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# ARTHROPODS AS PIONEERS: RECOLONIZATION OF THE BLAST ZONE ON MT. ST. HELENS

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## INTRODUCTION

My aim in this essay is to present a view of the recolonization of the blast zone on Mt. St. Helens from the perspective of the arthropods—the insects, spiders, and relatives. I hope to show that special features of these small animals, in particular their size and their mobility, underlie their expertise as pioneers. Paul Colinvaux (1984) has eloquently set the context for our studies of recolonization:

Mt. St. Helens set part of the clock of Holocene climatic change back to zero. It gave us bare land closely comparable to the bare land left by glaciers ten thousand years ago in that same place. So we can study the arrival of plants [and animals—J.S.E.] and the development of habitat...in a climate we know.

The eruption did much more than create bare land. With the aid of the prevailing wind, it showered a vast area with tephra—finely pulverized rock. The immediate biological impact of the tephra shower was widespread and diverse, both on land (Keller 1982) and in water (Edmondson 1984), but over most of the fallout area plants and animals seem to have returned to business as usual. It is in the blast zone, to the north of the breached crater, on bare mineral surfaces of diverse topography and texture, that the most cataclysmic effects occurred. Five years later the blast zone appears much as it did as the eruption subsided, a vast desert. That inhospitable area will be the focus of what follows.

The eruption may be seen as a major biological and economic catastrophe within the brief time scale of human civilization, but on the broader time scale of the indigenous flora and fauna, it was merely one more event in a sequence around the Pacific "Rim of Fire." The history of the Pacific Northwest has been marked by

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numerous episodes of volcanic activity superimposed upon the changing landscape of glacial advance and retreat. Retreating ice, floods, earthquakes, mud slides, and forest fires have all left in their wake bare land for animal and plant colonists and opportunists, hardy immigrants to barren ground. Indeed, the biota of Mt. St. Helens itself was still recovering from its last major perturbation, the eruption of 1800, when the most recent explosion occurred (Lawrence 1938). The plant and animal species that are returning to the mountain's slopes have seen it all before; for them, as species, it was no unique event, and our studies of colonization must take this into account.

For the biologist, however, there is a significant uniqueness to the eruption of Mt. St. Helens: it is the first opportunity proffered by nature to follow at close hand the events and the underlying mechanisms that form the leitmotif in a saga spanning ten thousand years or more. It is certainly not the first eruption to attract biological attention: Krakatau, Katmai, and Surtsey, for example, have contributed much to the literature of volcanic biology, but St. Helens is the first eruption that has not required expeditionary logistics, for it is in our backyard, and can be monitored closely.

## THE UNIQUENESS OF ARTHROPODS AS COLONISTS

Why study arthropods\*\* on the volcano when forests and elk herds are the most conspicuous non-human victims of the catastrophe? The answer may be partly that it is a matter of taste and expertise. But there is a more fundamental biological rationale for looking at insects and spiders, and that derives from their immense but poorly appreciated capacity for dispersal, and thus their potential to play the role of pioneer colonists.

We know from accounts of the earliest visitors to the blast zone—the rescue workers and geologists—that insects had preceded them. We also know that there must have been massive mortality in some arthropod groups, not only in the blast zone, but in the far greater downwind area of tephra fallout. Laboratory studies have shown that newly fallen tephra lethally accelerates water loss from the insect body by abrading the cuticle surface (Edwards and Schwartz 1981). And yet, because of their mobility and their evolutionary exploitation of the wind as a medium for dispersal, arthropods were returning to impacted areas before even the initial phases of the eruption had run their course. Our task during the five years since the eruption has been to attempt to set up a blast

zone balance sheet of arrivals, survivals, and deaths. This will be the major emphasis of what follows.

## THE ROLE OF REFUGIA IN RECOLONIZATION

Before turning to the consequences and implications of aerial dispersal, it should be noted that airborne immigrants—in Lindroth's term, "parachute forces"—were not the sole source of colonists to the shattered mountain. Since arthropods are small animals, they can occupy minute spaces; that is part of their success. The spaces within a scree or a rock debris pile, for example, while inaccessible to most vertebrates, can house a thriving microcosm of arthropod life. A buried stump, fault-shattered bedrock, or a miniature cavern can also provide niches for a diverse assemblage of insects and arachnids, affording shelter not only from predators, but also from extremes of the physical environment. In winter, a few centimeters of snow suffice to insulate underlying ground from extreme cold, and many arthropods in frigid places survive because the moderating effects of snowpack on ground temperature enable them to survive periods of extreme winter cold (Aitchison 1979, Lamb et al. 1985).

The timing of the May 1980 eruption was profoundly important in this respect, for deep snowpack covered many sites both outside the immediate blast zone and within in. Snowpack not only insulated small organisms—plants and vertebrates as well as arthropods—from heat and desiccation, it also served to moisten and compact tephra so that arthropods hatching from overwintering eggs, or emerging from winter shelter with the melting of a snowpack, encountered a changed habitat, but not necessarily a lethal one.

Two specific examples will illustrate the importance of refugia—places of local survival—on Mt. St. Helens. The first stems from observations made on my first visit to the blast zone in August, 1980, six weeks after the eruption. At one site near the former Eagle Creek, carpenter ants (*Camponotus modoc*) were seen feverishly foraging on the sun-baked sterile tephra surface. Their colony appeared to be based within a large log which had probably been deeply buried under a snowbank on a lee slope. The ants were taking dead, windblown insects from the tephra surface, and were also apparently harvesting a fungus or bacterial bloom at a seepage site.

The broad trends in the survival of ants, all of which must forage for protein (usually insects or seeds) and sugar (usually nectar and



honeydew) were revealed by sampling populations in clear cuts in a transect through the tephra fallout plume in 1982 (R. Sugg pers. comm.). At the margins, where tephra depths averaged 15 centimeters, nine ant species were taken, while areas covered with the greatest tephra depths (averaging 50 centimeters) yielded only one species.

The second example comes from Butte Camp, on the south side of the cone of Mt. St. Helens, where tephra fallout amounted to 10 centimeters. There, rock debris at the foot of the butte cliffs sheltered a number of arthropod species, among them the flightless grylloblattid, an earwig-like insect representative of a remarkable and little-known insect order (Edwards 1982), and fifteen species of spider known not to be aerial dispersers (Crawford 1985). These animals were taken in our pitfall traps during the first summer following the eruption, and could not have been immigrants. A scattering of such refugia resulting from accidents of topography and snowpack, some of them probably no larger than a few square meters, have provided foci for reinvasion in some otherwise devastated areas. In a similar fashion, but on a vastly grander scale, ice-free Pleistocene refugia sheltered organisms through the ice ages.

## ARTHROPOD DISPERSAL AND COLONIZATION

Some arthropods live relatively sedentary lives, passing their entire histories without moving far from where they hatched. Many island and alpine insects, for example, lack the power of flight possessed by close relatives. For these insects, as Charles Darwin recognized, the hazards of wind carriage in windy places may outweigh the advantages of aerial mobility.

But many arthropods are aerial dispersers, and the majority of flying insects have a more or less obligate period of flight, with dispersal thus built into their life histories. To complicate matters, many flightless insects have alternate passive means to ensure dispersal by wind carriage (e.g., Tussock moths, whose adult females are sedentary and whose hairy larvae are dispersed on the wind). Even the flightless arachnids achieve windborne aerial dispersal by means of aerodynamic surfaces (e.g., mites), by phoresy (hitchhiking) on insects (e.g., mites, pseudoscorpions), or, most dramatically, by ballooning (e.g., spiders)—a thread of silk is extended into the wind until the length is sufficient to carry the animal, sometimes for great distances. Additionally, many arthropods—notably beetles and plant bugs—are polymorphic, having, within

one species, both winged flying forms and flightless forms with variably reduced wings and associated muscles. The variable expression of the genetic capacity to fly can in many cases be related to the spatial and temporal predictability of habitat on scales ranging from seasonal to millennial, as Lindroth showed for postglacial distributions of carabid beetles (Lindroth 1970). The implications of polymorphism are far-reaching in the context of recolonization, but I shall not pursue that issue further here.

The profoundly important consequence of aerial mobility is that arthropods can explore and exploit a changing spatial and temporal mosaic of habitats at a range of scale from centimeters to hundreds of kilometers. In doing so they contribute to a surprisingly diverse and abundant "aeroplankton," as Glick (1939), in his classic study, showed by towing nets behind aircraft. Earlier, Coad (1931), using sticky traps on aircraft, found diverse insects up to 15,000 feet over Louisiana; even wingless forms were taken as high as 10,000 feet. On the basis of captures by tow nets fixed to kite lines over Yorkshire, England, Hardy and Milne (1938) calculated that there were about a million insects in the air column between 150 and 2,000 feet over a square mile.

Another index of aerial dispersal is based on the many observations of windblown insects above, or on, the open ocean (Bowden and Johnson 1976). One such example, based on insects derived from coastal lands bordering the North Sea, is relevant to lowlands west of Mt. St. Helens to the extent that the climate and land use are similar: Heydemann (1967) estimated that about 4.5 billion insects per day drift out over the North Sea on the wind, representing a total biomass for the months of July and August (derived from a 30-kilometer coastal strip) of 270,000 kilograms. A final example closer to Mt. St. Helens comes from nearby Mt. Rainier, where we have quantitatively sampled insects deposited on snowfields ranging from 2,000 meters elevation to 4,000-meter summit slopes. Representative data from snowfields at 2,500 meters in June show a mean of twenty-four insects per square meter, with a dry weight biomass of 6.7 milligrams per meter. Aphids, plant bugs, ants, and flies predominate.

It is obvious that the dispersive strategies of small arthropods, at the mercy of air movements, are wasteful to the extent that for every individual that finally alights in an appropriate place, many will terminate their flights in hostile environments—in the sea, on lakes, or on alpine snowfields, for example. These derelicts of dispersal are the food for what Hutchinson (1965) has termed the al-



lobiosphere, whose residents encompass the deep oceans, oligotrophic lakes, deserts, and high mountains—places where primary productivity derived from photosynthesis is absent or negligible and where animals must subsist on imported biomass. Swan (1963) coined the term aeolian zone for alpine regions in which the resident fauna depends on arthropod fallout. We have made estimates of the quantity and diversity of the fallout on Mt. St. Helens' neighboring alpine island, Mt. Rainier; here, birds of the alpine zone exploit the fallout by day and resident arthropods scavenge by night (Mann et al. 1980, Edwards 1985).

## ARTHROPODS AS PIONEERS ON MT. ST. HELENS

The hypothesis that aerial transport plays a significant role in recolonization sets the context for our studies of arthropod populations in the blast zone of Mt. St. Helens. Since the summer of 1981, we have sampled these populations on the surface of the stony deposits left in the wake of the events which immediately followed the May 18 explosion. A massive mud slide in spring of 1982 demolished our first site on the slopes below the breached crater at 1,100 meters. A second site established in summer 1982 eroded rapidly as a consequence of the drainage of Spirit Lake by the Army Corps of Engineers, and was in turn replaced by a third site situated at 1,000 meters on a broad ridge between Spirit Lake and the crater above.

Pitfall traps have provided much of our data. These are made from plastic cups set in the pyroclastic deposits so that their lips are at surface level. The cups are covered with a roofing square of plywood set about 1 centimeter above the surface, and are partially filled with ethylene glycol, which serves as a preservative. The pitfalls are augmented with collectors designed to simulate the pebbly desert surface that covers much of the blast zone. The collectors consist of 0.25-square meter trays with a nylon mesh base, filled with a single layer of close-packed golf balls. Spaces between and below the golf balls hold windblown material, but do not prevent the departure of live arthropods, so that samples should reflect the comings and goings in the natural desert surface. Arrays of these collectors are sampled at approximately ten-day intervals throughout field season, from shortly after snowmelt in June to the first snowfall in November. Microscopic organic material is separated from mineral deposits in the laboratory, then plant material is separated from arthropod fragments. Arthropods are further identi-

fied as far as possible, and dryweight biomass determined for each collector sample.

Pitfall trap and collector samples reveal a remarkably consistent seasonal pattern of fallout consisting of plant leaf fragments and seeds, as well as diverse arthropods comprising representatives from at least thirteen orders of insects, among which the Diptera—with at least forty families—are the most diverse. Measurements of fallout biomass indicate that a dry weight in the order of 10 milligrams per square meter per day for the approximately one hundred days of fallout activity arrive at our fallout collectors. A remarkable feature of the dipteran captures is the dominance of Culicidae (mosquitos) during the first two summers following the eruption. We ascribe this surge to transient events in freshwater ponds and pools that were heavily laden with organic material following the eruption, thus providing nutrients for blooms of microorganisms on which mosquito larvae fed. Mosquito larvae are uniquely suited to anaerobic water, since they breathe air from the surface by means of a snorkel. The larvae predominated until the freshwater biota processed the eruption debris and the microorganism population subsided. Mosquitos are known from previous studies to make long dispersal flights away from breeding sites (Johnson 1969).

Other groups strongly represented in the arthropod fallout are Homoptera and Heteroptera—for example, aphids and plant bugs—both of which are well known for their dispersive behavior (Johnson 1969). While numerous families (nearly twenty) of Coleoptera are represented in the fallout, the expected peak in bark beetles derived from the extensive kill of trees did not materialize. Fortunately for the forest industry, the timing of the eruption and its effect on impacted trees did not provide appropriate conditions for an epidemic of commercially harmful insects. All of the groups mentioned above, together with a remarkable diversity of insects represented in smaller numbers (e.g., seventeen species of Psocoptera), have no prospect of survival on the pyroclastic surfaces of the blast zone.

## SCAVENGERS AND PREDATORS

It was to be expected, however, that candidates for survival might be sought among scavengers and predators from insect orders such as the Coleoptera (beetles) and Dermaptera (earwigs) and from among the spiders. Earwigs have arrived in the fallout every summer, but have not established resident populations. Among the Coleoptera, it is the ground beetles (Carabidae) that have provided



the insect pioneers. More than thirty species of carabid have been airborne to the blast zone. Among these, *Bembidion improvidens* was the first we know to have overwintered, as evidenced by our finding adults sheltered under fragments of aerial survey markers in early spring of 1983. *Bembidion* larvae are now encountered in increasing numbers with each successive summer. This genus of known pioneers is in general restricted to disturbed habitats, and must be accorded the pioneer colonist role on desolate upland pyroclastic surfaces of the mountain. But that role in recolonization is a transient one, for *Bembidion* is seldom found in places with plant cover.

The fallout is also rich in spiders. Of the forty-three species that have been identified by R. Crawford, most will be unable to survive the rigors of the habitat, but it is probable that one or two species may have already successfully bred.

Arthropods provide food for the predator populations capable of surviving in the blast zone. The remainder presumably decay, and yield nutrients such as phosphorus and nitrogen to pioneer plants. With the establishment of plants, an assemblage of herbivores such as aphids and grasshoppers enters the habitat, and then, predators such as aphid-killing syrphid flies and the many varieties of insect parasites. It is clear that a food source for predators and scavengers has been arriving in the blast zone since the first days following the eruption. The limiting factor for survival appears to be the physical environment. Where fine textured surfaces provide no shelter from radiation and desiccation, the environment is too hostile for survival, but where the development of pebbly desert pavement provides shelter and adequate water balance, predators can establish, and can flourish, as we find with the carabid genus *Bembidion*.

Major volcanic eruptions are generally few and far between. Certainly they are not frequent enough to provide, in themselves, sets of niches for the evolution of pioneer colonists. But from the diminutive perspective of beetles a few millimeters in length, new potential habitats are continually arising along the changing courses of braided rivers, on the scars of land slides, and on the land left clear by shrinking glaciers or by changing sea levels. Species of the diverse genus *Bembidion*, along with other carabid beetles, are recognized as denizens of these disturbed habitats (Thiele 1977), where few plants may grow but where homeless and vulnerable dispersed arthropods provide a ready supply of prey. Thus, for the arthropods at least, Colinvaux's conception of the recolonization of Mt. St. Helens as instant replay of postglacial history holds good.

## CONCLUSION

What conclusions can be drawn from our studies of arthropods on Mt. St. Helens so far? Perhaps the broadest relates to the process of succession. The concept of succession is a venerable one in ecology, and has been the subject of voluminous controversy, but in essence it recognizes the general observation that a rather predictable sequence of organisms plays successive roles when bare surfaces yield to colonists and, in turn, to later occupants, until a self-perpetuating equilibrium, the climax, is achieved. The standard textbook account of primary succession on mineral surfaces emphasizes the role of microorganisms as early colonists, their nitrifying role leading to the establishment of vascular plants and then to herbivorous animals, with predators and scavengers as the last arrivals. Our results from areas of the blast zone where all life was destroyed on Mt. St. Helens reveal a disordering of that sequence, with immigrant predators and scavengers as pioneers dependent on copious arthropod fallout. The fallout not only supports the pioneering predators and scavengers, but it may, to a still unknown degree, also provide a source of nutrients for microorganisms, and subsequently for vascular plants, as the recolonization of Mt. St. Helens proceeds. It seems, then, that aerial arthropod dispersal has broader consequences for the pioneer ecosystem than has generally been appreciated. In their mastery of the air as a means for dispersal, the insects have ensured themselves ubiquity. Each dispersing species has achieved its own accommodation to the challenge of persistence in a changing environment. With the spread of vegetation over the once-barren surfaces of the blast zone, the habitat will become more complex, and the pioneering arthropods will yield their place to a changing spectrum selected both from residents and from the arthropod fallout of each successive season.

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## EDITOR'S NOTE

\*\* Arthropods are invertebrate animals with jointed legs and a segmented body. The arthropods include crustaceans, arachnids, insects, and myriapods.



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