AN ABSTRACT OF THE THESIS OF

Karl C. Fairchild for the degree of Honors Baccalaureate of Science in Fisheries and Wildlife presented on May 4, 2009. Avian Community Assembly Following Volcanic Disturbance at Volcán Arenal, Costa Rica, and Mount St. Helens, USA.

Abstract approved: ____
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Volcanism is an agent of major disturbance in many parts of the world. While the effects of volcanic disturbance are fairly well-known among some groups of species, few studies have been performed in bird communities. Likewise, few studies have attempted to compare how communities in temperate and tropical biomes respond to volcanism. This study examines how bird communities inhabiting areas recently disturbed by volcanism differ at Mount St. Helens in the United States, and Volcán Arenal in Costa Rica. I compare the two bird communities to evaluate patterns in species richness, species diversity and guild diversity and how those patterns fit with previously described differences in temperate and tropical bird communities. The two communities generally exhibited similarity in richness and diversity, although small sample sizes at Arenal may have influenced ability to detect differences. Nevertheless, my results suggest that the relatively low complexity of vegetation at these early successional study sites may explain the greater similarity than initially predicted. My results also suggest the greatest difference between the temperate and tropical sites is in the most structurally complex sites. Additional surveys at these and other sites are needed to reveal the generality of my results.

Avian Community Assembly Following Volcanic Disturbance at Volcán Arenal, Costa Rica and Mount St. Helens, USA

by

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I understand that my project will become part of the permanent collection of Oregon State University, University Honors College. My signature below authorizes release of my project to any reader upon request.

Karl C. Fairchild, Author

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INTRODUCTION

Volcanism is an agent of major disturbance in many parts of the world. Although the effects of volcanic disturbance are fairly well-known among some groups of species, such as insects and plants, few such studies have been performed in bird communities. Likewise, few studies have attempted to compare how communities in different biomes respond to volcanism. This study compares responses by bird communities to volcanism at Mount St. Helens in the United States, and Volcán Arenal in Costa Rica. Mount St. Helens is located in the temperate rainforest of Washington, USA while Volcán Arenal is located in tropical rainforest near La Fortuna, Costa Rica.

Structure and Niches

The response of bird communities to environmental, or habitat, disturbance and the changes in those communities through time has been widely studied, although mainly in temperate environments where recovery through secondary succession is occurring (Wiens 1989, p170). Secondary succession is characterized by having physical legacies (e.g., soils) and biological legacies, such as surviving plants and animals that remain after the disturbance. This contrasts with primary successional environments, typical of intense volcanic disturbance, where no physical and biological legacies remain following disturbance (i.e. Clements 1916).

It has long been known that plant communities change in species composition and in overall complexity of the vegetation as species are added to the community over time, with structural complexity increasing as a given community ages. Clements (1916) was one of the first ecologists to propose the concept that communities change over time and are generally not a static entity. MacArthur (1961) was one of the first to predict that an increase in the complexity of plant communities would also lead to a more complex bird community. He studied foliage height diversity, mostly in temperate forests, and found a strong positive correlation between foliage height and diversity of bird species present, even though foliage height diversity was also confounded with vegetative diversity. Despite the confounding factor, he concluded that the greater foliage height diversity led to the creation of more feeding niches, and hence more species were able to use the habitat. MacArthur later confirmed this hypothesis--that greater structural diversity provides more foraging niches and allows for higher species diversity--in another study, which examined the foraging patterns of boreal warblers and found that different species foraged in different portions of the spruce trees (MacArthur and Levins 1961).

Terborgh (1992) further examined MacArthur's idea that vegetation structure relates to niche partitioning. In addition, he incorporated hypotheses about decreased seasonality in tropical environments and how this potentially leads to a greater diversity of available structures and hence a greater number of possible niches. Terborgh (1992) examined the bird species present in a site in the Peruvian Amazon and compared it with one in South Carolina that was similar in terms of tree height, tree age, and lack of disturbance, yet found the tropical site had five times the number of species found at the temperate site. He found a possible explanation for this increased diversity by examining a community of antwrens at the Peruvian Amazon site, where he found that species used very similar but non-overlapping niches. Many of these foraging niches were highly specialized and relied on a single food source, available year-round and unique to the tropics. One species of antwren occupied a niche that exclusively gleans clumps of dead leaves that had become wedged in tree branches. Such a niche is only available in the tropics because it relies on a constant input of dead leaves falling from the canopy and becoming temporarily caught, before eventually falling to the ground. This condition would be unavailable in the temperate zone, because of deciduous trees that would contribute no leaves at all for many months. Terborgh also found a positive avian response to increased plant species diversity as well as to structural diversity. Since many tropical plants show flowering and fruiting phenologies independent from other species, some tropical bird species have been able to adapt to consuming a mixture of nectar and fruit year-round, where these resources would only be attainable separately, and for relative short periods of time during the year in the temperate zone (Terborgh 1992, pp57-71).

Terborgh's study is interesting because it suggests tropical species can become more specialized than temperate ones, as they do not have to adapt to as much seasonality and can occupy a narrower and more specialized foraging niche. When examined from the point of view of one investigating community reassembly at two latitudes, this suggests that there could be increased specialization and diversity in tropical colonists (both plant and animal), and also increased rates of structural development among plants due to the differences in seasonality. Furthermore, once some level of vegetative height diversity is established, one would expect to find proportionally more species using it.

Supertramp Colonization Strategy

Of the few studies that have been conducted on recolonization of areas defaunated by volcanic blasts, many have been conducted on islands in the southwestern Pacific Ocean in the area of Indonesia and New Guinea. Diamond (1974), after examining islands at different times after eruption, found that a certain predictable set of r-selected species were always found on islands with the least structural complexity and were most isolated from other islands. He determined that this set of species was adapted to extremely efficient colonization of islands through high levels of reproduction and high levels of emigration, and that they were resource generalists. Diamond discovered that there was a trade-off to this, however: the species were poor competitors when they competed with resource specialists. This led Diamond to conclude that these species were reliant on disturbed conditions and they would predictably assemble in recently disturbed areas. It is unclear, however, if species that use this life history strategy exist in mainland primary successional habitats.

Other Types of Primary Succession

While few studies have examined reassembly of bird communities in areas defaunated by volcanic eruptions, some studies have been done in areas defaunated to primary successional conditions in other ways, such as by strip mining. These studies are notable in that they are some of the few that explore primary succession in North American bird communities. Karr (1968) found a correlation between increased foliage height diversity and number of bird species. Likewise, birds showed increased richness with increasing time since strip mining had occurred on site. Karr only found five species on bare ground sites, while he found 18 in early shrub habitats that had only moderately more vegetative development. This value is similar to a study in Indonesia, which found nine species in an unrestored strip mine habitat, while a restored site with only small trees had 13 species (Passell 2000).

Previous Studies within Study Areas

Five studies have documented the effects of eruption from Mount St. Helens on bird communities; two of these were in close proximity to the volcano and three were located beyond the influence of the lateral blast in areas of cool ashfall deposition, mostly in eastern Washington, where prevailing winds blew much of the ash from the eruption.

Crisafulli and Hawkins (1998) studied avian community reassembly along a volcanic disturbance gradient at Mount St. Helens from 1981 through 1995 that included sites influenced by the 1980 lateral blast (blowdown zone) and pyroclastic flows. No birds survived the eruption at these sites and the authors predicted that during the reassembly process the structural complexity of the habitats should strongly influence species diversity, and the type and abundance of resources should influence the specific species colonizing these sites. In the blowdown zone, seven species colonized within one year of the eruption; these species were either ground foragers that nest on the ground or in cavities, or species that fly from perches to forage. A second reassembly phase occurred seven to 10 years after the eruption and was directly associated with the development of woody riparian vegetation. At this time, five additional species colonized and were those that gleaned insects from foliage or flew from perches to gather their prey; all nested in the shrub architecture. Avian colonization in the pyroclastic flow zone was slower than in the blowdown zone and involved a different mix of species. The pyroclastic flow zone remained relatively barren with patches of low stature herbs and only provided habitat for ground nesters and foragers, except for in wetlands where one species used cattail. None of the species colonizing the pyroclastic flow zone were species typically associated with montane coniferous forests.

Another study at Mount St. Helens examined the bird species present soon after the blast and examined the rates of nest predation in the Dark-eyed Junco (*Junco hyemalis*) in two levels of disturbance and a control in the summers of 1983 and 1984. It found nest predation to be higher in the tephra-fall site than in either the blowdown forest site or the control site. The authors proposed that the higher rates of depredation were caused by brown nests standing out clearly in an area of nearly homogenous white tephra, which was not present in the control site, making nests more obvious to predators. It was further proposed that the higher survival rate in the blowdown zone, which also exhibited a layer of white tephra, was due to the absence of predators, especially ground squirrels, since they were unable to survive the high intensity of the blast that affected the blowdown forest (Andersen 1986).

Bird species composition in subalpine habitats on Mount St. Helens was compared to that of neighboring mountains in a study from 1982-1985. Species were compared at two altitudes, and the only differences found existed were at sites where trees had been scorched by a July

1980 release of hot volcanic gas. In other areas, they found no eruption-based effects and they concluded that areas not significantly altered by the eruption showed few long-term effects. The authors also examined the foraging guilds present and found that guild presence and distribution was associated with altitude and intensity of disturbance, and that the guild composition was similar to that of subalpine areas in other parts of the US (Manuwal et al. 1987).

In an area of heavy ashfall in eastern Washington, a study examining nesting behavior in Ring-billed and California Gulls found that the gulls left their nests during the ashfall event, but returned within days and many were successful in excavating their eggs from the ash debris. The gulls that were unable to do so built new nests nearby soon after. Even though the nesting success of this gull colony was well below average the year of the eruption, the gulls returned to the colony the following year and nested with normal success rates (Hayward, Miller and Hill 1982).

Finally, another study noted the disappearance of breeding Bullock's Orioles at Oak Creek Wildlife Recreation Area Headquarters in Yakima, Washington after approximately 5 cm of ash from the May 18th eruption fell there. Several color-banded individuals returned and resumed normal breeding after a few weeks, but many birds did not (Butcher 1981).

No studies exist, to my knowledge, of avian responses to eruptions of Volcán Arenal, nor of any biological responses to eruptions there.

Objectives

From the body of research regarding association between foliage height diversity and bird community structure, the differences between temperate and tropical niches and foraging guilds, and colonization strategies, I expected to see: 1) differences within study sites due to differing levels of structure, 2) different species at each latitude, because of local ranges of species, and 3) different guilds, based on seasonality, vegetative structure, and available food resources. My objectives were to 1) determine whether structurally similar sites between the two latitudes have different numbers of species per guild, and 2) to determine whether there were differences in bird abundance and diversity based on latitude or vegetative structural complexity.

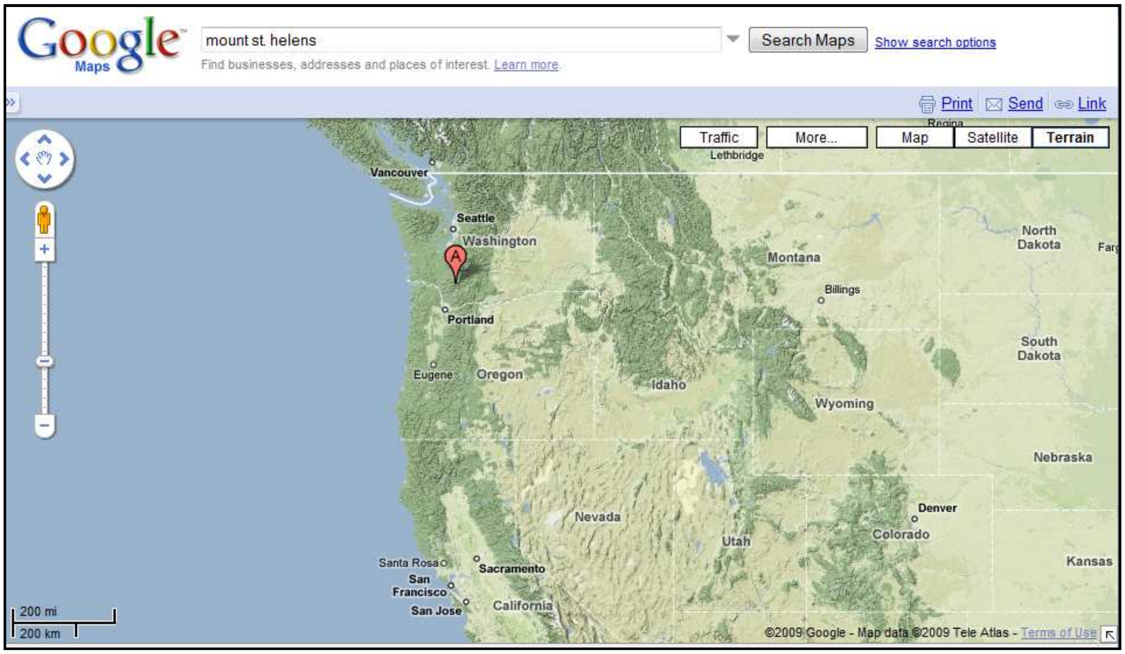
METHODS

Study Areas

Mount St. Helens

Contemporary Volcanic Activity

Mount St. Helens is a dacitic/andesitic stratovolcano, located in southwest Washington state, and the westernmost volcano in the Washington Cascades, located at 46.249 ° N and 122.162 ° W, with an elevation of approximately 2520 m (Fig. 1.1). The volcanic activity of the Cascade Range, including Mount St. Helens, is generated by the subduction of the Juan de Fuca plate beneath the Pacific Plate. After 123 years of inactivity, Mount St. Helens reawakened in the spring of 1980, with a climactic eruption on May 18th. This eruption began with a 2.5 km^3 landslide (the largest in recorded history) of the mountain's northern flank after a rapidly growing magma dome destabilized the slope. As this massive slide fell, it released the pressure on the magma chamber, causing a sudden depressurization, which unleashed a massive lateral blast. This blast rapidly overtook the debris slide and removed, leveled, uprooted, or scorched about 570 km^2 of forest. As the eruption progressed, dozens of pyroclastic flows descended from the mountain's vent onto the plain formed between the mountain and Spirit Lake. After this plain cooled, it became (and continues to be) a site of intense research into the biological and geological processes at play in the area, even though intermittent eruptive activity continues to this day, though is largely confined to within the crater (Dale, Swanson and Crisafulli 2005, pp 29-34, C. Crisafulli, pers. comm.).



mount st. helens

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Figure 1.1. Google Maps image of Mount St. Helens. ©2009 Tele Atlas (Google Maps 2009).

Climate

The climate of the northwestern United States where Mount St. Helens is located is temperate moist maritime, and the average annual rainfall in the Mount St. Helens area is 2373 mm, as measured at Spirit Lake before the 1980 eruption (Dale, Swanson and Crisafulli 2005, p 19). Much of the pumice plain, where research for this study was conducted, is covered intermittently in snow from mid-September to May. Average daily temperatures range from -2 ° C in January to 16 ° C in July, and the longest day of the year is 15 hours, 47 minutes, while the shortest is 8 hours, 36 minutes (Dale, Swanson, and Crisafulli 2005, pp 18-20, US Naval Observatory 2009).

Conservation

Much of the land affected by the May 18th, 1980 eruption of Mount St. Helens was owned either by the US Government and administered by the Gifford Pinchot National Forest, or Weyerhaeuser Inc., a private timber company. On Weyerhaeuser property, salvage logging was rapidly planned, and large swaths of land were soon logged and replanted. At the same time, the US Forest Service received a large volume of comments from scientists and members of the public, recognizing the value of the area for scientific and recreational purposes. This led Congress to pass the Mount St. Helens National Volcanic Monument Act, which created the Mount St. Helens National Volcanic Monument in 1982. This protection encompassed Mount St. Helens, the pumice plain, and large areas of blown-down and scorched forest, and undisturbed late-seral forest for a total of 43,300 hectares. However, within some of the blast area, outside of the Congressionally-created Monument, the US Forest Service did conduct reforestation efforts that included salvage logging and replanting (Dale, Swanson and Crisafulli 2004, pp282-283).

Study Sites

All four study sites at Mount St. Helens were located on the pumice plain located between the crater and Spirit Lake to the north at an altitude of approximately 1100 m. Two of the sites were located away from significant permanent stream channels and other sources of water, and were termed “upland” sites. By contrast, the other two sites closely followed existing stream channels and were termed “riparian.”

The two upland transects surveyed were each 800m in length and ran east to west across the pumice plain, and were known as Transect C and Transect D. The two transects were parallel to one another and were 500m apart. Riparian transects, by contrast, ran in a generally south to north direction and deviated from a straight line in order to follow the path of small (2-3m), naturally-occurring stream channels. The Willow Springs riparian transect followed Willow Springs Creek, while the Spirit Lake transect crossed a large seep and wetland area. The Willow Springs transect was 500m in length, while the Spirit Lake transect was 250m long.

In the upland study sites, vegetation was sparse and consisted of several herbaceous plant species and low densities of small willows and conifers. The most commonly occurring species were prairie lupine (*Lupinus lepidus*), penstemons (*Penstemon cardwellii.*), and paintbrushes (*Castelleja spp.*). Generally, vegetation in the upland sites was less than 50cm high and the scattered woody plants were typically less than 2 m in height. The riparian sites, by contrast had dense thickets of Sitka willow (*Salix sitchensis*) and alder (*Alnus rubra*, *Alnus crispa*), which were up to 6m tall on the Willow Springs site and up to 8m tall on the Spirit Lake site. In addition to the alder and willow growing at the Spirit Lake site, several large cottonwood trees, up to 12 m tall, were also present.

All four transects were surveyed six times from June 24th to July 18th, 2008 during the hours of 0600-1100. Birds were sampled using a line transect survey method, with distance along transect, perpendicular distance from transect, behavior, and height above ground recorded. Line transect sampling followed Burnham, Anderson and Laake (1980).

Volcán Arenal

Contemporary Volcanic Activity

Volcán Arenal is located at the northernmost point in the Tilarán mountain range of Costa Rica, latitude 10.471 ° N, longitude 84.722 ° W (Fig. 1.2). The surrounding terrain is approximately 500m in elevation, while the summit of the volcano is approximately 1695 m. The Tilarán mountains form a chain of volcanic activity that has migrated northwest since the late Pleistocene. This activity is fueled by subduction of the Cocos Plate by the Caribbean Plate. Volcán Arenal was dormant in recent history until it reawakened with an explosive eruption in 1968. This eruption, which lasted from July 29th to July 31st, opened several large summit craters and created a significant westerly blast, burning a large area of forest and devastating the towns of Pueblo Nuevo and Tabacón. A subsequent eruption in October 1968 deposited a large lava flow along the north edge of the 1968 blast. Many subsequent eruptions of lava and pyroclastic flows have deposited volcanic materials on the western flank of the volcano, including a lava flow in 1992 which extended toward the southern edge of the 1968 blast zone. On August 23, 2000, an atypically large pyroclastic flow descended the northeast flank of the volcano toward

Cedeño Lake. Eruptive activity at Volcán Arenal continues today, with primary activity concentrated on the southwest flank.

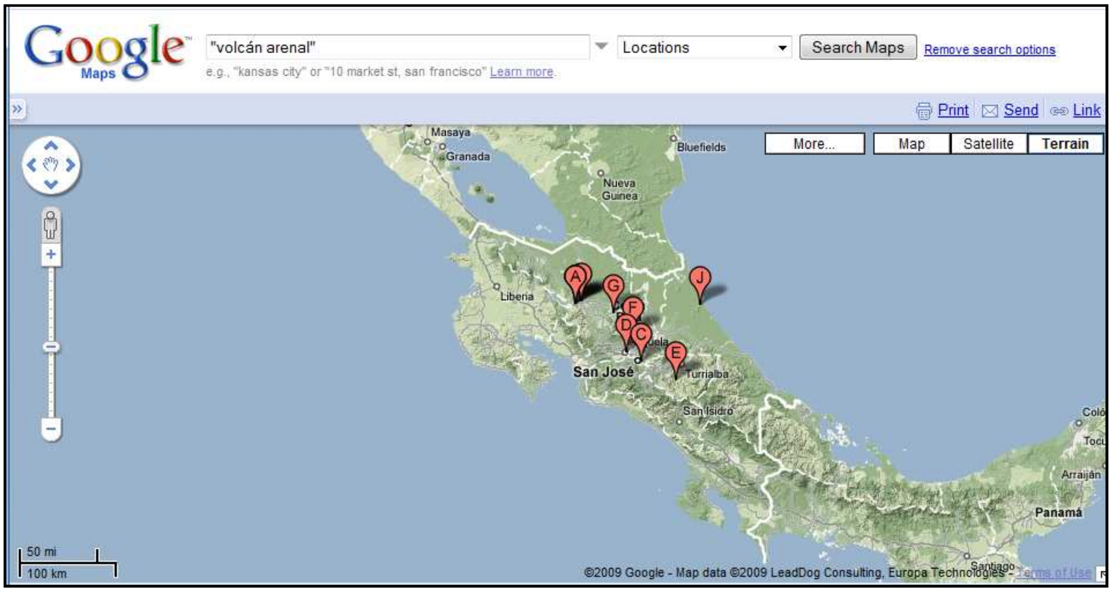

Figure 1.2. Google Maps image of Volcán Arenal. Volcán Arenal is Point A. © 2009, LeadDog Consulting, Europa Technologies (Google Maps 2009).

Climate

The study sites at Volcán Arenal are located in the Premontane Wet Life Zone, according to the Holdridge Classification System. Rainfall in the Volcán Arenal region varies between 2000 to 6000 mm/year, but the closest point of measurement, in the Caño Negro watershed on Arenal's southwest flank, records an annual rainfall of approximately 4000 mm. Pre-eruption vegetation in the area of the study sites was largely tropical moist forest. Vegetation in this area was heavily altered in some areas before the 1968 eruption, primarily for use as cattle pasture (Aylward, Echeverría, and Barbier 1995), and much of the area outside of the national park and tourist areas remains in this use today (personal observation). The annual temperature in the Arenal area ranges from 19 to 28 ° C. Day length in the Arenal area ranges from 11 hours, 31 minutes to 12 hours, 44 minutes (Aylward, Echeverría, and Barbier 1995, US Naval Observatory 2009).

Conservation

Much of the area damaged in the 1968 eruption of Volcán Arenal, along with areas considered in imminent danger from further eruptions, were acquired by the Costa Rican Government as the Arenal Forest Reserve in 1969 (Legislative Assembly of Costa Rica 1972). Even so, development of the surrounding area continued fairly rapidly. The area became a target of conservation interest in the 1980s, and the Arenal-Monteverde Protected Zone was created after a 1980 report from the non-profit Tropical Science Center established the area's conservation importance and suggested that a national park be created. This did not stop development, though the Monteverde Conservation League began purchasing small parcels for conservation (Aylward, Echeverría, and Barbier 1995). By 1991, tourism to the area was growing rapidly, and the importance of a more intensive regulatory framework became clear. In September 1991, Arenal Volcano National Park was created by presidential executive decree through Costa Rica's Ministry of Natural Resources, Energy and Mines (MIRENEM) (MIRENEM 1991). Since then, the park has been substantially expanded through another executive decree in October 1994 and renamed Arenal National Park (MIRENEM 1994). Management of the park has since been transferred to the National System of Conservation Areas (SINAC), a division of the Ministry of Environment and Energy (MINAE), after government restructuring in 1995 (Sánchez-Azofeifa et al. 2003).

Study Sites

Four study sites were established on the flanks of Volcán Arenal. One was on the northeast side and was located on a 2000 pyroclastic flow near the Los Lagos resort. The other three study sites were located on the northwest flank. One of these three sites was located on the 1968 lava flow at the privately-owned Arenal 1968 overlook and trail system, and the remaining two were located within Arenal National Park---one in the 1968 pyroclastic blast zone, and the other was located on a 1992 lava flow.

At each study site at Volcán Arenal, two to six point count stations were established, based on the number that could fit within each relatively homogenous habitat type, with the 50 m boundary encompassing only the target habitat type. Four points were established at the Los Lagos study site, four at the Arenal 1968 site, six at the 1968 lateral blast site, and two at the 1992 lava flow site.

Each study site was surveyed four times, and every point was sampled during the visit, using a 10-minute, 50 m -radius point count method adapted from Ralph et al. (1991). Distance to each individual bird was noted, and flyover birds were recorded separately. Surveys were conducted between December 6th and December 11th, 2008, from 700-1700hrs. Surveys were not stopped after the normal morning cutoff point since birds did not show a pronounced morning activity pulse. Additionally, heavy showers frequently made morning surveys impossible. At all study sites, whether at Volcán Arenal or Mount St. Helens, surveys were conducted in a random order to prevent biases.

At Mount St. Helens, all birds observed and recorded along the transect line were included in subsequent analyses. To make the data more comparable between Volcán Arenal and Mount St. Helens study sites, data from each point count station were combined at each of the Volcán Arenal study sites. Study sites at each study area were labeled 1-4 in order of increasing structural complexity, with 1 being the least structurally complex and 4 the most (structural complexity was visually estimated, taking into account the height, density and extent of vegetative cover). This designation was also preceded by "MSH" for Mount St. Helens sites and "VA" for Volcán Arenal sites to further aid in identification. At Mount St. Helens, Transect C (1) was determined to be the simplest, followed by Transect D (2), then the Willow Springs Transect (3), and finally, the Spirit Lake Transect (4), which was most structurally complex. At Volcán Arenal, the Los Lagos site from 2000 (1) was determined to be the simplest, followed by the 1992 lava flow site in Arenal National Park (2), then the Arenal 1968 lava flow (3), and finally, the Arenal 1968 blast zone (4).

Data Trimming

Since surveys performed at Mount St. Helens recorded all species observed within the transect length, regardless of distance from the transect, data at Mount St. Helens was trimmed to only include observations within 50 m perpendicular distance to either side of the transect line. This data trimming made the Mount St. Helens data more comparable to the Volcán Arenal data, which only recorded birds observed within 50 m of the point count.

To best sample bird usage of each habitat, further trimming was conducted with the goal of only including landbird species that bred in the general study area in the analysis. To accomplish this, all non-landbird species were excluded from the dataset, because too few individuals were observed to be able to draw any meaningful conclusions. Additionally, the way these species used the habitat differed from landbirds. Some species, such as vultures and guans (observed at Volcán Arenal), used resources in a distinctly different manner than did the landbirds present there.

Additionally, all recorded flyover birds at Volcán Arenal were excluded from the dataset, as many appeared to be passing over the study areas en route to adjacent forest habitat. Aerial foragers, such as swallows, were also excluded, since it was unclear if the insects they were foraging on originated from the study site. Flyover birds were also excluded at Mount St. Helens, though in a slightly different manner. Observations of birds flying at a height of more than 12 meters were excluded, with the exception that detections of Horned Larks (*Ermophila alpestris*) were included, regardless of height, since this species exhibits a towering flight song as part of its territorial behavior, and it frequently attains altitudes as high as 50 m when doing so (Ehrlich, Dobkin and Wheye 1988, p 396).

At Mount St. Helens, breeding was presumed of species present that were not classified as a flyover birds and had available nesting habitat. For example, species that utilize cliffs, tree cavities, or large trees were excluded from the analysis because no such habitat was present within the study site. This coarse approach may have included some species that were not actually breeders, and were instead post-breeding dispersers, such as Rufous Hummingbirds (*Selasphorus rufus*).

While most species detected at Mount St. Helens were considered breeders because most temperate species breed within the same time period, this was not the case at Volcán Arenal, especially since many of the species observed were overwintering North American migrants. The only effort made to distinguish between breeding and non-breeding species was to exclude these North American migrants, while assuming that all resident bird species, while perhaps not breeding at the time of my surveys, do breed in the area at some time during the year. Migrant/resident status was determined from Stiles and Skutch (1989), and where both migrant and resident populations occurred, it was assumed that birds observed were of the resident population.

Guild Classification

Taxonomy and nomenclature for birds observed at both study sites followed the AOU Checklist 7th Edition (2008). Each species was classified by foraging guild, based on its primary diet and what vegetation type or other substrate it uses for foraging. Diet and preferred foraging substrate were determined using Stiles and Skutch (1989) for birds at Volcán Arenal and Ehrlich, Dobkin and Wheye (1988), with supporting material from Cornell University's online Birds of North America (BNA) reference material (Cornell Laboratory of Ornithology 2009) for species found at Mount St. Helens. Where such accounts conflicted, for species at Mount St. Helens, secondary diet information from BNA, along with personal knowledge of the species, was used to aid in classification decisions.

Data Analysis

Accumulation Curves and Total Species Estimate

I created species accumulation curves, plots of the number of species observed as a function of the number of individuals observed, for each study site by combining the data from all surveys at each site. These curves were generated to gain an understanding of how completely each site was surveyed for avian community composition. If the accumulation curve displayed a clear asymptote in number of species observed, regardless of how many more individuals were examined, then a study site was considered to have been surveyed thoroughly. However, if the number of species continued to increase as more individuals were observed, with no clear asymptote, then it was considered a sign that the site had not been adequately surveyed and there were likely still more species present but not detected. Sites with incomplete accumulation curves were included in further analyses, but conclusions were drawn with these limits in mind, and all graphs resulting from these analyses were created with open (not colored) columns to identify these sites as such. In addition to creating the accumulation curve, I also calculated Chao's Estimator through EstimateS 8.0 (Colwell 2006) to estimate the actual number of species present at each study site.

Frequency Distributions

Percent frequency distributions of species at each study site were determined by calculating the percentage of the total individuals that each species represented relative to the total number of birds observed. These distributions are useful in determining how species compare to one another in terms of abundance. For instance, more diverse tropical communities would theoretically have more species that are proportionally less common. Sites determined to be incomplete based on the accumulation curves described above were included since these graphs are useful in describing the distribution of species present in the sites.

Descriptive Statistics

I calculated the following descriptive statistics for each site: number of individuals observed, species richness, Shannon-Weiner Diversity Index, evenness, and Margalef's Index. These descriptive analyses compare the most basic statistics across all sites, giving a general impression of the composition and diversity of bird assemblages at each site. All of these statistics were calculated using Microsoft Excel formulas. Guild and family richness were also plotted.

Community Comparison Indices

Sites at each latitude were compared to one another, using the Sorenson Classic Index and the Morisita-Horn Index. This analysis was first performed using the species of birds present, and then compared again using foraging guilds, and finally families. Next, sites were compared across latitudes, using all Mount St. Helens sites, but only the two at Volcán Arenal that had complete accumulation curves (VA2 and VA3). These analyses allowed me to examine which affected diversity more: vegetative diversity and foliage height diversity (if changes in complexity had more effect than latitude), or some inherent difference between temperate and tropical (in which case I would expect changes in latitude to have more of an effect). These indices were calculated using EstimateS 8.0 (Colwell 2006).

General Notes

Research at Mount St. Helens was conducted as part of a long-term monitoring project of the Forest Service on permanently established transects. Members of the public were required to stay on trails and did not venture near transects. Other researchers were also excluded from the transect area while surveys were taking place. This strongly contrasts to the survey setup at

Volcán Arenal. Research at Arenal was conducted exclusively for this project, and survey points were established exclusively in publicly-accessible areas. Even so, interference by members of the public was very limited in the VA1 and VA3 study areas. However, large tourist groups frequented the study sites in VA2 and VA4, which were located on or near public access trails. Every effort was made to avoid conducting surveys while these tourist groups were present. However, this was sometimes impossible, and disturbance may have been a factor at these sites.

In addition to the logistical constraints presented by the survey sites at Volcán Arenal, I also faced challenges in attempting to make the Mount St. Helens and Volcán Arenal data comparable. Due to limited time and resources to conduct the measurements and setup for line transect surveys, plus unstable and unsafe footing at several sites, point counts were established at Volcán Arenal in contrast to the line transects used at Mount St. Helens. This caused the two datasets to be fundamentally different in nature, something that was only exacerbated by the fact that each site at Mount St. Helens was surveyed six times, while the sites at Arenal were surveyed just four times. Still further complicating the analysis, many species had too few observations to be analyzed with the DISTANCE program to determine coefficients of detectability, and a blanket 50 m trim was used instead.

RESULTS

Accumulation Curves and Total Species Estimate

The accumulation curves for each study site at Mount St. Helens show a fairly distinct asymptote. Only the MSH1 site shows a possibility of a weakness in the asymptote. Accumulation curves from the Volcán Arenal sites showed distinct asymptotes only at the VA2 and VA3 sites, while the VA1 site showed little tendency toward an asymptote, and the VA4 site showed none at all (Figs. 2.1 and 2.2, notice that overlap between accumulation curves obscures some lines). All species estimates generated with Chao's Estimator show a higher mean value than the number of species observed. In addition, the observed values are also lower than the lower bounds of the 95 percent confidence intervals generated (Table 1.1).

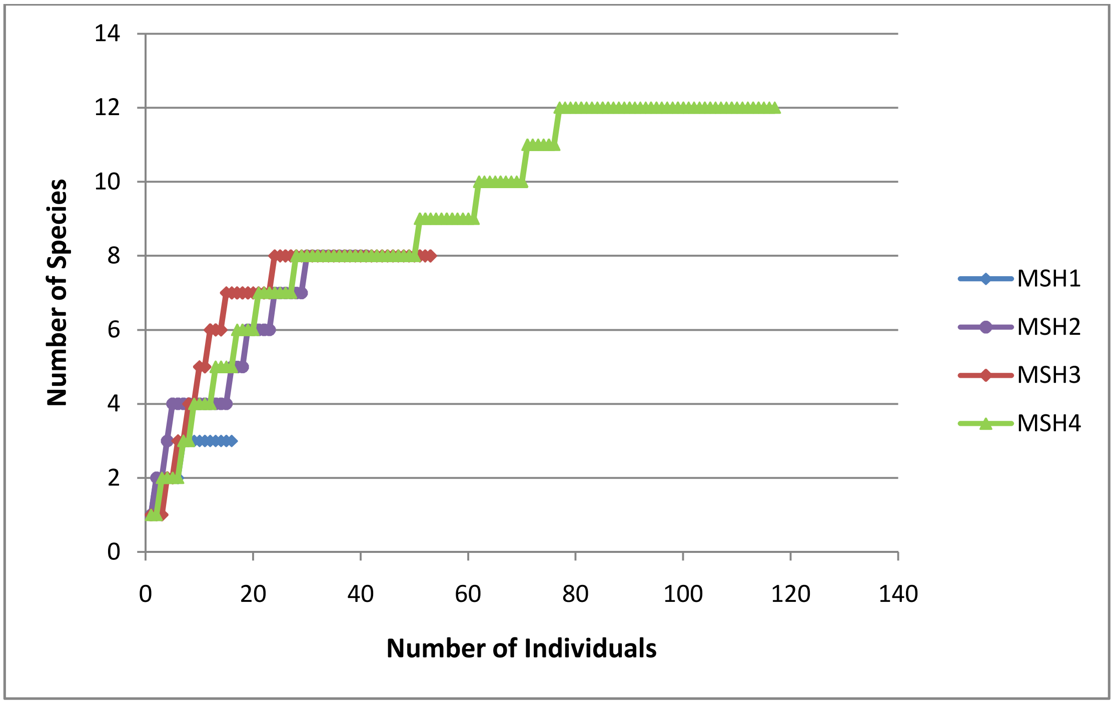

Figure 2.1. Accumulation curve of bird species present at four study sites on the Mount St. Helens pumice plain, summer 2008.

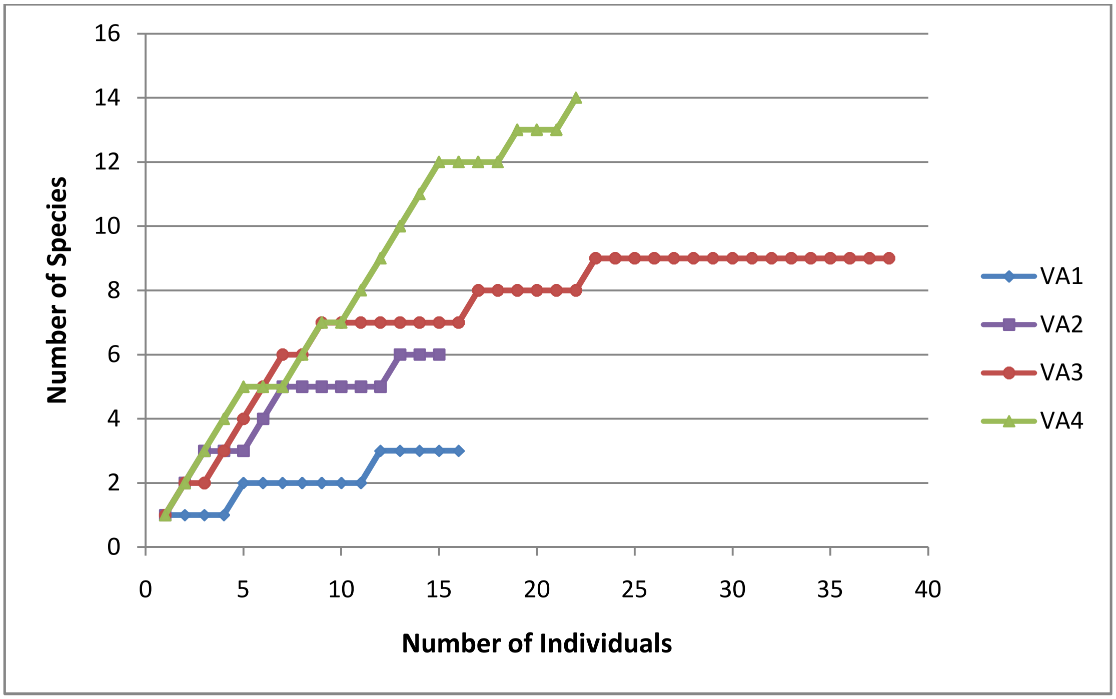

Figure 2.2. Accumulation curve of bird species present in four study sites at Volcán Arenal, Costa Rica, December 2008.

Table 1.1. Predicted number of species at each study site at Mount St. Helens, USA and Volcán Arenal, Costa Rica, as calculated with Chao's Estimator. Mean values are shown, along with 95 percent confidence intervals and actual numbers observed.

Site	Sobs	Mean	Lower	Upper
MSH1	3	7.48	7.39	9.18
MSH2	8	10.00	9.79	13.16
MSH3	8	13.00	13.00	13.00
MSH4	11	11.94	11.81	13.79
VA1	3	10.03	8.54	20.98
VA2	6	22.00	19.50	36.94
VA3	9	15.86	13.47	31.79
VA4	14	18.92	16.74	33.00

Frequency Distributions

Frequency distributions of study sites were examined for all sites, despite the incompleteness of several of the accumulation curves. The distributions from incomplete sites still showed trends in highly dominant species, even if they did not properly account for all species present. In several of these surveys, a distinct “fat tail” is noted. Overall, most distributions show a fairly gradual rate of taper, with the exceptions of the MSH1 site at Mount St. Helens and the VA1 site at Volcán Arenal (Figs 3.1 and 3.2).

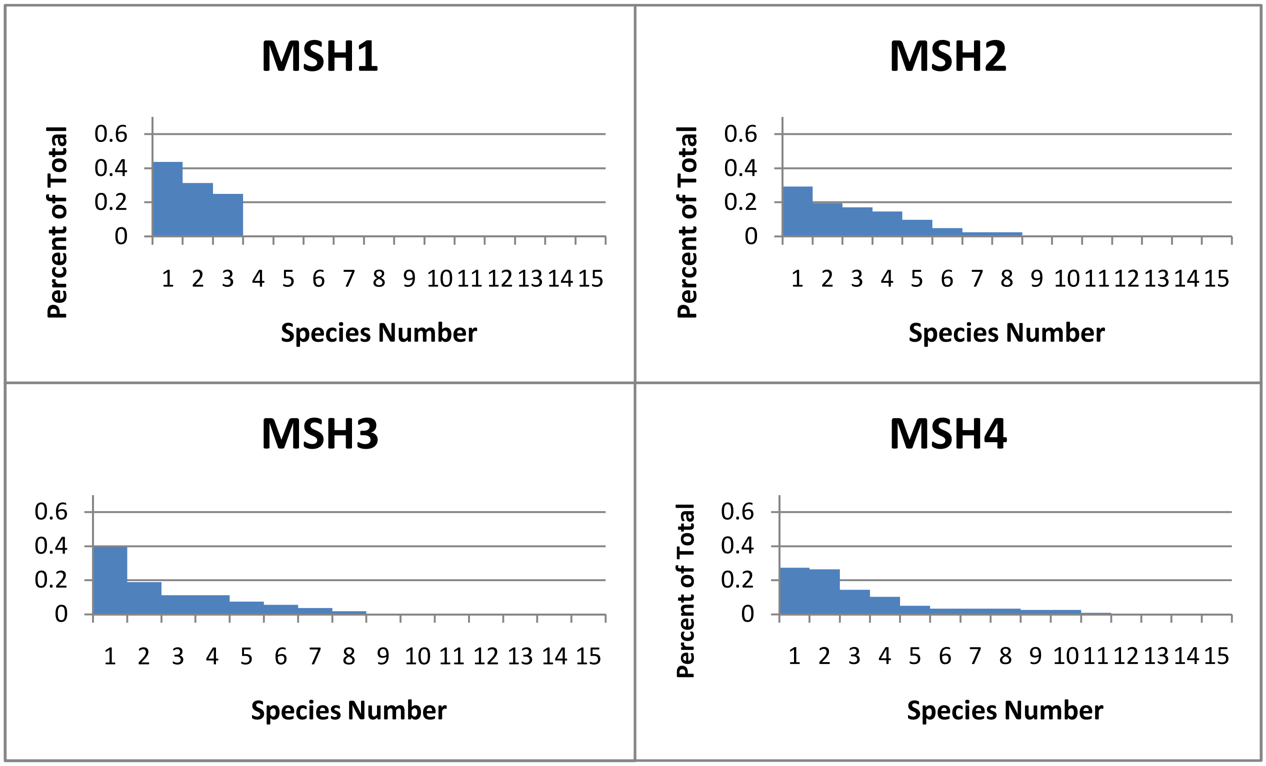

Figure 3.1. Frequency distributions of bird species present at Mount St. Helens. Species are ranked from most abundant to least abundant on the x-axis, while the percent of the total individual birds observed this species accounts for is on the y-axis.

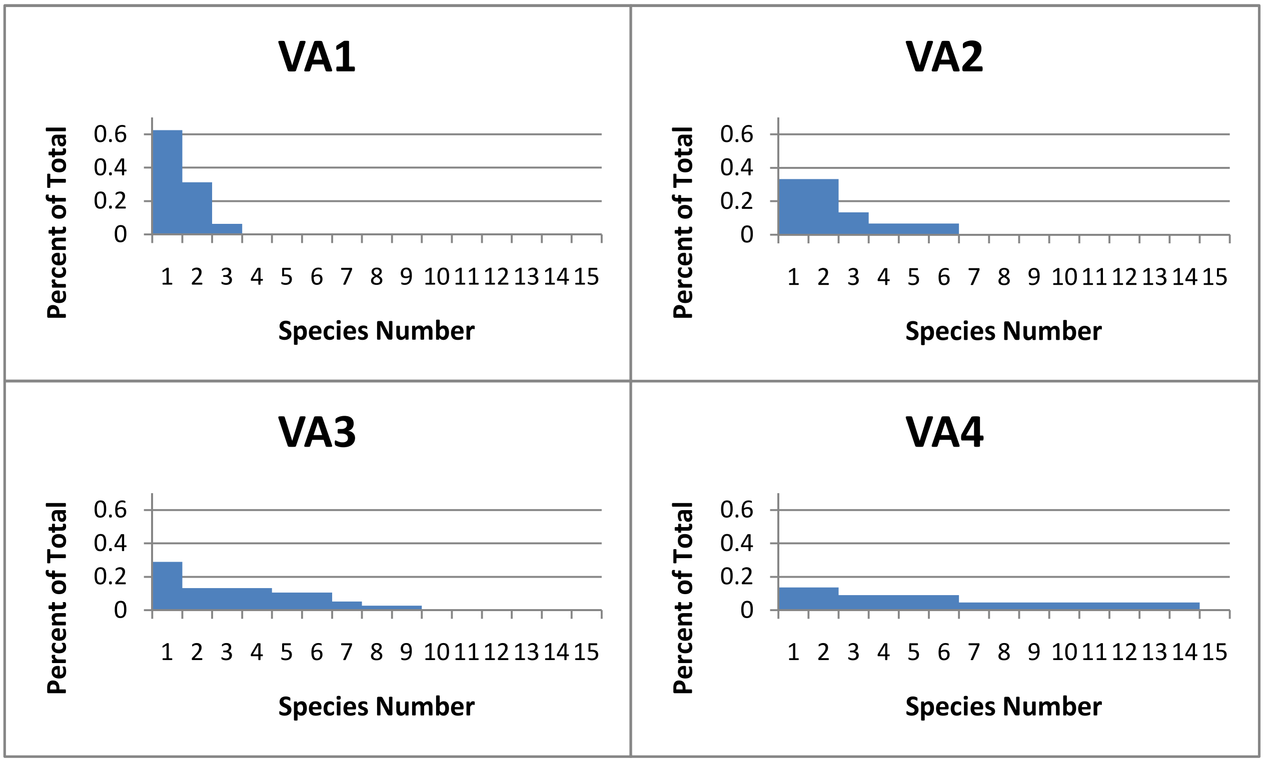

Figure 3.2. Frequency distributions of bird species observed at four study sites at Volcán Arenal, Costa Rica, December 2008. Axes are as in Fig. 3.1.

Descriptive Statistics

I observed a total of 13 species of birds that met criteria for site usage at Mount St. Helens, and 19 species at Volcán Arenal. I found that the vegetatively simple sites at both latitudes had the lowest numbers of species, though accumulation curves, especially for Volcán Arenal, were frequently incomplete. 14 criteria-meeting species were observed at the most vegetatively complex site at Volcán Arenal, the highest of any site, and the accumulation curve indicates far more species may be present. The most complex site at Mount St. Helens, by contrast, had only

11 criteria-meeting species, which was the highest number of species observed at any site there. Likewise, the highest number of individuals recorded at Mount St. Helens was also in the most vegetatively complex site, while the highest number of individuals observed at Arenal was in the second-most complex site. Other measures of diversity showed a similar positive relationship with vegetative complexity. Complete descriptive results appear in Figs. 4.1-4.3. In addition to calculating species richness, I also calculated the richness of foraging guilds and families present at each site, and found nearly twice as many foraging guilds at the most complex site at Volcán Arenal compared to the most complex Mount St. Helens site (Fig. 5.1).

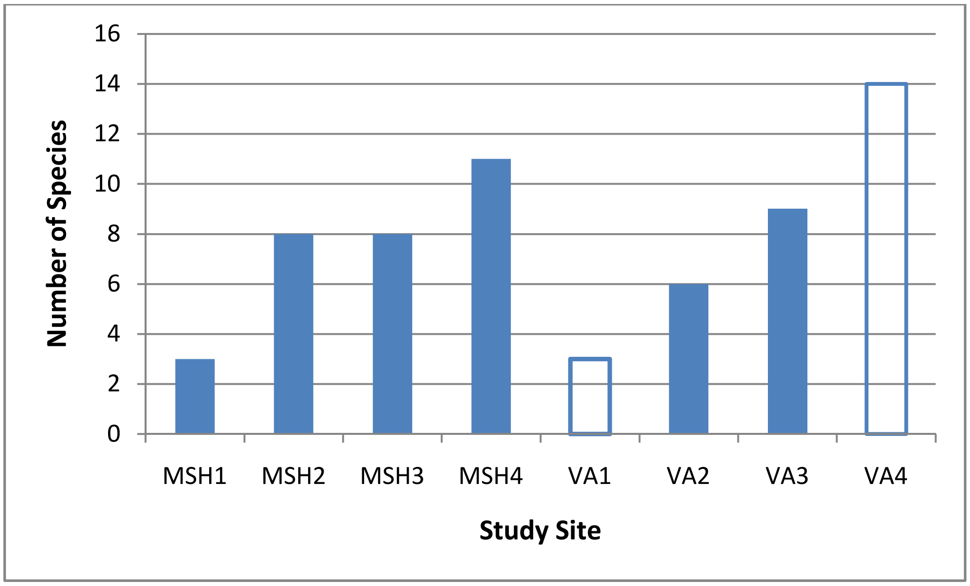

Figure 4.1. Number of species present at each study site at Mount St. Helens, USA and Volcán Arenal, Costa Rica.

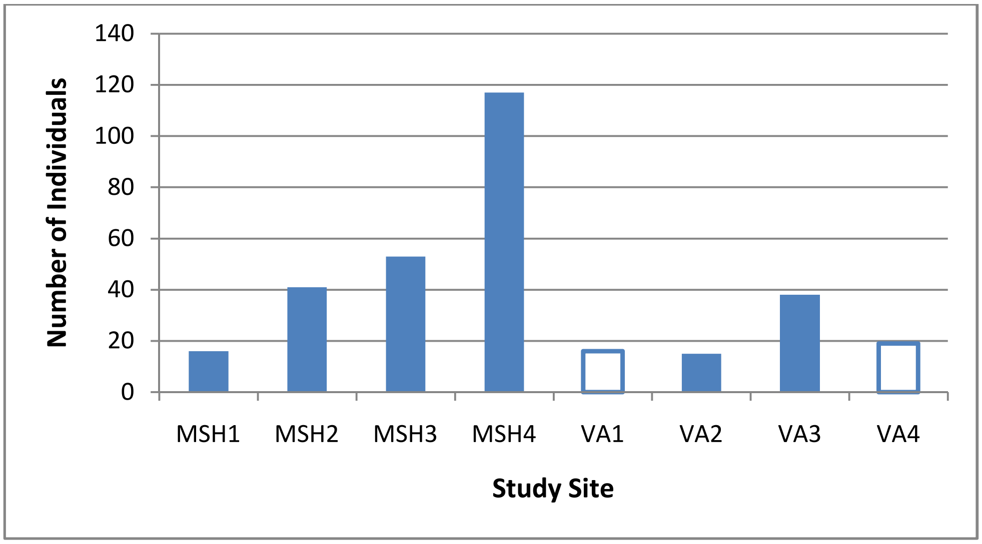

Figure 4.2. Number of individuals present at each study site at Mount St. Helens, USA and Volcán Arenal, Costa Rica.

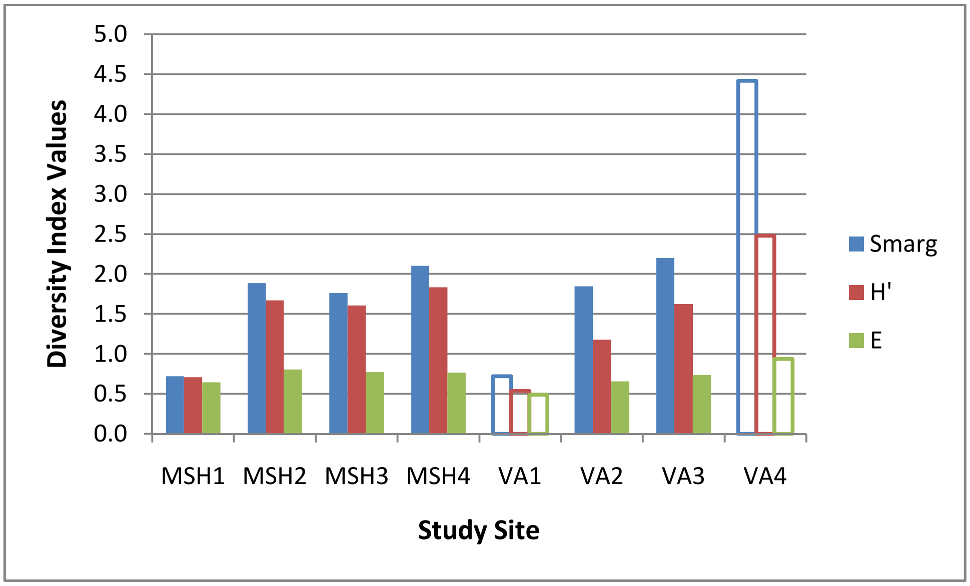

Figure 4.3. Margalef's Index, Shannon-Weiner Diversity Index, and evenness for each study site at Mount St. Helens, USA and Volcán Arenal, Costa Rica.

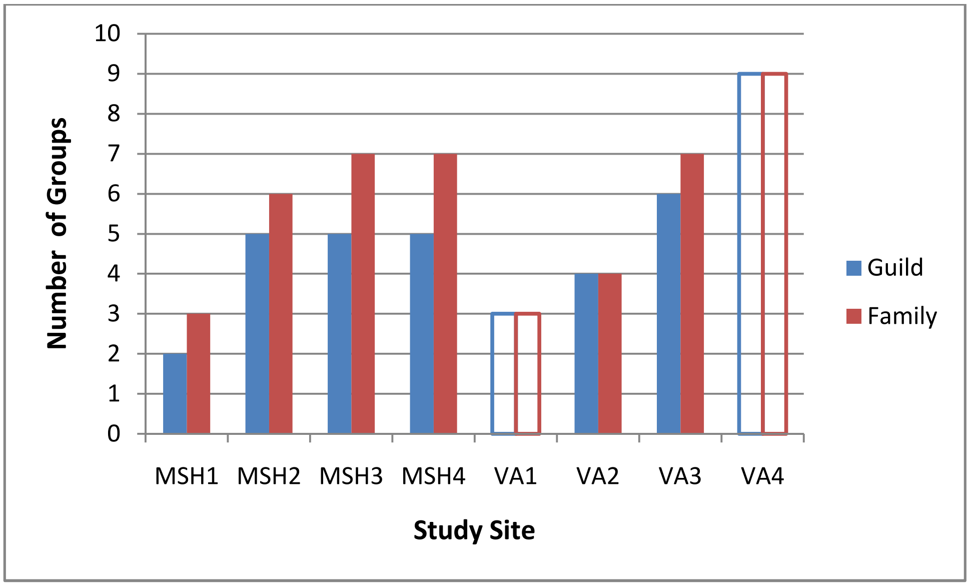

Figure 5.1. Number of foraging guilds and families observed at each study site at Mount St. Helens, USA and Volcán Arenal, Costa Rica.

Community Comparison Indices

Similarity of species was found to be greatest when habitats of similar levels of vegetative complexity were compared at Mount St. Helens, especially when the Morisita-Horn quantitative index was used (Tables 2.1, 2.2). The Sorenson qualitative index showed more variation. The vegetatively simple upland transects MSH1 and MSH 2 were found to be the most similar with the Morisita-Horn index, while vegetatively complex MSH3 and MSH 4 were also found to be very highly similar. At the Volcán Arenal sites, however, no such distinct trend existed. The simplest site was most different from all others, with the second-most complex site sharing the most diversity with the other two (Tables 3.1, 3.2). There were no criteria-meeting species shared between Mount St. Helens and Volcán Arenal, meaning that all of the indices of site similarity between the two latitudes were zero.

In addition to being most similar in terms of species composition, the Mount St. Helens sites with the greatest vegetative similarity also were the most similar in terms of guild composition (Tables 2.1, 2.2). As with species composition, guild composition also showed a much weaker relationship with structure at Volcán Arenal than at Mount St. Helens. The vegetatively complex sites VA3 and VA4 showed more similarity to each other to the other sites, while the simplest sites VA1 and VA2 also showed slight similarity (Tables 3.1, 3.2). When the sites at Mount St. Helens were compared with the Volcán Arenal sites that showed complete species accumulation, the Mount St. Helens sites only shared guilds with the VA3 site, and the values of similarity were much less than any of the values when any site was compared with others at the same latitude (Tables 4.1, 4.2).

Finally, families of birds present were also compared. Like the previous two comparisons, the sites that were most vegetatively similar at Mount St. Helens also showed the greatest similarity in families present, especially when measured with the Morisita-Horn index (Tables 2.1, 2.2). The same relationship appeared this time at Volcán Arenal as well, though it was much weaker and only appeared when the Sorenson qualitative measure was used (Tables 3.1, 3.2). When the Mount St. Helens families were compared to the Volcán Arenal families, similarity was very high in some cases, especially when complex sites were compared across latitudes. In some cases, these values were higher than when a simple site was compared to a complex site at the same latitude. The highest such correlation occurs when MSH4 is compared to VA3 qualitatively. The 0.7 value of similarity that results is higher than when MSH4 is compared to

MSH 1 (0.6) and when VA3 is compared to VA1 (0.4). The quantitative values generated by the Morisita-Horn comparison also show a similar relationship (Tables 4.1, 4.2).

Table 2.1 Comparison of similarity of bird species, foraging guilds, and families between study sites at Mount St. Helens, USA, using the Sorenson Classic Index. Species is listed first, followed by foraging guild and family in descending order.

Study Site	2	3	4
1	0.545	0.545	0.429
2	X	0.750	0.632
3	X	X	0.737
1	0.571	0.571	0.571
2	X	0.800	0.800
3	X	X	0.800
1	0.667	0.600	0.600
2	X	0.769	0.769
3	X	X	0.857

Table 2.2. Comparison of similarity of bird species, foraging guilds, and families between study sites at Mount St. Helens, USA, using the Morisita-Horn Index. Species is listed first, followed by foraging guild and family in descending order.

Study Site	2	3	4
1	0.837	0.329	0.243
2	X	0.360	0.257
3	X	X	0.828
1	0.984	0.442	0.375
2	X	0.422	0.365
3	X	X	0.984
1	0.899	0.383	0.357
2	X	0.454	0.439
3	X	X	0.876

Table 3.1. Comparison of similarity of bird species, foraging guilds, and families between study sites at Volcán Arenal, Costa Rica, using the Sorenson Classic Index. Species is listed first, followed by foraging guild and family in descending order.

Study Site	2	3	4
1	0.222	0.333	0.353
2	X	0.400	0.400
3	X	X	0.522
1	0.571	0.444	0.500
2	X	0.400	0.615
3	X	X	0.667
1	0.571	0.400	0.500
2	X	0.364	0.462
3	X	X	0.750

Table 3.2. Comparison of similarity of bird species, foraging guilds, and families between study sites at Volcán Arenal, Costa Rica, using the Morisita-Horn Index. Species is listed first, followed by foraging guild and family in descending order.

Study Site	2	3	4
1	0.279	0.327	0.265
2	X	0.515	0.410
3	X	X	0.404
1	0.448	0.489	0.286
2	X	0.734	0.484
3	X	X	0.624
1	0.444	0.499	0.383
2	X	0.753	0.648
3	X	X	0.644

Table 4.1. Comparison of similarity of bird foraging guilds and families between selected study sites at Mount St. Helens, USA and Volcán Arenal, Costa Rica, using the Sorenson Classic Index. Foraging guild is listed first, followed by family.

Study Site	2	3
1	0.000	0.250
2	0.000	0.182
3	0.000	0.182
4	0.000	0.182
1	0.000	0.400
2	0.000	0.615
3	0.182	0.571
4	0.182	0.714

Table 4.2. Comparison of similarity of bird foraging guilds and families between selected study sites at Mount St. Helens, USA and Volcán Arenal, Costa Rica, using the Morisita-Horn Index. Foraging guild is listed first, followed by family.

Study Site	2	3
1	0.000	0.077
2	0.000	0.050
3	0.000	0.064
4	0.000	0.045
1	0.000	0.192
2	0.000	0.238
3	0.207	0.338
4	0.529	0.618

DISCUSSION

Accumulation Curves and Total Species Estimate

Evaluation of the accumulation curves suggests that most study sites were adequately sampled and most if not all members of the avifauna at those sites were detected. However, the survey effort at two of the Arenal sites and possibly at one of the MSH sites appeared to be less than needed to accurately measure community composition. At Mount St. Helens, the MSH1 transect data appears sparse but fairly complete from an examination of the 50-meter trimmed curve. However, when the accumulation curve from the unlimited plot is considered, a lower plateau appears, before the data suddenly rise, nearly doubling in the number of species. Whether the lack of these species appearing within the 50 meters is due to insufficient surveying or to unsuitable habitat for this species within the 50 m is unclear. All of the other accumulation curves at Mount St. Helens appeared to be relatively complete, with new species appearing to reach an asymptote within three-quarters of the total observations. Even so, many of the curves show a somewhat “stepped” appearance, with at least one lower plateau before starting to increase again.

Accumulation curves at Volcán Arenal, however, frequently showed less complete survey results. Data from the VA1 transect appeared to increase linearly in a pattern of several steps, while data from the VA4 site simply increased linearly, with a slope of 1 in many locations. Especially in the case of the VA4 site, this discrepancy was likely caused by the behavior patterns of the birds present. The majority of birds observed were associated with mixed flocks of several species, frequently containing many individuals of both resident and migrant species. Many times, these flocks contained several or many species not previously detected on the surveys. With these mixed flocks passing through only occasionally, it is to be expected that the accumulation curve is incomplete for this site, since it would likely take much more time to encounter enough flocks for all the species in the area to be represented. It is worth noting that this steep and highly incomplete accumulation curve comes from the site with the most highly developed structure in the area.

The results generated by Chao's Estimator, by contrast, indicate highly incomplete surveys at all study sites. Values show especially incomplete surveys at MSH1 and all of the Volcán Arenal sites. The most incomplete survey of all, according to Chao's Estimator was at the VA2 study site. Overall, these highly incomplete values are not unexpected, especially at Volcán Arenal, where rainy conditions frequently reduced bird activity levels.

Frequency Distributions

Although it was predicted that species in tropical latitudes would show a greater difference in distribution in common and rare species, and that there would be more rare species present in the tropics, this prediction appears incorrect. The only site that had a relatively steep drop-off from common to rare species were the MSH3 and MSH4 sites, the most complex sites at Mount St. Helens, which also displayed a fairly long “tail” of rare species. At other sites, declines seemed more gradual. Interestingly, the shape of the graphs for the simplest sites, MSH1 and VA1, were fairly similar and the most abundant bird in each occupied a similar foraging guild. While these sites, especially the Arenal site, may have been undersampled, it appears that the most common bird in each occupies a similar foraging guild: a terrestrial granivore or granivore/insectivore, which may have descriptive value for the resources present in habitats with very little structural complexity.

In general, the lack of smooth curves and no significant change in frequency distribution between common and rare species in the tropics suggests that a small sample size confounded results. This appears to be especially true for the VA4 site, which showed no curve in descent and never had more than three individuals of any species. This difference may be simply due to the highly incomplete accumulation curve. In other sites, however, the difference may be caused by other factors, such as fewer individuals or species using the volcanically disturbed area, or becoming disproportionately successful at using its resources.

Descriptive Statistics

The strong relationship between number of species present and habitat complexity makes sense from an intuitive point of view and also contributes further evidence to MacArthur's hypotheses regarding structural and vegetative complexity, and possibly also to his hypotheses on the availability of more niches. However, even though the number of species is greater in the most vegetatively complex tropical site than in the temperate one, other sites are relatively comparable and there is pattern of greater diversity in the tropics. Of course, several of the sites at Volcán Arenal had incomplete accumulation curves, and an increased survey effort at the Arenal sites may have yielded different results.

Like the number of species, the number of individuals increased markedly with habitat complexity, especially in the temperate zone. However, the numbers in the two highly complex tropical areas do not show a sharp increase, and in fact decrease markedly in the most complex site, and are only one-fifth the numbers observed in the temperate zone. Even with this much smaller number of individuals, three more species were observed than in the most complex temperate habitat. If the accumulation curve at this site were more complete, it would likely present strong evidence for greater diversity in the tropics.

Perhaps most notable is that the number of guilds observed in the most vegetatively complex site at each latitude varied greatly, especially when one considers the number of observations these guilds are drawn from. Having nearly twice the number of guilds in one fifth the number of birds observed suggests that this community is beginning to fit the pattern of tropical richness that others have described.

Community Comparison Indices

Species, Family and Guild Comparisons within Latitude

As one would intuitively suspect, the sites with the most similar vegetative composition showed the most similarity, especially in the temperate zone. Since the similarity held true with both qualitative and quantitative indices, not only does it indicate that the same species were occurring in similar habitat structures, but also that the relative abundances of these species was fairly similar. This suggests that a fairly predictable set of species occur in a fairly predictable abundance in the two types of temperate study sites. A similar relationship existed with guilds and families at sites in both latitudes. However, the contrast was much weaker at the Volcán Arenal sites. This suggests that more of the same species or guilds may be using a wider range of habitats or that the habitat types are more similar and may in fact make up a gradient of habitats. This latter explanation seems reasonable, as the primary difference in the vegetative structure at VA2 as compared to VA3 was that the tall shrubs at VA3 were denser and there was a greater ground cover of grasses. This has interesting implications in terms of plant recovery, because both these sites have a thick lava flow substrate, but VA3 is 24 years older than VA2. These findings suggest bird communities may utilize them in similar ways, despite their large age difference.

Guild and Family Comparisons Across Latitude

The family similarity seen across latitudes suggests there may be a correlation between vegetative complexity and bird diversity, as predicted by MacArthur, which crosses latitudes. In some cases, similarity between families was higher in similar habitat structures at different latitudes when compared with different structural complexities within latitudes. However, this never applied to guilds. This could mean that even within a family, different guilds have appeared at different latitudes to utilize the resources present. However, it could also indicate too fine distinction being made in foraging behaviors. Or, when viewed from an ecological perspective, both of these two things could be occurring. Consider for example the Horned Lark and the Variable Seedeater, both of which are dominant in the least structurally complex site in temperate and tropical latitudes, respectively. Both are granivores. Even though they were classified as belonging to different guilds (they belong to different families as well), it is possible that they actually perform very similar ecological functions. Both will forage on bare ground, even though the seedeater requires some structure for roosting and nesting, while the lark is almost never found in any vegetative cover more than a few inches tall.

Conclusions

The basic goal of this study was to investigate and describe the reassembly of bird populations in two latitudes after volcanic blasts defaunated the areas. Even though I was not successful in completely sampling all the survey sites at Volcán Arenal, I was still able to gain valuable information. My findings support MacArthur's hypothesis of increasing vegetative complexity leading to increased bird diversity. In addition, I found some evidence, even though highly limited, that bird diversity in volcanic blast zones may be higher in the tropics, especially in communities that have recovered enough to have a fairly high level of vegetative complexity. I found no species overlap and little evidence of overlapping guilds or evidence of one family or one guild having a dominating presence over both habitats. I did find, however, that certain species were dominant in each habitat, especially in the temperate zone, with Horned Larks dominating the vegetatively simple habitats and Yellow Warblers showing high abundance in the complex sites. In some cases, I found a high degree of family overlap between the two latitudes, even though guilds were highly different, which suggests either that families differentiate themselves into a variety of guilds to take advantage of different foraging opportunities at different latitudes, or that I failed to classify species in guilds that were ecologically meaningful.

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