

# The Importance of Long-Term Studies of Ecosystem Reassembly after the Eruption of the Kasatochi Island Volcano

Roger del Moral\*

\*Department of Biology, Box 351800,  
University of Washington, Seattle,  
Washington 98195, U.S.A.  
moral@uw.edu

## Abstract

Kasatochi Island is a small volcanic island in the central Aleutian Islands that erupted on 7 August 2008. An interdisciplinary team visited the island and its vicinity in the summer of 2009 to describe the immediate consequences of the eruptions on terrestrial, coastal, and benthic communities. The initial effects of the eruptions on soils, oceanic waters, benthic terrain, terrestrial plants, land birds, shore birds, nesting sea birds, arthropods, marine algae, and marine invertebrates were described. This overview summarizes the conventional understanding of mechanisms that drive the reassembly of devastated ecosystems and shows how studies of Kasatochi Island may enhance our understanding of succession. The presence of residual soils and low mortality among sea birds will hasten early recovery, but significant erosion (removal of tephra and marine sediments) must occur to permit a return to a fully functional ecosystem. Long-distance dispersal over seawater will be needed to replenish the plant communities. While scavenger arthropods survived, dispersal will be needed to generate complete insect communities. Land birds were killed and their habitats destroyed, so their re-colonization awaits vegetation development. Ecosystem recovery will be facilitated by allochthonous inputs of nutrients and by plant establishment. Monitoring how the biota returns to a new equilibrium and comparisons to adjacent islands will allow tests of assembly and biogeographic theory and further our understanding of terrestrial-marine interactions. The study of Kasatochi Island's recovery will produce a valuable story of ecosystem reassembly.

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## Introduction

The studies found in this special issue detail immediate impacts of the Kasatochi Island volcanic eruption on its biota and geomorphology. In this paper, I suggest that Kasatochi Island (central Aleutian Islands) provides an unparalleled opportunity to clarify the understanding of ecosystem reassembly after intensive disturbances. Rarely has a devastating eruption occurred where there was an extensive understanding of preexisting vegetation and fauna. Comparison between the original biota and the reassembling communities can be used to address whether or not species assemble into communities according to rules (Weiher and Keddy, 1999) or by stochastic and contingent factors (Pickett et al., 2009; Simberloff, 2010). Do previously existing communities return in response to deterministic processes? This question may have different answers for various terrestrial communities (e.g., plants, sea birds, and arthropods) and for marine communities (e.g., algae and crustaceans). Can the numbers of species in a community be predicted by the equilibrium theory of island biogeography or do rapid successional processes blur patterns leading to a non-equilibrium state for some groups (cf. Bush and Whittaker, 1993)?

Table 1 summarizes how Kasatochi Island compares to some well known studies of succession on volcanoes. It is the sole case where pre-eruption conditions are known in detail. Each of the mechanisms highlighted are operational or likely to be operational on Kasatochi Island. A spectrum of biota has been studied and most groups are likely to be monitored. None of the other

volcanoes combine a potential for simple, characteristic recovery with monitoring focused on most organisms in both terrestrial and marine systems. In contrast to Surtsey, a new volcanic island that emerged between 1963 and 1967 south of Iceland, the previous marine, terrestrial and geological setting is well known. Surtsey, of course, had no biotic legacy, but is similar in other respects to Kasatochi Island. Permanent plot monitoring on Surtsey did not start for over 20 years, so studies of Kasatochi Island may benefit from establishing plots in the next few years. Floristic reconnaissance of Krakatau commenced within three years (Treub, 1888; Ernst, 1908) after its calamitous 1883 eruption, but ecological studies were not systematic for a few decades (Tagawa et al., 1985). Studies of Anak Krakatau, which emerged in the old caldera in 1930, have been detailed by several authors. The long record of observation and high diversity make the Krakatau Island group a center of biogeographic and successional investigation (Whittaker et al., 1989, 1992; Thornton, 1996). Studies of this group of volcanic islands have integrated succession with island biogeography and have provided significant insights into how dispersal limitations alter succession trajectories and the assembly of mature vegetation (Whittaker, 2004). Studies of the new island Motmot (formed near New Guinea within the caldera lake of Long Island) have demonstrated the importance of local conditions to recovery. Motmot emerged in 1968, but after 20 years the vascular flora was severely limited due to drought stress and freshwater barriers (Harrison et al., 2001). Other recently erupted volcanoes in the region had accumulated several times as many species in less time.

TABLE 1

Importance of major mechanisms to succession on volcanoes and habitats studied: comparison among well-studied volcanoes. Y = mechanism important; N = limited importance; TBD = to be determined; NA = not applicable; Monitoring: PLN = PLANNED; I = intermittent. Dispersal importance relative as it shifts during succession; 1 = most important; 3 = least important. Footnotes refer to principal papers dealing with succession on the several volcanoes. Kasatochi data are from papers cited in text.

Characteristic	Kasatochi USA	Surtsey Iceland <sup>1</sup>	Krakatau Indonesia <sup>2</sup>	Usu Japan <sup>3</sup>	Ksudach Russia <sup>4</sup>	St. Helens U.S.A. <sup>5</sup>
Prior data	Y	N	N	N	N	N
Erosion	Y	Y	Y	Y	N	Y
Legacy effects	Y	N	N	Y	Y	Y
Dispersal importance						
Wind	1	2	2	1	1	1
Vertebrates	2	1	1	3	2	2
Water	3	3	3	2	3	3
Physical amelioration	Y	Y	Y	Y	Y	Y
Biological facilitation	Y	Y	Y	Y	Y	Y
Assembly rules	TBD	Y	Y	Y	NA	Y
Monitoring	PLN	Y	I	Y	N	Y
Habitats studied						
Terrestrial	Y	Y	Y	Y	Y	Y
Shoreline	Y	Y	Y	NA	NA	NA
Marine	Y	Y	N	NA	NA	NA
Organisms studied						
Vascular plants	Y	Y	Y	Y	Y	Y
Lower plants	Y	Y	Y	Y	Y	Y
Terrestrial birds	Y	Y	Y	N	N	Y
Shore birds	Y	Y	Y	NA	NA	NA
Sea birds	Y	Y	Y	NA	NA	NA
Mammals	Y	N	Y	N	N	Y
Arthropods	Y	Y	Y	N	N	Y
Algae	Y	Y	N	NA	NA	NA
Marine invertebrates	Y	Y	N	NA	NA	NA

<sup>1</sup> Gunnarsson and Hauksson (2009); Magnússon et al. (2009); Petersen (2009).

<sup>2</sup> Tagawa et al. (1985); Thornton (2007); Whittaker and Fernández Palacios (2007).

<sup>3</sup> Tsuyuzaki (2009).

<sup>4</sup> Grishin et al. (1996).

<sup>5</sup> del Moral (1993); Dale et al. (2005); del Moral et al. (2005).

Katmai on the Alaska mainland (not listed in Table 1) produced the largest 20th century eruption in 1912, but it was not investigated ecologically for four years (Griggs, 1933). Its isolation and the severity of the climate hindered studies of recovery. Mt. Pinatubo, in the Philippines (not listed), the other great 20th century volcanic eruption (Gran and Montgomery, 2005) has been studied sparingly (Marler and del Moral, 2010) due to its isolation and political unrest. Only stable floodplains have developed greatly and the vegetation there is strongly influenced by agricultural species. Long-term studies on Hokkaido, Japan, have centered on Mt. Usu, where secondary succession from buried soils dominated recovery (Tsuyuzaki, 2009). Surviving species inhibited colonization of new species on Mt. Usu. Vegetation studies on Mt. Ksudach on the Kamchatka Peninsula, Russia (Grishin et al., 1996), explored disturbance gradients, but had no long-term component. The biota and geomorphic processes have been studied intensively on Mount St. Helens in Washington, U.S.A., and have provided many insights (Dale et al., 2005). Devastated habitats merged with those having less severe destruction, which allowed detailing of various processes of ecosystem assembly. Atypical factors such as fluctuations by the nitrogen fixing forb *Lupinus lepidus*, large elk populations, and invasion by exotic insect herbivores have reduced the generality of some conclusions.

An integrated study of terrestrial and marine systems on Kasatochi Island should facilitate the understanding of how

ecosystems develop and of mutual interactions between the landscape and the biota. It could provide more clear descriptions of assembly rules (which describe filters that allow community structure or composition to be predicted). Being a small, compact volcano, greater clarity may be obtained from Kasatochi Island than from large volcanoes. It provides a distinct combination of processes and biota. Similar to the Surtsey studies, those of Kasatochi Island can combine marine and terrestrial systems; like the Mount St. Helens studies, Kasatochi Island can include many ecosystem elements; and, like studies of Motmot and Krakatau, predictions based on island biogeography may be tested. Thus, the study of Kasatochi Island will likely generate a particularly valuable study of ecosystem reassembly, one that could elucidate the importance of deterministic factors in succession.

## Basic Lessons

Within the last two decades, the outline of what controls primary succession in terrestrial systems has been clarified (Walker and del Moral, 2003). Often, dearly held tenets of ecology have been overturned. Early succession does not necessarily depend solely on invasion by specialists (i.e., pioneers) and there is no strongly deterministic order of invasion. Rather, early succession often has been shown to be far more stochastic and opportunistic than expected (Fastie, 1995; del Moral et al., 2009). However, evidence is developing that over time vegetation develops tighter

ties with local environmental conditions (del Moral, 2009). What factors enforce such ties remains problematic, as does whether there are strong predictive rules describing the filters leading to particular vegetation. The initial findings at Kasatochi Island reported elsewhere in this issue confirm that many principles revealed by studies of early succession are valid, even under the extreme conditions found in the Aleutian Islands. While preliminary observations of Kasatochi Island suggested that life had been obliterated, subsequent studies showed that survivors were common. Here, I outline some of the processes that govern early succession in general and how they apply to the several ecosystems found on and surrounding Kasatochi Island in particular.

### *EROSION*

Erosion is both a constructive and destructive force on volcanoes. On Krakatau, huge pyroclastic deposits extended the island by many square kilometers. Subsequent down-cutting through these deposits created dissected landscape that may have hastened succession in places, but arrested it in others (Whittaker et al., 1989). Rill erosion on Mount St. Helens allowed ribbons of vegetation to survive while it perished beneath stable deposits (del Moral, 1993). Also on Mount St. Helens, erosion and deposition during extreme snowmelt events reset the “succession clock” (del Moral et al., 2005). On Surtsey, erosion is slowly shrinking and rearranging the island, which is projected to disappear beneath the waves within centuries (B. Magnússon, personal communication). On Mt. Usu, Tsuyuzaki (1994) found that erosion of tephra deposits allowed recovery of species surviving in old soil, but Tsuyuzaki and Haruki (2008) found that erosion from melting snow removed germinating seedlings, thus arresting succession (see also Tsuyuzaki et al., 1997). So, whether erosion supports ecosystem development, and thus is a form of physical facilitation, or inhibits it depends on local circumstances.

Erosion drives development of several components of the Kasatochi Island ecosystem. It removed deposits from steep slopes, and gullies were carved through pyroclastic deposits to the original surfaces. The exposed soils differ greatly in nutrients and acidity from new deposits (Wang et al., 2010 [this issue]). In the few places where soil was exposed, some plants reappeared from below-ground organs (Talbot et al., 2010 [this issue]); new propagules are likely to find suitable germination sites here. Erosion permitted nesting sites to reemerge, thus accelerating the return of seabirds and facilitating the importation of nutrients and seeds (Williams et al., 2010 [this issue]). Erosion of sediments in the sub-tidal is incipient, but is probable and is required if the reestablishment of kelp and crustose algae that require hard surfaces is to occur (Jewett et al., 2010 [this issue]). To the extent that some new deposits resist erosion, contrasts between vegetation developing on the two surfaces should be maintained for decades.

### *LEGACIES*

Remnants of ecosystems that escape total destruction can form islands in a sea of devastation. Such snippets of survival have been termed “relicts,” “refugia,” and “legacies.” “Legacy” is an apt term because it evokes a proper image of a bequest. The astonishing emergence of tiny areas of surviving vegetation within the blast zone of Mount St. Helens in 1981 alerted ecologists to the resilience of ecosystems (Dale et al., 2005). The legacy of soil includes much greater fertility and surviving plants and seeds, invertebrates, the occasional mammal, and mycorrhizae.

Fuller and del Moral (2003) found that refugia on Mount St. Helens remained floristically and structurally distinct from their surroundings after 20 years. However, refugia were invaded by wind dispersed species and the next generation colonized adjacent barrens. Surviving species contributed little to colonizing the new surfaces, and have declined in competition with invading species that are better adapted to stressful conditions. Thus, secondary dispersal is crucial to the reassembly of terrestrial ecosystems.

Against all odds, soil and organisms did survive on Kasatochi Island to provide small legacies that should hasten recovery. Soil was preserved in several locations determined by landscape position. Erosion revealed some of the soils buried to moderate degrees, especially along gullies. However, it is more likely that old soils will either have been sterilized, or the surviving species will be incapable of colonizing new surfaces. Talbot et al. (2010 [this issue]) found that while most of the island was devoid of plants, plant diversity reached its peak where erosion had effectively removed new material and revealed soils. These authors recorded 18 species, most of which had been present prior to the eruption, but five were newly recorded. They classified pre- and post-eruption vegetation into five types, four of which were post-eruptive. Relict soils promoted the cover and diversity of two of the five types, but new surfaces were scarcely inhabited. As with other eruptions (e.g., Mount St. Helens, Mt. Usu), survival on Kasatochi Island was due to heterogeneous impacts followed by erosion that allowed the emergence of plants from vegetative parts, not seeds. The direction of vegetation development, as with the introduction of additional species by long-distance dispersal, will be a focus of vegetation monitoring.

Ants survived on the cone of Mount St. Helens (del Moral, 1981), but colonies failed due to lack of resources. Relicts form an important initial step in ecosystem recovery. Buried vegetation can support arthropod communities until vegetation recovery is started. This pattern has repeated on Kasatochi Island. Arthropods found in 2009 were scavengers (necromass feeders), not herbivores (Sikes and Slowik, 2010 [this issue]), and the assembly of terrestrial arthropod communities has not truly begun.

Marine mammals and seabirds suffered comparatively little (Drew et al., 2010 [this issue]), while terrestrial birds had not returned in 2009 (Williams et al., 2010 [this issue]). Legacy effects were scarcely sufficient to permit the immediate recovery of terrestrial birds, because all sites were buried by tephra and impacted by toxic gasses. While plants and invertebrates may survive burial for periods of time, birds cannot. However, the presence of a few newly revealed substrates may hasten the return of terrestrial bird species.

The benthic community recovery also benefitted from legacy effects (Jewett et al., 2010 [this issue]). Due to the drastic change in substrate types (from rocks to sand), the composition of most of the impacted area changed. However, there was some kelp survival even where it was buried by over 20 m of sand due to the shoreline extension, and survival increased as the deposit attenuated. As with terrestrial survivors, habitat conditions may be less important to reestablishment than species immediately adjacent to the newly created sites.

### *DISPERSAL*

When new land appears (e.g., Surtsey) or the impact eliminates all life (e.g., Krakatau), recolonization requires dispersal (Walker and del Moral, 2003). Initial colonists are usually drawn from the more likely dispersers (Whittaker et al., 1992), although colonization can be subject to the vagaries of

chance, leading to cases of poorly dispersed species arriving first. For example, fruit bats on Krakatau transport seeds across water barriers, but have erratic behavior, leading to uncertain dispersal results (Whittaker and Jones, 1994). They also require substantial vegetation development to establish. Long Island (New Guinea) had 29 vertebrates, including several frugivorous bats after 350 years, while Motmot, which emerged from its crater lake in 1953, had only a single insectivorous bat (Cook et al., 2001). Wind, ocean currents, and flying vertebrates are the main vectors of plant dispersal to oceanic islands. On Surtsey, of the vascular plants noted between 1963 and 2008, 75% were bird dispersed, 16% wind dispersed, and only 9% were dispersed by sea; however, the first colonists were sea borne (Magnússon et al., 2009). Both wind and bird dispersal continue to add the occasional persistent species, but no new sea-borne species arrived after 10 years. Long-term monitoring of the developing communities on Surtsey (Jakobsson et al., 2009) demonstrated the mechanisms of dispersal for many types of organisms. Thus, the dispersal spectrum continues to shift, as it has done elsewhere. Kasatochi Island offers opportunities to expand our understanding of dispersal mechanisms and the stability of initially formed communities.

On Kasatochi Island the most prominent plant colonists in 2009 were dispersed by ocean currents (e.g., *Honckenya peploides*, also dominant on Surtsey), but wind dispersal and animal vectors can be important. *Leymus mollis* was common along the shore of Surtsey, but on Kasatochi Island it appears to have been introduced into upland sites by birds. *Leymus* colonizes volcanoes and other barren uplands in boreal regions, so its dispersal is likely to involve diplochory, i.e., dispersal by ocean drift and by birds. It is likely that wind dispersal will dominate the development of upland vegetation.

Surprisingly, most arthropods found in 2009 were survivors or their progeny (Sikes and Slowik, 2010 [this issue]). The best documented study of arthropods after a volcanic eruption is that of Edwards (1986; see also Edwards and Thornton, 2001), who found that wind transported most arthropods into barren sites on Mount St. Helens, but that most died. They formed short-lived scavenger-cannibalistic food webs that ultimately formed a basis for ecosystem development by enriching the soil (see *Facilitation*). This process also should be important on Kasatochi Island. At present, most immigrants will fail to find suitable habitats, so that while drift and wind continue to introduce organisms, most will die. Dispersal will lead to colonization only when the terrestrial system stabilizes, in large part in response to abiotic and external forces.

Seabirds nesting on Kasatochi Island were displaced, but few adults died (Williams et al., 2010 [this issue]). Recolonization will be required to establish shore birds such as black oystercatchers, but successful establishment awaits the recovery of shoreline habitats. Terrestrial birds (e.g., passerines) were exterminated by the eruption and have yet to return. They were among the last avian colonists on Surtsey (Petersen, 2009) because it required decades for forage and nesting sites to form. Pools of potential colonists occur on adjacent Aleutian Islands, so it is likely that terrestrial bird communities will reassemble quickly on Kasatochi Island once habitats develop. Because terrestrial birds need resources beyond nesting sites, the recovery of these groups will be slower than for shore and sea birds. For example, while sea birds became common on Surtsey within a decade, snow buntings were not common, although sporadically present (Petersen, 2009) for three decades and other terrestrial birds (e.g., crows) remained rare.

The impacts on Kasatochi Island's benthic communities, although severe, were spatially limited, so that pools of colonists

were available. In contrast to terrestrial systems, where even short distances limit dispersal (cf. del Moral and Ellis, 2004), aquatic systems can be colonized rapidly. Thus, newly created sandy benthic sites were dominated by mobile amphipods, not algae (Jewett et al., 2010 [this issue]). Dispersal of kelp will be ineffective until and unless suitable substrates are uncovered by erosion. Succession of benthic marine algae should proceed more rapidly than on Surtsey because colonists will not require long-distance dispersal (Gunnarsson and Hauksson, 2009).

#### AMELIORATION AND FACILITATION

Erosion is an important amelioration (Ashmole and Ashmole, 1988) process because it uncovers remnant soils and accelerates recovery (see *Erosion*). A diffuse amelioration by allochthonous nutrient inputs (arthropods, seeds, spores, seabird guano, and sea spray) is also an essential precursor to ecosystem development in sterile volcanic substrates (see *Dispersal*). Such inputs precede plant establishment that leads to more complex and stable ecosystems. Unique to an island situation is the presence of seaweed driven ashore by storms. While limited in extent, significant deposits of nutrients and organic matter, plus many arthropods clinging to seaweed, promote the stability of the shoreline and may accelerate development beyond the shore.

Facilitation is usually viewed as meaning modifications of the environment by plants that improve the chances of seedlings to establish and that promote growth (Gomez-Aparicio, 2009). Plants can add nutrients and organic matter and offer shade that reduces drought stress and wind. Note that competition can limit facilitation effects, that both have strong spatial components (cf. Krna et al., 2009), and that they interact in complex ways (Walker and Chapin, 1987; del Moral and Rozzell, 2005; Fayolle et al., 2009).

The delayed colonization of Surtsey by seabirds, followed immediately by the explosive development of land vegetation, demonstrated the critical importance of imported nutrients. Once seabirds began to nest, dense meadows developed to form communities similar to those on older Icelandic islands (Magnússon et al., 2009). In turn, dense vegetation stimulated the expansion and diversity of bird colonies and allowed other species to colonize, showing that facilitation can be reciprocal. Plant species turnover has been rapid, indicating strong competitive effects.

Earlier models of succession asserted that plants (especially mosses in moist habitats) were obligatory "pioneers" (Griggs, 1918), but subsequently it has been recognized that abiotic amelioration (del Moral and Bliss, 1993) and importation of organic matter are crucial precursors. Together, allochthonous inputs of air-borne arthropods (plus pollen, spores, and seeds), deposits of organic debris along the shore, and deposition of guano by seabirds accelerate ecosystem development greatly. Species characteristic of mature vegetation can often establish in relatively barren sites if they manage to arrive. Remnant soils also can facilitate ecosystem response, not only *in situ*, but also in the immediate surroundings (del Moral and Grishin, 1999). Clearly, residual soils have a reservoir of nutrients, seeds, plant vegetative parts, and microorganisms that can develop once erosion removes their blanket of tephra. Newly exposed surfaces are sparsely populated and therefore open to colonization. Colonists can thrive and disperse into the surrounding new substrates. It is likely that residual soils will play a central role in the recovery of the Kasatochi Island ecosystem (Talbot et al., 2010 [this issue]).

While seabirds went largely unscathed during the Kasatochi Island eruption, they have not yet reestablished breeding colonies.

Based on the Surtsey experience, their return will be a major turning point in the development of the terrestrial biota.

### ASSEMBLY

Ecosystem assembly has both theoretical interest and practical significance (Walker and del Moral, 2009). Clearly, reassembly starts with readily available pieces, so that younger systems appear more variable than mature ones. As vegetation becomes denser and as more species accrue, patterns become discernable (del Moral, 2009). Whether vegetation grows similar to that existing before the eruption is poorly understood (Holdaway and Sparrow, 2006), and there is evidence for both convergence and divergence. Most communities on Kasatochi Island have barely commenced assembly. Whether reassembled communities will be similar to the preexisting ones is an important question that bears on whether assembly is stochastic or deterministic. Because this flora is limited and old surfaces survived, vegetation could develop toward communities previously found on the island. The only species recorded after the eruption that were not previously found were bryophytes and a fungus. These species are unlikely to alter trajectories significantly, and may simply have been overlooked during earlier studies. Because there are wide expanses lacking vegetation, long-distance dispersal could yield alternative types of vegetation.

Seabirds survived and returned in similar numbers to the island, so reassembly has already occurred. Land birds and shorebirds have not had the opportunity to commence reassembly of their communities. Erosion and vegetation development will be required (Petersen, 2009). Immigration from surrounding islands offers the chance that different combinations of passerines will occur, although these differences may take several decades to become manifest.

### Importance of Kasatochi Island for Understanding Succession

The preliminary studies on Kasatochi Island presented few surprises other than in the details and support the current understanding of ecosystem reassembly following profound disturbances. However, the nature and location of the triggering disturbances do provide significant opportunities to refine our understanding of succession, particularly because there is a large body of pre-eruption data (DeGange et al., 2010 [this issue]). Taking advantage of these opportunities will improve the understanding of community reassembly. The research program will be greatly facilitated by the detailed understanding of the geology and impacts (Scott et al., 2010 [this issue]) and soils (Wang et al., 2010 [this issue]) created by the eruptions. I expect that our understanding of the mechanisms of community development will be enhanced by further studies of Kasatochi Island.

The recovery of this system after a major volcanic eruption is being driven by erosion in both terrestrial and marine habitats, exposure of residual substrates, import of nutrients, and recolonization of all systems. These drivers resemble those of other volcanoes, but when combined, they are unique. Continued study will allow for a better understanding of several aspects of ecosystem recovery and should improve how we approach the restoration of compromised ecosystems (Weiher, 2007; Svavarsdóttir and Walker, 2009).

The volcanic impacts and subsequent terrain modifications have created a spatially variable ecosystem with respect to tephra depths (cf. Pfitsch and Bliss, 1988), residual soils, and marine

deposits. Secondary disturbances will accentuate this variation. It is likely that even within an ecosystem, recovery will occur at different rates and certainly the various ecosystems will not recover synchronously. Thus, as in other volcanoes (Dirksen and Dirksen, 2007), heterogeneity will provide natural experiments to test hypotheses concerning succession mechanisms.

Legacies combined with isolation prejudice recovery toward the development of terrestrial ecosystems similar to those existing before the eruptions. Thus, Kasatochi Island itself may serve as a comprehensive test to determine if communities return to their former state.

Studies of the terrestrial-marine interaction during succession are rare. How terrestrial runoff, for example, affects recovering benthic communities is an open question. Does continued sedimentation provide a chance for opportunistic species to become entrenched, or will persistent species (e.g., kelp) return as disturbances abate?

Studies on Surtsey, where fish remains, guano, and seaweed are major determinants to the dynamics of upland meadows, have shown how marine systems can drive upland ones. There is an opportunity on Kasatochi Island to document a similar process and to explore how marine mammals and seaweed also affect upland development.

Unlike Surtsey, there is an opportunity to compare developing ecosystems on Kasatochi Island with those documented before the eruption. Particularly for more vagile groups, such comparisons may answer questions concerning assembly theory in different ecosystems.

### Unresolved Questions

Future work on Kasatochi Island could illuminate several ecological questions. What are the filtering mechanisms (assembly rules) for the various groups of organisms (cf. Temperton et al., 2004)? Each major group is likely to respond uniquely, so comparisons among groups would likely provide insights into the importance of such processes as priority effects and isolation. Will assembly rules in the form of deterministic processes such as strong competitive effects recreate plant communities previously found on the island? Alternatively, will isolation lead to stochastic immigration, possibly combined with priority effects, and to novel communities? Related to this last question is whether key plant species were extirpated during the eruption and how likely it is that they will recolonize. The absence of a key species can dramatically alter the vegetation through priority effects, a phenomenon seen in the intertidal zone. Thus far, legacies of arthropods and plants both appear to be limited and composed of a narrow spectrum of the available biota. Arthropods were mainly scavengers, so phytophagous and predatory insects must cross substantial barriers and await suitable habitats to develop. How will the functional vacancies be filled? While it is likely that, due to the limited regional diversity, communities similar to those that once existed will develop, it is possible that novel assemblages will form (cf. Simberloff and Wilson, 1970).

How will land bird communities develop? Will insectivores, feeding on imported food, establish prior to herbivorous birds and exclude some foraging guilds, or will both groups be limited by nesting sites until vegetation becomes well established?

More generally, once the landscape stabilizes, will any major group of organisms develop disharmonic species spectra due to differential dispersal or to competitive effects? Will the distribution of functional or dispersal groups stabilize in configurations different from the mainland? Isolation from intact communities

suggests that novel communities could develop (Whittaker et al., 1989). Alternatively, remnant vegetation could guide succession toward previously developed vegetation (convergence), or filters (e.g., competition, facilitation) could constrain the composition of successful assemblages (Thornton, 2007). Careful documentation of several land communities could provide a comprehensive test of island biogeographic theory, so monitoring community reassembly will be crucial. Marine benthic communities have substantially less history, so work in this habitat will be particularly valuable. Will priority effects, combined with chance dispersal, produce persistent novel benthic communities in the newly formed habitats described by Jewett et al. (2010 [this issue]) or will they be replaced by common assemblages?

As a veteran of 30 years of monitoring on Mount St. Helens, I recognize the difficulties of maintaining any long-term study. Kasatochi Island offers challenges, but the rewards of making regular, systematic, and standardized sampling of each component of the island's biota and geomorphic changes will be substantial (cf., DeGange et al., 2010 [this issue]). Modern succession theory can rarely be examined comprehensively. Studies on Kasatochi Island will make it likely that answers to such questions as posed above will emerge.

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### References Cited

- Ashmole, N. P., and Ashmole, M. J., 1988: Insect dispersal on Tenerife, Canary Islands: High altitude fallout and seaward drift. *Arctic and Alpine Research*, 20: 1–12.
- Bush, M. B., and Whittaker, R. J., 1993: Non-equilibration in island theory of Krakatau. *Journal of Biogeography*, 20: 453–458.
- Cook, S., Singidan, R., and Thornton, I. W. B., 2001: Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. IV. Colonization by non-avian vertebrates. *Journal of Biogeography*, 28: 1353–1363.
- Dale, V. H., Swanson, F. J., and Crisafulli, C. M. (eds.), 2005: *Ecological Responses to the 1980 Eruption of Mount St. Helens*. New York: Springer, 342 pp.
- DeGange, A. R., Byrd, G. V., Walker, L. R., and Waythomas, C. F., 2010: Introduction—The impacts of the 2008 eruption of Kasatochi Volcano on terrestrial and marine ecosystems in the Aleutian Islands, Alaska. *Arctic, Antarctic, and Alpine Research*, 42: 245–249.
- del Moral, R., 1981: Life returns to Mount St. Helens. *Natural History*, 90(5): 36–49.
- del Moral, R., 1993: Mechanisms of early succession on Mount St. Helens. In Milne, J., and D. W. H. Walton. (eds.), *Primary Succession on Land*. London: Blackwell, 79–100.
- del Moral, R., 2009: Increasing deterministic control of primary succession on Mount St. Helens, Washington. *Journal of Vegetation Science*, 20: 1145–1154.
- del Moral, R., and Bliss, L. C., 1993: Mechanism of primary succession: insights resulting from the eruption of Mount St. Helens. *Advances in Ecological Research*, 24: 1–66.
- del Moral, R., and Ellis, E. E., 2004: Gradients in heterogeneity and structure on lahars, Mount St. Helens, Washington, USA. *Plant Ecology*, 175: 273–286.
- del Moral, R., and Grishin, S. Y., 1999: Volcanic disturbance and ecosystem recovery. Chapter 5. In Walker, L. R. (ed.), *Ecosystems of Disturbed Ground*. Goodall, D. W. (editor-in-chief), *Ecosystems of the World Series*. Amsterdam: Elsevier Science, 137–160.
- del Moral, R., and Rozzell, L. R., 2005: Effects of lupines on community structure and species association. *Plant Ecology*, 180: 203–215.
- del Moral, R., Wood, D. M., and Titus, J. H., 2005: How landscape factors affect recovery of vegetation on barren surfaces. In Dale, V. H., Swanson, F. J., and Crisafulli, C. M. (eds.), *Ecological Responses to the 1980 Eruption of Mount St. Helens*. New York: Springer, 93–109.
- del Moral, R., Sandler, J. E., and Muerdter, C. P., 2009: Spatial factors affecting primary succession on the Muddy River Lahar, Mount St. Helens. *Plant Ecology*, 202: 177–190.
- Dirksen, V. G., and Dirksen, O. V., 2007: Vegetation dynamics and ecological consequences of the 1996 eruption in Karymsky Volcanic Center, Kamchatka. *Journal of Volcanology and Seismology*, 1: 26–38.
- Drew, G. S., Dragoo, D. E., Renner, M., and Piatt, J. F., 2010: At-sea observations of marine birds and their habitats before and after the 2008 eruption of Kasatochi Volcano, Alaska. *Arctic, Antarctic, and Alpine Research*, 42: 325–334.
- Edwards, J. S., 1986: Derelicts of dispersal: arthropod fallout on Pacific Northwest volcanoes. In Danthanarayana, W. (ed.), *Insect Flight: Dispersal and Migration*. New York: Springer, 196–203.
- Edwards, J. S., and Thornton, I. W. B., 2001: Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. VI. The pioneer arthropod community of Motmot. *Journal of Biogeography*, 28: 1379–1388.
- Ernst, A., 1908: *The New Flora of the Volcanic Island of Krakatau*. Cambridge: Cambridge University Press (translated by A. C. Seward), 74 pp.
- Fastie, C. L., 1995: Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology*, 76: 1899–1916.
- Fayolle, A., Violle, C., and Navas, M. L., 2009: Differential impacts of plant interactions on herbaceous species recruitment: disentangling factors controlling emergence, survival and growth of seedlings. *Oecologia*, 159: 817–825.
- Fuller, R. N., and del Moral, R., 2003: The role of refugia and dispersal in primary succession on Mount St. Helens, Washington. *Journal of Vegetation Science*, 14: 637–644.
- Gomez-Aparicio, L., 2009: The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. *Journal of Ecology*, 97: 1202–1214.
- Gran, K. B., and Montgomery, D. R., 2005: Spatial and temporal patterns in fluvial recovery following volcanic eruptions: channel response to basin-wide sediment loading at Mount Pinatubo, Philippines. *Geological Society of America Bulletin*, 117: 195–211.
- Griggs, R. F., 1918: The eruption of Katmai. *Nature*, 101: 497–499.
- Griggs, R. F., 1933: The colonization of Katmai ash, a new and inorganic “soil.” *American Journal of Botany*, 20: 92–111.
- Grishin, S. Y., del Moral, R., Krestov, P. V., and Verkholat, V. P., 1996: Succession following the catastrophic eruption of Ksudach volcano (Kamchatka, 1907). *Vegetatio*, 127: 129–153.
- Gunnarsson, K., and Hauksson, E., 2009: Succession and benthic community development in the sublittoral zone at the recent volcanic island, Surtsey, southern Iceland. *Surtsey Research*, 12: 161–166.
- Harrison, R. D., Banka, R., Thornton, I. W. B., Shanahan, M., and Yamuna, R., 2001: Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. II. The vascular flora. *Journal of Biogeography*, 28: 1311–1337.

- Holdaway, R. J., and Sparrow, A. D., 2006: Assembly rules operating along a primary riverbed-grassland successional sequence. *Journal of Ecology*, 94: 1092–1102.
- Jakobsson, S. P., Magnússon, B., and Gunnarsson, K. (eds.), 2009: *Surtsey Research 12*. Reykjavík, Iceland: The Surtsey Research Society.
- Jewett, S. C., Bodkin, J. L., Chenelot, H., Esslinger, G. G., and Hoberg, M. K., 2010: The nearshore benthic community of Kasatochi Island, one year after the 2008 volcanic eruption. *Arctic, Antarctic, and Alpine Research*, 42: 315–324.
- Krna, M. A., Day, T. A., and Ruhland, C. T., 2009: Effects of neighboring plants on the growth and reproduction of *Deschampsia antarctica* in Antarctic tundra. *Polar Biology*, 32: 1487–1494.
- Magnússon, B., Magnússon, S. H., and Fridriksson, S., 2009: Developments in plant colonization and succession on Surtsey during 1999–2008. *Surtsey Research*, 12: 57–76.
- Marler, T. E., and del Moral, R., 2010: Primary succession along an elevation gradient 15 years after the eruption of Mount Pinatubo, Luzon, Philippines. *Pacific Sciences*, 65: in press.
- Petersen, A., 2009: Formation of a bird community on a new island, Surtsey, Iceland. *Surtsey Research*, 12: 133–148.
- Pfitsch, W. A., and Bliss, L. C., 1988: Recovery of net primary production in subalpine meadows of Mount St. Helens following the 1980 eruption. *Canadian Journal of Botany*, 66: 989–997.
- Pickett, S. T. A., Cadenasso, M. L., and Meiners, S. J., 2009: Ever since Clements: from succession to vegetation dynamics and understanding to intervention. *Applied Vegetation Science*, 12: 9–21.
- Scott, W. E., Nye, C. J., Waythomas, C. F., and Neal, C. A., 2010: August 2008 eruption of Kasatochi Volcano, Aleutian Islands, Alaska—Resetting an island landscape. *Arctic, Antarctic, and Alpine Research*, 42: 250–259.
- Sikes, D. S., and Slowik, J., 2010: Terrestrial arthropods of pre- and post-eruption Kasatochi Island, Alaska, 2008–2009: a shift from a plant-based to a necromass-based food web. *Arctic, Antarctic, and Alpine Research*, 42: 297–305.
- Simberloff, D., 2010: Invasions of plant communities—More of the same, something very different, or both? *American Midland Naturalist*, 163: 220–233.
- Simberloff, D. S., and Wilson, E. O., 1970: Experimental zoogeography of islands—A 2-year record of colonization. *Ecology*, 51: 934–937.
- Svavarsdóttir, K., and Walker, L. R., 2009: The value of Surtsey for ecological research. *Surtsey Research*, 12: 149–151.
- Tagawa, H., Suzuki, E., Partomihardjo, T., and Suriadarma, A., 1985: Vegetation and succession on the Krakatau Islands, Indonesia. *Vegetatio*, 60: 131–145.
- Talbot, S. S., Talbot, S. L., and Walker, L. R., 2010: Post-eruption legacy effects and their implications for long-term recovery of the vegetation on Kasatochi Island, Alaska. *Arctic, Antarctic, and Alpine Research*, 42: 285–296.
- Temperton, V. M., Hobbs, R. J., Nuttle, T., and Halle, S. (eds.), 2004: *Assembly Rules and Restoration Ecology—Bridging the Gap between Theory and Practice*. Washington, D.C.: Island Press, 424 pp.
- Thornton, I. W. B., 1996: *Krakatau—The Destruction and Reassembly of an Island Ecosystem*. Cambridge, Massachusetts: Harvard University Press, 346 pp.
- Thornton, I. W. B., 2007: *Island Colonization: the Origin and Development of Island Communities*, New, T. (ed.), Cambridge: Cambridge University Press, 302 pp.
- Treub, M., 1888: Notice sur la novella flore de Krakatau. *Annales du Jardin Botanique de Buitenzorg*, 7: 213–222.
- Tsuyuzaki, S., 1994: Fate of plants from buried seeds on volcano Usu, Japan, after the 1977–1978 eruptions. *American Journal of Botany*, 81: 395–399.
- Tsuyuzaki, S., 2009: Causes of plant community divergence in the early stages of volcanic succession. *Journal of Vegetation Science*, 20: 959–969.
- Tsuyuzaki, S., and Haruki, M., 2008: Effects of microtopography and erosion on seedling colonisation and survival in the volcano Usu, northern Japan, after the 1977–78 eruptions. *Land Degradation & Development*, 19: 233–241.
- Tsuyuzaki, S., Titus, J. H., and del Moral, R., 1997: Seedling establishment patterns on the Pumice Plain, Mount St. Helens, Washington. *Journal of Vegetation Science*, 8: 727–734.
- Walker, L. R., and Chapin, F. S. III, 1987: Interactions among processes controlling successional change. *Oikos*, 50: 131–135.
- Walker, L. R., and del Moral, R., 2003: *Primary Succession and Ecosystem Rehabilitation*. Cambridge: Cambridge University Press, 442 pp.
- Walker, L. R., and del Moral, R., 2009: Lessons from primary succession for restoration of severely damaged habitats. *Applied Vegetation Science*, 12: 55–67.
- Wang, B., Michaelson, G., Ping, C.-L., Plumlee, G., and Hageman, P., 2010: Characterization of pyroclastic deposits and pre-eruptive soils following the 2008 eruption of Kasatochi Island volcano, Alaska. *Arctic, Antarctic, and Alpine Research*, 42: 276–284.
- Weiherr, E., 2007: On the status of restoration science: obstacles and opportunities. *Restoration Ecology*, 15: 340–343.
- Weiherr, E., and Keddy, P. (eds.), 1999: *Ecological Assembly Rules: Perspectives, Advances and Retreats*. Cambridge: Cambridge University Press, 432 pp.
- Whittaker, R. J., 2004: The island biogeography of a long-running natural experiment: Krakatau, Indonesia. In Fernández Palacios, J. M., and Morici, C. (eds.), *Ecología Insular/Island Ecology* Asociación Española de Ecología Terrestre (AEET)–Cabildo Insular de La Palma, 57–59.
- Whittaker, R. J., and Fernández Palacios, J. M., 2007: *Island Biogeography: Ecology, Evolution, and Conservation*. Second edition. Oxford: Oxford University Press, 416 pp.
- Whittaker, R. J., and Jones, S. H., 1994: The role of frugivorous bats and birds in the rebuilding of a tropical forest ecosystem, Krakatau, Indonesia. *Journal of Biogeography*, 21: 245–258.
- Whittaker, R. J., Bush, M. B., and Richards, K., 1989: Plant recolonization and vegetation succession on the Krakatau Islands, Indonesia. *Ecological Monographs*, 59: 59–123.
- Whittaker, R. J., Bush, M. B., Asquith, N. M., and Richards, K., 1992: Ecological aspects of plant colonization of the Krakatau Islands. *GeoJournal*, 28: 201–211.
- Williams, J. C., Drummond, B. A., and Buxton, R. T., 2010: Initial effects of the August 2008 volcanic eruption on breeding birds and marine mammals at Kasatochi Island, Alaska. *Arctic, Antarctic, and Alpine Research*, 42: 306–314.

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