from $r^2 = 0.62$. The slopes of the individual regressions did not differ significantly. The intercepts were variable and the difference among them was significant ($P < 0.02$). Mean richness beyond 8 m differed little, though it demonstrated a linear regression with logarithm of distance ($P < 0.0001$, $r^2 = 0.48$). Neither the slopes nor the intercepts of transects, calculated as above, were different. In addition to the expansion of species present in 1997, a few additional species were encountered (e.g., *Lupinus latifolius*, *Achillea millefolium*, *Phacelia hastata*, *Lomatium martindalei*, and *Carex rossii*). These species increased richness and cover.

H' and D declined with distance to 24 m, then both in-

Figs. 2–3. Structure of vegetation along transects leading from refugia onto barren pumice. Differences along transects were significant (ANOVA, $P < 0.0001$). Points along a line with the same letter are not different (Bonferroni test, $P < 0.05$). **2.** Mean cover percentage and mean species richness. **3.** Diversity (H') and dominance ($D = 1 -$ Simpson's index). R = refugia. Distance axis is logarithmic.

tural features were compared as with the similarity comparisons. The 2002 data reflected greater structural development near the refugia (Table 4), as well as at greater distances. Mean richness was higher, often statistically significantly so, in 2002. Cover, not subject to the sampling bias, was higher in each comparison. H' and D also tended to be higher in 2002, indicating reduced dominance as rarer species have expanded on the transects.

Comparisons between the 25 barren site samples from 1997 with the 32 samples each at 64 and 124 m from refugia provide insight into development patterns. As expected, percent cover was significantly and substantially greater in 2002 than in 1997. However, in 1997 mean richness, H' and D were higher than in 2002. This result suggests that by 2002 a few species had become more dominant, thus reducing local richness and diversity, even though the total number of species in the samples increased from 25 in 1997 to 39 in 2002. *Lupinus lepidus* (other dispersal) and *Penstemon* (tumbler) were much more abundant in 2002, while parachute species such as *Chamerion angustifolium* declined in absolute abundance. *Lupinus lepidus*, in particular, has expanded dramatically since 1999, both geographically and in local abundance. It is likely that competitive effects of such species have altered the dominance hierarchy.

Distribution of dispersal types—Patterns observed here should reflect dispersal and the ability of a species to persist and expand. The distributions of species along transects were analyzed using one of seven dispersal categories. Refugia were dominated by bird-dispersed species and mesophytic herbs with poor dispersal. The inclusion of refugia data guarantees large differences along transects, so refugia were excluded from statistical analyses. The maximum cover of each dispersal category was next to the refugia. Cover declined with distance, but dispersal types declined to different degrees, all of which were significant (Fig. 4). Wind-dispersed species (parachute, glider, tumbler) all declined sharply, reaching a "baseline" between 16 and 24 m. Thereafter, other factors dictated the details of species composition. Bird-dispersed species dropped to near zero within 4 m, while species dispersed by other means (primarily *Aruncus viridus* and *Lupinus latifolius*) occurred up to 16 m from refugia.

Shifts in dispersal-type composition are readily visualized when relative cover at each sample distance is plotted (Fig. 5). Parachute species declined rapidly, from 33 to 8% of the total, reflecting the origin of most seedlings on the margins of the refugia (Fuller and del Moral, 2003). Beyond 32 m, their distribution relative to other species was variable. Gliders, nev-

creased (Fig. 3). The linear relationship of each to distance was highly significant ($P < 0.0001$), despite increases at farther distances that reduced the power of the relationship. The transects demonstrated no significant differences in the slope of the relationship for either H' or D, indicating the generality of the result. However, both were affected by the nature of the refugia because the intercepts of the regressions did differ significantly ($P < 0.0001$). By 8 m, there does not appear to be a significant impact of refugia on community structure, and there was certainly no effect beyond 24 m. Changes still further from refugia reflected topographic, spatial, and stochastic factors.

Comparisons between the 1997 and the 2002 transects confirmed that the vegetation had developed substantially. Struc-

TABLE 4. Comparison of structure along transects leading from refugia, 1997–2002. Bare samples were over 100 m from refugia in 1997, and 64 m (A) and 128 m (B) in 2002.

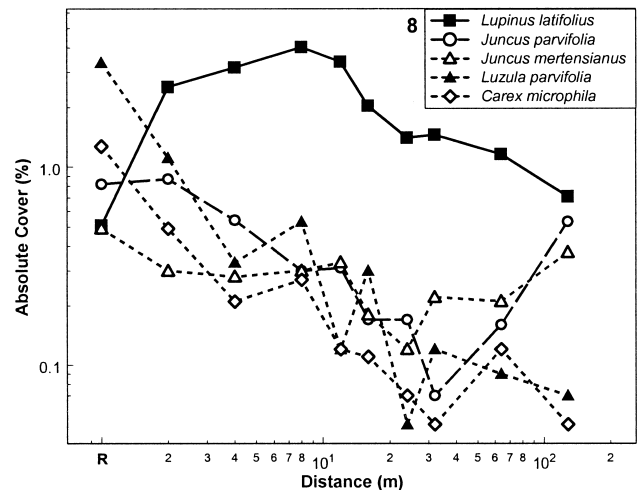| Sample	Richness[1]		Cover (%)		H'		D	
	1997	2002	1997	2002	1997	2002	1997	2002
A	8.1	11.4[a]	24.3	34.9[a]	1.41	1.69[a]	0.658	0.698
B	6.2	6.9	13.8	19.9[a]	1.28	1.02	0.598	0.594
C	5.1	6.6[a]	8.2	15.6[a]	1.02	1.27[a]	0.516	0.592
D	4.9	5.9	6.5	10.6[a]	0.97	1.26[a]	0.475	0.606[a]
Bare	8.0		4.2		1.67		0.744	
A. Bare		6.0[b]		7.1[b]		1.39[a]		0.659[a]
B. Bare		6.4[a]		7.7[b]		1.44[a]		0.675[a]

[1] Superscripts indicate significant differences between years determined by t tests: [a] $P < 0.05$; [b] $P < 0.001$.
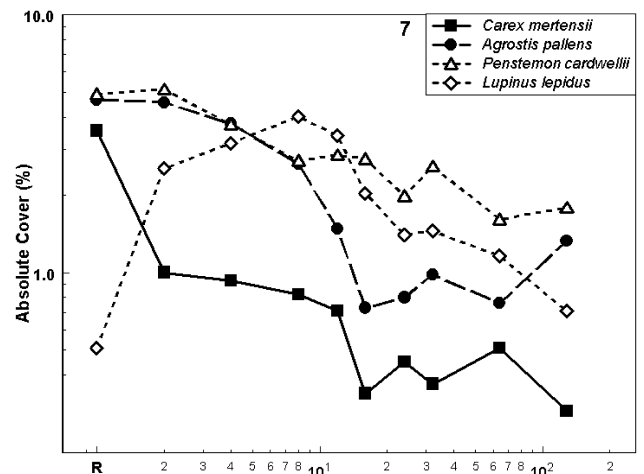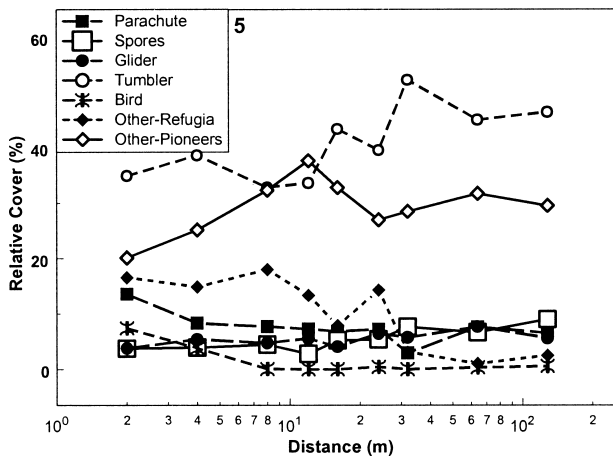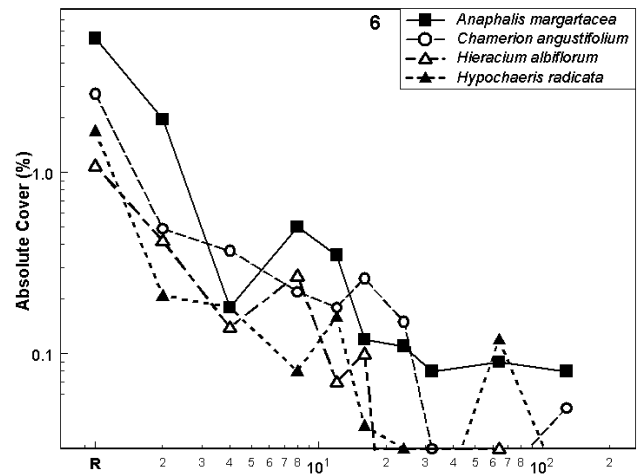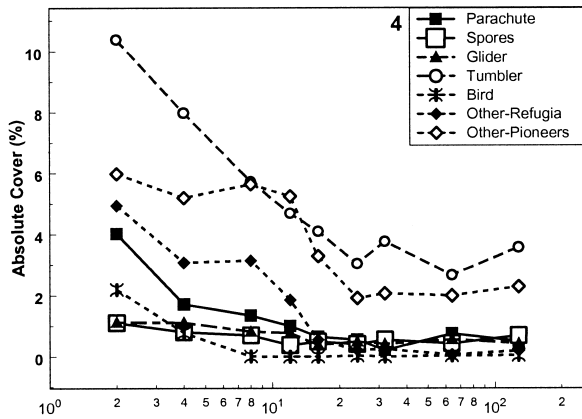
Figs. 4–5. Cover of dispersal types along transects leading from refugia. Refugia are excluded to highlight changes on transects. **4.** Absolute cover, all patterns significant by one-way ANOVA ($P < 0.001$ for parachute and tumbler species; $P < 0.01$ for spores, gliders, and other-refugia species; $P < 0.05$ for birds and other-barrens species. **5.** Relative cover. Distance axis is logarithmic.

Figs. 6–8. Distribution of species on transects leading from refugia. **6.** Parachute species. **7.** Glider and tumbler species, plus *Lupinus lepidus*. **8.** Species without special dispersal mechanisms. R = refugia. Distance axis is logarithmic.

er abundant, gradually decreased proportionately with distance, from 11 to 7%. Only the gliders *Carex mertensii* and *Cistanthe umbellata* were common beyond the 2 m. Tumblers such as *Penstemon*, *Agrostis pallens*, and *A. scabra* became proportionately more common with distance, but the overall proportion changed little. The vegetative expansion of the first two species was substantial after they established. Bird-dispersed species declined to insignificance close to refugia, reflecting the lack of attractions for birds in the barren pumice. Species found in refugia dispersed by other means declined to near zero by 32 m. Other pioneer species expanded from 6 to 29% of the totals.

Distribution of typical species—The distributions of species reflect the patterns of dispersal. The species present were drawn from among those common on the barrens. Cover of parachute species declined with distance (Fig. 6), due to low background seed rain (Wood and del Moral, 2000) and be-

cause early colonists have become senescent. They formed a very small fraction of the total beyond 32 m. Many other wind dispersed species were abundant in and immediately adjacent to refugia (Fig. 7). They all declined with distance, but not to the same degree as parachute species. *Lupinus lepidus* did not invade refugia or their margins. Though uncommon in 1997, it subsequently expanded rapidly on the Pumice Plains (Bishop, 2002). Seedling establishment has declined in recent years because safe sites have been usurped by long-lived species or have disappeared as erosion and weathering reduce the physical habitat complexity of the pumice barrens. This phenomenon helps species that spread vigorously.

Species lacking specific dispersal mechanisms tended to decline with distance (Fig. 8). *Lupinus latifolius* has a large seed, but can be dispersed over short distances by ants. Pods may sometimes tumble over land, and it could be distributed by water. It survived in some refugia and has expanded from them. The other species shown have small seeds and declined sharply at least to 32 m. They are species that might have survived in some refugia (e.g., *Luzula*) and those that somehow reached the fertile margins of refugia, from which they expanded somewhat.

*Wetlands—Floristic patterns—*The wetlands data were analyzed by NMS, which indicated that there was only one dimension of floristic change. The DCA axes were strongly correlated with distance ($r^2 = 0.47$; log-linear regression $P \ll 0.0001$), so we used distance rather than the statistical construct.

DCA identified a strong floristic gradient from the wetlands to dry uplands. The correlation between distance from 1 to 32 m and DCA-1 on each surface was significant ($r^2 = 0.84$; $P < 0.005$). Herbaceous wetland species, such as *Typha*, *Juncus* spp., *Equisetum* spp., and wetland mosses, were dominant, with scattered *Salix* spp. Though physiographically similar, the flora of these wetlands differed greatly. Unlike wetlands associated with perennial streams on the Pumice Plain, *Salix* and *Alnus* were not dominant (del Moral, 1999b). Cover of most species declined with distance from wetlands, but *Lupinus lepidus* increased substantially and upland mosses were variable from 1 to 32 m. These species, however, are unlikely to benefit directly from wetland effects. Rather, they were common throughout the area. Most other upland species displayed lower cover with distance from the wetlands. These included widely distributed parachute species such as *Epilobium anagallidifolium*, *Hypochaeris*, *Salix commutata*, *Carex mertensii*, *Juncus mertensianus*, *Castilleja miniata*, and *Anaphalis*. Many wetland species also expanded slightly beyond the wetland into plots dominated by upland species that were dry on the surface during sampling. These included *Salix sitchensis* and *Epilobium ciliatum*, which declined gradually to 16 m, *Juncus articulatus* and *Equisetum arvense*, which extended to 4 m, and mosses and liverworts found up to 2 m distant.

*Vegetation structure—*Richness declined steadily along the transect, continuing until a baseline appeared to be reached beyond 16 m (Fig. 9). Cover declined sharply beyond the wetland, but none of the sites beyond 1 m differed significantly from one another. However, when the cover of *Lupinus lepidus* and upland mosses was excluded, there is a strong pattern of decline that continued to 32 m. We excluded these widely distributed species because they do not appear to require soil
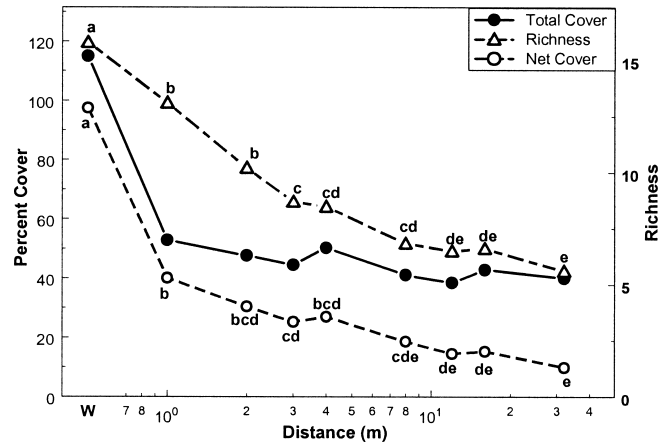

Fig. 9. Richness and cover on transects leading from wetlands. Net cover excludes *L. lepidus* and upland mosses. For each measure, differences along transects were significant (ANOVA, $P < 0.0001$). Points along a line with the same letter are not different (Bonferroni test, $P < 0.05$). W = wetland. Distance axis is logarithmic.

development on the Pumice Plain (del Moral and Jones, 2002). They, therefore, could mask facilitation effects of the wetland.

H' declined outside wetlands, suggesting that the wetland provided resources for species to reduce dominance. When mosses and *Lupinus lepidus* were excluded, the pattern was similar (Fig. 10). This pattern was reflected in D as well (Fig. 11). Both measures of structure declined with distance, and plots 16–32 m distant were less diverse than exhibited near wetlands.

*Dispersal patterns—*The pattern of dispersal types near wetlands revealed a weak effect. Species were grouped into dispersal types, with necessary additions for wetland species. Species typical of wetlands (Titus et al., 1999) were considered separately. Parachute species declined with distance (Fig. 12). Even 1 m from the wetland, upland parachute species dominated wetland ones. Wetland species declined from over 62% cover in the wetland, while upland mosses increased from zero. By 32 m, upland parachute species may have reached equilibrium.

Gliders, predominantly *Alnus viridus*, were common up to 4 m, with a spike at 16 m. Tumbler species demonstrated no clear pattern with distance (Fig. 13). Bird-dispersed species dropped to a baseline within 3 m and wetland tumbler species were uncommon from 1 m.

Species with other dispersal mechanisms included *Lupinus lepidus*, other pioneer species, and species of refugia, declined. Other species with poor dispersal found in refugia extended to 12 m at levels above background and may be enjoying facilitation from wetland effects. There does not appear to be an effect on pioneer species (Fig. 14). These patterns are summarized in terms of relative cover (Fig. 15). The proportion of most dispersal types declined with distance from the wetland due to the increasing cover of upland mosses.

The relationship among the common dispersal types found in wetlands demonstrated how parachute and glider species declined, while pioneer species increased along transects. Wetland and refuge species did not extend more than 4 m, but invading pioneers appear to have first established on wetland margins.
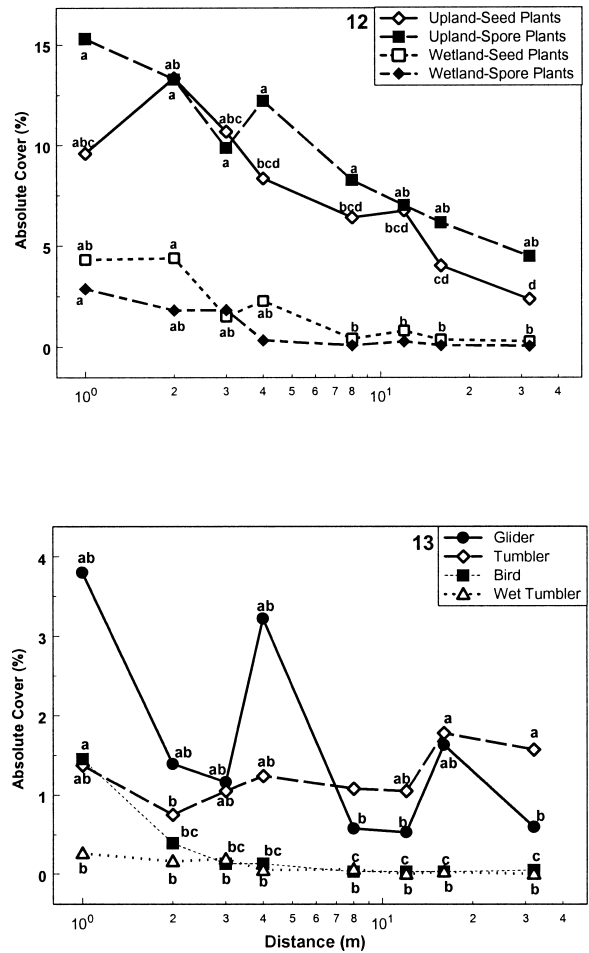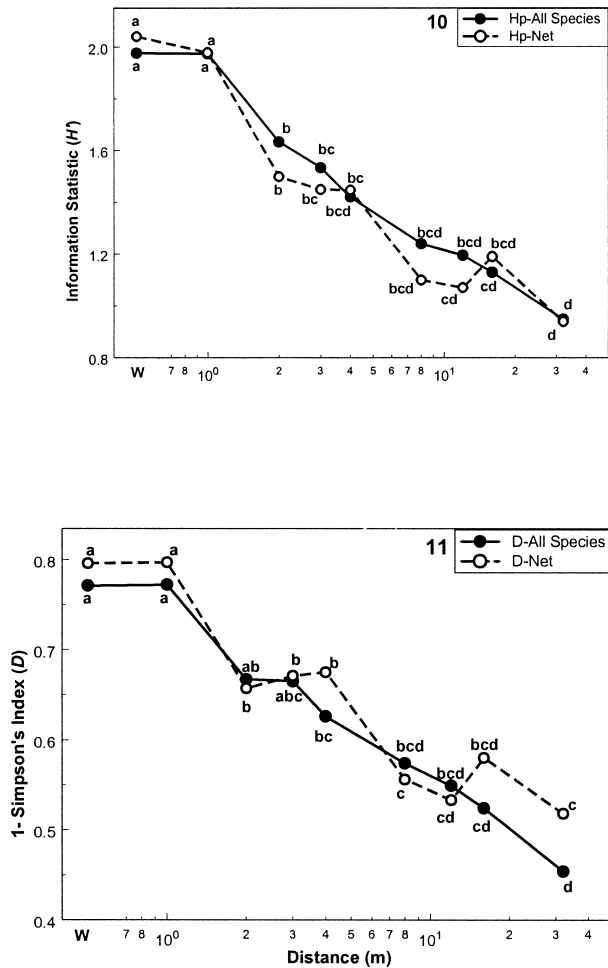
Figs. 10–11. Structure on transects leading from wetlands. For each measure, differences along transects were significantly different (ANOVA, *P* < 0.0001). Points along a line with the same letter are not different (Bonferroni test, *P* < 0.05). **10.** *H'* determined from all species and after excluding *Lupinus lepidus* and upland mosses. **11.** *D* determined from all species and after excluding *Lupinus lepidus* and upland mosses. W = wetland. Distance axis is logarithmic.

Figs. 12–13. Dispersal types on transects leading from wetlands. Points along significant lines with the same letter are not different (ANOVA, followed by Bonferroni test, *P* < 0.05). Cover in wetland not shown. **12.** Parachute species. **13.** Glider, tumbler, and bird-dispersed species. Distance axis is logarithmic.

DISCUSSION

Floristic changes—DCA—The floristic gap between refugia and barrens was sharp, which is consistent with the environmental gap. The floristic contrast between wetlands to their nearest upland sample (1 m distant) was even greater. On the barrens, the floristic gradient between samples at 2 and 32 m was 0.62 half-change, while near wetlands the same distance encompassed 1.00 half-change. The steeper floristic gradient leading from the wetlands suggests that the habitat contrast between uplands and wetlands is greater than that between refugia and pumice barrens.

The environments near refugia and near wetlands do not change significantly, yet DCA reveals that the vegetation changes gradationally. This implies that much of the immigration is linked to the refugia or wetlands. This is weak evidence that "hot spots" influence the direction of primary succession. Plants found on the margins of patches likely produced the majority of seedlings of most species found within 16 m. This effect attenuates with distance, so that beyond 32 m, invasion is dominated by species from the general seed rain.

Species composition changes—Soon after the 1980 eruption, parachute species found a suitable habitat on edges of refugia and soon produced copious seeds. This translated into relatively dense populations of parachute species (e.g., near refugia *Anaphalis, Chamerion, Hieracium, Hypochaeris*; Fuller and del Moral, 2003). In contrast, some species, including *Lupinus lepidus, Luetkea pectinata, Juncus mertensianus, J. parryi, Saxifraga ferruginea, Cistanthe umbellata*, and *Salix commutata*, have patterns that are irregular with respect to refugia. These species are more likely to have invaded from the general seed rain. *Lupinus lepidus*, in particular, established in concentrated patches over much of the Pumice Plain in areas far removed from refugia. By 2002, proportions in the barrens had changed significantly. Within 20 m of the refugia, parachute species, gliders, and tumblers declined, while pioneers increased. These patterns suggest that the advantages offered by refugia on wind-dispersed species are overcome by the slower dispersing, more persistent species.

The pattern differs subtly with respect to wetlands. Unlike the margins of refugia, wetland margins present a strongly contrasting environment to the barrens. Soils are wetter, shade is more common, and competition is more intense. The wetlands were invaded soon after the eruption, primarily by moss-
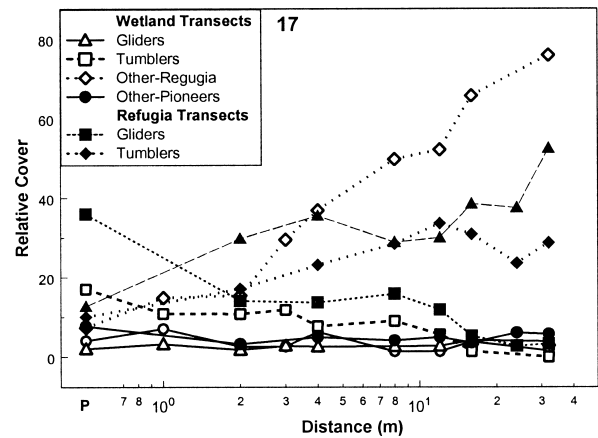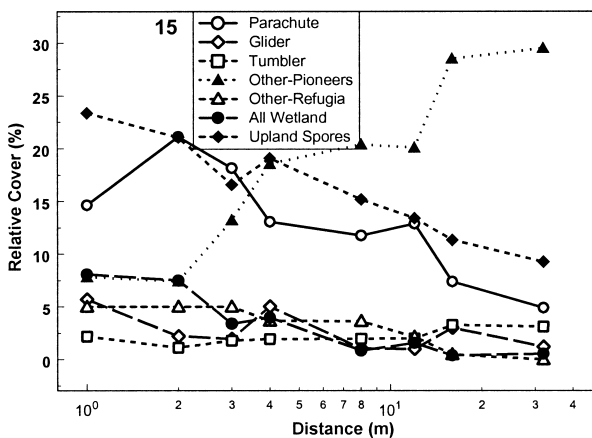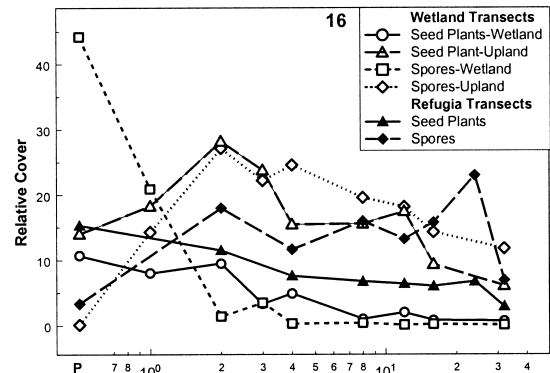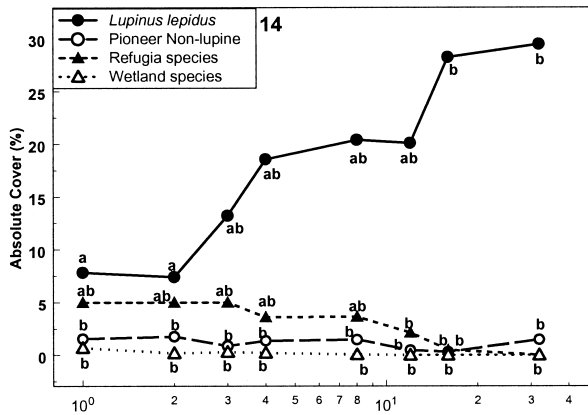
Figs. 14–15. As in Figs. 12–13. **14.** Other dispersal mechanisms. **15.** Relative cover of common types. Distance axis is logarithmic.

Figs. 16–17. Comparisons of transects from refugia with those from wetlands with respect to dispersal types. **16.** Parachute species. **17.** Gliders, tumblers, and other species. Refugia transects truncated at 32 m. P = patch (either wetland or refugium). Distance axis is logarithmic.

es, horsetails, small-seeded rushes, and some willows (Titus et al., 1999), as well as upland parachute species. Isolated wetlands did not support dense willow populations, and did not cast much shade beyond the wetland. Upland parachute species declined with respect to wetlands, reaching a baseline within 16 m. Species such as *Hypochaeris*, *Salix commutata*, and *Chamerion* were abundant near the edges of wetlands and, presumably, have expanded from these founder populations, much as parachute species have done from refugia. Gliders and tumblers were erratic with respect to wetlands. However, species with other dispersal mechanisms, such as *Luzula*, *Castilleja*, *Juncus mertensianus*, and wetland species declined regularly from peaks near the wetland. Of these species, all but *Hypochaeris* do best in moist environments. *Lupinus lepidus* increased dramatically from wetlands, suggesting that it is not benefited from wetland effects.

Dispersal-type changes—The two core habitats were dominated by different concentrations of dispersal types (Figs. 16–17). Wetlands and nearby barrens had substantially more parachute species and abundant spore plants, but parachutists were not so dominant near refugia. This effect is due primarily to the abundance of *Hypochaeris radicata* and *Salix commutata* surrounding wetlands. Spore-bearing plants were also more abundant surrounding wetlands. Wetland mosses and ferns ex-

panded to some degree beyond wetlands, while upland species were particularly common. Upland mosses increased proportionately along refugia transects because other species declined in the harsher pumice. Gliding species were relatively sparse in both samples. Tumblers were more abundant, and increased to a greater degree around refugia than wetlands. This effect may be due to the greater abundance of *Agrostis* and *Penstemon* at higher elevations and the stronger winds in the vicinity of the refugia transects. In addition, soils surrounding wetlands were derived from pyroclastic materials and are less stable than the pumice found above the refugia. This may limit the ability of these species to establish. Bird dispersed species did not extend far from the wetlands or the refugia. Species common to refugia and wetlands with limited dispersal dropped off rapidly in both cases. Pioneer species lacking obvious dispersal mechanisms increased dramatically outside wetlands, less so above the refugia. The contrasting nature of these habitats, and their contrasting landscape positions appear to translate into different types of floristic gradients around biologically rich habitats.

There also have been changes on barren sites since 1997. Parachute seed plant species declined, particularly in the more distant samples, while mosses increased dramatically. Gliders

remained a small fraction of the total, but increased in cover due to expansion by *Carex mertensii*. Tumblers did not change significantly, while bird dispersed species, though uncommon, increased slightly at more distant sites. There were no significant differences among other-dispersed species near refugia, but they have increased on the barrens. These changes were driven by increases in *Lupinus lepidus*, *Juncus parryi*, and *J. mertensianus*.

Similarity—Vegetation developed significantly between 1997 and 2002 on the barrens transects. Within 20 m of refugia, where floristic gradients are strongest, similarities between adjacent samples have increased markedly. Thus the vegetation is becoming more homogeneous. It is unlikely that this process will lead to high levels of similarity because herbaceous and low shrub vegetation responds to many variables that maintain heterogeneity. These include habitat variations (del Moral, 1993), recurrent disturbances, and localized herbivory. Increasing similarity between samples adjacent to refugia and more distant barrens implies that competitive effects and persistence of a few species are beginning to override the effects of local dispersal due to refugia. From 1997, parachute species (excluding spore bearing species) declined in absolute cover from 1.40 to 0.70%. Gliders did not change (0.45 in 1997, 0.43 in 2002), while tumblers increased from 2.00 to 3.57%. Other pioneer species increased strongly from 0.30 to 4.26%. Longer lived, larger, and more persistent species are exerting dominance over parachute species that were able to colonize barrens soon after the eruption by building up populations on refugia margins.

Structural changes—The central question of this study is whether productive sites can enhance the vegetation of their surroundings by providing an initial pulse of seedlings. Clearly both refugia and wetlands do. There are floristic gradients leading from both, and both total cover and species richness decline with distance from these patches. On the barrens, cover does not change significantly beyond 24 m, and major effects may not extend beyond 8 m. Surrounding wetlands, the effect may extend no more than 16 m. Richness near refugia and wetlands was not affected beyond 16 m.

Diversity measures confirmed the limited scope of productive site effects. H' and D both declined sharply away from refugia as the number of species declined and a few species became dominant. On the wetland, both H' and D declined sharply to the end of the transect, at values lower than the lowest on the barrens. The pattern was similar after excluding the effects of *Lupinus lepidus* and upland mosses.

Clearly, the effects of productive sites of contrasting types are weak beyond 16 m. As yet, vegetation has not developed attractions for birds at greater distances that would alter this condition. Bird-dispersed species are notably lacking from plots even 8 m from productive sites. When perches become available, we predict that community development will accelerate.

Implications—This study provides insight into the importance of remnant vegetation. While remnants serve an important function during early primary succession, their effects are indirect. Surviving species fail to invade surrounding barren sites, but refugia and wetland provide oases for the rapid establishment of species capable of long-distance dispersal. It is these pioneering species that reproduce and disperse into the surroundings. Restoration ecologists are aware of the importance of dispersal for recovery. Here, we demonstrate that over ten to 20 years, short distances from potential colonists impede establishment. There were pronounced gradients in dispersal types surrounding both a remnant habitat and new wetlands. Though they differed in detail, the effects of both habitats were limited to less than 30 m. Such limitations must be considered in planning rehabilitation or restoration and for studying the effects of landscape fragmentation. The paucity of successful invasion events in a hostile habitat also implies that migration rates of many species, in the face of global warming, may be less than anticipated by many dispersal models.

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