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Posteruption Arthropod Succession on the Mount St. Helens Volcano: The Ground-Dwelling Beetle Fauna (Coleoptera)

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10.1 Introduction

Arthropods are important components of ecosystems because of the roles they play in pollination, herbivory, granivory, predator–prey interactions, decomposition and nutrient cycling, and soil disturbances. Many species are critical to the structure and functioning of their ecosystem, although some (particularly insects) are considered pests in farmlands and forests because of their detrimental effects from feeding on foliage and transferring pathogens to trees and crops. Arthropods also constitute a high-protein prey resource for vertebrate wildlife (especially small mammals, birds, reptiles, and amphibians), thus contributing to the existence and stability of these wildlife species. As such, studies of arthropod population dynamics and changes in species assemblages following natural disturbances are important for understanding ecosystem responses. In the case of the Mount St. Helens volcanic eruption, studies of arthropods not only can provide information on natural history and ecology of many different species but also are relevant for evaluating theories of disturbance ecology and postdisturbance successional processes.

The 1980 eruption of Mount St. Helens provided researchers with an opportunity to test a wide range of theories concerning the structure and functioning of ecosystems. In particular, the existence of a continuum of disturbance intensity across a large landscape made possible a suite of comparative studies that evaluated the influence of different levels of volcanic disturbance on the survival and initial recolonization patterns of plants and animals. For example, researchers to date have documented the survival and reestablishment of a number of plant species and described the patterns and rates of vegetation successional processes of the disturbed ecosystems (see Lawrence, Chapter 8, this volume; Antos and Zobel, Chapter 4, this volume; Dale et al., Chapter 5, this volume; del Moral et al., Chapter 7, this volume; and references therein). In addition, numerous faunal studies have quantified the eruption's impacts on survival and subsequent short-term responses of small mammals (Andersen 1982; Andersen and MacMahon 1985a,b; Adams et al. 1986a; Johnson 1986; MacMahon et al. 1989; Crisafulli et al., Chapter 14, this volume), birds (Andersen and MacMahon 1986), amphibians (Karlstrom 1986; Hawkins et al. 1988; Crisafulli and Hawkins 1998; Crisafulli et al., Chapter 13, this volume), and arthropods (Edwards et al. 1986; Sugg 1989; Edwards and Sugg 1993; Crawford et al. 1995; Sugg and Edwards 1998; Edwards and Sugg, Chapter 9, this volume).

Information collected on the fauna and flora of Mount St. Helens during the past 20 years facilitates the analysis of recolonization patterns in the context of two ecological theories: relay successional processes (MacMahon 1981) and the intermediate-disturbance hypothesis (Connell 1978). The term relay succession refers to the sequential replacement of species (plant and animal) in an ecosystem recovering from some form of disturbance. This process typically begins with species that either survived the disturbance or immigrated to the site shortly thereafter. Some of these species are well adapted to the disturbed conditions of the site and can greatly increase in abundance, whereas others are poorly adapted and become locally extinct. Biotic interactions (competition, predation, herbivory, and parasitic and disease infections), coupled with abiotic factors (extremes of temperature or moisture), often determine the success or failure of each species survival. Through time, as different species colonize the site, they alter the environment's characteristics (e.g., plant regrowth provides shade, cools soil surface temperatures, increases soil moisture and organic matter, and provides substrate for fungi and vegetation for herbivores). As the environmental conditions change, new opportunities are created for additional species to colonize and dominate, eventually replacing established species that have become competitively inferior in the altered environment; hence, the "relay" of species during postdisturbance succession. This process applies to both plant and animal species assemblages and inherently involves complex interactions among plants and animals (MacMahon 1981).

The second theory, the intermediate-disturbance hypothesis (Connell 1978), addresses the patterns of species richness across a gradient of disturbance. The theory predicts that both undisturbed sites and sites suffering severe, frequent, or large-scale disturbances should have fewer species than sites subjected to “intermediate” levels of disturbance intensity, frequency, or areal extent. The theory is based on the assumption that, in undisturbed sites, certain species are dominant because of their superior competitive abilities and exclude less-competitive species, thereby depressing overall species numbers. On severely disturbed sites, only a few species are capable of surviving in the disturbed environment; and the higher frequency, intensity, or spatial extent of the disturbance resets or arrests the successional process, thereby also depressing species numbers. Under intermediate levels of disturbance, species elements of both undisturbed and disturbed species assemblages would be present on a site, thereby exhibiting a greater composite number of resident species. Hence, over a range of disturbance intensities, frequencies, and/or sizes, the predicted pattern of species richness would be approximately bell shaped, with a peak in species numbers at the intermediate disturbance level (see Figure 1 in Connell 1978, p. 1303). Although intuitively attractive, the intermediate-disturbance hypothesis appears to apply in only limited situations (see Mackey and Currie 2001), suggesting that further testing of the theory is warranted.

The purpose of our study of the Mount St. Helens ground-dwelling beetle assemblages was to assess and analyze the posteruption successional processes with this taxonomically and ecologically diverse group of arthropods. Ground-dwelling beetles were selected for four reasons:

- By examining the *ground-dwelling* species, we can study species inhabiting a similar substrate (the ground’s surface) common to all the sites impacted by a volcano’s eruption. (Such is not the case with *plant-dwelling* arthropod species in forests and clear-cuts, because plants in some of these sites were totally removed by the eruption.)
- Beetles as a group are fairly well known taxonomically and can, in most cases, be readily and reliably identified to the species level.
- Ground-dwelling beetles are abundant and easily sampled with passively operating pitfall traps.
- Beetle assemblages not only comprise a taxonomically diverse group but also contain members of a wide variety of trophic groups (predators, herbivores, granivores, fungivores, scavengers, carrion feeders, dung feeders, parasitoids, etc.).

This last factor allows us to analyze the posteruption development of beetle trophic composition across the disturbance gradient of the Mount St. Helens region. Finally, previous research has shown that arthropods can have significant influences on successional processes on Mount St. Helens (Fagan and Bishop 2000; Bishop 2002), suggesting that further studies on the composition and temporal changes of the beetle assemblages would be of value for understanding the overall pattern of succession on the volcano.

Our specific goals for the study were to (1) describe the ground-dwelling beetle assemblages in the context of both taxonomic and trophic composition for sites previously supporting forested and clear-cut habitats on the Mount St. Helens volcano; (2) compare these beetle assemblages across the disturbance gradient from the highly disturbed Pumice Plain near Spirit Lake to the undisturbed sites well outside the eruption-affected area; (3) examine the temporal changes in species composition and abundances to ascertain the rate and extent of species turnover (relay succession) on different sites; (4) evaluate the disturbance-intensity component of the intermediate disturbance hypothesis with respect to the beetle assemblages; and (5) describe and compare the trophic composition of the beetle assemblages through time and across the disturbance gradient of the volcano. Our study ran from 1987 to 2000 and thus, when coupled with the extensive work on ground-dwelling arthropods from 1981 to 1985 by Edwards and Sugg (see Chapter 9, this volume), portrays a nearly complete record of change at Mount St. Helens.

10.2 Study Areas and Methods

The sampling sites for this study were located within the Pacific silver fir (*Abies amabilis*) zone, ranging in elevations from 1040 to 1175 m (Franklin and Dyrness 1973). The region had a long history of forest harvesting and had become a mosaic of clear-cuts, replanted forest stands of even-aged trees, and old-growth forest stands. As such, the study was designed to examine the succession of ground-dwelling beetle assemblages within areas that, just before the eruption, had been either standing old-growth forest or young-aged (∼15-year-old) clear-cut plantations. Study sites were selected that were of comparable elevation, slope, aspect, and (for clear-cut sites) age since the most recent harvest and replanting. Seven study areas were chosen (Figure 10.1), representing two states of preeruption conditions (forested or clear-cut) and four levels of volcanic disturbance: (1) a single site within the pyroclastic-flow zone on the Pumice Plain located between the pediment slopes of the volcano and the newly formed shore of Spirit Lake (Figure 10.2a,b); (2) two sites within the tree blowdown zone: a clear-cut area in the Smith Creek watershed and a previously forested site near Norway Pass (Figure 10.2c,d); (3) two sites within the tephrafall zone (a clear-cut area and a forested site, known locally as the Hemlock Forest area; Figure 10.3a,b); and (4) two reference sites (a clear-cut and a forested site) unaffected by the volcanic eruption and located on Lonetree Mountain, about 40 km north-northeast of Mount St. Helens (Figure 10.3c). [See also Crisafulli et al. (Chapter 14, this volume, Table 14.1) for quantitative measures of vegetation and abiotic characteristics of these study sites.]

Within each study area, 10 arthropod pitfall traps were installed to sample the ground-dwelling beetle assemblages.

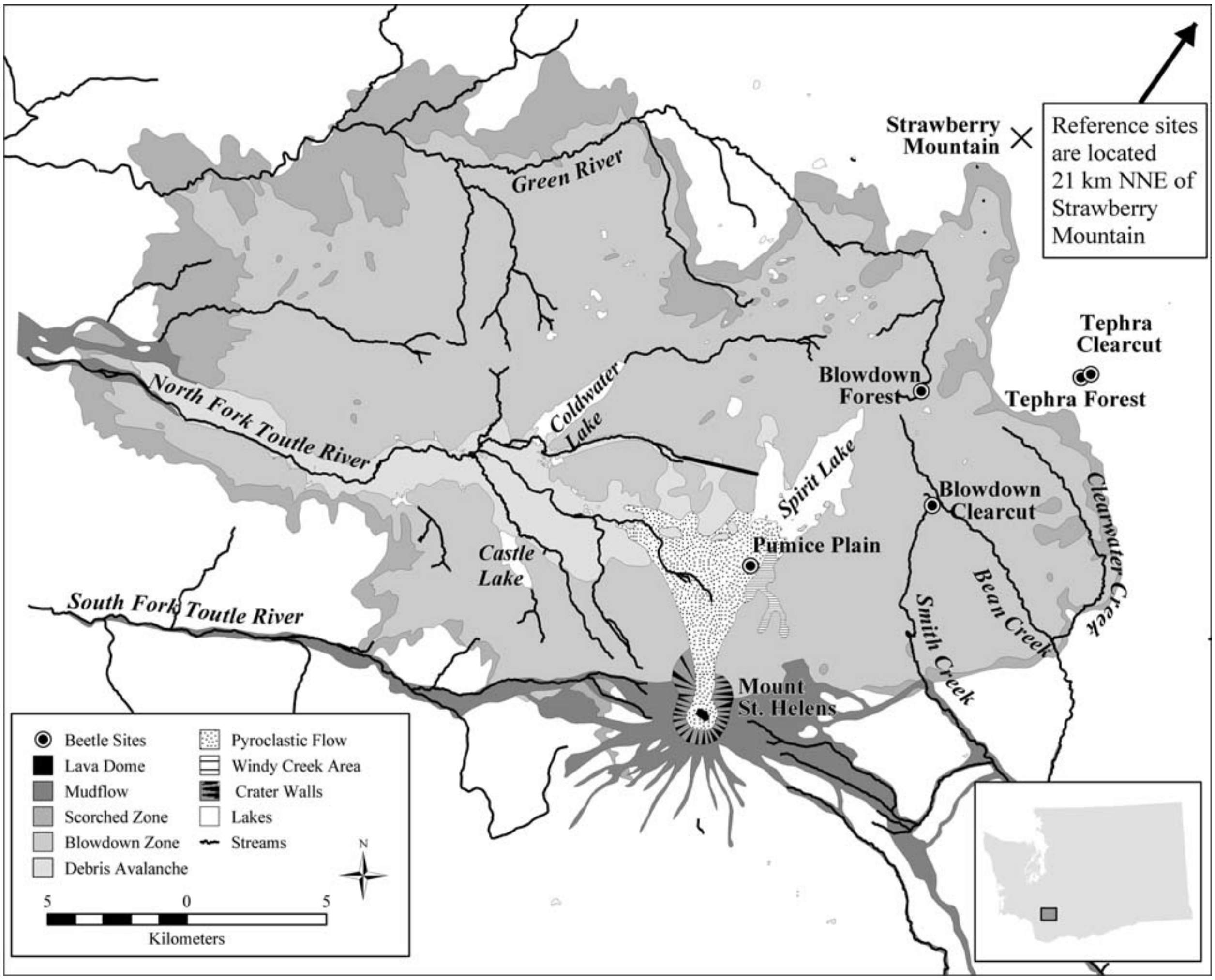

FIGURE 10.1. Locations of study sites within the Mount St. Helens eruption zone.

Traps consisted of metal cans or plastic cups inserted into the ground so that their tops were flush with the soil surface. A second plastic cup filled with propylene glycol was placed inside the trap; this fluid served to preserve captured arthropods, but also prevented freezing or evaporation. Traps were placed at 10- to 15-m intervals across each study area. Traps were opened in the spring (late May to mid-June, depending on time of snowmelt), left open continuously between sample collection times, and closed in autumn at the end of the growing season. Arthropods were collected from the traps in July, August, September, and October of 1987, 1990, 1995, and 2000. All arthropods were preserved in 70% ethanol, transported to the laboratory, sorted, identified, and counted. Species identifications were made by G. Parsons at Michigan State University, and series of voucher specimens are archived in the Division of Arthropods, Museum of Southwestern Biology, University of New Mexico, Albuquerque.

Once the beetle species from each site had been identified and counted, the beetle assemblages of the different study areas were compared with a similarity index that produced percentage similarities of species composition between pairs of study plots. The similarity index (S) was calculated as

$$S_{1,2} = [a/(a + b + c)] \times 100$$

where $a =$ the number of species common to both sites 1 and 2, $b =$ the number of species unique to site 1, and $c =$ the number of species unique to site 2. These paired similarity indices were assembled into a resemblance matrix for each sample year (1987 to 2000) to evaluate patterns of similarity among the study areas and through time.

Patterns of beetle species relay succession on the study sites were evaluated by plotting the mean number of individuals per species collected on each site through time and comparing the temporal abundances of each species. If relay succession was occurring on the sites, then a series of species replacements would be expected in the disturbed study areas, and this phenomenon would be more pronounced in the more heavily disturbed areas of the volcano. For these analyses, we only used

FIGURE 10.2. (a) Northward view of the Pumice Plain study site in 1987, showing the bare tephra/pumice-covered substrate in the foreground and Spirit Lake in the background. (b) Southward view of the Pumice Plain in 2000, with Mount St. Helens in the background. Note the dense cover of lupines and other forbs and grasses; the *white squares* are the rain covers of the arthropod pitfall traps. (c) Norway Pass (blowdown forest) study site in 1986, illustrating the symmetrical patterns of logs from the old-growth forest leveled by the blast wave of the eruption. (d) Norway Pass study area in 2000. Note the surviving Pacific silver firs (*Abies amabilis*) as well as the settling of the logs into the soil's surface.

the most common species (i.e., those with large sample sizes) to reduce the chance of including apparent random extinctions and recruitments caused by small sample sizes [e.g., pseudoturnover, as denoted by den Boer (1985)].

Finally, to evaluate the trophic structure of the beetle assemblages among the study areas and through time, the proportion of species belonging to five general trophic groups was determined. Those groups were predators, herbivores, omnivores, fungivores, and scavengers. These proportions were then compared across the disturbance gradient and over the time of the study (1987 to 2000). The predicted successional pattern was one of increasing importance of herbivores and fungivores through time as the disturbed sites recovered and as vegetation and decomposing litter (leaves and wood that provide substrate for fungi) became more abundant. Concomitantly, the more heavily disturbed sites would have relatively higher proportions of predators and scavengers in the early posteruption years when compared to the reference areas because of the lack of vegetation resources for herbivores and fungivores. Trophic-group assignments for each species were based on natural history information contained in Arnett and Thomas (2001) and Arnett et al. (2002) and references therein.

10.3 Results and Discussion

10.3.1 The Beetle Assemblages of Mount St. Helens

During this study, we collected 27,074 beetles representing 279 species and 39 families (Table 10.1). The most species rich families included the rove beetles (Staphylinidae, 75 species), ground beetles (Carabidae, 40 species), "click" beetles (Elateridae, 24 species), round fungus beetles (Leiodidae, 21 species), and weevils (Curculionidae, 18 species); the

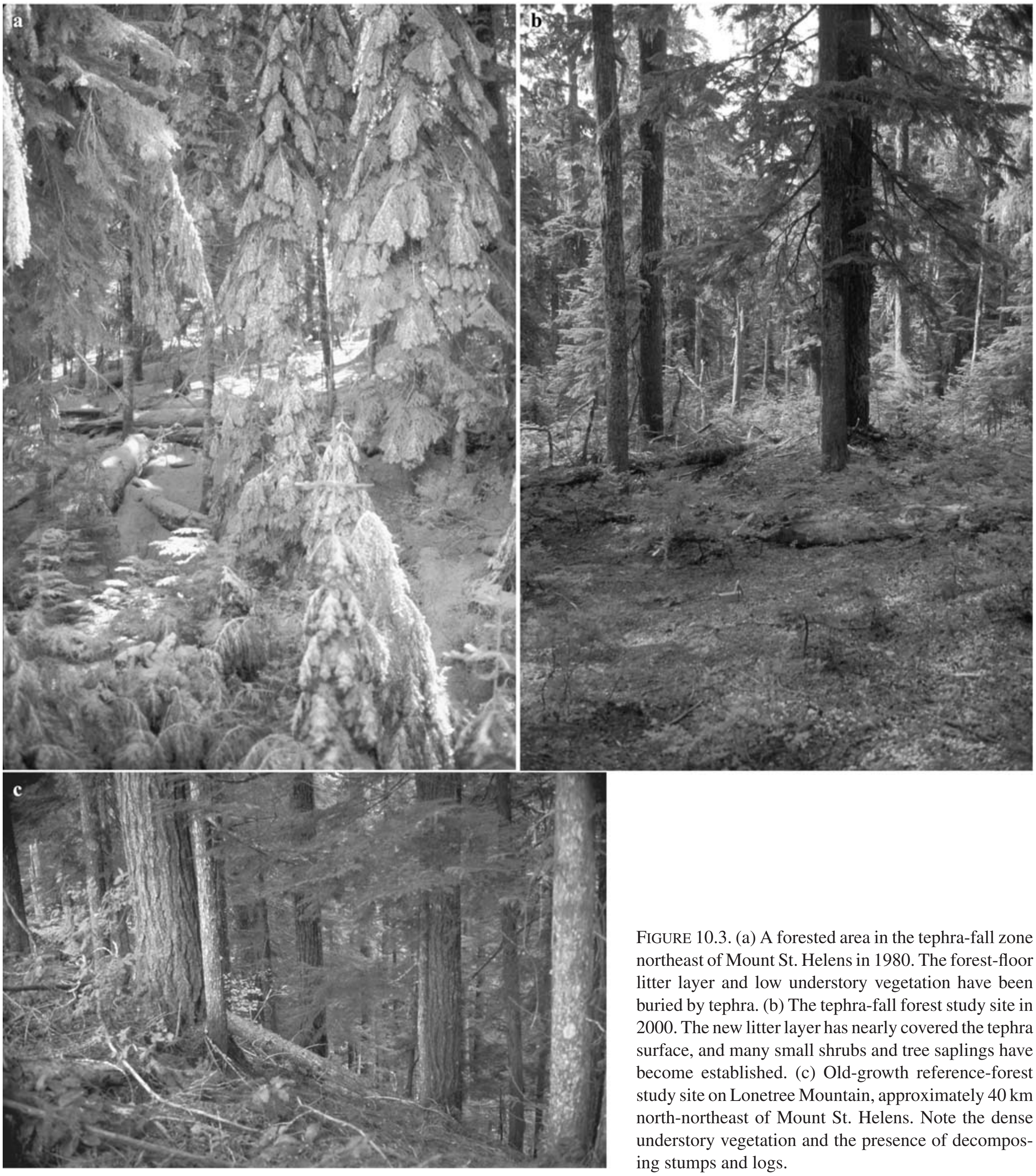

FIGURE 10.3. (a) A forested area in the tephra-fall zone northeast of Mount St. Helens in 1980. The forest-floor litter layer and low understory vegetation have been buried by tephra. (b) The tephra-fall forest study site in 2000. The new litter layer has nearly covered the tephra surface, and many small shrubs and tree saplings have become established. (c) Old-growth reference-forest study site on Lonetree Mountain, approximately 40 km north-northeast of Mount St. Helens. Note the dense understory vegetation and the presence of decomposing stumps and logs.

178 species from these 5 families comprised 64% of all the species collected. In the sample, 16 families were represented by only a single species. It should be noted at the outset that pitfall traps would not be expected to capture all beetle species living on the study areas, particularly those species that typically live on upper layers of vegetation (e.g., shrubs and trees); hence, many of the rarer species in our data set were likely the result of accidental captures of individuals during short

Table 10.1. List of the 39 beetle families (with numbers of species, totaling 279) sampled on the study sites at Mount St. Helens from 1987 to 2000.[a]

Family	Number of species
Agyrtidae	2
Anthicidae	1
Bothrideridae	1
Byrrhidae	8
Cantharidae	2
Carabidae	40
Cerambycidae	6
Chrysomelidae	6
Coccinellidae	7
Corylophidae	1
Cryptophagidae	13
Cucujidae	1
Curculionidae	18
Dermestidae	1
Derodontidae	1
Elateridae	24
Endomychidae	2
Eucnemidae	1
Lampyridae	1
Latridiidae	5
Leiodidae	21
Lycidae	1
Melandryidae	2
Melyridae	1
Mordellidae	1
Nitidulidae	8
Oedemeridae	1
Ptiliidae	1
Salpingidae	1
Scarabaeidae	6
Scraptiidae	2
Scydmaenidae	6
Silphidae	1
Staphylinidae	75
Tenebrionidae	2
Throscidae	4
Trachypachidae	2
Trogossitidae	1
Zopheridae	2

[a] The complete data set for this study can be found on the Mount St. Helens National Volcanic Monument web page: http://www.fsl.orst.edu/msh/.

periods of activity on the ground surface. Nonetheless, most of the common families and species of beetles collected during the study were typical ground-dwelling taxa and would have been appropriately sampled with the pitfall traps.

A comparison of the total numbers of beetle species collected on each site during each year is shown in Table 10.2. Note that no samples were collected from the tephra-fall sites in 1987 because of extensive trap disturbances by elk. (*Cervus elaphus*) Several patterns are apparent in Table 10.2.

First, although the sampling effort was consistent among years, the 1987 sample yielded considerably fewer species (99) than the samples from later years (145 to 169 species); this difference even extended to the reference forest and clear-cut sites, indicating that some widespread phenomenon was responsible. The period from 1984 to 1987 was characterized by unusually dry summers (following the wet El Niño period of 1982 to 1983), and this dry period may have had a cumulatively negative effect on the beetle fauna. In addition, this drought may have had an influence on other faunal groups in the region; for example, MacMahon et al. (1989) reported a decline in small mammals during 1987 compared to the years from 1983 to 1986.

Second, in comparing the beetle species-richness values of the paired forest/clear-cut sites within each disturbance zone, we noted little consistent difference in the numbers of species; in some years, we found more species in the forests, while in other years we collected more species in the clear-cuts. Only the tephra-fall sites exhibited more species in forests than in clear-cuts in every year.

The third pattern that emerges in Table 10.2 is that the most disturbed site, the Pumice Plain (a former forest buried in the debris avalanche of the eruption), supported fewer species after 1990 than did most of the forested sites.

The fourth pattern is the apparent lack of species accrual between 1990 and 2000; none of the sites showed an increase in beetle species numbers during this decade. The numbers of beetle species per site collected during 1990 to 2000 varied from 26 to 84, but no obvious trend in the number of species was observed.

Finally, with respect to the intermediate-disturbance hypothesis, the Mount St. Helens eruptions of 1980 essentially provided a single event that created a disturbance-intensity gradient from the crater outward for tens of kilometers. As a result, we could examine the intermediate-disturbance hypothesis only in the context of this disturbance intensity because there was no range of disturbance frequencies (there was only one cluster of eruptions during the period) nor range of disturbance patch size (just one volcano with one large patch). Moreover, we did not conduct any sampling between 1980 and 1986. At that point, what we did was to test for disturbance intensity across the disturbance gradient. These constraints notwithstanding, in the early posteruption years, we expected to find more species on the sites subjected to intermediate disturbances (the tephra-fall and blowdown sites) than on the more-disturbed or less-disturbed sites (i.e., the Pumice Plain and reference sites). Such a pattern was observed in 1987 for the blowdown sites versus the other sites, but these numerical differences diminished in later years as the site vegetation recovered. The tephra-fall sites failed to exhibit consistent increases in species relative to any of the other sites. Thus, from these results, we conclude that, during the period from 1987 to 2000, there was only weak evidence in support of the intermediate-disturbance hypothesis. Given the limitations of this study, however, a more pronounced species pattern, perhaps more consistent with the intermediate-disturbance hypothesis, may have existed on Mount St. Helens shortly after the 1980 eruption, and it could have dissipated by the time we started conducting our study in 1987.

TABLE 10.2. Numbers of beetle species collected on the study sites at Mount St. Helens from 1987 to 2000.

Year	Study site							
	Reference forest	Reference clear-cut	Tephra-fall forest	Tephra-fall clear-cut	Blowdown forest	Blowdown clear-cut	Pumice Plain	Total species
1987	17	16	—	—	53	38	31	99
1990	62	50	50	36	60	84	52	169
1995	40	43	46	26	48	45	37	145
2000	60	36	45	29	51	62	41	169

10.3.2 Successional Patterns of the Beetle Assemblages

In examining the abundances of particular beetle species on the disturbed plots, we found considerable evidence of relay successional patterns through time. Beetle species that were abundant in 1987 on the Pumice Plain and on sites within the blowdown zone were often absent or greatly reduced in number by 2000. Comparative-abundance graphs for some of the common species on the Pumice Plain (Figure 10.4) and in

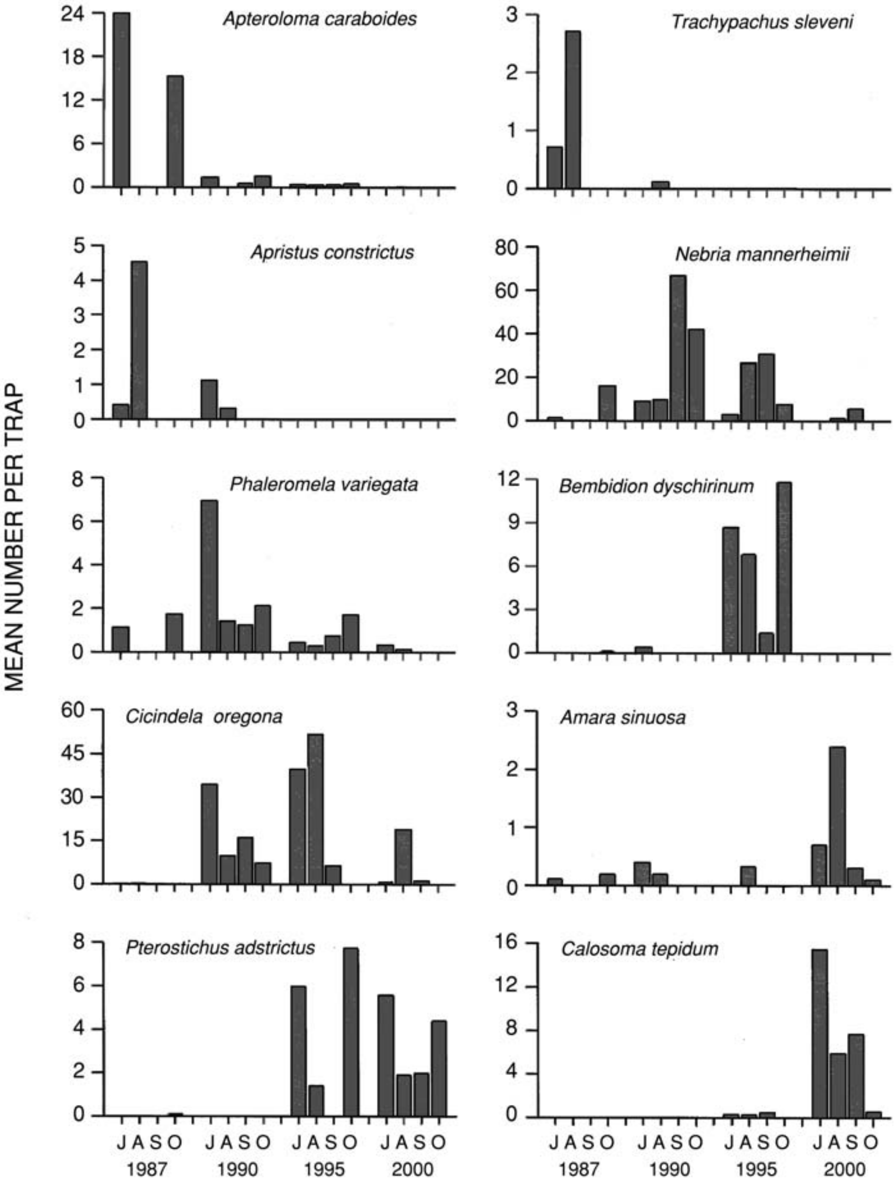

FIGURE 10.4. Temporal changes in the abundances of common beetle species on the Pumice Plain study site from 1987 to 2000. Species are sequentially replaced through time (relay succession). Sample dates reflect the beetles collected during the 4- to 5-week period before the date; J = July, A = August, S = September, and O = October. Note that the scale changes in the abundance axes.

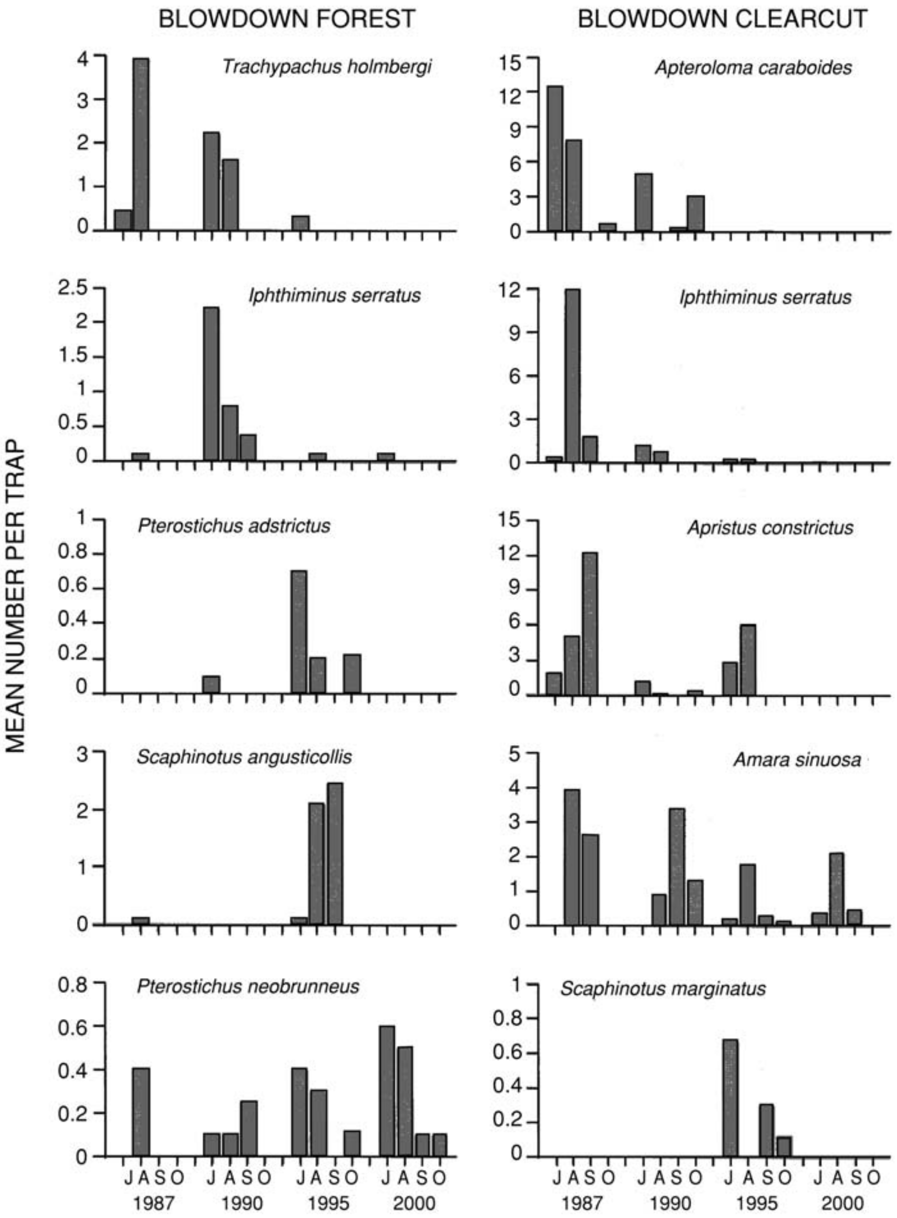

FIGURE 10.5. Temporal changes in the abundances of common beetle species on the two blowdown-zone study sites from 1987 to 2000. Species are sequentially replaced through time (relay succession). Sample dates reflect the beetles collected during the 4- to 5-week period before the date; J = July, A = August, S = September, and O = October. Note that the scale changes in the abundance axes.

the two blowdown-zone sites (Figure 10.5) illustrate this phenomenon. Edwards and Sugg (Chapter 9, this volume) documented 30 species of beetles on the Pumice Plain from 1981 to 1985, of which *Apteroloma caraboides* and *Apristus constrictus* were among the dominants (see Figure 9.5). These species were still common on our Pumice Plain study site in 1987, but became less abundant in 1990 and had nearly disappeared by 2000. Similarly, the various species of *Bembidion* observed by Edwards and Sugg (Chapter 9, this volume) on the Pumice Plain had been replaced by other *Bembidion* species, particularly *B. dyschirinum*. We also noted the appearance of new species at different times on the Pumice Plain; the carabid ground beetles *Nebria mannerheimii* and *Pterostichus adstrictus* appeared in large numbers in 1990 and 1995, respectively. Populations of the tiger beetle (*Cicindela oregona*) virtually exploded between 1990 and 1995, becoming one of the most abundant predatory beetles on the Pumice Plain. Similarly, the caterpillar hunter beetle, *Calosoma tepidum*, became highly abundant between 1995 and 2000, coincident with the large increase in herbaceous plant cover and the increase in moth caterpillar larvae (Fagan and Bishop 2000; Bishop 2002). Thus, the pattern of relay succession was well evidenced in the beetle species of the volcanically disturbed landscape.

In analyzing the patterns of the beetle assemblages among the study sites through time, we compared the percentage species similarities in all paired combinations within each sample year (Table 10.3). From these computations, the impacts of the different levels of volcanic disturbance become

TABLE 10.3. Similarity coefficients and numbers of shared beetle species among study sites across the Mount St. Helens disturbance gradient from 1987 to 2000.

	Reference forest	Reference clear-cut	Tephra-fall forest	Tephra-fall clear-cut	Blowdown forest	Blowdown clear-cut	Pumice Plain
1987							
Reference forest	—	14			9	12	0
Reference clear-cut	4	—			15	17	2
Blowdown forest	6	9			—	34	17
Blowdown clear-cut	6	8			23	—	23
Pumice Plain	0	1			12	13	—
1990							
Reference forest	—	32	56	24	23	20	11
Reference clear-cut	27	—	32	34	29	26	17
Tephra-fall forest	40	24	—	25	26	22	15
Tephra-fall clear-cut	19	22	17	—	23	22	23
Blowdown forest	23	25	23	18	—	41	30
Blowdown clear-cut	24	28	24	22	42	—	26
Pumice Plain	1	15	13	12	26	28	—
1995							
Reference forest	—	22	32	22	22	18	8
Reference clear-cut	15	—	22	17	21	19	8
Tephra-fall forest	21	16	—	26	25	17	6
Tephra-fall clear-cut	12	10	15	—	16	16	7
Blowdown forest	16	16	19	10	—	33	15
Blowdown clear-cut	13	14	13	10	23	—	22
Pumice Plain	6	6	5	4	11	15	—
2000							
Reference forest	—	37	38	24	28	16	4
Reference clear-cut	26	—	37	25	26	20	7
Tephra-fall forest	29	22	—	35	30	19	5
Tephra-fall clear-cut	17	13	19	—	23	15	4
Blowdown forest	24	18	22	15	—	19	8
Blowdown clear-cut	17	16	17	12	18	—	16
Pumice Plain	4	5	4	3	7	14	—

Upper-right portions of matrices show percentage species-similarity values; lower-left portions show numbers of shared species.

clear. Table 10.3 is arranged to show increasing levels of disturbance from left to right (reference forest through Pumice Plain). In all the sample years, percentage similarity in beetle species composition also declines from left to right, indicating lesser similarity in species with increasing disturbance level. For example, in 1987, the Pumice Plain had no beetle species in common with the reference forest, and the most similar beetle assemblage was found on the blowdown clear-cut site (23%). Similar patterns are seen in later years. As expected, the reference forest has the highest similarities with the tephra-fall forest (see Table 10.3). The sites in the blowdown zone have many species in common with both the reference sites and with the Pumice Plain, but, as described above (Table 10.2), the blowdown-zone sites did not consistently have an overall total species number in excess of the other sites.

The other pattern of interest in Table 10.3 is the inconsistent progression in similarity from 1987 to 2000 among the sites. If successional processes during this period had allowed the sites to substantially recover from the eruption disturbance, we would have expected to see a pattern of increasing similarity between the disturbed sites and the reference sites. In the most favorable example, the reference-forest and blowdown-forest comparisons yielded values of 9%, 23%, 22%, and 28% from 1987 to 2000. However, such was not usually the case; for example, similarity percentages between the reference forest and the tephra-fall forest in 1990, 1995, and 2000 were 56%, 32%, and 38%, respectively. Even the Pumice Plain showed little directional change in relation to the reference forest, fluctuating from 0% similarity in 1987 to 11%, 8%, and finally 4% in subsequent years. So, we conclude from these analyses that, although the sites were clearly changing through time in a relay successional fashion, their beetle assemblages after 20 years of posteruption recovery were still not comparable to their presumed preeruption species composition. This pattern was obviously produced by the differences in site characteristics (vegetation, soils, and microclimate) that have resulted from site-specific successional processes and by the fact that we would not expect convergence of all the beetle assemblages until all the sites have developed similar habitat attributes (i.e., old-growth coniferous forest, such as that existing on the reference sites).

10.3.3 Trophic Structure of the Beetle Assemblages

As described earlier, the ground-dwelling beetle fauna on each site consisted of a large number of species, and these assemblages were made up of a wide variety of species feeding on an even wider variety of food items. The success of any species in surviving and reproducing in their environment depends upon (among other things) finding sufficient food resources. In the harsh environment of the Pumice Plain immediately after the 1980 eruption, only scavenger and predator species could survive on the aeolian rain of dispersing arthropods (Edwards and Sugg 1993; Sugg and Edwards 1998) because other food resources (e.g., plants or fungi) were not present. However, as plants slowly established in the disturbed areas, herbivorous arthropods began recolonizing as well, followed by other predators, fungivores, and carrion and dung feeders (taking advantage of carcasses and dung of mammals and birds).

In an effort to view the succession of the beetle assemblages from a functional-role perspective, we analyzed our beetle data set with respect to the trophic groups represented within each site's assemblage. We considered only five broad categories: predators, herbivores, omnivores, fungivores, and scavengers. Although the dietary habits of some species were either speculative or unknown, the majority of the species has reasonably well-known food preferences and could thus be classified into one of the five categories (Arnett and Thomas 2001; Arnett et al. 2002).

In comparing the trophic structure of the ground-dwelling beetles in the forested sites (Figure 10.6), we found that, between 1990 and 2000, the trophic structure remained relatively stable in the reference forest. In this site, predators (mostly Carabidae and Staphylinidae) dominated the assemblage, with fungivores being the second most common trophic group (fungi were abundant on the decaying logs and litter of the old-growth forest floor). Herbivores, omnivores, and scavengers made up a relatively small proportion of the assemblage. The tephra-fall forest exhibited greater change in trophic structure, with increases in herbivorous and omnivorous beetle species and a decrease in predators, fungivores, and scavengers. The blowdown-forest site showed a relatively stable trophic structure through time. This site was characterized by large numbers of decomposing logs with abundant fungi (e.g., the coral tooth mushroom, *Hericium abietis*) and a variety of polypores, which presumably contributed to the large percentage of fungivorous beetles found on this site (see Figure 10.6).

In the clear-cut sites and on the Pumice Plain site (Figure 10.7), notable differences in beetle trophic structure existed between the levels of disturbance, and some proportional change occurred between 1987 and 2000 (species numbers also increased markedly; see Table 10.2). The reference clear-cut, much like the reference-forest site, was dominated by predators and fungivores; the blowdown clear-cut, having less decomposing woody debris than the blowdown forest (see Figure 10.2c,d), was dominated by beetle predators, herbivores, and omnivores instead of fungivores (compare Figures 10.6 and 10.7). The Pumice Plain beetle trophic structure was dominated by predators but did show an increase in herbivores (from 6 to 10 species) and omnivores (from 4 to 11 species) between 1987 and 2000; this observation corresponds to the increase in herbaceous vegetation during this same period (see Figure 10.2a,b). Hence, the beetle trophic structures of the study areas on and around Mount St. Helens corresponded well with the predicted patterns, based on the availability of food resources (plants, fungi, and other arthropod prey species).

It is interesting to note that the patterns observed in the beetle trophic groups on Mount St. Helens correspond to the posteruption observations made on another volcano, Krakatau, during the late 19th and early 20th centuries. A Dutch naturalist, K.W. Dammerman, studied the successional patterns of plants and animals after the Indonesian volcano exploded in 1883 and noted that, among the animals, the "first [to] come [are] those animals that subsist upon refuse—chiefly vegetable debris, but sometimes also animal waste [carrion and dung]; then come omnivorous species, equally undiscriminating as to their food; the true herbivorous species follow later, while the predaceous animals and the parasites are the last to settle" (Dammerman 1948, p. 201).

10.4 Conclusions and Lessons for the Future

In total, our study found that the patterns of ground-dwelling beetle recolonization and succession on the volcanically disturbed sites were consistent with predicted patterns from relay successional theory, with individual species being sequentially replaced through time as the environmental characteristics of each site changed. The beetle assemblages exhibited predictable patterns of similarity across the landscape, with the least similar assemblages being at opposite ends of the disturbance gradient. Trophic structures of the assemblages also conformed to predicted patterns based on the available food resources of the sites. The major pattern that did not wholly concur with predictions was that from the intermediate-disturbance hypothesis; we did not consistently observe a greater number of beetle species on sites subjected to intermediate volcanic disturbance when compared to undisturbed or severely disturbed sites. Finally, from our analyses of the first 20 years of posteruption recovery, it appears that the beetle fauna of the disturbed sites bears little resemblance to that of the undisturbed (reference) forested and clear-cut sites and that considerable development of the beetle assemblages will be occurring in future decades.

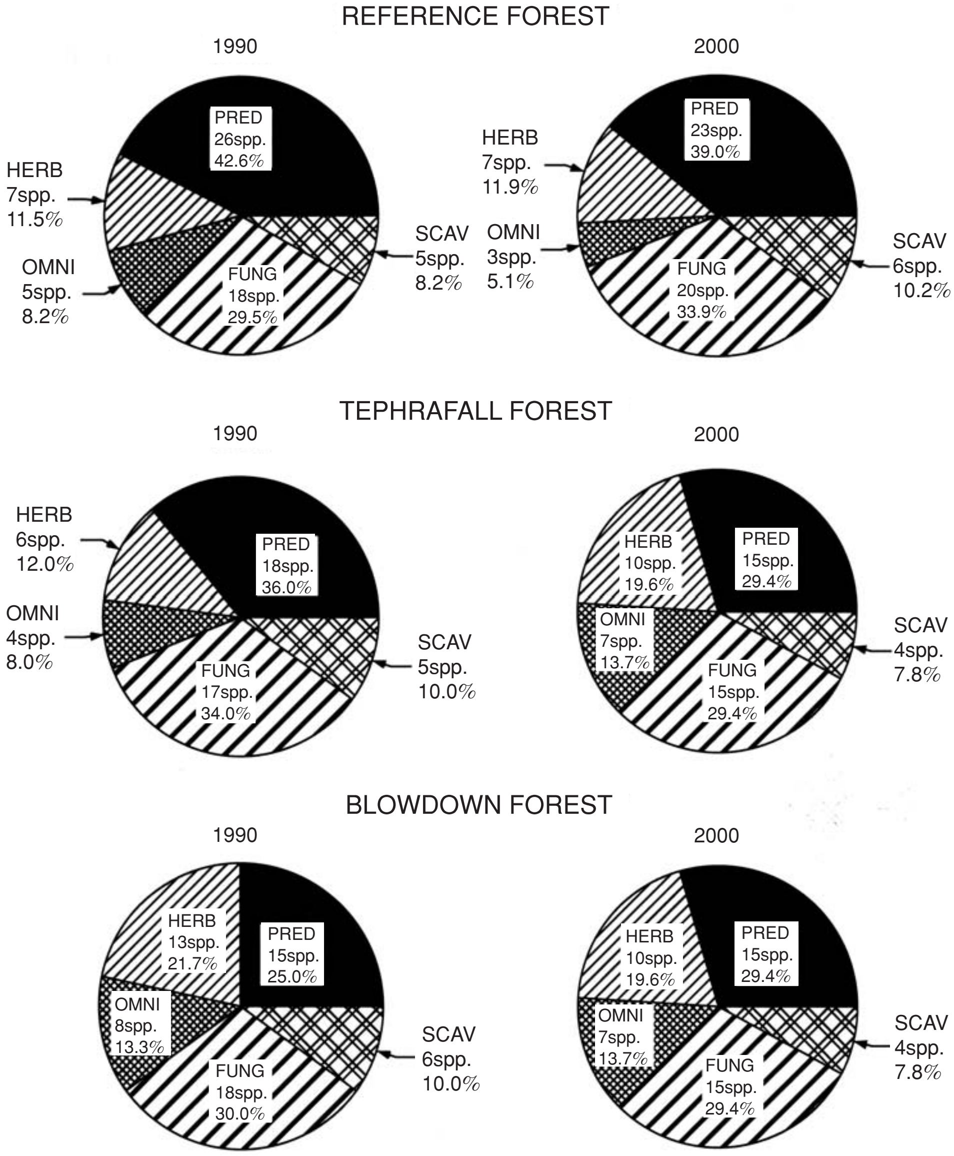

FIGURE 10.6. Comparisons of beetle-community trophic structure among forest sites in 1990 and 2000. The beetle community in the reference-forest and blowdown-forest sites remained relatively stable during this time, while the tephra-fall forest's beetle community exhibited a small shift toward herbivores and omnivores.

A final question is: What might future changes in the beetle assemblages look like? In the absence of further large-scale disturbances (more eruptions, fire, and anthropogenic development), the various sites on Mount St. Helens will likely continue to progress toward a forested ecosystem (presumably similar to the preeruption forests on the volcano). During this successional process, each site's biotic and abiotic characteristics (vegetation composition and structure, soil development, litter, and microclimate) will possibly converge in similarity, thus providing a more homogeneous forested landscape conducive to domination by forest beetle species. This successional process will proceed at different rates and time steps for the variously disturbed sites. Although the beetle assemblages of forests and clear-cuts in the tephrafall and blowdown zones might converge with the reference sites within several decades, the areas on the Pumice Plain may require centuries to attain a forest assemblage.

In addition to the need for appropriate habitat characteristics for successful establishment, different beetle species have varying capabilities of dispersal and will exhibit differences in their abilities to immigrate to areas of suitable habitat. Although many species are strong fliers and can easily move from distant source populations, others are poor fliers or are completely ambulatory, while still others are polymorphic for wingedness. These latter species may need to await the development of continuous suitable habitat corridors or archipelagos of habitat islands through which the beetles could safely disperse.

Clearly, beetles form a species-rich and trophically diverse group of animals that will play important roles in the successional processes on disturbed areas of Mount St. Helens. The 279 beetle species identified from the pitfall traps in this study represent only a fraction of the total number of beetles that inhabit the area. Many more undoubtedly live higher up

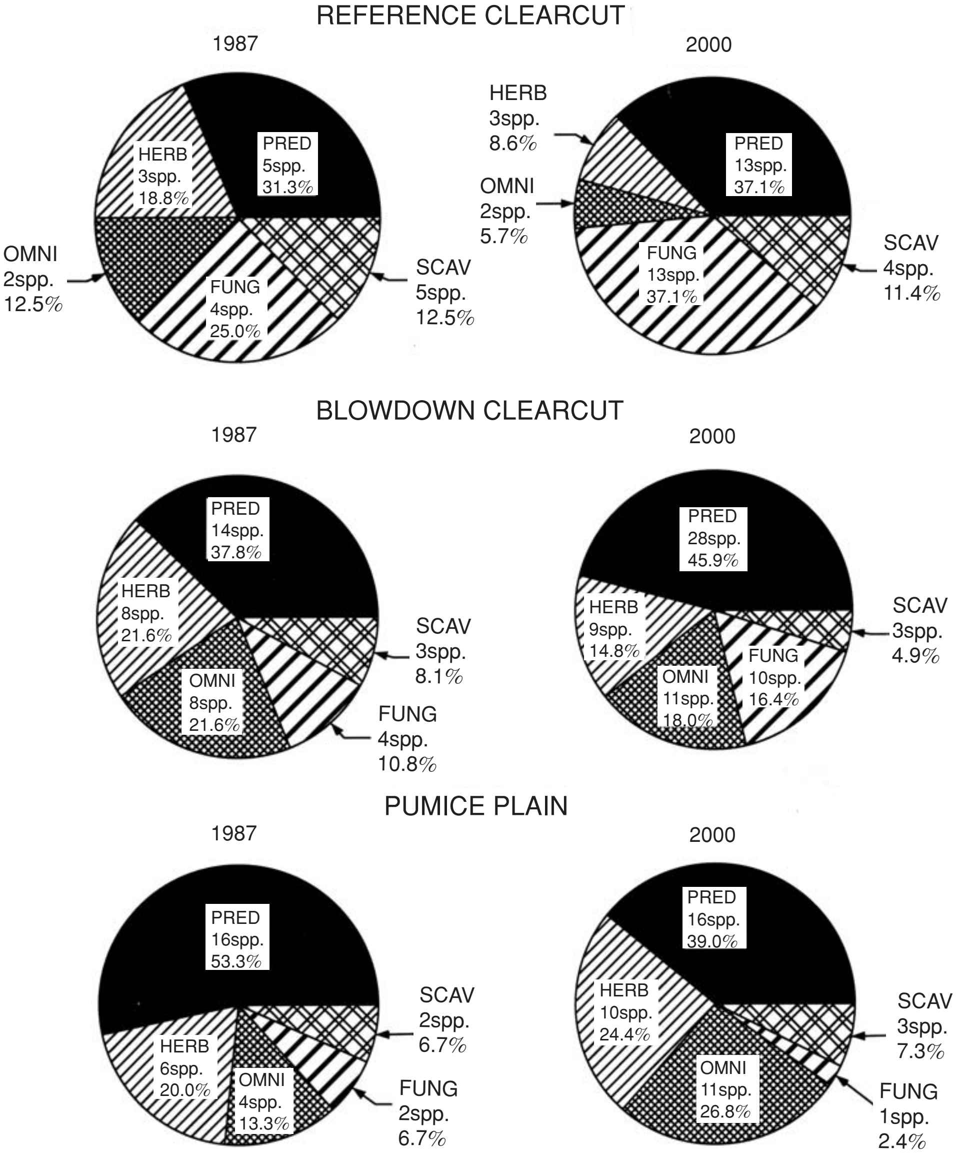

FIGURE 10.7. Comparisons of beetle-community trophic structure among the clear-cuts and the Pumice Plain site in 1987 and 2000. Herbivores and omnivores on the Pumice Plain site increased from 1987 to 2000.

in vegetation and in specialized microhabitats that we did not sample. These species will continue to influence ecological processes through their activities of herbivory, predation, nutrient cycling, pollination, soil disturbance, and dispersal of fungal spores. These activities, in turn, may prove critical in determining the rate of each site's succession, the pathways of successional trajectories, and perhaps even the species composition of other taxa (plants and animal) in the later successional stages. Future studies on these important and conspicuous beetle groups, and other arthropod taxa, will undoubtedly provide valuable insights into the ecosystem responses to the 1980 eruption of Mount St. Helens.