CHAPTER 9

The Maturation of Vegetation

A rainbow augers a nice day on the Muddy River Lahar (July, 1999).

Introduction

As communities of vegetation mature, available space becomes occupied, biotic interactions develop and species composition starts to reflect its surroundings. This chapter explores factors that driving succession on Mount St. Helens. I will explore how plant strategies change from readily dispersed, short-lived herbs to poorly dispersed, persistent perennials. The links between species composition and environmental drivers will be explored. Because the flora was meager in 1980 due to isolation and frequent disturbance, few species were able to invade barren sites. Because biotic constraints on species success were relaxed, unusual combinations of species were initially common.

Vegetation on Mount St. Helens is developing on new terrain, surrounded by exotic species not present when the volcano last erupted. A particular habitat might have supported communities like those previously found on Mount St. Helens, but the new biota and the new landscape will lead to new plant communities. It is possible that "alternative states", two or more communities found in similar habitats, have developed. Because habitats remain characterized only in general terms, and the vegetation continues to develop, there are as yet no unequivocal examples of alternative states on Mount St. Helens. I will explore this question using new methods of analysis.

Trajectories

Succession trajectories were discussed by Walker and del Moral (2003) among others. The effects of landscape, historical events and chance were ignored, or if acknowledged, it was asserted that vegetation on similar sites would eventually overcome these effects and that identical communities would emerge. Repeatable and therefore predictable interactions such as competition and tight coupling between species and the controlling environment inevitably led to same *climatic climax*. This view failed to recognize that trajectories could arrive at the same stable end-point by alternative routes (hysteresis). It did not accept that random events could produce persistent results or that new species combinations could develop. Rather, this view asserted that all trajectories converged to one predictable community.

Each pattern has been observed on Mount St. Helens. Succession on Mount St. Helens is a complex, messy network of trajectories that describe community replacement more in terms of intersecting links than as convergent trajectories. Alternative trajectories can result from many factors, including priority effects that are the result of different species establishing in similar sites. Below I provide an overview of convergence, divergence and priority effects.

Convergence. Convergence occurs in homogeneous habitats if there are a few competitively dominant species. It is more likely when general factors like the climate rather than local factors like soil control development. It is more likely when taller species dominate the landscape, creating homogeneous understory conditions. Functional groups describe species aggregated by similarities in morphological and physiological traits (Alday et al. 2011). Habitat factors can exclude species based on such functional traits. For example, only species that tolerate low nitrogen levels could survive in habitats deficient in nitrogen. However, which of a group of tolerant species tolerant actually establishes might by unpredictable. Thus, the vegetation in different parts of a particular infertile habitat may have different dominant species forming communities with similar structure and function (Clark et al. 2012).

If competition by a persistent species can eliminate pioneer species and if this species is competitively superior to others, then convergence should occur. Persistent associations then may be formed by complementary combinations. For example, a rhizomatous graminoid such as bentgrass can grow with a prostrate shrub such as partridgefoot with little adverse effect on either (Fig. 9.1). Because there may be several functionally equivalent species combinations (e.g., Merten's sedge with beardtongue), floristic convergence is not assured.

Divergence. Divergence may occur if small initial differences are exaggerated by feedback mechanisms that involve priority effects and competition. If two similar sites receive colonists that affect the site differently and change the environment in dissimilar ways, then later colonists are likely to be different as well. Local habitat heterogeneity also can produce divergence (Tsuyuzaki 2009). If broadly tolerant species colonize the habitat, they persist until more several specialized competitors, attuned to differences in the habitat, may become dominant. Once floristically homogeneous, plots would have become more variable, that is, the trajectories would have diverged.

Priority effects. Priority effects are fundamental to understanding trajectories. Each site within a homogeneous habitat may receive any of several colonists able to establish. The early arrival of one species rather than another may start local environmental changes, attract different subsequent colonists and inhibit the establishment of other species. Thus, further succession on that site may be arrested if the first colonist is a strong competitor (e.g., pinemat manzanita). Alternatively, it may be that species like pearly everlasting create a more hospitable site, allowing succession to proceed with species adapted to infertility. If that first colonist were to be prairie lupine, then yet another cascade of interactions would develop. Each case produces an alternative trajectory. Since similar habitats can produce different results, the unexplained variance in studies that compare environmental factors to vegetation may be substantial.

Fig. 9.1. *Partridgefoot and bentgrass are one example of a functionally compatible combination.*

Trajectory patterns

Each site promotes different patterns of recovery and each offers an alternative view of vegetation maturation. Here I summarize studies that explored trajectories under different conditions.

Plains of Abraham. Persistent species gradually replaced readily dispersed pioneer species. Subtle habitat variation, annual weather fluctuation and landscape effects combined to produce communities responsive to topographic variation (del Moral et al. 2012). These few pioneers established a sparse community (A) dominated by pearly everlasting, with a smattering of cat's ear, fireweed and white hawkweed. Two other pioneer communities occurred in special habitats. Lupines and sedges developed in a gully near survivors (B). Beardtongue and pussypaws joined the pioneers in a few plots (C). Pussypaws was locally common and combined with pioneers to form a transitional community (D). As grasses and low shrubs like beardtongue and partridgefoot invaded, a more developed community became prevalent (E). Three communities were common at the end of the study. One developed with willows (F). A second had a layer of mosses (G). Finally, one had the common persistent species and abundant Parry's rush (H). It is likely to be the eventual pervasive community until conifers become established.

Plots may transition from one community to another in any given year; there are no fixed successional stages. About 78% of the time, plots did not change and the time spent by a plot in a community increased with time. Transitions were marked by an increase in the persistent species, and by 2001, the pioneer communities were gone. From 1999 to 2008, there was some rearrangement among persistent communities, but most transitions were to community F (116 in 1999 to 175 in 2008) as willows expanded. Transitions followed different pathways that demonstrated divergence (from A to other communities) and net-like transitions. Much of the pattern appeared random, although the persistent communities occupy spatially distinct sites within slightly different habitat conditions.

The grid also showed significant change in the ordination analyses (DCA), but the patterns differed from conventional wisdom. At first, plots were floristically similar and most had only a few pioneer species. As they developed, once similar plots diversified. In order to highlight trajectory development, I divided the grid into 20 groups of 20 plots each and analyzed mean species composition using DCA. Trajectories for ten groups show the floristic changes (Fig. 9.2). The starting points were close together (Euclidean distance [ED] = 16.6 DCA units), but by 2010, the groups had diverged and were more than twice as distant (ED =36.2). This result also showed that vegetation developed at different rates and traversed different trajectories.

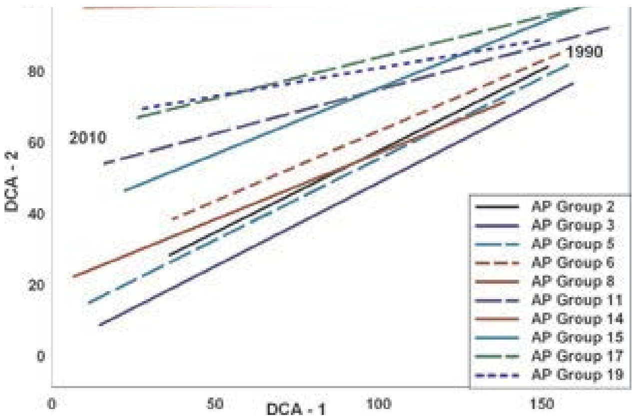


Fig.9.2. *DCA trajectories of ten representative composite plots produced on the Plains of Abraham that showed overall changes in floristic composition over 20 years. The trend suggests that the vegetation is diverging from a similar initial condition...*

Pumice zone. In order to explore trajectories, the pumice zone grid was divided into eight groups each with 16 plots. I determined trajectories of these spatial groups in floristic space and plot only starting and ending points (DCA Fig. 9.3). The trajectories in parallel, demonstrating similar floristic development. The groups initially differed by an average of 63 DCA units, while after 20 years, differences averaged 55 DCA units, a significant difference (t-test, P < 0.02). Convergence appears to be a response to the general of lupines, graminoids, beardtongue and mosses.

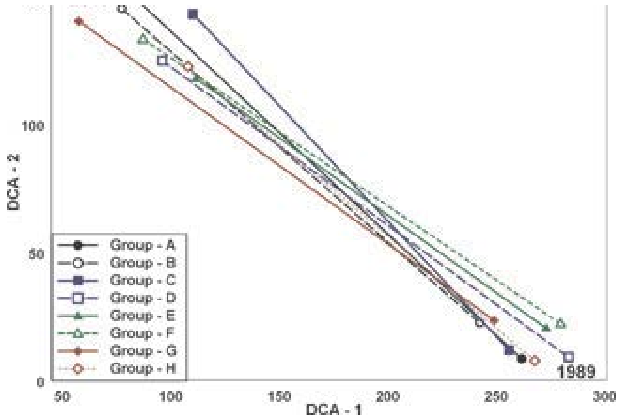
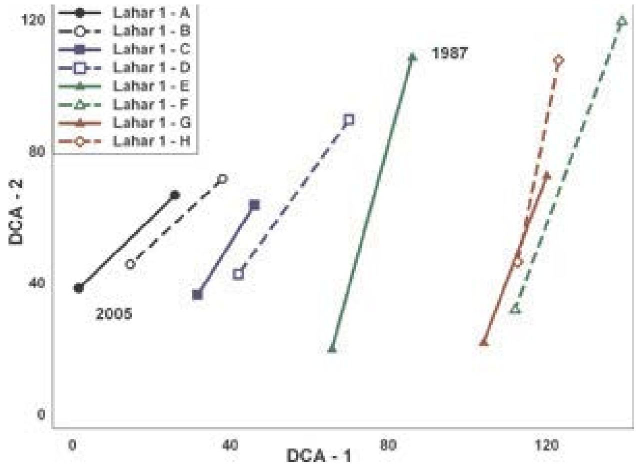


Fig.9.3 *DCA trajectories of eight composite groups in the pumice zone grid. Groups consisted of 16 contiguous plots. The starting and ending points for each group was the mean DCA position of the plots in a group.*



F**ig.9.4** *DCA trajectories of eight composite groups on the Lahar 1 grid. Groups formed as described for Fig. 9.3.*

Lahars at Butte Camp. The Lahar 1 grid presents a different interpretive challenge. Because of the distance gradient from the forest, the eight groups of 16 plots had markedly different starting and ending points (Fig. 9.4). Each moved in a similar way. Conifers were initially sparse away from the edge and common near the forest. By 2005, conifers were common throughout, but dominant near the forest. These differences produced most of the differences in DCA trajectories. The Euclidian distance between groups in a year was low between adjacent groups and increased with distance both in 1987 and in 2005. The trajectories represented unique spatial conditions on the lahar, and changes were essentially parallel.

The Lahar 2 grid provides a final view of trajectories. It was divided into eight groups of 24 plots each. The resulting trajectories show a weak divergence (Fig. 9.5). Relatively homogeneous plots became more distinct at the end of the study.

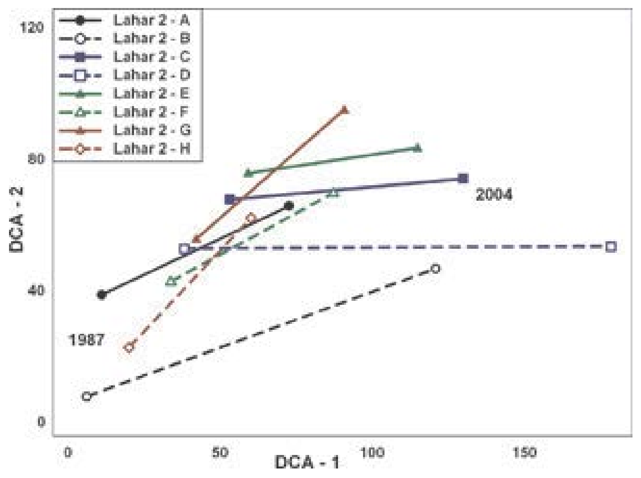


Fig.9.5. *DCA trajectories of eight composite groups on the Lahar 2 grid. Groups were blocks of 24 plots (6 by 4) distributed in a checkerboard fashion.*

Summary of divergence and convergence. The grids provided a good way to explore trajectories. Grid habitats were relatively homogeneous and their different conditions provided insights into what controls trajectories. Where strong gradients of immigration existed, there were significant differences in the initial communities. These differences persisted until the dominants have spread across the site. Then, convergence might be expected. Convergence also may occur if strong dominance develops. On the pumice zone grid, the episodic dominance of prairie lupine and the consequent abundance of mosses produced convergence. Species convergence overwhelmed topographic differences that might allow divergence. Isolated plots received essentially the same set of immigrants, so divergence was more likely. Early vegetation was composed of a few species and plots were floristically homogeneous. Over time, local environmental differences and priority effects will allow different plots to develop differentially.

Plant Strategies

Raunkiaer (1934) had developed the concept of plant life-forms over 40 years (see Appendix I. In essence, species were categorized by how they survived the harshest time of year. For example, regenerative buds always could be exposed well above the ground (taller shrubs and trees) or buried as bulbs or rhizomes. Later, Grime (1974) developed the plant strategy concept to reflect plant adaptations to the forces of natural selection. Having demonstrated that environments differ only in their degree of disturbance and their production potential, he described three primary strategies, each adapted to a one combination of conditions. Habitats may be stressed by infertility, drought or cold, or they are offer few direct constraints on productivity. Alternatively, habitats may be stable and relatively free from disturbance, or disturbances may be frequent and intense. Stressed, undisturbed habitats have selected for species that grow slowly and reproduce slowly (stress-tolerant species, S). Productive habitats that are frequently disturbed allow for species that grow rapidly and reproduce copiously (ruderal species, R). Productive, undisturbed habitats select for large, fast growing species able to occupy the available space and competing for resources (competitive species, C).

Plant strategies dominant on a site change through succession because prevailing conditions change. Grime and Pierce (2012) showed how site location is a filter that limits the available immigrants while habitat conditions select from that pool of immigrants. Other factors, such as periodic drought, may select from these species to limit the flora further. Finally, as habitats develop and conditions change, species with different traits are favored. Therefore, when plots are analyzed over time by growth-forms, life-forms or adaptive strategies, they reveal trajectories like those found when species are used. Growth-forms inform us more directly about factors that control succession.

It is difficult to obtain the data needed to categorize species by the Grime system. Instead, I classified all species with longevity, growth form, life form (Raunkiaer system), degree of clonal growth and nitrogen fixing ability. The result was 10 "functional groups." Placing species into these groups helps to assess factors that shape successional responses. If trajectories lead to different species composition, but the species reflect similar patterns of functional groups, it may be that environmental filters exist, but that they work on traits, not on species.

Pumice zone grid. Common functional groups showed distinct changes over time (Fig. 9.6A, B). By 1999, the vegetation was dominated by erect forbs (e.g., pearly everlasting) and rhizomatous graminoids. It appeared that low shrubs were destined to exert their dominance. In 2000, overall cover was still less than 5%, but most functional groups had significant cover. The system then shifted dramatically to one dominated by N-fixers (prairie lupine) and mosses. The other groups accounted for less than 10% of the total; while they continue to increase in absolute terms, their "market share" declined. It may take many years, but eventually conifers should be able to establish dominance

and the functional dominance will shift again as trees (not shown), tall shrubs and mosses become dominant.

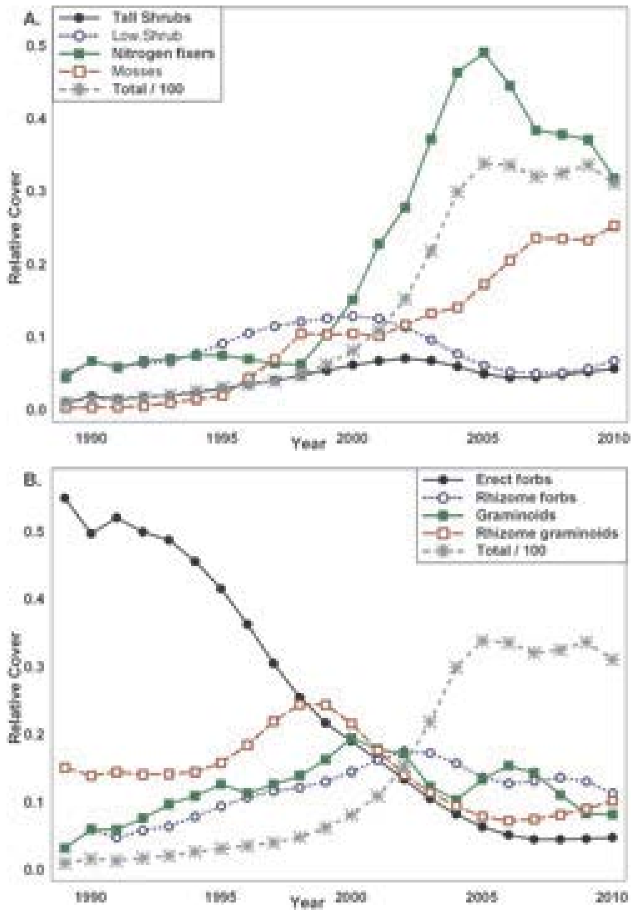


Fig.9.6. *Relative cover of functional groups on the pumice zone grid, 1989-2010: A. tall and low shrubs, N-fixers and mosses; B. erect and rhizomatous forbs, graminoids and rhizomatous graminoids. In both graphs, the total absolute cover is shown, divided by 100.*

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Lahar deposits. A similar analysis was conducted with data from Lahar 1. Plots were divided into those within 60 m (near) of the forest and over 100 m away (far) from the forest and mean composition by functional type was determined annually (Fig. 9.7). In this way, the effect of distance could be determined. Cover increased from 2.6% to 47%. Near the forest, conifers consistently exceeded 80% of the cover and other species accounted for under 20% of the cover, their values declined as tree cover stabilized by 1996 at about 85%. All other functional groups declined and remained low after 1996. The more distant plots showed a different pattern. The tree decline in 1988 was due to the jump in the rhizomatous forb yarrow. The other common groups were typically more prevalent on the far plots than on the near plots.

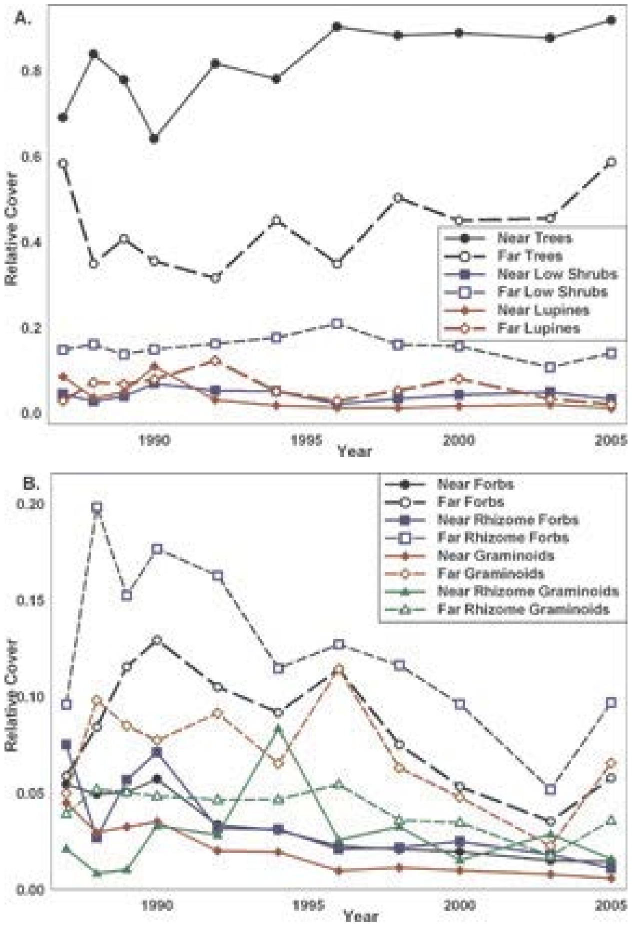

Fig.9.7. *Relative cover of functional groups on the Lahar 1 grid. The data were divided into plots near the forest and those distant: A. trees, low shrubs and lupines; B. forbs, rhizomatous forbs, graminoids and rhizomatous graminoids*

On Lahar 2, functional groups changed over the study, but these changes were in response to the pulse of N-fixing lupines in the final years of the study (Fig. 9.8). In fact, most groups simply continued to increase slowly. Because the vegetation was sparse (all functional groups were less than 4% except for lupines), competitive interactions that might shift dominance had not yet occurred.

Summary. That functional group composition changes though succession suggests that there is a premium placed upon longevity and persistence. At present, succession in isolated habitats from which all vegetation was removed by the eruption is in an intermediate successional stage where nitrogen fixers, mosses, persistent grasses and low shrubs dominate the vegetation. This analysis demonstrated that changes in functional groups do not occur without competitive interactions.

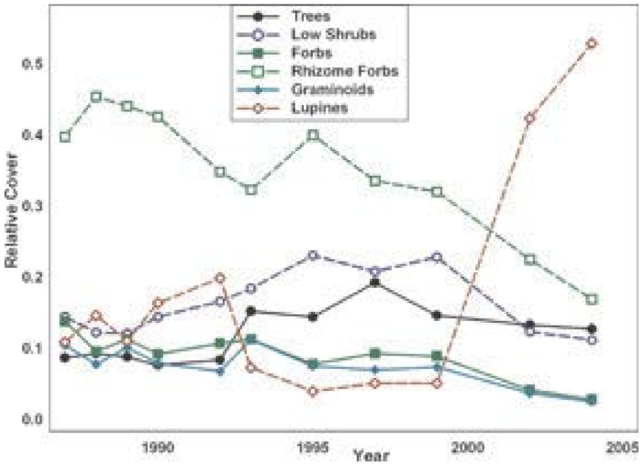

Fig. 9. 8. *Relative cover of functional groups on the Lahar 2 grid. All plots were essentially equally distant from sources of potential colonists.*

Relating vegetation patterns to the environment

Early in succession, the species of a site have wide tolerances and occur because they arrived before more adept species. They persist over an array of conditions not because they are particularly well suited, but because better competitors have yet to arrive. As vegetation develops, environment and competitive effects should provide a significant filter (Baasch et al. 2009). Thus, measures that express the relationships between species composition and the environment should strengthen.

Over the years, my colleagues and I have conducted several studies to investigate correlations between vegetation and its environment. Patterns remain weak, but trends have emerged. Initial patterns of species composition are affected by dispersal patterns, which are strongly influenced by landscape effects, accidents and chance, but not local conditions such as moisture and fertility. As the years unfold, local factors assert control over the distribution and growth of individual species, to forge ever-tighter links between the vegetation and resources. As importance of spatial factors has declined, the overall relationship has strengthened, but remained weak (Table 9.2). In this table, I note the year during which a study related "explanatory" variables to species patterns. These include the fraction of the explained variation that was either environmental or spatial in nature, the total percentage of the variation explained by these factors and the strength of the correlation with the first axis of variation.

That explained variation and the correlations were low suggests that further strengthening of the relationships will occur. In this section, I review studies that have explored this question using "direct gradient analysis," in which species composition and environmental data are compared using a method called redundancy analysis (RDA; ter Braak and Šmilauer 2007).

Wetlands. Wetlands between Spirit Lake and the lower slope of the cone were studied in 1994 (Titus et al. 1999), in 1998 (del Moral 1999b) and again 2004 (Titus unpublished). Despite different environmental data and different samples, these studies showed that local factors increasingly controlled the vegetation. In 1994, wetlands were heterogeneous; the many recognized communities had no relationship the local habitats. RDA revealed that several factors had weak relationships to vegetation, but only 19% of the variation was attributed to the predictor variables and location effects accounted for about 2/3 of this variation.

Five years later, I found that the predictability of wetland vegetation had increased. Wetland vegetation was responding to both internal factors (e.g., erosion, degree of dry conditions, water pH and water source) and geographic factors. These factors accounted for 31% of the variation between species composition and environmental factors. About 60% of the explained variation was from environmental factors and 40% from spatial factors (Fig. 9.9).

Fig. 9.9. *Wetland derived from fresh spring water, showing dominance by wetland herbs such as purple monkeyflower (July 21, 2011).*

I ran a detailed analysis of the 2004 data that suggested that willows had become a significant competitive filter. Now, over 80% of the explained variation was due to local effects related to factors like sediments and water pH. These analyses demonstrated that an increasingly tight control of vegetation by environmental factors developed, mediated by the expansion of a dense willow canopy.

Potholes. I studied potholes, those small depressions found in the pumice zone, since 1992 (del Moral 2009). Initially barren (Fig. 9.10), they have accumulated a diverse collection of species. Periodically, I have related the species composition in these depressions to their environment. Overtime, explained variation increased consistently, due to local factors; spatial factors remained unchanged. The correlation of the first axis of the analysis (*r*) increased from 0.59 to 0.77 between 1993 and 2008. The 2008 relationships are summarized in a bi-plot showing the average position of pothole vegetation grouped by communities and the vectors of significant explanatory variables. The strength of the relationship is shown by the length of the lines (Fig. 9.11). Moisture, lupine abundances three years earlier, pH, soil texture and elevation were all significant. This analysis explained 36% of the variation and of this, 63% was associated with environmental factors. Over the study, environmental factors developed from having no effect to this significant effect. Thus, it appears that predictable relationships between persistent species and their environment are developing, but remain relatively weak.

Fig. 9.10. *Typical pothole in 1992 (August 10, 1992). There were few plants and few species represented. Here, pearly everlasting and fireweed are the most abundant.*

Muddy River Lahar deposit survey. Along with Claire Muerdter and Jeremy Sandler, I described vegetation on the upper Muddy River lahar deposit in 2007 (Fig. 9.12; del Moral et al. 2009). We explored how landscape factors determined species composition. We sampled 151 plots to explore this question using RDA to determine and partition variation. Factors that best predicted species composition were elevation, latitude and degree of isolation, primarily spatial factors. Only 31.6% of the variation was related to predictor variables, indicating that the vegetation is remained dynamic, that chance factors remained important and that factors with good predictive potential (e.g., competition) remained unimportant. Landscape factors continued to dominate vegetation control (60% of the explained variation). There are strong dispersal gradients along both sides of the lahar. The elevation range of this study is large and elevation affects both dispersal and the growing season. In most plots, vegetation cover was sparse, suggesting that competition is not yet a strong factor.

Pumice Plain survey. We conducted a survey of Pumice Plain vegetation in 2002 (del Moral and Lacher 2005) intending to compare it to the 1993 survey of the same area (del Moral et al. 1995). During the earlier study, only spatial factors had been significant, and they accounted for only 15% of the variation. The 2004 survey demonstrated twice the explained variation (29%) and modest correlations to several variables. Spatial factors continued to dominate the analysis, but environmental factors now accounted for almost 40% of the explained variation. Comparison of the two analyses of vegetation on the Pumice Plain, conducted nine years apart, suggested that environmental factors, while hardly predominant, were starting to exert some control on the initial patterns established in response to landscape factors.

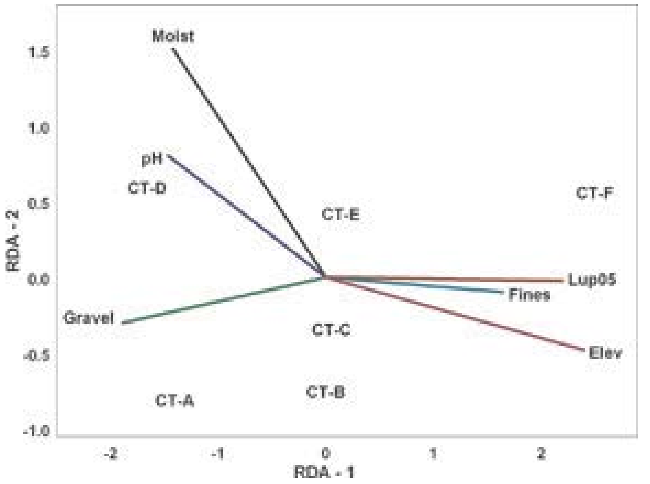

Fig. 9.11*. Graph (bi-plot) describing main results from redundancy analysis of pothole data, 2008. The vectors, starting from the 0, 0 point, run an equal distance in the opposite direction as shown. Their lengths suggest the relative importance of environmental variables. The 80 sample potholes were classified into communities, whose mean position in this space is shown. LUP05 was the concentration of lupines in 2005 and was used to indicate soil fertility. The other variables with significant explanatory value were fines, gravel, elevation, moisture and soil pH.*

Plains of Abraham grid. The vegetation on this grid remained sparse (Fig. 9.13). Weak statistical relationships between habitat variables and vegetation had developed by

2008 on this grid, but they were low (del Moral et al. 2010) and the correlation to explanatory values was only 0.57. The environmental factors used account for over 60% of this variation. Priority effects, secondary disturbances, elk grazing and seasonal fluctuations will all affect the development of this vegetation, rendering it unlikely that explained variation will become large before forests develop. Infertility is unlikely to be ameliorated because lupines occur sporadically and have never been common. For years to come, the existing vegetation is likely to persist.

Fig. 9.12. *The Muddy River Lahar deposit remained only moderately developed, but there was a strong gradient leading away from the edges (July 30, 2007).*

Fig. 9.13. *. The Plains of Abraham remains sparsely vegetated (August 17, 2009). Beardtongue and Parry's rush dominate this section of.*

Summary: environmental control of vegetation. The studies that related vegetation patterns to environmental and spatial factors yield some generalizations. Unexplained variation continues to dominate in each case, but for different reasons. When the study area is large chance reduces the link between vegetation and the environment. Priority effects, the establishment and persistence of inferior species, accentuate chance effects. When vegetation is young, competition does little to filter species. Isolation slows succession (see Chapter 8) and extends the time before competitive dominance can be achieved. Spatial gradients affect species composition across environmentally homogeneous habitats, weakening statistical relationships between vegetation and environment. At a local scale, the potential for demonstrating stronger environmental relationships to vegetation exists because all sites are equally isolated and smaller plot size meant that recorded environmental data was closely associated with the vegetation.

Novel species assemblages

If species assembly is dominated by unique events and by geographic factors that influence dispersal, then some early plant communities should be species combinations not yet observed in the Pacific Northwest. Plants from different habitats that find themselves in the same place might coexist for extensive periods before competitive factors exert control. Bruce Clarkson (1990) suggested that novel assemblages should be common in early succession because competition cannot yet enforce dominance, and many species expand into many open habitats, encountering new neighbors. Dispersal limitations can produce unique vegetation compared to sites with a dense seed rain (cf., Tagawa 1964). Novel communities may persist by virtue of a priority effect. On Mount St. Helens, the common joint occurrence on lahars and pumice of both lupine species is an example (Braatne and Bliss 1999).

There are several problems with demonstrating that novel communities exist. Communities that I suggest as being novel may exist, but have escaped notice. The best general collection of plant communities is the US National Vegetation Classification. Of 41 communities listed that could occur in the vicinity, only three were at all comparable. Many of the communities described thus far in my studies may be novel because they have not been formally recognized.

Wetland communities. Most wetland communities found in wetlands in the pyroclastic zone were dominated by Sitka willow with various associates (del Moral 1999). These communities had roughly analogous communities in the Pacific Northwest and do not strongly sustain the concept of novel communities. However, the community dominated by horsetails seems to lack a model in the region, and is a candidate for being a novel community.

Uplands. Communities were noted in several habitats for a variety of purposes, and at different scales. Reviewing classifications from the Plains of Abraham, Lahar 2, Muddy River Lahar survey and the Pumice Plain survey suggested only a few distinct communities at a scale like that used in the National Classification. All of these communities are immature and will continue to develop. However, there is a strong suggestion that the vegetation currently clothing the landscape is distinct from that in surrounding higher elevation, open habitats such as those at Mount Rainier and Mount Adams. The communities are listed in Table 9.3 by habitat with an assessment of how likely they are to be novel in this region.

On the Plains of Abraham, vegetation is poorly developed, yet succession produced several communities. The surviving vegetation is dominated by combinations of beardtongue, bentgrass, pussypaws and Parry's rush. It is very likely that this is a novel community. Lahar 2 contains some conifers, but the dominants are long-lived plants. Buckwheat in combination with fleeceflower and prairie lupine is extensive and, due to the abundant lupine, is likely to be novel. The community dominated by lupine and fleeceflower is probably novel. The Muddy River lahar deposit contained four communities. The bent grass-partridgefoot and prairie lupine-beardtongue communities are likely to be novel, while the pinemat manzanita community has analogs many regional habitats. Rock moss-lupine community occurs here and on the Pumice Plain. It probably occurs in other dry pumice desert habitats in the region. The Pumice Plain had prairie lupine with bentgrass and I could find no reference to this type, so it may be novel. I found no mention of a prairie lupine-willow community. The habitat of the pumice zone was barren, but moist, an unusual combination, so it is unlikely that the lupine-willow combination will be found elsewhere.

Although the evidence is weak, there are several candidates for novel communities Mount St. Helens. Thus, processes molding vegetation are contingent on available species, and their availability is spatially constrained. That novel communities appear to be common on Mount St. Helens suggests that community assembly within one habitat could produce several communities. The combination of a limited species pool, dispersal barriers and an immature landscape appear to lead to communities never previously observed. That these assemblages are functioning well (their species persist and reproduce) suggests that these habitats can sustain multiple options. It follows that when these communities develop fully, they should form alternative states. In the next section, I discuss this concept and explore vegetation patterns for evidence that may support their existence on this volcano.

Alternative states

Alternative states occur when two or more communities occupy a single habitat. At the scale of plots used in these studies, it is difficult to provide clear evidence either way. It is possible to demonstrate only that a given result is consistent with alternative states. Some habitats on Mount St. Helens are homogeneous over wide areas, so we should expect them to support similar vegetation throughout their extent. However, because early species assembly had a large random element and because many species have broad ecological tolerances, it is equally likely that a community would occupy multiple habitats. Over time, deterministic processes linking competition to habitats may shift dominance patterns so that only one community occurs. Below, I describe several situations that suggest that alternative vegetation types currently occupy similar habitats.

Side Bar 9.1. Danger from above, part 2 (1999)

Mountains in the Pacific Northwest spawn notorious weather. Most bad weather happens during that long stretch from September to May when we can't do plant research. Sometimes, however, these mountains conjure spectacular summer thunderstorms. Mount St. Helens, isolated from others, attracts violent storms and intensifies them. Chad Jones, Christina Wolfe and I prepared to settle into our tents after a long climb to Butte Camp and a tasty meal. We were on a broad bench around 1300 m, the old Butte to our backs and the cone stunningly beautiful in the golden sunset. Clouds were gathering in the east, so we made sure everything was secure. While Chad and I chatted, Christina snuggled into her tent. Outside, the wind picked up and soon there were raindrops. Cell phones were not then ubiquitous, and then as now, cell service was tenuous. Chad called his new wife, Elise, to touch-base and to assure her that we were safe-and-sound. Just as he said this, the first thunderclap shattered the calm. Not to close, but not too far away, either and Christina, now awake, asked if we were all right. We assured her. Chad continued his talk for a few moments…then a second clap of thunder, very loud this time, and the sky immediately flashed white. Chad's call was dropped. "Are you guys all right?" shouted a shaken Christina. "Oh, yes," I managed. Chad tried to call home several times between sheets of lightening that seemed to surround us, and the rain poured down. Each call was dropped. Finally, the storm moved on and Chad's call went through. For me, it was a very harrowing experience and Christina shared the feeling. Chad, however, claims to have had no worries…at least that's what he told Elise. I can only imagine what she went through when each tremendous explosion cut off the connection.

Most studies that have recognized alternative states on terrestrial sites have involved disturbances (e.g., fire or grazing). However, alternative states have been proposed due to dispersal limits (Chase 2003) and to complex, nonlinear interactions among dominant species and environmental constraints (Smith 2012).

I explored this question by comparing communities and habitats in several situations. Ideally, each habitat would have one community, and each community would occur in only one habitat. This is unlikely. In order to make it more difficult to reject the single state hypothesis, each example divided the vegetation samples into more habitats than communities. In this way, species variation within a habitat is more likely to be smaller than that of the communities.

Habitats were classified using only factors related to the plot; spatial factors were omitted. Communities were classified using only vascular plants, and fewer communities were recognized than in the original studies to make it less likely that alternative communities would be found. Each of these cases showed relationships between the vegetation and local environments, making it more likely that single communities in each habitat would be observed.

Muddy River lahar survey (2007). The mean similarity within communities was modest (61.5%) but that of the habitats was significantly lower (50.1%), implying that each habitat sustains vegetation more variable than that in a loosely defined community (Table 9.4). The DCA values in both dimensions are much more variable in the habitats than communities. Multiple communities appear to occur in a single habitat.

Pumice Plain survey (2004). The floristic data were combined into only six communities over the entire landscape. Twelve habitats were formed. Nonetheless, the communities were more cohesive than when these plots were clustered by habitat. The pattern persisted when variation in the DCA-1 scores was compared. There is no evidence that a habitat supports only one community.

Plains of Abraham grid (2010). The grid on the Plains of Abraham is an ideal place to find a homogeneous habitat supporting only one community. However, floristic similarity of plots in six communities was higher than that of plots in the nine habitats. Variation in the DCA scores of communities and habitats was lower than in the other analyses, suggesting limited floristic variation. The larger habitat variation indicated that these groups were not floristically homogeneous as would be expected under the one community per habitat hypothesis.

Pumice zone grid (2010). The six communities on this grid were more homogeneous than the 10 habitats, whether the assessment was by similarity or variation within a group, demonstrating that each habitat contained representatives of several communities. Variation in DCA space was significantly greater in the habitat-based groups. Again, there was no evidence to support the single community per habitat hypothesis.

Potholes (2008). In contrast to the other studies, sample area was only 4-m^2 and habitat measures included moisture and other soil factors measured in close association with the vegetation. Indeed, similarities in the five communities and in the seven habitats were substantially higher, but percent similarity in habitats remained significantly lower and more highly variable. Variation in the DCA scores was the same in both sets of data. The pothole study does not demonstrate that a single community occupies a single habitat, but it suggests that future studies of this question must define habitats in more detail.

Summary

One of the more interesting topics in the study of succession is the nature of trajectories. Does vegetation in one habitat become more or less similar as time goes on? The studies on Mount St. Helens provided conflicting answers. The answer depends on when you start the study. Initially sparse vegetation on the Plains of Abraham diverged as plots accumulated different species at different rates, and development was net-like. The overall pattern of development showed divergence in response to subtle topographic features. In the pumice zone, where the study started with more vegetation, vegetation developed in parallel, with only a slight tendency to converge. Lahar 1 was strongly affected by a dispersal gradient, leading to slower development at increasing distances. Trajectories on different parts of this lahar ran in parallel. Given several more decades, when conifers cover the lahar, these trajectories might converge. Lahar 2 displayed divergence. Thus, there is no rule that dictates convergence and vegetation patterns on a homogeneous habitat may develop in several ways.

Plant strategies demonstrate a consistent pattern. Pioneering vegetation is dominated by species able to colonize from long distances. After more than 30 years, vegetation is dominated by long-lived woody species and grasses. In most places, prairie lupines are periodically abundant and because this short-lived perennial produces copious seeds, it is persistent.

The results gleaned from vegetation patterns on Mount St. Helens fail to show close relationships between habitats and species. While it is to be expected that groups based on species composition would be more homogeneous than those based on habitats, the large disparities between the two analyses imply that similar habitats still sustain several community types. Granted, all the examples of vegetation discussed remain in flux, and it is possible close relationships will develop. At present, however, the record does not reject the proposition that alternative states of vegetation do exist in similar habitats. There is little evidence that this *condition* will change. Similarly, novel species assemblages may not persist, yet there is no evidence that they are transient. Disturbance where there is limited species richness and species recently added to the pool of available species may be expected to produce new species groups.

Table 9.1. Overall trajectories on the Plains of Abraham grid. First set is transition from nearly barren sites to intermediate development in 1999. Second set is transition from 1999 to 2008. Values are the percentage of the possible transitions and do not total 100% because in a few cases, the plot remained in the same community during the interval.

CT-90	ID	%	CT-99	ID	CT-99	ID	%	CT-08	ID
A	Pion	2.00	D	Pion-PuPa-PaRu	D	Pion-PuPa-PaRu	1.00	F	PeCa-SiWi-BeGr-PaFt
A		52.75	E	PeCa-PaFt-PuPa-Pion-BeGr	D		0.50	G	PeCa-PuPa-BeGr-Moss
A		24.75	F	PeCa-SiWi-BeGr-PaFt	E	PeCa-PaFt-PuPa-Pion-BeGr	1.00	F	PeCa-SiWi-BeGr-PaFt
A		7.50	G	PeCa-PuPa-BeGr-Moss	E		14.00	G	PeCa-SiWi-BeGr-PaFt
A		7.00	H	PuPa-PeCa-PaRu-BeG	E		27.25	H	PuPa-PeCa-PaRu-BeGr
B	Lupine	1.50	E	PeCa-PaFt-PuPa-Pion-BeGr	F	PeCa-SiWi-BeGr-PaFt	1.25	E	PeCa-PaFt-PuPa-Pion-BeGr
B		0.50	F	PeCa-SiWi-BeGr-PaFt	F		3.75	G	PeCa-PuPa-BeGr-Moss
B		0.50	H	PuPa-PeCa-PaRu-BeGr	F		0.50	H	PuPa-PeCa-PaRu-BeGr
C	PeEv-PuPa	0.75	E	PeCa-PaFt-PuPa-Pion-BeGr	G	PeCa-PuPa-BeGr-Moss	1.00	E	PeCa-PaFt-PuPa-Pion-BeGr
C		0.25	G	PeCa-PuPa-BeGr-Moss	G		2.75	F	PeCa-SiWi-BeGr-PaFt
D	Pion-PuPa	0.75	E	PeCa-PaFt-PuPa-Pion-BeGr	G		1.00	H	PuPa-PeCa-PaRu-BeGr
D		0.25	H	PuPa-PeCa-PaRu-BeG	H	PuPa-PeCa-PaRu-BeGr	0.50	F	PeCa-SiWi-BeGr-PaFt
					H		1.75	G	PeCa-PuPa-BeGr-Moss

Code: Pion = mix of pioneer species (see text); Lupine = prairie and broadleaf lupines; PeEv = pearly everlasting; PuPa = pussypaws; PaRu = Parry's rush; PeCa= Cardwell's penstemon; PaFt = partridgefoot; BeGr = bentgrass; SiWi = Sitka willow; Moss = rock moss and juniper moss.

Table 9.2. Summary of studies of the relationship between explanatory data and vegetation patterns. The study areas are described in the text. The correlation coefficient (*r*) describes the relationship between the explanatory variables and the pattern of the vegetation samples in the first axis of variation. The explained variation is the percent of the total variation in the species data that is related to the explanatory data. The variation explained by spatial and environmental factors, respectively, generally exceeds this total because some variation is attributed to both kinds of variation. The contribution of each was adjusted to be a percentage of the total explained variation.

Site	**Year**	**Spatial (%)**	**Environment (%)**	**Explained (%)**	***r***
Wetlands	1994	68.7	30.3	19.5	0.750
	1998	39.1	60.9	32.2	0.856
	2004	10.2	89.8	41.1	0.829
Potholes	2001	59.6	40.4	29.7	0.650
	2006	29.8	70.2	29.6	0.770
	2008	37.1	62.9	36.0	0.774
Muddy Lahar	2007	59.9	40.1	31.6	0.899
Pumice Survey	2002	60.8	39.2	29.1	0.688
Pumice Grid	2010	48.5	51.5	27.6	0.844
Plains of Abraham	2008	38.5	61.5	15.0	0.570

Table 9.3. Community types recognized in several habitats of Mount St. Helens at a scale comparable to that used in the National Vegetation Classification.

Name	**Location**	**Novel**
Pearly everlasting-fireweed-cat's ear	Plains of Abraham	ephemeral
Pearly everlasting-pussypaws-bentgrass	Plains of Abraham	likely
Penstemon-bent grass-pussypaws	Plains of Abraham	very likely
Buckwheat-knotweed-prairie lupine	Lahar 2	likely
Prairie lupine-knotweed	Lahar 2	likely
Bent grass-partridgefoot	Muddy River	likely
Prairie lupine-penstemon	Muddy River	likely
Broadleaf lupine-penstemon	Pumice Plain	possibly
Prairie lupine-willow	Pumice Plain	very likely

Table 9.4. Summary of comparisons between communities (CT) and habitats (HT) in five sets of data. Vegetation data were clustered floristically or by habitat and examined by mean floristic similarity in each type, variation (SD) of similarities and variation of DCA-1 and DCA-2 scores (SD). * indicates that HT values are significantly less similar or more variable than the comparison CT score, based on a t-test (P < 0.05)

Characteristic	Muddy Survey	Pumice Survey	Plains of Abraham	Pumice Grid	Potholes
CT Mean Similarity (%)	61.5	59.96	64.99	65.29	62.35
HT Mean Similarity (%)	50.1*	35.7*	52.52*	47.67*	55.47*
CT Mean SD (%)	12.02	15.5	10.78	11.62	10.48
HT Mean SD (%)	17.1*	22.1*	12.55	16.49*	13.07*
CT DCA-1 Mean SD (%)	33.64	31.48	21.92	30.76	43.90
HT DCA-1 Mean SD (%)	50.6*	53.58*	28.57*	41.61*	40.01
CT DCA-2 Mean SD (%)	27.88	34.84	22.01	23.05	30.22
HT DCA-2 Mean SD (%)	34.61*	35.63	28.26*	27.98	28.17

Sample sizes: Muddy Survey, CT = 7, HT = 10; Pumice Plain Survey, CT = 6, HT = 12; Plains of Abraham Grid, CT = 6, HT = 9; Pumice Grid, CT = 6, HT = 10; and Potholes, CT = 5, HT = 7.