

ABSTRACT

Title of Document: AVIAN COMMUNITY RESPONSES TO
ECOLOGICAL DISTURBANCE AND RECOVERY
AT MOUNT ST. HELENS, WA, USA

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Community assembly occurs through the complex interaction of local and regional processes which contribute to the differential colonization and extinction of species within a local site. Understanding these processes is of fundamental importance to ecology because it enables predictions for the trajectory of recovery in ecological systems following disturbance. In this dissertation I combined field studies of the Mount St. Helens bird community with historical and regional data to better understand the processes contributing to local assembly in a mainland community following large scale volcanic disturbance.

First, I applied a novel spatial approach to examine avian colonization patterns at Mount St. Helens and approximate the geographic extent of the region influencing local community assembly in the first thirty years of recovery. Despite the prevalence of regional sources, avian colonization of Mount St. Helens has occurred slowly over thirty years. By approximating ‘minimum source regions’ for local communities across time, I developed a new approach for examining the spatiotemporal dynamics of colonization and found that species from a broad geographic area extending beyond the Cascade mountains have colonized Mount St Helens. I then focused on the primary successional

habitat of the Mount St. Helens Pumice Plain to examine what ecological processes have contributed to avian community assembly. Testing multiple assembly hypotheses I found evidence of niche-based assembly through nestedness and habitat filtering but no support for competition-based assembly rules. Finally, I addressed the specific mechanism of local recruitment in maintaining populations of birds on the Pumice Plain by monitoring nest success across species. I found observed nest success lower than previously recorded in other habitats for several common ground-nesting and shrub-nesting species. I determined that in the absence of sufficient local recruitment, repeated colonization from the surrounding region may contribute to the persistence of some species on the Pumice Plain. Overall, my results found evidence of habitat filtering rather than interspecific competition in limiting early assembly and supported the importance of continued colonization processes drawing from a range of regional habitats.

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RECOVERY AT MOUNT ST. HELENS, WA, USA

By

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Dedication

To my husband Jerry, and to my parents Lida and Ron.

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First and foremost, I would like to thank my mentors, Bill Fagan and Charlie Crisafulli, from whom I have learned so much and without whom I could not have done this work. I am grateful to them both for their unfailing support and cannot put into words everything they have taught me. Throughout my time at the University of Maryland, Bill has mentored my development as a scientist, grounding my work and research perspective in the foundations of ecological theory. From defining interesting ecological research questions, to conducting rigorous research and conveying results effectively, Bill has demonstrated how to conduct exceptional research and pushed me to become a better scientist. Complementing Bill's guidance in understanding and participating in quantitative ecological research, Charlie Crisafulli provided invaluable support and assistance in developing a deep understanding of the Mount St. Helens system in which I conducted my dissertation research. He has demonstrated the management of complex field research projects and provided guidance and encouragement through the logistical details of field work as well as our ongoing analysis and collaborations. Both have provided me with wonderful opportunities for professional development, and I could not have asked for a better pair of mentors. I am also grateful for the University of Maryland faculty and other scientists who have served on my advisory committee and helped guide me throughout this process: Mary Ann Ottinger, Gerald Wilkinson, Irv Forseth, Nathan Kraft, Marjorie Reaka, and Bill Bowerman.

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Chapter 1 : Introduction

Community Assembly

The process of local community assembly is a central theme in community ecology. The goal of community assembly research is to determine the underlying mechanisms for patterns observed in local species assemblages in order to better explain and predict patterns observed in local diversity and species composition (Weiher and Keddy 2001). Community assembly has often been studied in the context of equilibrium. However, species composition patterns develop over time (Fernández-Juricic 2000) and the extent to which community assembly processes are detectable following disturbance is unclear (Drake et al. 1999, Stokes & Archer 2010). Understanding the structure of communities during ecological recovery is critical for biodiversity conservation efforts in the face of ongoing anthropogenic and natural disturbance (Cash et al. 2012).

Volcanic Disturbance

Though volcanic activity is an important source of natural disturbance around the world, few studies have examined the impact of volcanic disturbance on bird communities, particularly in a mainland context. Much of the existing work on avian responses to volcanic disturbance comes from Mount St. Helens following the 1980 eruption (Butcher 1981, Hayward 1982, Andersen & MacMahon 1986, Manuwal et al. 1987, Crisafulli and Hawkins 1998, Fairchild 2009). I am not aware of any other studies addressing longterm avian responses to eruptions in a mainland setting. However, there

are numerous examples of both short and long-term avian studies following volcanism from volcanic islands (e.g., Brattstrom 1956, Byrd 1980, Whittaker and Jones 1994, Dalsgaard et al. 2007, Petersen 2009, Drew et al. 2010, Bond 2012). Several studies have focused on impacts of tephra (solid material ranging from ash to pebble-sized rock) and tephra fall events and have demonstrated initial declines in avian diversity and abundance, and detrimental effects of tephra fall on waterbird nesting sites and breeding colonies. However, studies persisting multiple years have observed quick recovery of local breeding populations following these minor eruptive events. Long-term colonization patterns have also been studied in the context of volcanic islands with known historic eruptions, and led to Diamond's (1975) community assembly rules.

Mount St. Helens

Prior to the eruption in 1980, the area around Mount St. Helens was predominantly forested, a matrix of old-growth and managed coniferous forest. The 1980 eruption of Mount St. Helens was a major catastrophic disturbance comprising several processes which changed the local landscape. The major eruptive event began with a 5.1 magnitude earthquake on May 18, 1980 which caused the north face of the volcano to collapse (Swanson and Major 2005). The collapsed face of the volcano created the largest debris avalanche recorded, which flowed northeast and northwest and radically altered Spirit Lake and the North Fork Toutle River valley. The collapse of the north face of the volcano also released pressure on the volcano's magma body leading to a blast of superheated gas, rock and ash directed laterally across the landscape to the north of the volcano. This blast toppled trees and scorched aboveground life over 570

km² of land as well as depositing a layer of debris from sandy gravel to sandy silt, ranging in depth from 0.01 to 1.5 m. Following the blast, searing hot (300-850°C) pyroclastic flows surged from the crater for about four hours creating a vast sterile plain. In addition, tephra was ejected from the volcano in a vertical plume for approximately nine hours and deposited across the landscape, primarily to the east-northeast. Subsequent to the main May 18th event the area was influenced by additional pyroclastic flows, lahars (mudflows with volcanic debris) and tephra falls (Swanson and Major 2005). At the time of the eruption any birds present in the Blast Area, which included bird communities of winter residents, permanent residents and early migrants were immediately killed.

The 1980 eruption of Mount St. Helens created a patchwork of habitats which were identified by the types of disturbance they underwent during the eruption (Figure A1-1). The area identified as the Pumice Plain was most devastated by the eruption, being buried several tens to > 100m beneath the debris avalanche caused by collapse of the north face of the volcano, being hit by the laterally directed blast surge, and finally being buried under pyroclastic flows (Table A1-1). Though no life survived on the Pumice Plain, [non-avian] biological legacies were common in much of the Blast Area, where secondary succession ensued. The majority (approximately 370 km²) of about 570 km² along a 180° arc north of the mountain was designated as Blowdown Zone. In this area the lateral blast of the eruption removed, toppled, or scorched most aboveground vegetation, followed by tephra deposits typically 0.01-1m thick (Swanson and Major 2005). Beyond the Blowdown Zone, the Scorch Zone designates areas where the heat of the lateral blast killed above-ground vegetation, leaving a forest of standing dead trees.

These areas received shallower tephra deposits (typically 0.01-0.1 m deep). Beyond the Scorch Zone, areas to the east and northeast of the volcano were impacted primarily by tephra fall, and were identified as the Tephra Fall Zone. The creation of these different disturbance zones in the resulting post-eruption landscape provided an outstanding opportunity to study avian community assembly in a mainland context.

Previous Work

The majority of previous work on bird community responses to mainland volcanism have focused on secondary successional sites where there were residual components of the pre-disturbance community (although all birds present at the time may have perished), addressed short-term impacts of volcanic disturbance, and/or were conducted on volcanic islands. At Mount St. Helens, effects of volcanic disturbance on bird communities were primarily considered in terms of temporary effects in areas of tephra fall during the first fifteen years following the 1980 eruption (Butcher 1981, Hayward 1982). In the Blowdown Zone between 1981 and 1984, bird densities were low and only three to six species were observed annually, with the Dark-eyed Junco (*Junco hyemalis*) most common (Andersen and MacMahon 1986). Mountain Bluebirds (*Sialia currucoides*) and Common Ravens (*Corvus corax*) were also observed. Manuwal et al. (1987) found an altered guild structure of birds in the Scorch Zone through reductions in the tree foliage-insectivore and tree seed foraging guilds and dominance of species associated with ground vegetation and the understory. Between 1980 and 1993, two waves of colonization were observed in the Blowdown Zone. Within one post-eruption year, ground nesters and cavity nesters that foraged on the ground, on tree boles, or from the air column colonized the area, followed in the late 1980s by a suite of foliage

gleaners and flycatchers (Crisafulli and Hawkins 1998). Colonization was far slower in the primary successional habitat of the Pumice Plain, where many different habitat affinities were represented in the colonist species in the first decade following the eruption.

Dissertation Work

In this dissertation, I considered three aspects of community development to better understand the community assembly processes at work in the bird community at Mount St. Helens. First, I looked at the spatiotemporal dynamics of colonization by approximating the geographic region from which colonist birds may originate. Colonization is the first critical step in community assembly, and relies on dispersal from an external population source. While many studies consider community assembly processes within a regional context, the definitions of “local” and “regional” vary among taxa and among studies within a given taxon. Using a novel spatial approach that leveraged regional bird observations from the U.S. Breeding Bird Survey (BBS) and Monitoring Avian Productivity and Survivorship (MAPS) programs, I estimated the extent of the geographic region contributing to community assembly processes at Mount St. Helens by mapping possible source locations for colonizing species. Using this approach I examined the change in the extent of the source region for different disturbance zones across time, quantifying the spatial patterns of colonization across time for Mount St. Helens bird communities. I considered each disturbance zone of Mount St. Helens separately to identify whether the degree of disturbance affected the colonization patterns observed during ecological recovery.

Although community assembly has been addressed in many contexts, few studies have addressed assembly processes in relation to disturbance or the assembly of mainland bird communities. I addressed post-disturbance avian community assembly in the primary successional habitat of the Pumice Plain in more detail, testing multiple assembly hypotheses against observations of the local bird community. Using historical data collected by the U.S. Forest Service and conducting additional bird surveys, I considered patterns in bird diversity and composition during two time periods within the first thirty years of ecological recovery following the 1980 eruption. For the more recent time period (2007-2010) I compared bird communities in sparsely vegetated upland habitats to those of more structurally complex wetland habitats. I examined the relative evidence for stochastic assembly and deterministic assembly through selective colonization (eg, habitat filtering) and extinction (eg, competition) processes. To determine the support for alternative assembly hypotheses I considered abundance distributions, consistency in rank abundance, and diversity partitioning for local bird communities. In addition, I tested these communities for body-size dispersion, nestedness, and guild proportionality. I compared my observations from the local bird communities to predictions from niche and neutral models using null models.

In order to address the specific mechanism of local recruitment in maintaining populations of birds on the Pumice Plain, I conducted a nest monitoring study on the Pumice Plain across three breeding seasons. Though my sample sizes were small, I estimated nest success for ground-nesting and shrub-nesting birds and the effect of surrounding vegetation on nest success. I also calculated species-specific success rates for the most commonly observed species and compared them to published nest success

rates from other locations, in order to estimate the extent to which local recruitment contributed to maintaining local populations. These studies together combine a detailed mechanistic approach with rigorous testing of assembly hypotheses and interpretation of broad colonization patterns to assess community assembly processes of birds in the post-eruption landscape of Mount St. Helens, WA.

Chapter 2 : Local and regional colonization in successional habitats at Mount St. Helens, WA

Co-authored with: *W. F. Fagan and C.M. Crisafulli*

Abstract

The regional context of a local community is critical to assembly processes at both local and regional scales. However, defining the region for a local community is sometimes difficult, particularly in a mainland habitat. While several traditional approaches define static regional species pools (RSPs) for testing community assembly hypotheses, no standard approach adequately defines the geographic extent of the region in question or considers the dynamic nature of assembly processes. Here we developed a novel spatial technique to leverage regional species sightings as potential source locations of colonizing species and to define the physical ‘minimum source region’ of a focal community and its associated RSP. Using this new technique we examined the spatiotemporal patterns of colonization and determined the geographic extent of the region likely influencing local community assembly. For the Mount St Helens bird community this region comprised a large geographic area extending beyond the Cascades range. We further demonstrated that as local species richness increased across time, the geographic area necessary to account for possible source locations increased as well. In addition, more highly disturbed sites attracted species from across a larger geographic area than sites with less disturbance. Our results demonstrated the role of disturbance intensity and assembly time on the geographic region contributing to local community assembly.

Introduction

Community ecology has long explored the contributions of local and regional processes to patterns of local occupancy and diversity. A large body of this work relies upon the concept of regional species pools (RSPs), which provide a way to study the ecological processes that lead to different patterns of diversity across a range of spatial and temporal scales (Cornell and Lawton 1992, Cam et al. 2000, Ricklefs 2000, Algar et al. 2005, Brotons 2005, Jung et al. 2010). RSPs are defined by biogeographic processes at large spatial scales and evolutionary processes at large temporal scales, while local occupancy is shaped by ecological processes at more immediate spatial and temporal scales (Cornell and Lawton 1992). As such, RSPs are an important tool for assessing the relative importance of ecological processes for local communities. In particular, RSPs often provide the means to test competing hypotheses in community assembly, such as the relative importance of (1) local versus regional processes and (2) neutral versus niche processes (Hubbell et al. 2001, Fargione et al. 2003, Algar et al. 2005, Weiher et al. 2011). RSPs also provide important context for studies addressing local diversity and richness, as any analysis of the saturation or completeness of local communities must address regional richness to be meaningful.

The results of these studies depend on the composition of the respective RSPs and the rules used to define them (Graves and Gotelli 1983, Schoener 1988). Despite the broad use of RSPs in ecological studies, there is no consistently applied methodology for identifying RSPs (Butaye et al. 2002). Even within a given taxon, species pools are defined in a number of ways. Common approaches include the combined samples approach, the state atlas approach and the range-map approach. The combined samples

approach is commonly applied in studies with large sample sizes and experimental manipulations (e.g., Drake 1991, Butaye et al. 2002, Chase 2007). In this approach the RSP is assumed to be the compilation of all species observed in the study. This approach may be appropriate for many specific questions in community ecology, but can be problematic when species detection is imperfect. Additionally, in order to have an independent species pool, the sample in question should always be excluded from the species pool used to interpret the local condition (Cam et al. 2000).

The state atlas approach defines a physical region, determined by geographic or political boundaries, and uses a compiled list of species for this area as the species pool (e.g., Algar et al. 2005, Blackburn and Gaston 2001). For this approach to be effective, the range of the atlas used should have some ecological meaning. However, many atlases are defined according to political boundaries, which are not ecologically significant (Gaston 1990). Thus, this approach is most effectively applied to island systems. State or country atlases commonly provide information about local occurrence patterns of species by counties or grid cells of a state or comparable entity, though advances in GIS have led to the availability of more detailed mapping in some cases (Smith et al. 1997). Similar species lists may be collated for a defined area from published data or long-term monitoring programs (Cam et al. 2000). Monitoring programs such as the North American Breeding Bird Survey have a network of sites where the presence of species have been observed and recorded, providing excellent data once an appropriate physical region is determined.

The range map approach considers species presence on a broader scale. Rather than defining a physical region, this approach defines the RSP as the set of all species

whose range maps overlap the location of interest (e.g., Belmaker and Jetz 2012, Stevens and Willig 2002). This approach does not consider an actual physical region for a RSP, but instead identifies the species that may potentially be found at a particular location. However, the nature of range map information creates potential problems in RSPs. First, the limits of resolution on range maps place methodological constraints on the process of defining a regional pool for a given location. A buffer is often applied around the location of interest, due to the poor spatial resolution of species range maps (e.g., 100km buffer, Belmaker & Jetz 2011) Also, discrepancies in scale between local data and range maps may complicate this approach, leading to overestimation of species occurrence at local scales (Hurlbert and White 2005, Hurlbert and Jetz 2007).

Cutting across all of these approaches are several commonalities. For any definition of a RSP, the spatial scale and resolution of the data should be appropriate for the study system in question. However it is constructed, the RSP should include all species capable of colonizing the local community. To limit species pools to species with a reasonable probability of colonization, the composition of the RSP is often restricted by guild, most commonly according to habitat use (see Zobel 1997, Brotons et al. 2005, Lessard et al. 2011). Limiting RSPs by habitat accounts for one aspect of the niche assembly hypotheses and increases the likelihood of detecting stochastic processes in assembly (Schoener 1988). RSPs following any of these traditional approaches generally provide a list of species that may be present in a focal community according to location, but the breadth of inclusiveness may vary significantly depending on the rules applied to define the RSP. Additionally, these RSPs provide no insight into the spatial

context of the community and the extent of an ecologically meaningful ‘region’ around it.

The concept of the RSP is based in part on the ability of species to immigrate to the focal community via dispersal. Dispersal is a key mechanism that connects RSPs to local communities and shapes the local and regional contributions to local community assembly (Graves and Rahbek 2005). Given a RSP including all species capable of colonizing the local community, dispersal is a necessary step determining which species succeed and become a part of the community. Conversely, the limits on dispersal are important in determining local occurrence and may maintain beta diversity through spatial variation in local colonization and extinction (Vallecillo et al. 2009, Chase 2010). Colonization is limited by dispersal and appears to be a primarily local process in some post-disturbance bird communities (Brotons et al. 2005).

Using the concept of dispersal from a source region, we developed a novel spatial technique for defining the physical region of a focal community and its associated RSP. For many well-studied taxa, location-specific species information is becoming more readily available through monitoring programs. These data may be leveraged to develop new ways of addressing regional and local contributions in community ecology. Instead of imposing a predetermined region on the analysis, this approach uses spatially explicit species presence data to define a ‘minimum source region’ and construct its RSP. For each species in the focal community, a ‘nearest neighbor’ location for that species is identified as the nearest observation of that species from independent regional data. The collection of ‘nearest neighbor’ locations for all species from the focal community are used to define the spatial extent of the ‘minimum

source region.’ Combining potential source locations across species yields a minimum spatial extent of the source region for a local community. This region consists of some number of locations of species observations and may include sites that are not a ‘nearest neighbor’ site. All species observed within the geographic area of the ‘minimum source region’ comprise its corresponding species pool. The ‘minimum source region’ for a focal community thus has the potential to change with colonization by new species. Conceptually this approach provides an alternative framework to the RSP for studying dispersal, colonization and assembly patterns. By estimating possible source locations and directly considering the dispersal process, this approach is fundamentally different than defining an RSP through traditional methods and provides a tool to consider the patterns of dispersal and colonization to local communities in a spatially explicit context.

The goal of this study was to determine to what extent post-disturbance bird communities at Mount St. Helens have been colonized from local and regional sources and to approximate the spatial extent of the region contributing colonist species to the local community (Figure 1). A further goal was to examine community assembly using the spatial patterns of colonization across a gradient of disturbance and through time during ecological recovery. Combining survey data with independent regional datasets of bird observations, we developed and applied a spatial approach to map source regions for local bird communities across thirty years of ecological recovery following volcanic disturbance (1981 – 2010) at Mount St. Helens, WA.

Methods

1. Field Site

The May 1980 volcanic eruption of Mount St. Helens (Washington, USA) caused dramatic and large-scale changes to the landscape, with the blast creating a series of disturbance zones that were determined primarily according to direction and distance from the volcano (Table 1-1). Closest to the volcano, the Pumice Plain was sterilized and buried under pyroclastic flows, killing everything above- and below-ground in the area. In the Blowdown and Scorch Zones, the vast majority of plants and animals were killed, but refugia created by topography and snowbanks allowed for the survival of some plants and animals, many of which were subterranean. While some migratory birds may not have arrived at Mount St. Helens for the breeding season at the time of the eruption, any birds present in the Pumice Plain, Blowdown Zone, or Scorch Zone would have been killed. No breeding birds were observed in these areas during the year following the eruption. We therefore assume that all bird species observed in this field study colonized after the eruption. Beyond the Scorch Zone is the Tephra Fall Zone in which tephra (solid material ranging from ash to pebble-sized rock) from the eruption, primarily in the form of ash, was the primary disturbance; in this zone, bird communities include legacy species that survived the eruption.

Catastrophic disturbances such as volcanic eruptions have the capacity to create rare and ephemeral habitats which may attract unusual species combinations. Within the Mount St. Helens area, the interaction of the eruption, the topography, and the ecological recovery across thirty years has contributed to a spectrum of habitats that differ in many ways from the Cascade Mountains surrounding Mount St. Helens, which

are dominated by old-growth and managed forests. Each of these areas has been and continues to be modified by successional recovery processes since the 1980 eruption, creating a unique mosaic of habitats atypical for the Cascade Mountains. This mosaic of successional habitats provides opportunities for unusual species combinations within the local communities, which we analyze at the level of disturbance zones.

2. Data Sources

2.1 Field Data

We sampled local breeding bird community at Mount St. Helens through distance-sampling using line transect surveys (Anderson et al. 1979) performed between 1982 and 2010 throughout the disturbed areas at Mount St. Helens. Twenty five transects, stratified across the disturbance zones of the Mount St. Helens area, range from 250 m to 1 km in length, according to topographic constraints and habitat continuity. In addition, two reference sites are located approximately 40 km to the northwest of the volcano. We conducted repeated surveys of breeding birds along these transects between 1982 and 1993, and again between 2007 and 2010. Not all transects were surveyed all years. We surveyed active transects four or more times per year between 0600 and 1000 on mornings with moderate weather conditions during the late May to early August breeding season (Emlen 1977). We included all birds observed within 100 m of a transect in the surveys.

We defined separate local community samples by aggregating across multiple transect locations within each disturbance zone at Mount St. Helens and for the entire Mount St. Helens area using available survey data. Combining species observations by

sample year across transect locations, we created 37 community samples specific to Mount St. Helens disturbance zones: 13 on the Pumice Plain, 10 in the Blowdown Zone, 5 in the Scorch Zone, 7 in the Tephra Fall Zone and 6 in the Reference Area. Each community sample aggregates a list of species from all transect surveys for the disturbance zone, for the given year and all previous years, to focus on colonization processes. For example a 2010 community sample for the Pumice Plain includes all species observed in surveys at any Pumice Plain transect from 2010 and all prior years. The 2010 community samples therefore include all species which have colonized the Mount St. Helens landscape and been observed since the 1980 eruption. In addition, community samples were combined across disturbance zones for each year during which bird surveys were conducted to identify 17 years of community species lists for Mount St. Helens as a whole.

2.2 Regional Data

We used large-scale avian monitoring programs in the Pacific Northwest as independent sources of regional observation sites for breeding birds observed at Mount St. Helens. Spatially explicit records of bird species observations in the region were drawn from both the North American Breeding Bird Survey (BBS) and the Monitoring Avian Productivity and Survivorship (MAPS) program sites. We included sites within 600 km of Mount St. Helens as regional observation sites, because this area included the entire political boundary of the Washington Breeding Bird atlas and was sufficient to observe the birds present in the field data from Mount St. Helens.

The BBS is the most extensive monitoring program for birds in North America. BBS monitoring efforts are well distributed throughout the Pacific Northwest region, with 190 sites located in Washington State (Figure A2-1 Panel A). BBS surveys take place as a series of roadside point counts, and surveys are conducted annually during the breeding season. Each site consists of 50 point counts along a 40 km route, which allows a single 'site' to include a variety of habitats. For our purpose, each BBS site is geo-referenced by the midpoint of the route. Given the years of longitudinal data collection at each BBS site and the even distribution of BBS sites across the region, we consider the BBS dataset to be a reasonable proxy for actual species occurrence for a broad range of taxa, but recognize that some species are not well sampled (for example, nocturnal species and species utilizing wetlands) and the spatial resolution is coarse. The MAPS program consists of fewer sites that have a clumped spatial distribution, but are monitored more intensely than BBS and conduct mist netting and banding. Bird observations between 1992 and 2006 at 149 MAPS stations within 600 km of Mount St. Helens (Figure A2-1 Panel B) were included in the MAPS regional observation sites (Michel et al. 2006). From the BBS, we included bird observations from 1968 to 2010 for 289 routes (Figure A2-1; PWRC 2012). Because detection is imperfect and varies across species and habitats, an individual survey year or even multiple survey years may not include all species present (Donovan and Flather 2002). Therefore we combined all observations across all years of sampling to create species lists for all BBS and MAPS sites, a conservative approach that does not account for effects of habitat or climate change. One BBS route was located within the disturbed area of Mount St. Helens. This

route was excluded from the regional dataset, and considered as a separate source of local community data.

Regional monitoring programs do not necessarily provide unbiased reports of species locations. The roadside nature of BBS surveys is a source of bias in species observations that was not directly addressed (Keller & Scallan 1999). Another source of bias in regional data was poor representation of alpine specialists. In both MAPS and BBS data, alpine species were observed at few if any locations within 600 km of Mount St. Helens despite being present in the Cascades region. Because alpine species are common in the Mount St. Helens field data, it was important to account for this bias in the regional observations. To counteract this systematic bias, we identified Mount Rainier (75 kilometers away) as an additional regional observation site for the American Pipit, Gray-crowned Rosy-finch, Horned Lark and White-tailed Ptarmigan. These alpine birds have been consistently documented at Mount Rainier for over 90 years (Taylor 1922, National Park Service 2011).

3. RSPs

3.1 Traditional RSPs

We defined traditional RSPs for the Mount St. Helens area to provide context for interpretation of the minimum source region approach. We used two commonly accepted methods for RSPs, the state atlas approach and the range map approach. Because the Mount St. Helens area comprises a wide range of habitats, we did not limit the traditional RSPs according to habitat or other ecological factors. The state atlas RSP adopted the political boundaries approach and included all bird species with confirmed

evidence of breeding in Washington State, according to the 1987-1996 Washington Breeding Bird Atlas (Breeding Bird Atlas 2012). The range map RSP identified all species whose digitized range map overlapped a circle of 100 km radius centered on the Mount St. Helens Pumice Plain, using publically available geo-referenced range maps from NatureServ (Ridgely 2007). Maps overlays were performed in ArcGIS 10.1.

3.2 Novel RSP: Minimum Source Regions

By applying a spatial approach to source regions, we tested hypotheses about colonization and assembly processes. As species accumulate through colonization, the colonists may originate entirely from within the local area, or may draw upon a broader region (Figure 2-1A). The minimum source region protocol described here provides a measure of the physical extent of the region from which colonists may disperse, based on existing species occurrence data. The broader the region contributing colonizing individuals to the local community, the larger the minimum source region should be. When the regional observation sites provide a reasonable proxy for actual species occurrence across a landscape, we can glean more about colonization and dispersal from the set of minimum source regions. Moreover, if the minimum source region and the community are relatively stable over time, then the areal extent of the minimum source region quantifies the scale of the ‘region’ contributing to local colonization.

If colonization is entirely through short distance dispersal from local populations, then the minimum source region may never expand beyond a small number of very local regional observation sites. In contrast, if colonization involves long distance dispersal either by drawing haphazardly from a large region or by attracting species to specific

habitats (e.g., supertramp species, Diamond 1974) then we expect the minimum source region to include a larger geographic area (Figure 2-1A). In the context of successional processes and community assembly, the distance between the focal community and species-specific ‘nearest neighbor’ locations represent an upper bound on the closest source for each colonist species. As time passes, averaging the proxy dispersal distance across species in a community indicates the relative contributions of short and long distance dispersal to the community. If assembly is neutral, the average proxy dispersal distance would be expected to stay constant or to increase with increasing size of the minimum source region (Figure 2-1B). However, if average proxy dispersal distance decreases as a function of minimum source region, this suggests a shift from long-distance dispersal to short-distance dispersal, which may indicate niche assembly processes such as habitat filtering.

We identified spatially explicit minimum source regions using spatially-referenced species observations taken from large-scale monitoring programs. Using the species composition of a local community, we defined a minimum source region for each assemblage as follows (Figure 2-2). Independent data provided occurrence locations in the vicinity of the focal community (Figure 2-2A). Species observations were associated with location data and identified as species-specific regional observation sites. For each species within the focal community, the regional observation sites are identified (Figure 2-2B) and the nearest regional observation site was determined as its ‘nearest neighbor’ location (Figure 2-2C). Obviously, this location represents only one possible source of colonist individuals to the focal community, but it is the closest one for which any data were available. The distance between each ‘nearest neighbor’

location and the location of the community was termed the ‘proxy dispersal distance.’ The proxy dispersal distance denoted an upper limit on minimum dispersal distance for each colonizing species.

The minimum source region is determined by the collection of all nearest neighbor source locations across species within a community (Figure 2-2D). These sites were used to define a convex polygon which contained all nearest neighbor locations, named the ‘minimum source region’ (Figure 2-2E) Each minimum source region included within its boundaries a small area around the geographic location of the local community, as represented by the black circle in Figure 2-2D. Including this area in every minimum source region addressed two concerns. First, it ensured that all minimum source regions include the geographic location of the local community. Second, it allowed a polygon to be constructed when fewer than three source locations were necessary to account for all species in the community, a consideration that was most relevant for species-poor local communities. These physically defined minimum source regions were quantified by their area and mapped. The species pool for each minimum source region comprised all species observations for all regional observation sites within the defined polygon (Figure 2-2F). The pattern of species colonization sources for a local community was characterized by the distribution of proxy dispersal distances, summarized by the mean and maximum distances across species within the community, and by the area of the minimum source region.

4. Data Analyses

4.1 Test of the Minimum Source Region Protocol

We tested the methods for defining minimum source regions using annual surveys from BBS sites within Washington State. Because locations of BBS sites were selected randomly and are distributed across the state, we considered them a good test of the minimum source region across a range of representative habitats. While some BBS sites may show significant change in local land use and community composition over time, others would have more stable composition.

We defined a local community sample for a given BBS site and a given year as all species observed in any survey before or during the year in question. That is, for each survey year, we constructed the associated community sample by appending any newly observed species to the list of species observed in previous years. This provided an inclusive list of possible colonists which provided a more direct comparison to our Mount St. Helens work focused on colonization. In addition, studying BBS sites separately allowed us to consider the effects of sampling effort and species richness on the minimum source region outside of the context of successional change.

Using the regional observation sites of all species observations at 462 BBS sites in Washington, Oregon, Idaho and Montana, excluding the BBS site of interest, we calculated 2000 minimum source regions. We applied the minimum source region to all Washington State BBS sites to test the feasibility of the spatial approach and to provide a baseline expectation for the minimum source region and how it changes over time.

4.2 Identification of Mount St. Helens Minimum Source Regions

Spatially explicit minimum source regions for the Mount St. Helens community were identified using the regional observation sites from the BBS and MAPS datasets. For each of the 54 community samples collated from survey data a minimum source region was defined following the methods explained previously (Figure 2-1). In addition, minimum source regions were identified for 13 years of community samples drawn from the BBS route located within the Tephra Fall Zone of Mount St. Helens as an additional source of local community data. To ensure that a minimum source region could be calculated even for species-poor community samples and that Mount St. Helens was always within its bounds, each 'minimum source region' included within its boundaries an ellipsoidal area around Mount St. Helens approximately 20 km in radius and 1256 km² in area (see Figure 2-2D). In order to test the differences in regional datasets, source regions were calculated using BBS data alone, MAPS data alone, and the combined dataset. We created 67 minimum source regions (i.e., the polygons generated for each of the 5 disturbance zones across 17 years with surveys, all Mount St. Helens field observations combined, plus 13 years of surveys on the Mount St. Helens BBS route).

4.3 Comparison between Mount St. Helen communities and statewide community data

We compared the spatially defined minimum source regions from Mount St. Helens field data to those calculated for the Washington State BBS sites. We only considered the first 17 annual surveys for each BBS community to allow for direct comparison of change over time with the 17 years of Mount St. Helens surveys. These

surveys were not from the same years at Mount St. Helens surveys, but selected to parallel the sampling effort and length of elapsed time of the Mount St. Helens surveys. From the minimum source regions we extracted the across-species mean and maximum of proxy dispersal distances, and the area of the minimum source region to characterize the pattern of species colonization sources for the Mount St. Helens community samples. To differentiate between changes in minimum source regions due to increased sampling from those due to changes in observed species, we used a generalized linear model to examine what variables affected metrics defining the minimum source region (mean distance, maximum distance, and area). Community identity (e.g., Pumice Plain) was included as a random effect. We estimated the direct fixed effects and interactions of observed species richness, number of sampling years, and community source (Mount St. Helens disturbance zone v. Washington BBS site). The best model was selected using the minimum AIC value.

4.4 Comparison between Mount St. Helen communities and traditional RSPs

Within each resulting minimum source region, we compiled a list of species for the corresponding RSP. All regional observation sites that were located within the geographic range of each minimum source region were identified, and the list of species observed at least once at those sites constituted the spatial RSP. The compositions of these spatial RSPs were compared to traditional RSPs. We identified the completeness of the RSPs for including all local species, the total number of species in each RSP, and the species absent from some RSPs.

Results

RSPs

Traditional and spatial RSPs were defined for the Mount St. Helens bird community as a whole. The species richness of RSPs determined by State Atlas, Range Map, and the spatial approach were similar but not identical (Table 2-1). The total species richness of the traditional RSPs was approximately 250 species in each case, though composition varied (Table A2-1). Among all traditional and spatial RSPs, 312 bird species occurred in at least one RSP, but only 153 occurred in all RSPs. The State Atlas RSP included 118 passerines versus 108 for the Range Map approach. The spatial RSPs included a similar richness of passerine species compared to the Range Map RSP, but fewer non-passerines (Table 2-1). The Range Map also approach identified six additional species that were excluded from the RSP, as only their winter ranges overlapped with the Mount St. Helens area. The State Atlas and the Range Map approach both included all 62 passerine species observed at Mount St. Helens, but did not include all observed birds (Table 2-1). Of the species observed at Mount St. Helens, the State Atlas RSP did not include three raptors and one shorebird, and the Range Map RSP was missing one woodpecker species.

In contrast, the spatial RSPs by definition included all species observed at Mount St. Helens, though the BBS dataset and the MAPS dataset each lacked one alpine species (Table 2-1). In the BBS, the closest observation of Gray Crowned Rosy-Finch (*Leucosticte tephrocotis*) was 686 km from Mount St. Helens in Alberta, Canada. In the MAPS regional data, the American Pipit was not observed. When the BBS and MAPS species observations were combined, both alpine species were observed at exactly one

location within 500 km of Mount St. Helens. By including Mount Rainier as an additional regional observation site for alpine specialists, we prevented this systematic bias from influencing the results of the minimum source regions. All other species from Mount St. Helens were observed in the regional datasets within 450 km.

While the spatial extent of the “region” of traditional RSPs was ecologically arbitrary, the spatial RSPs define a region according to the species occurrence data in the local and regional datasets. The spatial minimum source regions differed according to the regional data used (Table 2-1). Higher data density in the BBS led to smaller minimum source regions, but this did not correspond to smaller RSPs. When both MAPS and BBS data were considered, the source region necessary to find all species observed at Mount St. Helens between 1982 and 2010 was 34,516 km² in extent, with the maximum distance to a regional observation of 254 km. BBS and MAPS observations in this region yielded a total of 110 identified passerine species. When the spatial RSP approach was applied to only one of the regional datasets, the spatial extent of the minimum source region required was larger and fewer species were included in the associated RSP.

The two regional sources resulted in very different source regions. The BBS minimum source region was 51,774 km² in size and contained observations of 108 passerine and 104 non-passerine species (Table 2-1). In the BBS RSP, the larger spatial area corresponded to more total species, though fewer passerines, than in the smaller spatial RSP when using both BBS and MAPS datasets. Due to its clustered site locations and fewer total sites, the MAPS data required a minimum source region over twice the size of the BBS minimum source region for the Mount St. Helens bird community

samples. Despite the large spatial extent, the MAPS RSP included fewer species than the combined Spatial RSP with 110 passerine and 86 non-passerine species.

Minimum Source Regions

Minimum source regions were used to quantify the potential extent of the ecological regions from which birds colonized Mount St. Helens bird communities. The spatial extent was determined by the species composition of local community samples and each species' nearest neighbor location in the regional dataset. Because the qualitative patterns observed in the minimum source regions were similar for each regional dataset and the BBS provides a more consistent distribution of regional sites both for this study and across the U.S., we have limited further results to the BBS regional data.

As expected, the accumulation of species across time within the disturbance zones of Mount St. Helens led to minimum source regions with increasing area. The minimum source regions across disturbance zones increased quickly within the first few years of surveys, plateaued within five years of the eruption, and showed little variation between 1985 and 1993. However, the minimum source regions for Blowdown Zone and Pumice Plain increased again after surveys were resumed in 2007 (Figure 2-3A). These disturbance zones were the most changed by the eruption, and showed the most successional change in habitat structure during the ecological recovery. The recent increase in the size of the minimum source region indicates that these habitats continue to be colonized by long-distance dispersal of regional species, as opposed to colonization strictly from local sources (Figure 2-4). Though the minimum source region

for the Pumice Plain includes the farthest nearest-neighbor location for Greater Yellowlegs (*Tringa melanoleuca*) 445 km from Mount St. Helens and is the largest region defined for a disturbance zone community at 11,175 km², it does not quite include the entire region necessary for the Mount St. Helens bird community as a whole, whose minimum source region covers 12,996 km² (Figures 2-3, 2-4). Also, the same ‘nearest neighbor’ locations appear in the minimum source regions of different disturbance zones at different times during ecological recovery. The Scorch Zone, Tephra Fall Zone, and Reference Area show only small increases in minimum source region after 1985, indicating that they may have been primarily colonized through shorter-distance dispersal.

Unlike the total area of the minimum source region, the mean of species-specific proxy dispersal distances may increase or decrease over time. The average distance to species-specific nearest neighbor locations is expected to increase when the minimum source region grows larger, but for a constant minimum source region, the average distance will depend on where within the minimum source region the species-specific nearest neighbor locations are distributed. The mean distances across species in the Scorch Zone, Tephra Fall Zone, and Reference Area tend to increase in the first years of surveys and remain consistent in later surveys. The mean distances across species in the Pumice Plain and Blowdown Zone of Mount St. Helens are non-monotonic across time (Figure 2-3B), consistent with the hypothesis of assembly processes including habitat filtering. The mean proxy dispersal distance for the Pumice Plain community was very high in 1983 followed by a decrease and consistent lower mean distance through the rest of the 1980s surveys. When surveying resumed in 2007, the distances show greater

variation and another increase corresponding to the increase in the extent of the minimum source region. In contrast, the mean proxy dispersal distance for the Blowdown Zone community shows a gradual increase and then decrease over 1982-1993. When surveys were conducted again in 2007, the average dispersal distance within the community again increased. These fluctuations in the community-wide average of species' proxy dispersal distances suggest that habitat selection may be contributing to assembly patterns in the local community.

Comparison to statewide BBS

The BBS communities showed a fast increase in minimum source region size during the first few years of surveys due to sampling effects, after which transects tended to reach an asymptotic minimum source region. Over the entire sampling period, the minimum source regions for the Mount St. Helens communities grew faster than for the BBS communities (Figure 2-5). In a generalized mixed-effect linear model, the best fit model for change in minimum source region across 17 sample years, as measured by mean proxy dispersal distance, maximum distance, and areal extent, was the full model that included the interaction between community source (Mount St. Helens disturbance zone v. BBS site), the number of years sampled, the species richness of the focal community, and community identity (e.g., Pumice Plain). Estimates for Mount St. Helens sites had large variances due to the very small number of disturbance zone communities at Mount St. Helens (Table 2-2). Notably, the relationships between observed richness of a community and the minimum source region metrics were significantly more positive for Mount St. Helens communities than for BBS

communities. For example, the effect of observed local richness on community-wide mean of proxy dispersal distances was not significantly different from zero (-1.6 ± 2.8 standard error) for BBS communities but was highly positive (82.2 ± 9.8 standard error) for MSH communities. This indicates that the number of species in a local community at Mount St. Helens is more likely to correspond to the size of the minimum source region than the number of species in a BBS community. In total, 93 species were observed in the Mount St. Helens community, and the mean observed richness for community samples was 40 species, while the BBS community samples averaged 78 species and had up to 138 species observed in a single community. Thus, the high effect size for observed richness on the minimum source region size for Mount St. Helens communities may be due to the relatively low species richness in these communities.

Discussion

Our spatial approach to defining source regions for a community provides a new way to consider community colonization and assembly from a spatiotemporal perspective. Though different in composition, the RSPs originating from this spatial approach were comparable in species richness to traditional approaches and satisfied the requirement that a good RSP must include all the species observed in the local community (after we had accounted for the lack of alpine sites in regional data). This contrasts with the traditional Atlas and Range Map RSPs that failed to include all species observed in the local communities. Despite their widespread use, the traditional RSPs did not always satisfy the basic requirements for defining a species pool.

Spatially explicit source regions, embodied by the spatial RSP analyses, quantify the dynamics of colonization patterns for a community across time and space. Although RSPs determined by State Atlas and Range Map RSPs provided a standard, temporally constant context for species colonization, the minimum source region approach demonstrated spatiotemporal expansion of the area potentially influencing a focal community during colonization. As each disturbance zone accumulated species through colonizations, we observed the community minimum source region increase in areal extent as well (Figure 2-3). Assuming that the regional observation sites are a reasonable proxy for actual species occurrence across the landscape, this pattern demonstrates that long distance dispersal from a non-local region is contributing to assembly of the Mount St. Helens bird communities. Most colonist species occurred in independent communities within 100 km of the disturbed areas of MSH; however, some colonist species occurred only at a significant distance from Mount St. Helens, and required long distance dispersal. Some of these long distance colonists, such as Brewer's Sparrow (*Spizella breweri*), are habitat specialists found regionally in specific locations (e.g., shrublands east of the Cascades) whose characteristics were replicated in the midst of the Cascade Mountains by the volcanic disturbance, or species typically migrating further north for the breeding season (Greater Yellowlegs). Within a given species, dispersal distances are often 'long-tailed' in which there are relatively few long-distance dispersal events (Kot et al. 1996). Thus, if colonization draws from a wide geographic region, dispersal limitations across species should constrain the temporal rate of increase in the spatial extent of the minimum source region. However, it is important to keep in mind that these results are limited by the locations of available data through monitoring

programs. In this case, the BBS provided a more complete sampling of regional bird observations than MAPS. As new location-specific species observations data and databases continue to become available, the precision and accuracy of these analyses will continue to improve. For birds, the eBird program (www.ebird.org) organized by the Cornell Lab of Ornithology is one such effort that is beginning to provide excellent location- and time- specific sightings data.

Given the high dispersal ability of many birds across land and the prevalence of migratory populations (Clobert et al. 2001), it is not surprising that long distance dispersers have arrived to Mount St. Helens. However, inhospitable environments or geographic features may still have acted as dispersal barriers for some species (Sharov and Liebhold 1998). Dispersal and gene flow between populations may be limited by habitat connectivity in some bird species (e.g., Segelbacher et al. 2003). Although this study considered only Euclidean distance between locations and selected the “nearest neighbor” sites as the most likely source of colonist species, incorporating ‘least cost’ paths and habitat connectivity into distance measurements could improve ecological realism and affect the shape and size of calculated minimum source regions (Moilanen and Nieminen 2002). However, such paths and connectivity measures are typically species specific (Tischendorf and Fahrig 2000, Calabrese and Fagan 2004), making them impractical in an analysis of whole communities as we have here.

The thirty years of ecological recovery at Mount St. Helens discussed here are only the beginning of a lengthy successional process. However, it is enough time to begin to address how local communities are assembling and from where colonizing species may disperse. The disturbance zones of Mount St. Helens demonstrated a stark

contrast between areas with high levels of disturbance (Pumice Plain and Blowdown Zone) and areas with lower levels of disturbance (Scorch Zone, Tephra Fall Zone, and Reference Areas). Although the disturbance in the Scorch Zone was significant, it was more similar to wildfire disturbance, and these sites were in close proximity to the less highly disturbed tephra fall zone. The Scorch Zone and Tephra Fall Zone may have been largely colonized from the local surroundings, while the more highly disturbed Blowdown Zone and Pumice Plain drew colonist species from further afield. This may be due to the habitats created on the Pumice Plain and Blowdown Zone following the eruption, which were least like the habitat in the surrounding Cascade Mountains region, and had the highest potential for attracting long-distance colonists. The increase in mean source distance in the first ten years of surveys in the Blowdown Zone indicates the importance of long-distance dispersal events in bird community assembly (see Figure 3B). However, as time passed and the minimum source region remained stable, the decrease in mean source distance indicates that short distance dispersal was a consistent contributor of new species to these communities. This may be due in part to plantations of *Pseudotsuga menziesii* and *Abies procera* planted soon after the 1980 eruption, which have attracted forest birds from the Cascades as they have developed a forest habitat at a much faster pace than the natural ecological recovery. The long distance dispersal made evident by the Mount St. Helens source regions is an important ecological process with the potential to feed back into regional diversity dynamics. Long distance dispersal, even when rare, is an important mechanism for gene flow, and can facilitate range shifts, expand geographic ranges, and enable invasion by exotic species (Nichols and Hewitt 1994). Moreover, long distance dispersal of birds can have far-reaching community-

level effects as birds are known vectors of dispersal for a wide variety of seeds and invertebrates (Green and Figuerola 2005, Merow et al. 2011, Gillespie et al. 2012).

Both Pumice Plain and Blowdown Zone communities showed an increase in maximum distance to species-specific nearest neighbor locations and community-wide minimum source region area following repeated years of sampling (Figure 3). Future colonizations on the Pumice Plain, an area undergoing primary succession, will shed further light on the expected patterns in source regions over time. As ecological recovery continues, we expect the Blowdown Zone and Pumice Plain to continue to be colonized by a mix of short distance and long distance dispersers. Considering the recent expansion of the minimum source regions for the Blowdown Zone and Pumice Plain, there is no reason to expect these source regions have reached their maximum extent. We expect that these areas will continue to be colonized by a combination of short and long distance dispersers from throughout a broad geographic region and for the minimum source region around Mount St. Helens to grow further.

Minimum source regions cannot identify where colonizing individuals actually originate. However, they can provide realistic proxies for source populations based on regional occurrence data. The minimum source region uses monitoring data to define a physical geographic area within which to address community ecology questions. Previously, the spatial geometry of regional source pools had only been characterized through overlaying species range maps. The union of the geographic ranges of species present in an assemblage defines that assemblage's dispersion field (Graves and Rahbek 2005). Because of their reliance on range maps, which overestimate local species occurrence, this approach only works at coarse spatial resolution, e.g., for continental

species pools and assemblages defined by 1° latitude/longitude quadrats. Consequently, the range map approach is valuable for studying large scale patterns in species richness, but not appropriate for examining colonization sources in local assembly.

In this study, species were accumulated in community samples across years and the possibility of local extinctions was ignored. This was considered the best approach given the lack of data between 1993 and 2005, as well as limited sampling at Mount St. Helens since 2005. However, 11 species observed at Mount St. Helens before 2005 have not been observed since 2005. Additional surveys would be required to truly identify how many of these species are locally extinct versus how many are present but unobserved in the most recent surveys. Incorporating local extinction dynamics would be a beneficial extension of the minimum source region, particularly in studying heterogeneity and spatial patterning of habitats and communities in a spatiotemporal framework. Similarly, our approach could be modified to further restrict regional observations by the year of observation relative to local sampling to facilitate application to networks of interacting communities.

Using minimum source regions we found evidence for both short- and long-distance colonization in mainland post-disturbance habitats. In contrast to traditional RSPs, the spatial approach presented here addresses the spatiotemporal variation in colonization by explicitly identifying potential source locations for colonist species. By approximating the geographic area of interactions between a local community and its surroundings, the minimum source region explicitly examines the scale of the ecological “region” within which a local community is situated. Each measure of the source region (e.g., mean distance) provides additional information on colonization patterns. The

distribution of proxy dispersal distances, along with summary statistics such as those presented here, provide insight into the overall patterns of dispersal to a local community during colonization and characterize its overall similarity to the surrounding region. Maximum distance and source region area are dominated by the dynamics of the few species which appear to colonize a site via long distance dispersal, as evident in the contrast between the pattern for minimum source region area and across-species mean of proxy dispersal distances. By explicitly considering the spatial occurrence of species in the region, this approach allows researchers to address the dynamic features of colonization and the landscapes in which they occur.

Tables and Figures

Table 2-1. Species inclusion in regional species pools using traditional and spatial approaches.

Results of alternative approaches to determining regional species pools (RSPs), applied to survey data from Mount St. Helens, WA. For each RSP, the number of species (total and passerine) in the ‘region’ is given. Of the species observed at Mount St. Helens, the number of those species observed in the RSP, and the identities of any missing species, are provided. Note that for the BBS and MAPS datasets, missing alpine species (*) were accounted for by including Mount Rainier as a regional observation site for distance and area calculations. For the focal Mount St. Helens community, the across-species mean and maximum proxy dispersal distances and the area of the resulting ‘minimum source region’ [convex polygon] are given.

	State Atlas	Range Map	Spatial-BBS	Spatial-MAPS	Spatial-All
# Species	249	245	212	196	206
# Passerines	118	108	108	110	110
# MSH Species	89	92	91*	91*	93
# MSH Passerines	62	62	60*	60*	62
Missing MSH Species	Golden Eagle, Northern Goshawk, Prairie Falcon, Greater Yellowlegs	Red-naped Sapsucker	American Pipit, Gray-crowned Rosy-finch*	Horned Lark, American Pipit*	N/A
Mean Distance (km)	N/A	N/A	37	511	35
Maximum Distance (km)	N/A	N/A	445	1075	254
Area (km ²)	184800	7854	51774	137183	34516

Table 2-2. Regression parameters for effects of year and species richness on minimum source region statistics.

Estimates of slope of minimum source region parameters (across-species mean of proxy dispersal distances, across-species maximum of proxy dispersal distances, area of minimum source region) for longitudinal samples of up to 17 years of Mount St. Helens (MSH) communities (by disturbance zone) and Washington state BBS routes, according to best-fit generalized linear models. For each of the three metrics of the minimum source region, the best-fit model according to AIC included both number of years sampled (Year) and number of species in the local community (SR), with community location (Mount St. Helens disturbance zone or BBS route) as an interaction term for both Year and SR. Community identity (e.g., Pumice Plain) was included as a random effect.

Metric	Model Parameter	Slope Estimate ± SE
Mean Distance	Year (MSH)	-11.5 ± 45.9
Mean Distance	Year (BBS)	4.0 ± 8.5
Mean Distance	SR (MSH)	82.2 ± 9.8
Mean Distance	SR (BBS)	-1.6 ± 2.8
Max Distance	Year (MSH)	626.3 ± 1139.7
Max Distance	Year (BBS)	-186.1 ± 193.5
Max Distance	SR (MSH)	3094.3 ± 233.4
Max Distance	SR (BBS)	85.0 ± 59.6
MSR Area	Year (MSH)	9.9 ± 211.4
MSR Area	Year (BBS)	204.9 ± 37.4
MSR Area	SR (MSH)	265.2 ± 44.1
MSR Area	SR (BBS)	109.9 ± 12.0

Figure 2-1. Predicted patterns in minimum source region area over time.

Predicted patterns in minimum source region for community samples across time. Panel A shows areal extent of minimum source regions. Colonization from either local or regional sources is expected to plateau within a given area that represents the ecologically significant region from which dispersal to the focal community occurs. The rate at which the minimum source region reaches its maximal extent will be determined by the dispersal limitation of the potential colonists. Panel B shows the across-species mean of proxy dispersal distances. Neutral assembly from either local or regional sources predicts a monotonic curve. Niche processes such as habitat filtering may lead to non-monotonic curves over time.

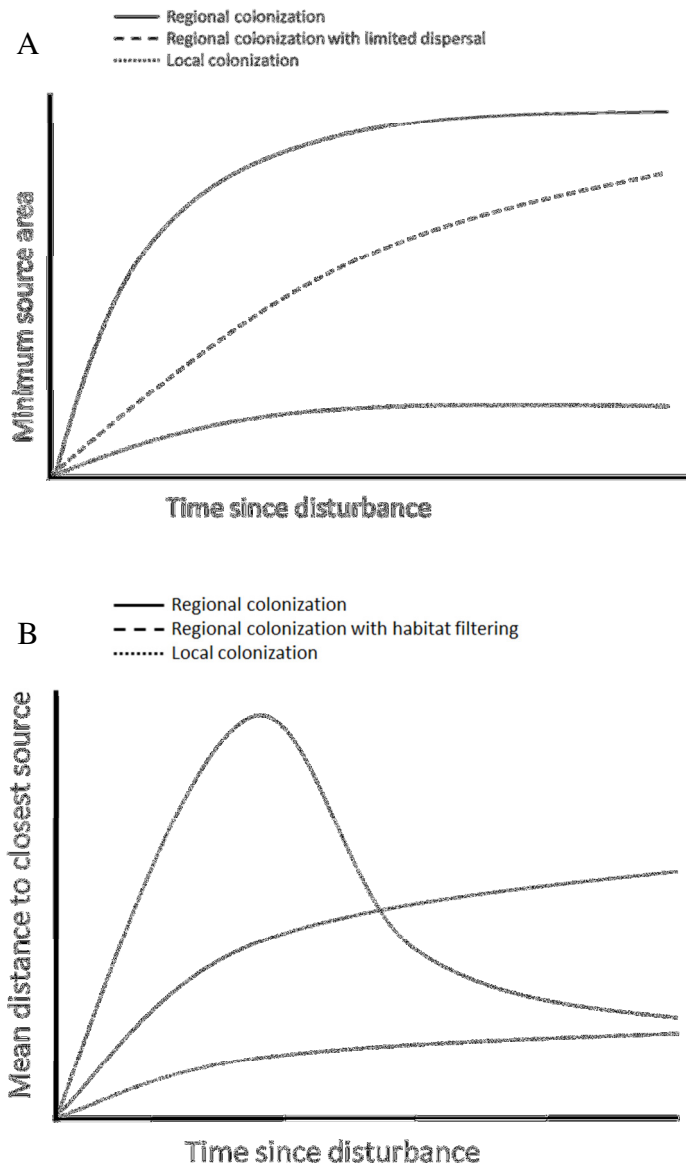


Figure 2-2. Diagram of methodology defining minimum source region.

Method to define minimum source region and associated RSP. Panel **A** shows a map of the focal community (Mount St. Helens) represented by the triangle and surrounding regional source locations (BBS routes) as circles. From the regional source locations, the closest location for each species present in the focal community is identified. In panel **B**, the regional observations for Species X are identified (diamond outlines). Panel **C** identifies the closest source location for Species X (black diamond). Panel **D** shows the suite of closest sites which combined include all species in focal community, identified as black diamonds, and a minimum circle around the focal community. In panel **E**, the minimum convex polygon that includes all required source locations is defined as the minimum source region (denoted by black lines). In panel **F**, all the source locations within the minimum source region are identified (union set of black circles and black diamonds). The regional reference community comprises all the species observed at all source locations within the minimum source region.

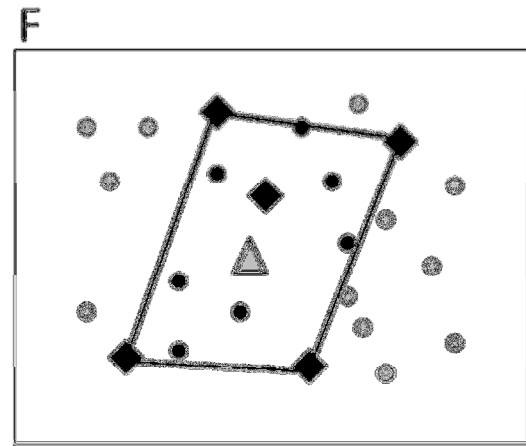
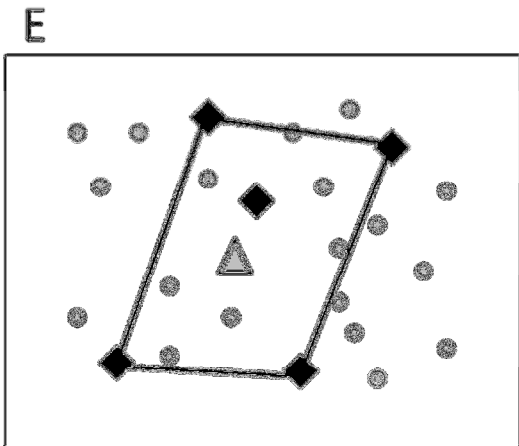
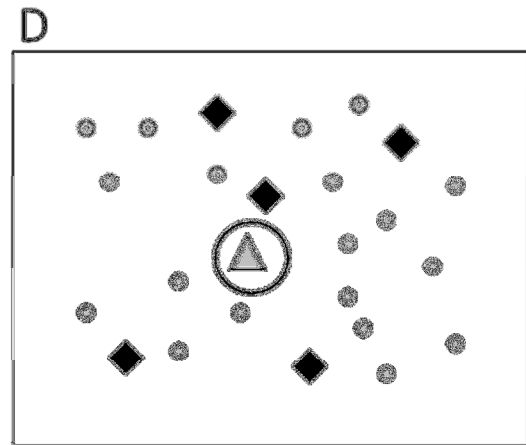
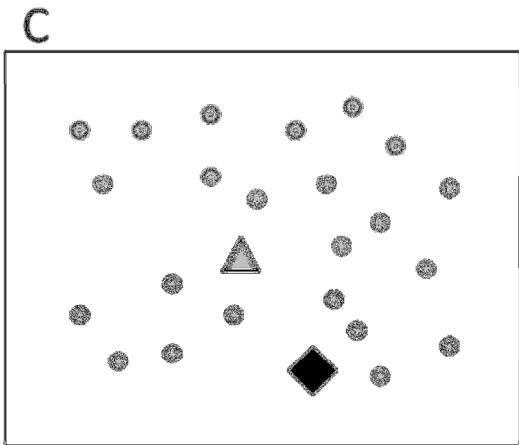
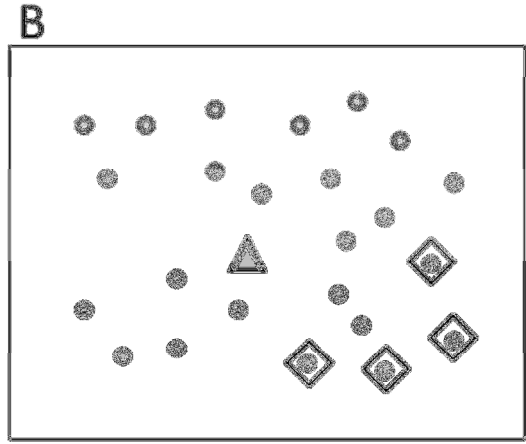
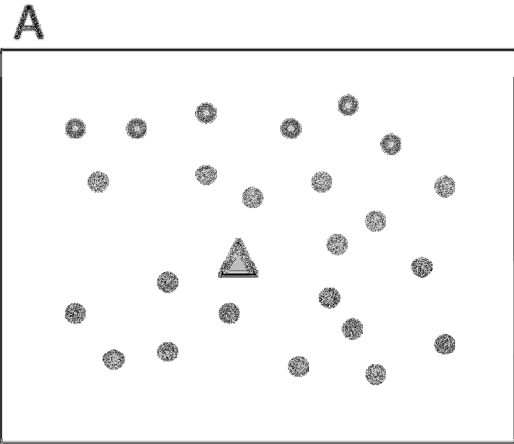


Figure 2-3. Observed patterns in minimum source regions across time.

Observed patterns in minimum source region for community samples across disturbance zones and years. Panel A shows areal extent of minimum source regions (km²) on a log scale. Panel B shows the across-species mean of proxy dispersal distances (km) within each community sample.

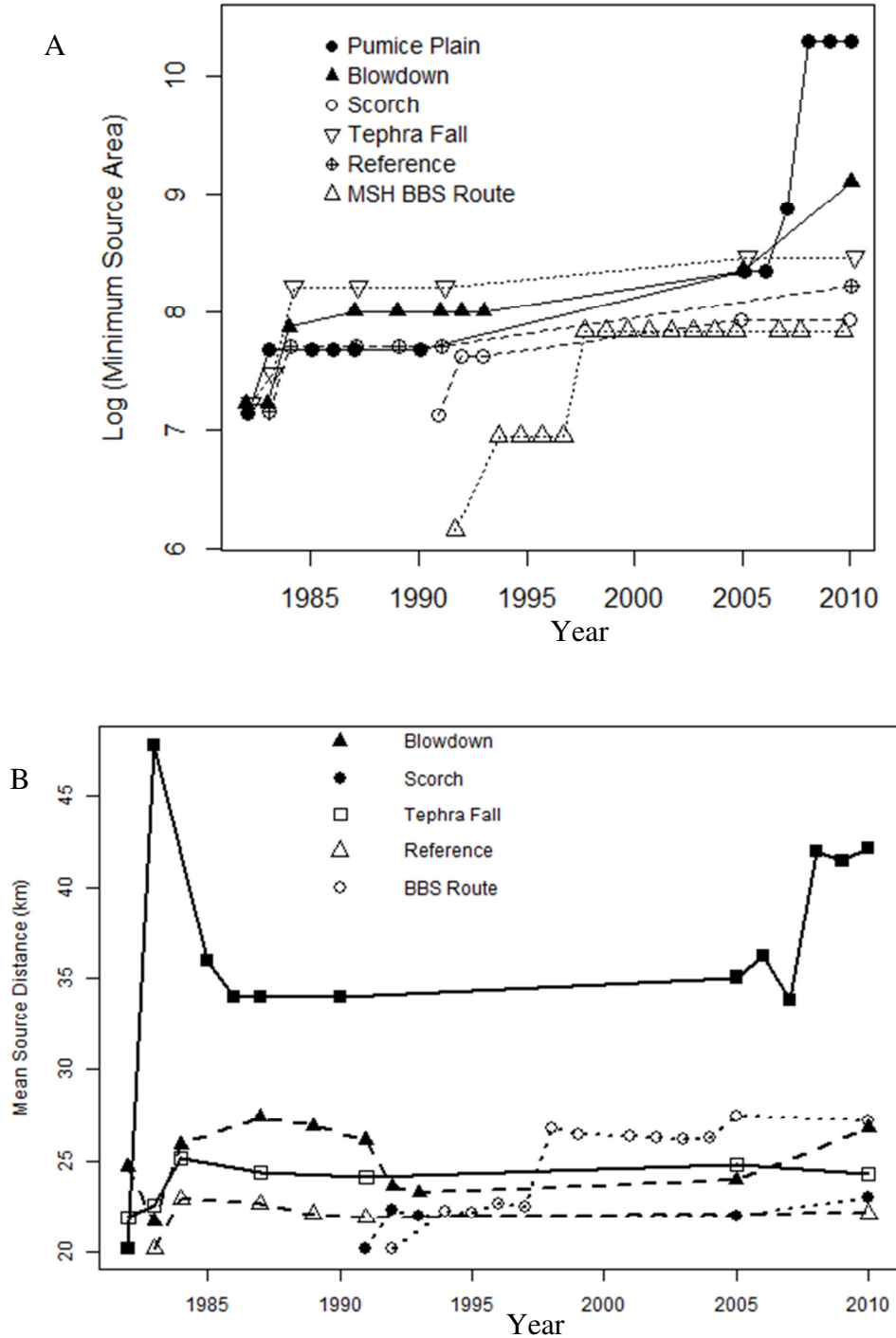


Figure 2-4. Maps of Minimum Source Regions for Mount St. Helens birds.

Maps of 'Minimum Source Regions' for data subsets at Mount St. Helens. Black triangle indicates Mount St. Helens. For each year, all species observed since the start of data collection are included. Each minimum source region is the minimum convex polygon that contains regional locations of all species observed in the community. Maps in the 'All Zones' column are based on species observed during field surveys at Mount St. Helens in all disturbance zones. Maps in the 'Blowdown Zone' column are based on species observed during field surveys at Mount St. Helens in the Blowdown disturbance zone. Maps in the 'BBS Route' column are based on species observed during independently conducted surveys along the Mount St Helens breeding bird survey route in the tephra fall zone of Mount St. Helens.

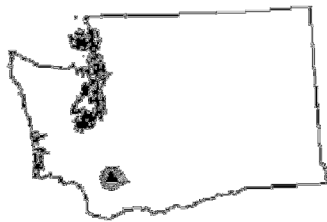
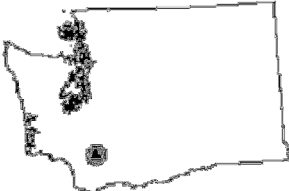
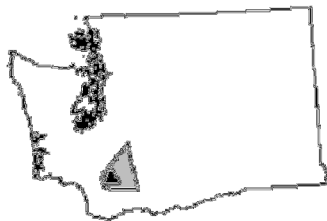
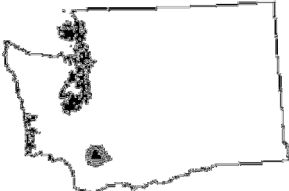
Year	Mount St. Helens: All Zones	Mount St. Helens: Blowdown Zone	Mount St. Helens: BBS Route
1982			
1983			

Figure 2.4 continued.

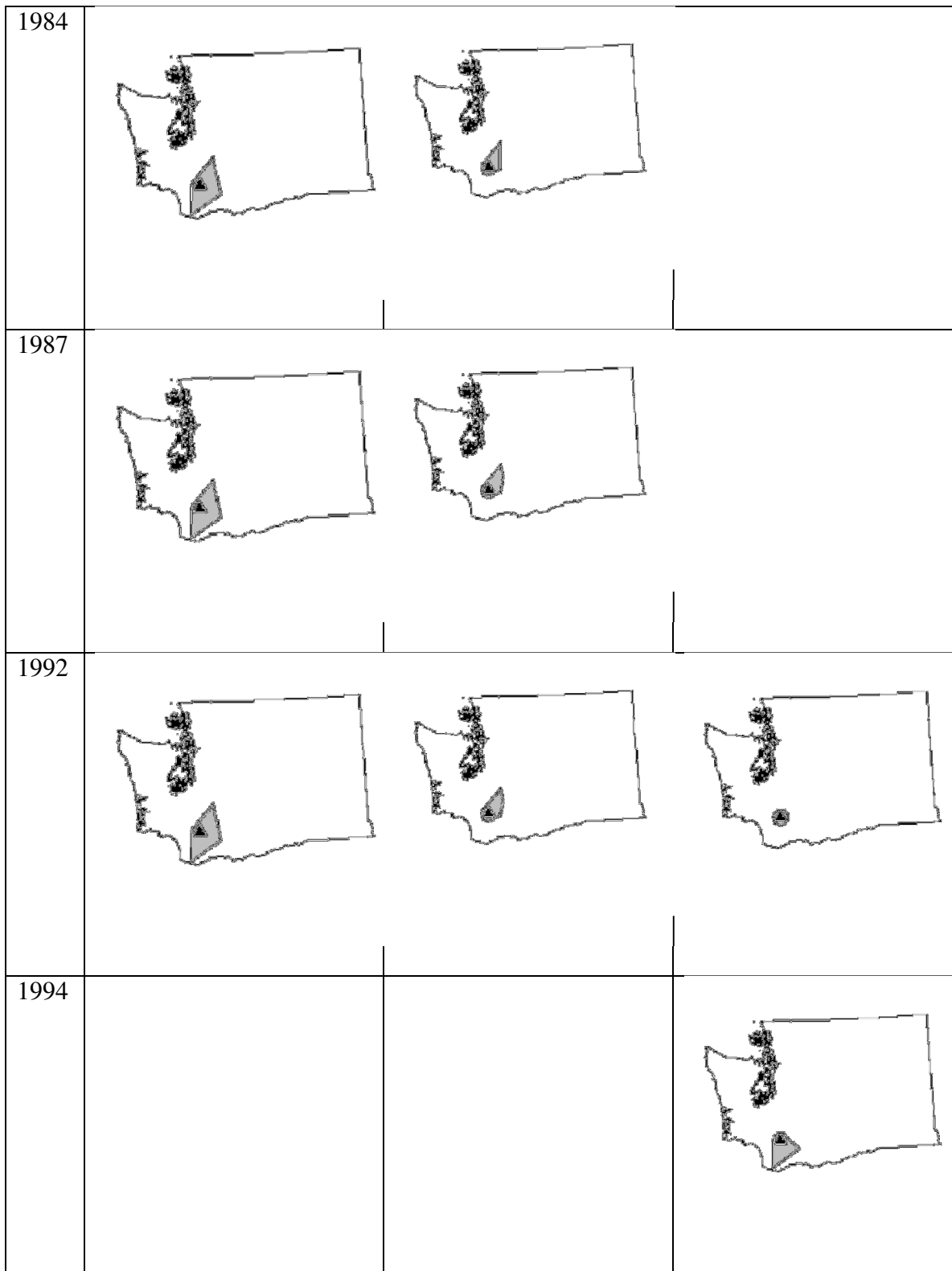


Figure 2.4 continued.

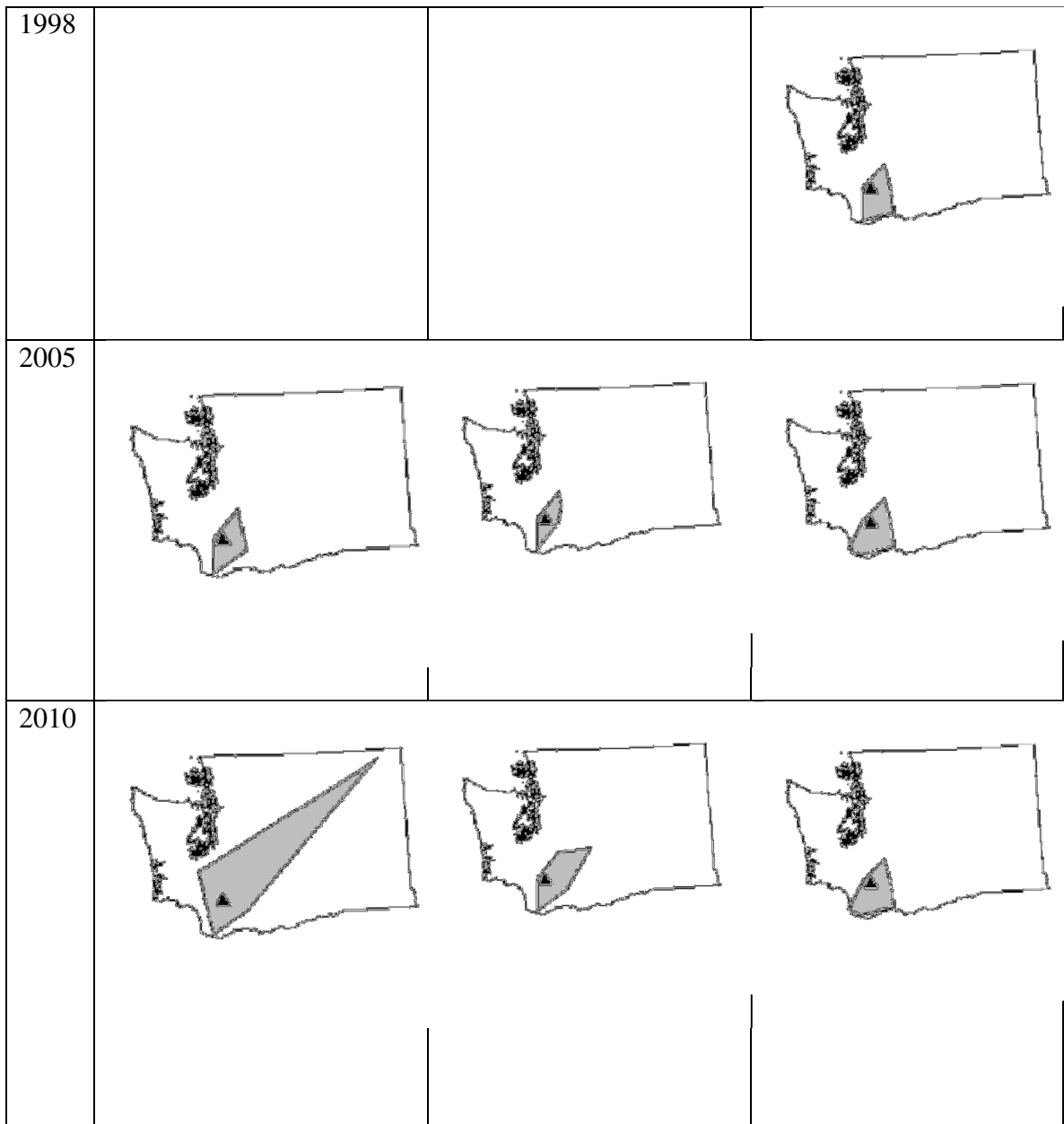
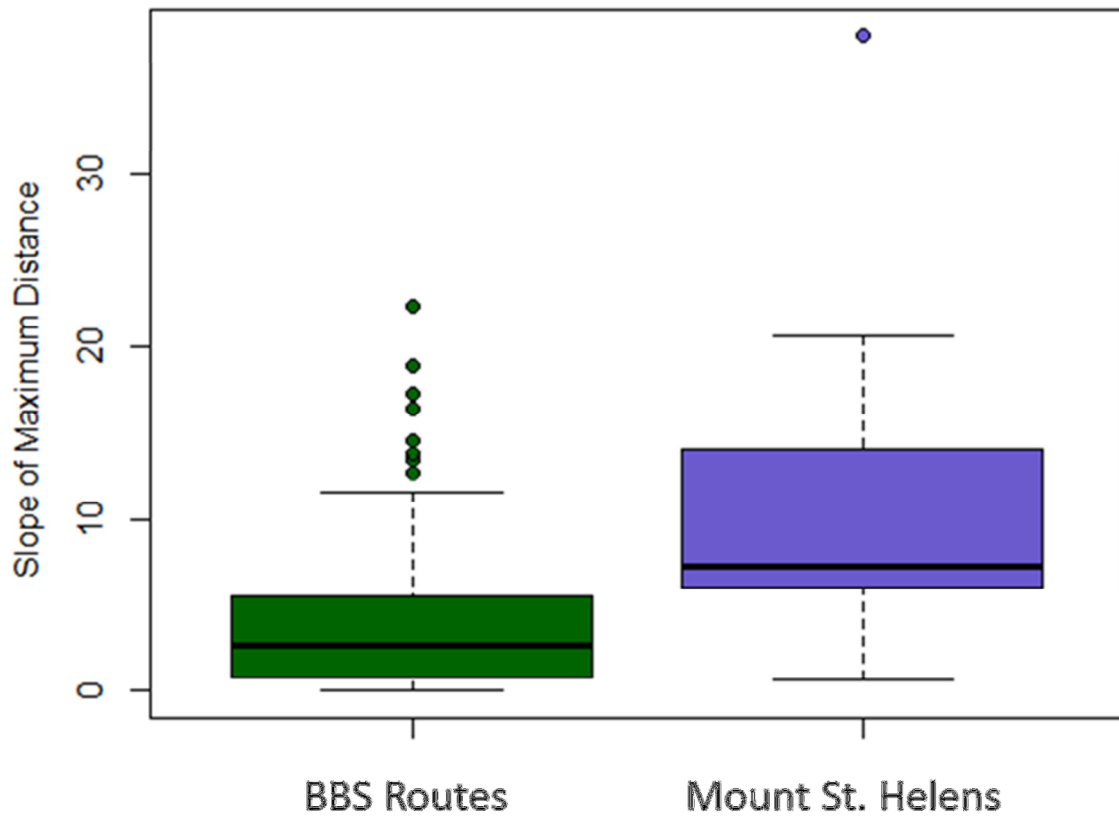


Figure 2-5. Temporal change in community-specific maximum of species' proxy dispersal distances.

The rate of increase in maximum distance across 17 years of surveys is typically higher in Mount St. Helens disturbance zone communities than in Washington State BBS site communities.



Chapter 3 : Evidence of assembly processes during primary succession at Mount St. Helens, WA

Co-authored with: *W. F. Fagan and C.M. Crisafulli*

Abstract

Understanding what processes regulate the structure and composition of local communities is a critical question in community ecology. While the role of species' responses to local conditions as determined by their niche have long been recognized, stochastic processes have more recently been included in the discussion of community assembly. In this study we considered community assembly in the bird communities of early primary successional habitats at Mount St. Helens following volcanic disturbance. We tested multiple niche-based assembly hypotheses against null models representing stochastic processes using relative abundance distributions, guild proportionality, nestedness, and body-size dispersion of birds during two time periods in early primary succession. While the bird communities present showed evidence of nestedness and habitat filtering, they did not support predictions based on assembly processes involving intraspecific competition. Our results suggest that the bird assemblages at Mount St. Helens have been shaped primarily by differential colonization according to classic environmental filtering models.

Introduction

Understanding community assembly processes is a fundamental component of community ecology, with ecologists long debating the roles of deterministic and stochastic processes. Historically, research has focused on environmental filters and

species interactions to explain deterministic patterns in community structure and composition. Models employing “assembly rules” identify patterns in community assembly and seek to explain the assembly processes underlying those patterns (Diamond 1975, Weiher and Keddy 2001, Weiher et al. 2011). In testing assembly rules, species are defined by traits influenced by environmental filtering, including ecological tolerances, habitat associations, and dietary guilds. These traits in turn influence the interactions among colonist species. Classic community ecological processes such as inhibition, facilitation, and priority effects all rely on species interactions consistent with niche processes.

The development of the neutral theory of community ecology has enlivened the debate over assembly processes (Caswell 1976, Hubbell 1997, 2001). Neutral theory posits community assembly to depend purely upon stochastic processes of births and deaths, speciation and extinction, and dispersal. Neutral theory provides a striking contrast to niche assembly, emphasizing event probabilities instead of species differences. However, neutral theory has also been criticized for its limitations in predictive ability and for its assumption of species functional equivalence (Gaston and Chown 2005, Gotelli and McGill 2006, McGill 2003). In addition, parameterization of neutral models of community ecology is often troublesome because such models frequently depend on parameters that are hard to estimate, such as rate of migration and metacommunity population size (Gotelli and McGill 2006). Though the neutral model of Hubbell (2001) and its extensions (eg, Etienne and Olf 2004, Ulrich 2004, Rangel & Diniz-Filho 2005) are often identified as a process-based description of community

assembly, such models are more correctly identified as specific forms of a null model (Gotelli and McGill 2006).

Today, both neutral and niche processes are recognized as potential contributors to community assembly. Early studies that incorporated both neutral and niche theories of community assembly often presented them as two competing hypotheses (e.g., Algar et al. 2005). However, they are now accepted as two ends of a continuum, where communities may undergo both niche and neutral processes (Tilman 2004, Gaston and Chown 2005, Gravel et al. 2006, Yang et al. 2013). Recent research has applied niche process models in the context of null models and multiple hypothesis testing to develop a more robust understanding of both niche and neutral community assembly processes (Algar et al. 2011, Chase and Myers 2011, Mutshinda and OHara 2011).

The use of neutral models and other robust null models for testing hypotheses has broadened our understanding of both neutral and niche processes in community assembly (Blackburn and Gaston 2001, Gotelli and McGill 2006). Neutral models of assembly are commonly tested based on patterns of species distributions, abundances, and species-area relations. Under neutral assembly processes, models predict both high β -diversity and low consistency of species rank abundance among local assemblages. Chance dispersal, particularly following disturbances is a key driver (Chase and Myers 2011, Cash et al. 2012). Priority effects, in which early colonizers influence the success of later colonizers, may contribute to this pattern (Chase 2007). Nestedness patterns, in which the species present at species-poor sites are subsets of the species at species-rich sites, may indicate selective colonization or extinction, or may be a result of passive sampling (Wright et al. 1997, Wang et al. 2011).

Commonly identified niche assembly processes include habitat filtering and interspecific competition (e.g., Diamond 1975, Keddy 1992, Fargione et al. 2003,) which predict opposing patterns in species traits within a community. Habitat filtering presumes that species with shared ecological tolerances and habitat requirements should find the same habitats attractive for colonization. Thus habitat filtering leads to assemblages with more similar traits than would arise from neutral assembly. When either habitat filtering or interspecific competition related to niche overlap and body size similarity drives species local colonization success, observed assemblages should feature specific patterns of co-occurrence, guild proportionality, and trait dispersion (Driscoll and Lindenmayer 2010). For example, competition may limit co-occurrence of species pairs with overlapping resource bases, leading to proportional sampling across guilds (Wilson 1989). Habitat filtering processes should lead to co-occurrence of species with more similar character traits while competition-based assembly should lead to the opposite (i.e., overdispersion of traits within the assemblage). Under competition-based models, species pairs adjacent in ranking of body size should exhibit larger average body size ratios, larger minimum size ratios, and smaller standard deviation of size ratios within the community than stochastically assembled communities (Case et al. 1983, Wang et al. 2011).

Disturbance

On the landscape scale, disturbance processes maintain overall landscape heterogeneity and related β -diversity (Swanson et al. 2010), and the intensity and frequency of disturbance should affect community dynamics (Pickett 1985). While the

1980 eruption of Mount St. Helens represents the less-studied extreme of high intensity – low frequency disturbance, lessons from lower intensity, higher frequency disturbance may still inform our understanding of assembly processes following this catastrophic disturbance. Disturbance is expected to increase “disorderliness” or stochasticity in community assembly (Fowler 1990), and this is particularly true under primary succession scenarios (del Moral and Grishin 1999). Frequent disturbance could obscure evidence of assembly rules if the disruptions occur on a timescale faster than the timescale of equilibration (Holdaway and Sparrow 2006, Driscoll and Lindenmayer 2010). Thus following disturbance, the accumulated effects of assembly processes would be expected to become more evident as more time passes. However in a study of macroinvertebrate communities across a gradient of disturbance, Lepori and Malmqvist (2009) observed β diversity to be lowest at intermediate levels of disturbance and highest in sites without disturbance, suggesting stochastic processes were more important when disturbance was low and that the role of niche processes was most important at intermediate levels of disturbance. Community assembly processes may still be evident in non-equilibrial communities recovering from disturbance (Cash et al. 2012), though few studies have addressed this topic.

Here, I examined the roles of niche and neutral processes in avian community assembly within the context of an early primary successional landscape following volcanic disturbance. Applying null models of stochastic community assembly, I tested local bird communities from wetland and upland primary successional habitats at Mount St. Helens, WA, for evidence of alternative assembly hypotheses (guild proportionality, nestedness and size-structure) and for species abundance patterns consistent with neutral

or niche hypotheses testing the importance of habitat filtering, interspecific competition, and neutral processes in assembly. Because the Mount St. Helens avifauna is assembling in early primary successional habitat, I expect stochastic processes to play a major role in assembly processes (Belyea & Lancaster 1999, Drake et al. 1999, Stokes & Archer 2010). Therefore I predict that niche-based assembly processes will not be detected in assembly patterns in the Mount St. Helens bird community. Examining assembly hypotheses in the context of the avian communities at Mount St. Helens offers a unique perspective of the role of assembly processes in recovery from large scale disturbance.

Methods

Field Site

Previous research on bird community responses to volcanic disturbances has focused largely on secondary successional sites that featured residual components of the pre-disturbance community, addressed short-term impacts of the disturbance, and/or were conducted on volcanic islands. For example, several researchers have studied both short and long-term avian responses to disturbance on volcanic islands (e.g., Brattstrom 1956, Byrd et al. 1980, Whittaker and Jones 1994, Dalsgaard et al. 2007, Petersen 2009, Drew et al. 2010, Bond 2012). Comparable studies, focusing on the impact of volcanic disturbance on bird communities in a mainland context, are largely absent from the literature. Much of what does exist in this area focuses on avian community recovery following the 1980 eruption of Mount St. Helens, WA, USA (Butcher 1981, Hayward 1982, Andersen & MacMahon 1986, Manuwal et al. 1987, Crisafulli and Hawkins 1998, Fairchild 2009), and we build on this literature in several ways.

Field work was conducted in 1981-1990 and 2007-2010 on the Pumice Plain at Mount St. Helens, which, prior to the 1980 eruption, was predominantly forested, a matrix of old-growth and managed coniferous forest. During the 1980 eruption, the Pumice Plain area was affected by several types of disturbance. First it was buried several tens to > 100m beneath a debris avalanche caused by collapse of the north face of the volcano, followed by a laterally directed blast surge, and then culminated in searing hot (> 300 °C) pyroclastic flows that surged from the crater for about four hours creating a sterile plain approximately 600 ha in size. Subsequent to the main 18 May 1980 volcanic eruption the area was influenced by additional pyroclastic flows, lahars, and tephra falls (Swanson and Major 2005). At the time of the eruption any birds present, including winter residents, permanent residents, and early migrants were immediately killed. The 1980 eruption and the resulting post-eruption landscape provide an outstanding opportunity to study avian community assembly in a mainland primary successional context. To the north, east and west, the Pumice Plain is surrounded by the Blast Area, which was severely impacted by the 1980 event; to the south the area was disturbed primarily by tephra fall although some areas were influenced by small lahars. Though no life survived on the Pumice Plain, remnants of the pre-eruption biota, identified as biological legacies, were common in much of the Blast Area, where secondary succession ensued.

At Mount St. Helens, impacts of volcanic disturbance on bird communities were addressed by a handful of investigators during the first fifteen years following the 1980 eruption. Most of this work focused in areas receiving cool tephra deposits >20 cm thick and reported ephemeral effects such as temporary abandonment of territories and nesting

sites (Butcher 1981, Hayward 1982). However, Andersen and MacMahon (1986) in addition to working in the Tephra Fall zone, investigated sites subjected to intense blast forces that toppled late seral forest over 370km² and deposited blast material and tephra several decimeters thick over the landscape. They reported a depauperate avifauna ranging from 3 to 6 species observed each year and low densities of species colonizing the blowdown zone during 1981-1984, dominated by the ground-nesting Dark-eyed Junco (*Junco hyemalis*). They found low depredation rates for artificial nests in the blowdown zone, where Mountain Bluebirds (*Sialia currucoides*) and possible nest predator Common Ravens (*Corvus corax*) were also observed. Manuwal et al. (1987) investigated avian responses in high-elevation forest on the south and southeast flanks of the volcano which received two levels of volcanic impact: tephra fall and scorch. Not surprisingly, they found that the effect of the eruption on bird communities was related to the extent of impact and that areas of shallow tephra supported communities similar to their reference sites, whereas in the scorched forest area they noted reductions in the tree foliage-insectivore and tree seed foraging guilds. Dominant species were associated with ground and understory vegetation. Crisafulli and Hawkins (1998) reported avian responses to the Mount St. Helens 1980 eruption in both secondary and primary successional sites over a 13 year period (1980-1993). In the Blowdown Zone they documented the establishment of seven bird species by the second post-eruption growing season (1981) that included ground nesters/foragers and cavity nesters that foraged on the ground, tree boles, or from the air column within one post-eruption year, followed by a second wave of colonization about six years later that included a suite of foliage gleaners and flycatchers. In the Pumice Plain, where all vestiges of the pre-

eruption biota were eliminated, they documented a much slower colonization rate and an overall bizarre community composition that included species drawn from many different habitat affinities (Crisafulli and Hawkins 1998).

During 2007-2010, the vast majority of the Pumice Plain was “upland” habitat in early stages of succession and dominated by low statured forbs and graminoids, *Lupinus lepidus* and sparse shrubby vegetation, primarily *Alnus sp.* and *Salix sp.* and occasional coniferous trees. For this study, four transects, 800-1000 m in length, were established running east-west through upland habitat, distributed uniformly across the Pumice Plain with 2 km separating parallel transects. Wetland habitat was dominated by dense thickets of *Salix* and *Alnus* with canopy height of 1.5 to 5m. Three transects 250-500m in length sampled the entire extent of wetland habitat that existed in 2007. Riparian habitat was also dominated by dense thickets of *Salix* and *Alnus* though canopy height did not exceed 4m. Two 500m transects were located along the eastern edge of thin riparian corridors, which provided the most effective method for surveying birds in these habitats. Wetland and riparian habitats occupied less than five percent of the total Pumice Plain landscape and were therefore more exhaustively sampled than upland habitats.

Bird Surveys

Between 1980 and 1990, initial colonization of the Pumice Plain was documented by the U.S. Forest Service conducting bird surveys along two transects on the Pumice Plain. In 1981 a 500m transect was surveyed twice. In 1982 the transect had been destroyed by a lahar, but surveys were conducted in the same area. In 1983 – 1990,

bird observations were recorded during multiple visits along one transect 3km in length on the Pumice Plain. Data available for this time period consisted only of the species identities observed each year.

Between 2007 and 2010, bird surveys were resumed on the Pumice Plain using distance sampling along the nine transects described above. Each transect was surveyed 4-7 times each year, 2007-2009. In 2010, only 5 of the 9 transects were surveyed. Surveys were conducted between 0600 and 1000 in the morning during June and July. Weather conditions were recorded at the start and end of each survey including the air temperature, cloud cover, precipitation, and wind. Based on habitat width (i.e., vegetation physiognomy) and post-hoc examination of survey results, bird observations were excluded if based on sightings beyond 100m perpendicular distance from a transect line in upland areas, and beyond 80m in wetland areas. Because of the narrow linear form of riparian habitats, only observations recorded between the transect line and 20 m west were included for riparian surveys. These limits in perpendicular distance were used to limit observations to the habitat targeted at that site. Bird observations included perpendicular distance to transect to allow these cut-offs to be made.

At all sites, records of birds flying through habitat were excluded from the analysis, and raptors, waterbirds and shorebirds were excluded from the study, as survey sites and techniques did not target these species. Records of the three most commonly recorded species were examined for habitat overlap where species in one habitat were observed from a transect in a different habitat. Specifically, records for Horned Larks (*Eremophila alpestris*) in wetland transects were examined and eliminated if actually occurring in surrounding upland habitat. Similarly, records for Yellow Warbler

(*Setophaga petechial*) and Willow Flycatcher (*Empidonax traillii*) in upland habitat were examined and eliminated if occurring in encroaching wetland habitat. Species trait information including diet guild, foraging behavior, nest location, length (cm), and mass (grams) were collated for each species observed at Mount St. Helens using Birds of North America species accounts (Poole 2005).

We stratified our study sites into “upland” or “wetland” habitats where “wetland” habitats included both riparian and wetland areas. For analysis, local sites were defined as 200m segments of each transect with $\geq 100\text{m}$ buffers between sites, resulting in 12 upland sites and 8 wetland sites.

Detection and Occupancy

To account for the presence of undetected birds, hierarchical occupancy models were used to estimate species-specific detection rates, site occupancy, and species richness within each habitat type (Zipkin et al. 2009). Initial occupancy was modeled as a Bernoulli random variable $z_{i,j,t} = \text{Bernoulli}(\Psi_{i,j,t})$ with probability $\Psi_{i,j,t}$ for species i at site j during year t (MacKenzie et al. 2002, Ruiz-Gutiérrez et al. 2010). For sampling in 2007 ($t=1$), we modeled species-specific occupancy by habitat type using the logit scale (Kéry & Royle 2009):

$$\text{logit}(\Psi_{i,j,1}) = w1_i \text{habitat}_j + w2_i (1 - \text{habitat}_j)$$

where $\text{habitat} = 1$ for upland sites and $\text{habitat} = 0$ for wetland sites, such that $w1_i$ is the probability of occupancy in upland sites and $w2_i$ is the probability of occupancy in wetland sites. Because upland sites were larger in area than wetland sites, the occupancy values should not be directly compared. The larger area of upland sites was expected to

be balanced by the higher densities of birds in wetland sites, For each subsequent survey year, occupancy was modeled by:

$$\begin{aligned} \text{logit}(\Psi_{i,j,t>1}) = & (1 - \epsilon 1_i) z_{i,j,t-1} \text{habitat}_j + (1 - \epsilon 2_i) z_{i,j,t-1} (1 - \text{habitat}_j) \\ & + a 1_i (1 - z_{i,j,t-1}) \text{habitat}_j + a 2_i (1 - z_{i,j,t-1}) (1 - \text{habitat}_j) \end{aligned}$$

where $\epsilon 1_i$ and $\epsilon 2_i$ represent probability of local extinction, such that $(1 - \epsilon 1_i)$ gives the probability of continued occupancy in year t given presence in year $t-1$. Similarly $a 1_i$ and $a 2_i$ represent colonization probabilities for each habitat, or the probability of occupancy in year t given that the species was not present in year $t-1$.

The detection of a given species in a survey was modeled as a Bernoulli random variable $x_{i,j,t,k}$ which denotes whether a species was recorded ($x=1$) or not recorded ($x=0$) for a given species i (i in 1-87; 37 observed species and 50 potential unobserved species) during a given survey identified by site j (1-20), year t (2007-2010), and sampling replicate k (1-7). Detection depends on the true occupancy z such that $x_{i,j,t} = \text{Bern}(\theta_{i,j,t,k} z_{i,j,t})$ where θ gives the probability of detection during sampling event k given that species i is present for species i at site j in year t . Probability of detection $\theta_{i,j,t,k}$ was assumed constant for a given species within a given habitat type:

$$\text{logit}(\theta_{i,j,t,k}) = v 1_i \text{habitat}_j + v 2_i (1 - \text{habitat}_j)$$

This model used data regarding detection and non-detection for each survey and each of the 37 species observed on the Pumice Plain. Species richness for each habitat was also estimated within the community model by summing probabilities of occurrence by year. Species-specific parameters for initial occupancy, local colonization and extinction probabilities from 2007 to 2010 were assumed to come from a normal prior distribution for the community, the mean of which came from a uniform distribution between 0 and

1 (Zipkin et al. 2010). Separate distributions were used for each habitat. This approach allowed us to incorporate all observations, including poorly represented species, within the analyses without making assumptions about community structure. Model parameters were estimated using a Markov chain Monte Carlo (MCMC) simulations in a Bayesian analysis implemented in WinBUGS (Spiegelhalter et al. 2003) and AIC was used for model selection. 20,000 iterations of three MCMC were run, with a burn-in of 10,000 discarded iterations and thinning the remainder to every fifth sample.

Diversity Metrics

Species diversity for the Pumice Plain was partitioned into α - and β - diversity. Observed species richness was the primary indicator of alpha diversity, due to the format of available 1981-1990 data. For 2007-2010, α -diversity was estimated using the nonparametric abundance-based jackknife1 estimator, which is robust to the scale of sample aggregation (Hortal et al. 2006). The jackknife estimator is precise across a range of spatial scales and allows an estimation of standard error. Additionally, the community occupancy models provided an additional estimate of α -diversity through the summed occupancy estimates of observed species and unobserved dummy species. Species accumulation curves were used only to demonstrate that sampling effort was sufficient in 2007-2010, and not to provide a formal estimate of specie richness. Raw relative abundances from the maximum number of individuals observed y site and year were fitted with broken-stick, log-normal, Zipf, and Mandelbrot-Zipf distributions. The best fit distribution for each habitat was determined using AIC.

To examine temporal and spatial variation in the Pumice Plain bird community between 2007 and 2010, β -diversity was calculated using the additive model $\beta_{Add} = \gamma$ -

$\bar{\alpha}$. The variation among community samples was partitioned hierarchically across habitats, years, and sites. Considering the context of colonization during 1981-1990 and the community during 2005-2010, turnover in the Pumice Plain bird community across time was determined using the Raup-Crick approach to β -diversity (Raup and Crick 1979), which uses species presence/absence data and a probabilistic null model to account for the effect of variation in α -diversity on the measurement of community similarity (Anderson et al. 2011, Chase et al. 2011). The Raup-Crick metric ranges from -1 (more similar) to 1 (more dissimilar), with 0 representing the dissimilarity expected by random chance.

Community Metrics

Community metrics were calculated for upland and wetland sites separately, and for the Pumice Plain as a whole. Metrics were compared to simulated assemblages from regional data (see below). Observations were aggregated across surveys and years for each site. Niche assembly processes are expected to increase the consistency of species identities in rank abundance distributions across sites. Consistency of rank abundance across sites within and among habitats was compared to the random expectation by an IV index:

$$IV = 2 \left(\frac{Cr_{obs}}{Cr_{obs} + Cr_{null}} \right) - 1$$

which is greater than 0 when observed rank consistency (Cr_{obs}) is greater than expected by random chance and is less than 0 when ranks are less consistent than random expectation (Watkins and Wilson 1994, Cash et al. 2012). Rank consistency was calculated for each habitat and Cr_{null} was calculated as the mean rank consistency for

100 permutations of the rank abundance matrix in which the ranks of species with non-zero abundances within each site were randomized. The Cr index ranges from 1 when rank abundances are identical among plots to -1 when they are as different as possible. One sample t-tests were used to determine if the mean rank consistency index for each habitat was significantly different than zero.

Nestedness of assemblages present on the Pumice Plain was estimated following the BinMatNest approach which holds constant the row and column sums when randomizing the species-site occupancy matrix (Ulrich et al 2009). The temperature index of the community matrix, which ranges from 0 to 100 where 0 indicates perfectly nested communities and 100 indicates minimal nestedness, was calculated among sites within each habitat and across the Pumice Plain. The null expectations for nestedness temperature were calculated with fixed column and row marginal sums using the vegan package in R (R Core Development Team 2010).

Community structure for species trait guilds was considered for foraging behavior, food type, and nest placement to assess the roles of habitat filtering and competition in assembly. For these analyses, null models were constructed from regional species pools compiled from the 1968-2009 surveys of USGS Breeding Bird Survey (BBS) routes within 500 km of the study site. Given the mainland nature of the study site, the extent of the region used here was selected because all birds observed at Mount St. Helens can be found within the BBS data at this radius. The number of individual BBS routes where each species has been observed was used as a proxy for species' range size. The regional species pools were limited to the taxonomic orders and guilds observed at Mount St. Helens. Each species observed in the regional datasets was

classified according to diet guild, foraging guild, and nest placement using Birds of North America species accounts (Poole 2005). Null models used random sampling from a regional pool following Blackburn and Gaston (2001), where each species in the regional pool was weighted by the number of regional sites occupied to account for regional abundance. A distribution of values for the null expectation was drawn from 1000 community simulations for each test. For null model predictions of diversity and guild structure, communities containing the same number of individuals as the target community were simulated. The proportion of individuals in each guild and the variance in guild proportionality were tested against null model expectations. The proportion of species in each guild in Pumice Plain assemblages and the variance in proportions among sites were compared to the probability distribution of null assemblages built from the regional species pool (eg, Blackburn and Gaston 2001, Algar et al. 2005). A Bonferroni correction was made to control for multiple comparisons of guild proportionality.

The influence of interspecific competition on community assembly was also tested by comparison of species pair body size ratios within the community, using weight (grams) and length (cm). For each Pumice Plain habitat x guild combination, body size ratios (BSR) were calculated for species pairs adjacent in body size rank (Case et al. 1982, Etienne and Olf 2004). Body size ratios were only examined for diet guild assemblages with three or more species. Overall patterns in body-size overlap were tested by standardizing the observed BSR from each assemblage (BSR_{obs}) to the null distribution using the standardized effect size ($SES = \frac{BSR_{obs} - BSR_{sim}}{sd(BSR_{sim})}$). Assembly patterns unaffected by interspecific competition predict on average, an SES not

significantly different from zero (Case et al. 1983, Wang et al. 2011). This hypothesis was tested using a one-sample t-test to determine whether SES values for the group of assemblages was different from 0; upland and wetland assemblages were considered separately.

Results

Bird Community and Occupancy

Only seven landbird species were observed on the Pumice Plain in the first ten years following the 1980 eruption (Figure 3-1). The Common Raven was the first bird species observed on the Pumice Plain following the eruption, followed in 1983 by the Gray-crowned Rosy-finch (*Leucosticte tephrocotis*) and American Pipit (*Anthus rubescens*), both ground-foraging species commonly found in alpine barrens. By 1985 three additional landbirds were present, including the aerial-foraging Barn Swallow (*Hirundo rustica*). Additional colonists were the ground-foraging Dark-eyed Junco and Rock Wren (*Salpinctes obsoletus*). In 1986 Tree Swallows (*Tachycineta bicolor*) were first observed, an aerial forager not reliant on vegetation for nesting habitat.

By 2010, 37 landbird species were observed in surveys of the Pumice Plain. Of these, 18 were observed at upland sites and 27 were observed in wetlands. The species observed included 33 Passeriformes, two species of Apodiformes [Rufous Hummingbird (*Selasphorus rufus*) and Vaux's Swift (*Chaetura vauxi*)], one Caprimulgiformes (Common Nighthawk - *Chordeiles minor*) and one Piciformes (Northern Flicker - *Colaptes auratus*). Species accumulation curves show that species richness approached an asymptote in each habitat (Figure 3-3), indicating that our sampling effort sufficiently

captured the species present at each site. The relative abundance distributions for the Pumice Plain assemblages were best fit by the Broken-Stick model (Table 3-1), which implies relatively high evenness across species (Wilson 1991).

Overall species richness for the Pumice Plain was estimated at 42.6 ± 5.2 species. In upland sites, the nonparametric abundance based estimate of α -diversity (jackknife 1) was 22.6 ± 3.1 species (mean \pm SE). However, the hierarchical community model estimated species richness for the upland sites to be slightly higher, at 28.8 ± 8.7 species. This is because the jackknife 1 estimate only considers the patterns of observation of observed species to predict unobserved species, while the hierarchical model incorporates dummy species for which it estimates unobserved occupancy using parameters drawn from the community distribution. In wetland sites, α -diversity was estimated at 32.6 ± 3.8 species, although the hierarchical community model estimated species richness for the wetland sites significantly higher, 58 ± 4.8 species. While wetland sites had higher α -diversity than upland sites, both habitats demonstrated lower α -diversity than predicted by random assemblage.

Temporal turnover was significant, with Raup-Crick β -diversity across the first ten years of sampling consistent with expectations under randomization ($0.79 \pm .32$). Also, between 2007 and 2010 β -diversity within each habitat did not differ from expectations under randomization ($\beta_{site} = 10.08$, $p=1$). However, additive β -diversity was significantly higher than expected between upland and wetland habitats and across years during 2007 - 2010 ($\beta_{habitat} = 6.87$, $p=0.002$; $\beta_{year} = 15.25$, $p<0.002$). Similarly, Raup-Crick β -diversity was 0.00036 ± 0.0004 in upland sites and 0.0038 ± 0.0066 in wetland

sites, demonstrating spatial turnover within each habitat also did not differ from expectations.

In upland sites, species-specific detection probabilities were estimated to be less than 0.15 with the exceptions of Horned Lark (0.731 ± 0.033), Dark-eyed Junco (0.223 ± 0.057) and White-crowned sparrow (0.377 ± 0.054). Local site occupancy (within 200 m transects) ranged from 0.52 to 0.96 (Table A2-1). In wetland sites, 27 species were observed and α -diversity (jackknife 1) was 32.6 ± 3.8 species, although the hierarchical community model estimated species richness for the wetland sites significantly higher, 58 ± 4.8 species. Detection rates from the occupancy models in wetland habitat were estimated to be less than 0.5 with the exceptions of White-crowned Sparrow (0.590 ± 0.050), Willow Flycatcher (0.828 ± 0.039), Yellow Warbler (0.845 ± 0.034), and Lincoln's Sparrow (0.862 ± 0.045). Estimated occupancy rates were also significantly higher than in upland sites ($p < 0.003$) with Yellow Warbler demonstrating the highest estimated occupancy at 0.97. When considering the greater area of upland sites, this indicates a dramatic disparity in occupancy and bird densities between habitats. Equal occupancy of upland and wetland sites would indicate greater density in upland sites, because upland sites are larger in area. However, higher occupancy was observed in wetland areas due to the higher bird densities in these areas.

Assembly Processes

Species distributions across sites showed significant evidence of niche assembly processes, contrary to my predictions. For example, early colonization of the Pumice Plain shows clear patterns of habitat filtering. Early colonists were primarily

insectivorous or omnivorous, ground or cliff nesting, and less reliant on vegetation than later colonists. During 2007-2010, the consistency of rank abundances was very high for wetland sites at 0.686, while C_r for upland sites was equivalent to random expectation at 0.07. However, the IV index for rank abundance consistency was significantly greater than zero for both habitats, indicating that rank abundances were more consistent across sites within each habitat than expected by chance (Table 3-2). The local Pumice Plain assemblages were also highly nested within each habitat. The temperature index was 16.7 in upland habitats and 12.1 in wetland habitats, in both cases significantly lower than null model predictions for each occupancy matrix.

In comparing guild structure in upland and wetland assemblages to null models of assembly, we found significant deviations from the expected pattern of guild proportionality. In upland habitats, significantly more omnivorous, granivorous and nectarivorous individuals and fewer insectivores were observed than expected (Table 3-3). Unsurprisingly, ground foragers were overrepresented in upland habitats, as were aerial foragers and hovering foragers. Similarly, there were significantly more ground nesters than in the null model (Figure 3-5). In wetland habitats, slightly fewer insectivores and more nectarivores were observed than predicted by the null model. Ground foragers were still more prevalent than in the null model, though to a lesser degree than in upland sites. In addition, there were more shrub and ground nesters present in the wetland sites than in the null model. Overall, tests of guild proportionality repeatedly supported the hypothesis of habitat filtering. However, sample sizes were too small to test the variance of guild proportionality across sites.

Body size ratios of species within both wetland and upland sites were lower than expected based on previous studies (Case et al. 1983, Wang et al. 2011). Average body length ratios were less than 1.3 for every guild examined. Body mass ratios ranged from 1.2 to 2.4, but the majority of values were less than 2.0. In addition, body size ratios of both mass and length demonstrated a standardized effect size significantly greater than zero, opposite the pattern predicted by interspecific competition (Table 3-4).

Discussion

Our study examined bird assemblages in two primary successional habitats at Mount St. Helens, WA, for evidence of community assembly patterns. Such patterns, which include relative abundance distributions, guild proportionality, nestedness, and body-size dispersion, have been commonly studied separately. However, only recently have individual studies addressed the relative merits of these hypotheses (Algar et al. 2005, Driscoll and Lindenmayer 2010, Cash et al. 2012), and the relative roles of niche and neutral assembly processes in shaping post-disturbance communities remain a topic of ecological discussion (Stokes & Archer 2010, Mutshinda and Ohara 2011, Rosindell et al. 2011).

The avifauna on the Pumice Plain of Mount St. Helens demonstrated a higher α diversity of birds in wetlands than in uplands (Figures 3-2, 3-4). This is expected given the advanced development of vegetation in wetland areas relative to uplands, and the higher potential for niche differentiation (MacArthur 1965, Pianka 1966). Beta-diversity indicated turnover consistent with niche assembly processes between habitats and across

years. However, within each habitat, β -diversity was consistent with neutral assembly processes.

Species compositions of local assemblages, particularly within each habitat type, were highly nested, possibly indicating that community assembly is shaped by selective colonization or extinction processes. In this mainland context, the observed nestedness may be due to frequent colonizations of regional species, due to the high dispersal ability of colonizing species (Cook and Quinn 1995). These results were consistent across both habitat types considered and are similar to patterns found in other assemblages (Wang et al. 2011). However, it's important to note that nestedness alone may emerge from several mechanisms, including effects of passive sampling (Wright et al. 1997, Ulrich & Gotelli 2007).

Some patterns identified in the Mount St. Helens community are contrary to what was expected given the early stage of ecological response or development (Magurran 2007, McGill et al. 2007). For example, the broken-stick distribution fit of relative abundances seen in Table 3-1 is surprising. The lognormal distribution, which would indicate lower species evenness than the broken-stick model, is more commonly fit to relative abundance distributions (Magurran 2007). Evenness is generally expected to increase with time and the Pumice Plain communities are in relatively early development. Also, while β -diversity was consistent with neutral processes in upland sites, the concordance of rank abundance distributions across sites suggests niche assembly processes, which suggests deterministic processes and could be attributed to habitat filtering or competitive interactions (Cash et al. 2012). In addition, the positive

species co-occurrence patterns between ecologically-similar species at Mount St. Helens suggest the importance of environmental filtering mechanisms in assembly processes.

The patterns of bird occupancy at Mount St. Helens are consistent with habitat filtering but do not show evidence of interspecific competition in assembly processes, as seen in the guild proportionality and body size dispersion analyses. Overall patterns of guild structure were not consistent between upland and wetland habitats. Upland habitats included more ground foragers and nesters, while wetland habitats with greater vegetation complexity supported more foliage-gleaners shrub-nesters (Table 3-3). These patterns show clear evidence of habitat filtering from the regional species pool in colonization of local sites.

Under the influences of intraguild competition body size ratios should be approximately 1.3 for body length and 2.0 for body mass (Hutchinson 1959, Case et al. 1983). For both measures of size, average body size ratios of Pumice Plain habitats were lower than these expected values and lower than predicted by null assemblages, arguing against competition as a driver in community assembly. Recent studies of species co-occurrence patterns (Driscoll and Lindenmayer, 2010, Wang et al., 2011) likewise found little evidence of interspecies competition shaping assembly processes. In contrast to our work, however, Wang et al. emphasize the impact of local extinction processes (mediated by area effects) on local occupancy and community structure rather than colonization after disturbance. The lake island bird communities studied by Wang et al. have assembled over nearly twice as many years since disturbance as the Mount St. Helens communities studied here, yet show similar support for niche-based (habitat filtering) and neutral assembly processes. Likewise, Cash et al. (2012) tested the

assumption that community structure is stronger in undisturbed, equilibrium communities by testing several assembly patterns and hypotheses in avian communities in areas with varying levels of disturbance. The researchers found only limited support for the expectations that niche-based assembly rules would have larger impacts in undisturbed communities or that local assemblages at different sites would become more similar over time following disturbance.

Community assembly occurs through a combination of niche and neutral processes, but how these processes change in importance over time since disturbance remains in question. Following disturbance, community assembly may be initiated by an early pioneer stage characterized by stochastic colonization, before transitioning to an intermediate building stage characterized by local spread of colonist species (Gitay and Wilson 1995). The role of disturbance has been typically examined through selection of study sites experiencing different disturbance regimes, and few studies have addressed systems in early assembly.

Here we examined the evidence for neutral and niche processes in community assembly after thirty years of primary succession following intense large-scale forest disturbance. Overall, the structure of the avian community at Mount St. Helens shows evidence of habitat filtering during both periods of bird surveys, but little other indication of niche assembly processes. Patterns of diversity and nestedness observed on the Pumice Plain are better explained by selective colonization based on habitat suitability rather than competitive interactions. This suggests that in the context of post-disturbance recovery of mainland habitat, niche-based processes may determine the trajectory of early community assembly.

Tables and Figures

Table 3-1. Model fitting for species abundance distributions

Model selection results for site-wide abundance distributions according to AIC. Number of sites for which each standard species abundance distribution model was the best fit is given, along with AIC values (site mean \pm standard deviation) for Pumice Plain species abundance distributions for each habitat aggregated across 2007-2010, which demonstrate that the broken-stick model is consistently the best fit distribution.

Model	Fit in Upland Sites	Fit in Wetland Sites
Broken-Stick	11 sites (17.46 \pm 9.86)	8 sites 33.24 \pm 20.38
Zipf	1 site 19.53 \pm 7.68	0 sites 34.97 \pm 19.83
Log-normal	0 sites 20.02 \pm 8.58	0 sites 35.00 \pm 19.69
Mandelbrot-Zipf	0 sites 22.72 \pm 7.54	0 sites 36.49 \pm 19.13

Table 3-2. Consistency of rank abundances for birds on the Pumice Plain

Consistency of rank abundances of species across sites, within each Pumice Plain habitat. The IV Indices for rank abundances were more consistent than expected by random chance, as demonstrated by the students t-test.

Habitat	<i>Cr</i>	IV Index (mean \pm sd)	Student's t	P value
Upland	0.067	0.249 \pm 0.209	13.9	$<1 \times 10^{-10}$
Wetland	0.686	4.54 \pm 3.26	11.9	$<1 \times 10^{-10}$

Table 3-3. Actual and expected guild proportions of birds on the Pumice Plain.

Proportions of dietary, foraging, and nesting guilds observed on Pumice Plain compared to null model assembly from the regional species pool. Proportions of species observed within each guild were compared to corresponding null model results within each habitat of the Pumice Plain.

Trait	Guild	Simulated	Actual (Upland)	Actual (Wetland)
Dietary	Insects	0.76 ± 0.03	0.59*	0.73*
Dietary	Nectar	0.01 ± 0.01	0.06*	0.07*
Dietary	Omnivore	0.07 ± 0.02	0.11*	0.07
Dietary	Seeds	0.16 ± 0.02	0.24*	0.13
Nesting	Burrow	0.01 ± 0.01	0.04*	0.01
Nesting	Cavity	0.31 ± 0.03	0.25*	0.17
Nesting	Cliff	0.04 ± 0.01	0.18*	0.05
Nesting	Ground	0.13 ± 0.02	0.34*	0.27*
Nesting	Shrub	0.15 ± 0.02	0.06	0.26*
Nesting	Tree	0.31 ± 0.03	0.12	0.21
Foraging	Aerial foraging	0.15 ± 0.02	0.17*	0.17*
Foraging	Flycatching	0.08 ± 0.02	0.04	0.05
Foraging	Foliage gleaning	0.28 ± 0.03	0.05*	0.17
Foraging	Ground foraging	0.48 ± 0.03	0.68*	0.55*
Foraging	Hovering	0.01 ± 0.01	0.06*	0.07*

Table 3-4. Body size ratios for Pumice Plain assemblages.

Overall body size ratios were smaller than expected according to interspecific competition assembly hypotheses.

Habitat	Size Measure	Mean Ratio	SES (Atlas pool)	SES (BBS pool)
Upland	mass	1.7035	0.4515	0.3976

Wetland	mass	1.4826	0.5029	0.2565
Upland	length	1.1119	0.8607	0.7658
Wetland	length	1.0969	0.8613	0.8693

Figure 3-1. Satellite images of Pumice Plain bird transects.

Satellite images of sections of Pumice Plain bird transects showing general vegetation patterns for wetland and upland habitats during 2007-2010 for the Mount St. Helens Pumice Plain. Black bars represent 50 m lengths to indicate scale.

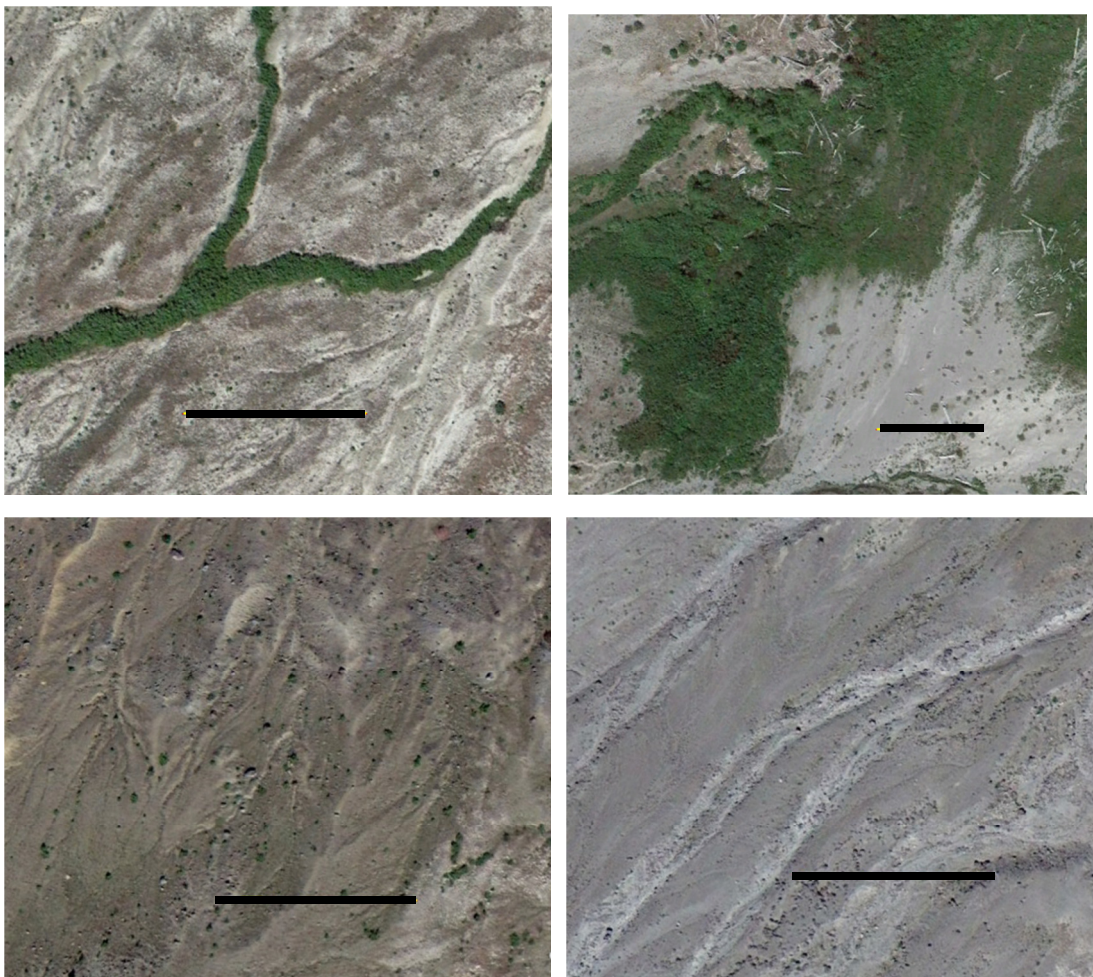
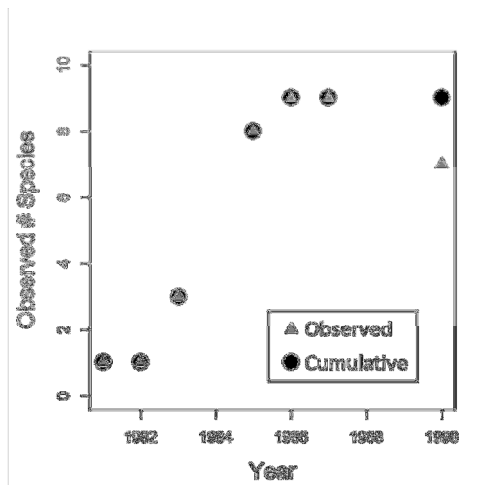


Figure 3-2. Observed species richness on the Pumice Plain, 1981-1990 and 2007-2010.

Observed species richness on the Pumice Plain, 1981-1990 (A) and 2007-2010 (B). Heavy lines represent cumulative species observed across years, thin lines represent species observed in a given year. For 1981-2006, only upland habitats were surveyed. For 2007-2010, solid lines represent species richness combined for both upland and wetland habitats. Dashed lines represent species richness observed in upland habitats only.

A.



B.

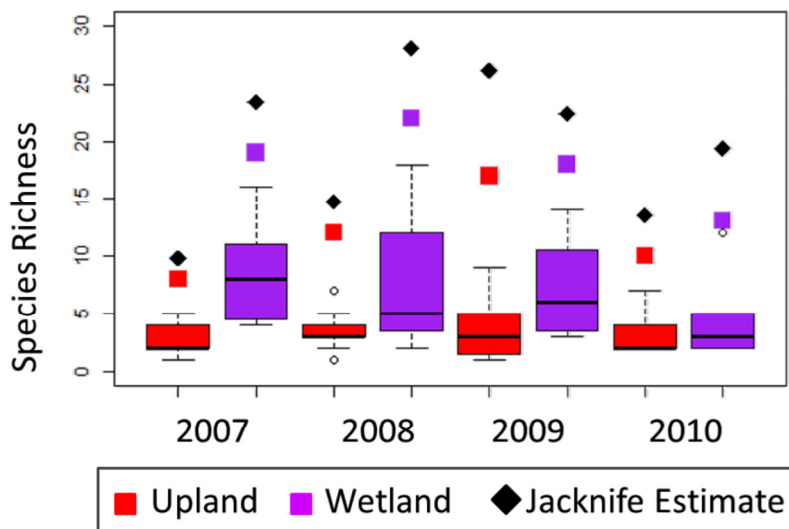


Figure 3-3. Diversity partitioning of Pumice Plain species, 2007-2010.

Partitioning of diversity across sites within each habitat, habitats, and years 2007-2010. The light gray bars (Alpha) shows the average species richness at each hierarchical level. The dark gray bars (Beta) shows the additive beta diversity at each level.

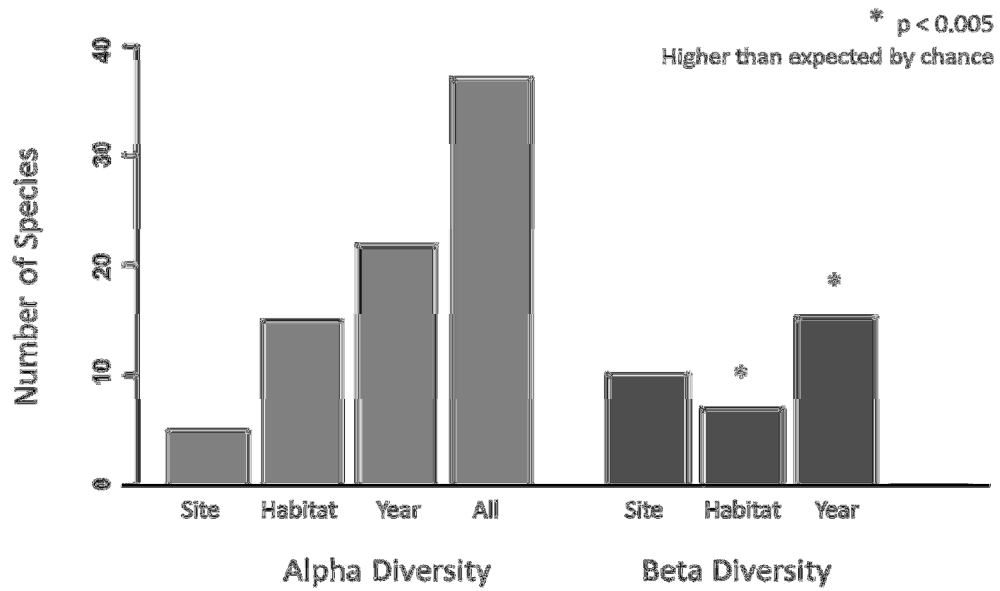


Figure 3-4. Species accumulation curves for Pumice Plain habitats, 2007-2010.

Species accumulation curves across sites for wetland and upland habitats on the Pumice Plain during 2007-2010.

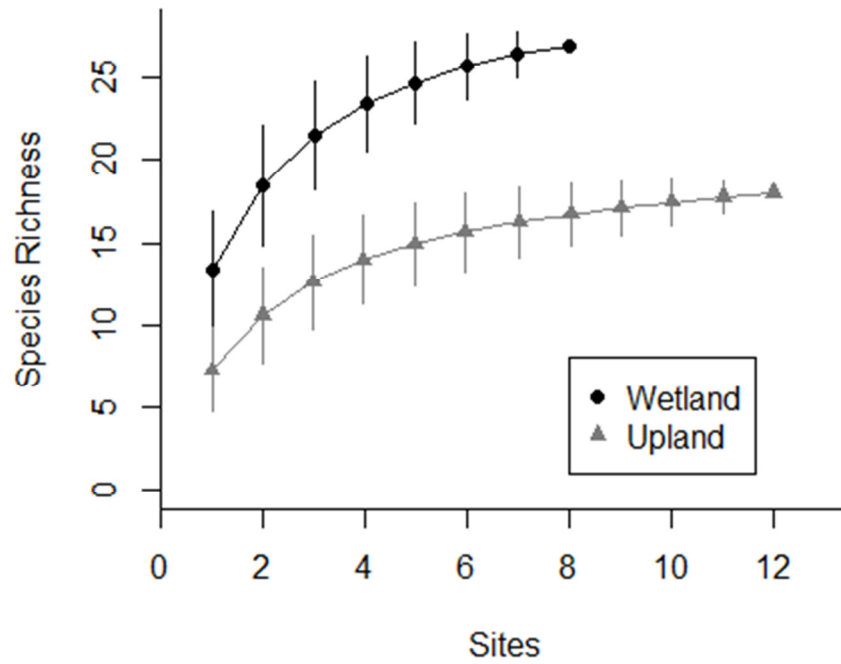


Figure 3-5. Observed richness of avian dietary guilds on the Pumice Plain.

Observed species richness of avian dietary guilds present on the Pumice Plain, 1981-1990 and 2007-2010.

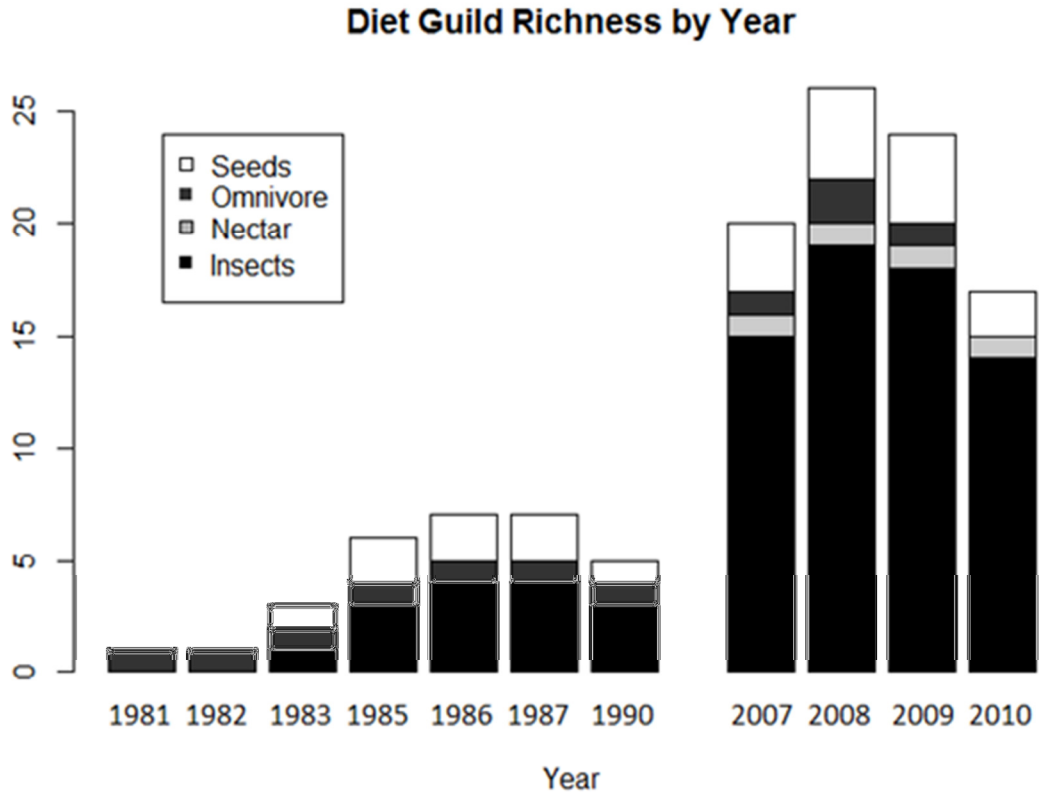


Figure 3-6. Observed richness of avian foraging guilds on the Pumice Plain.

Observed species richness of avian foraging guilds present on the Pumice Plain, 1981-1990 and 2007-2010.

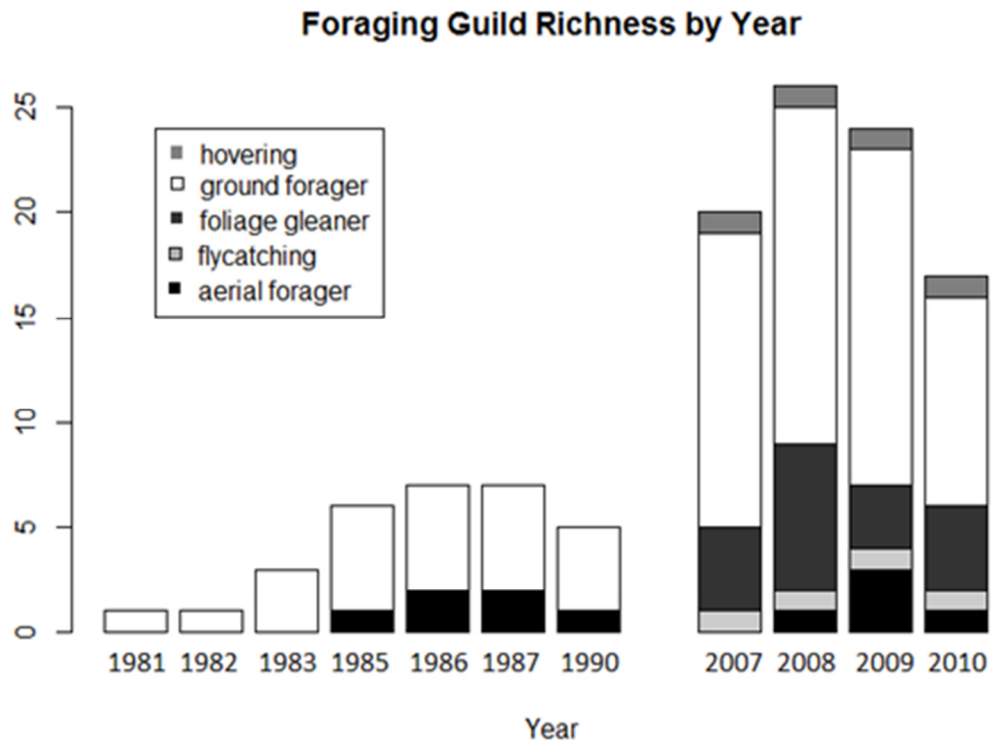
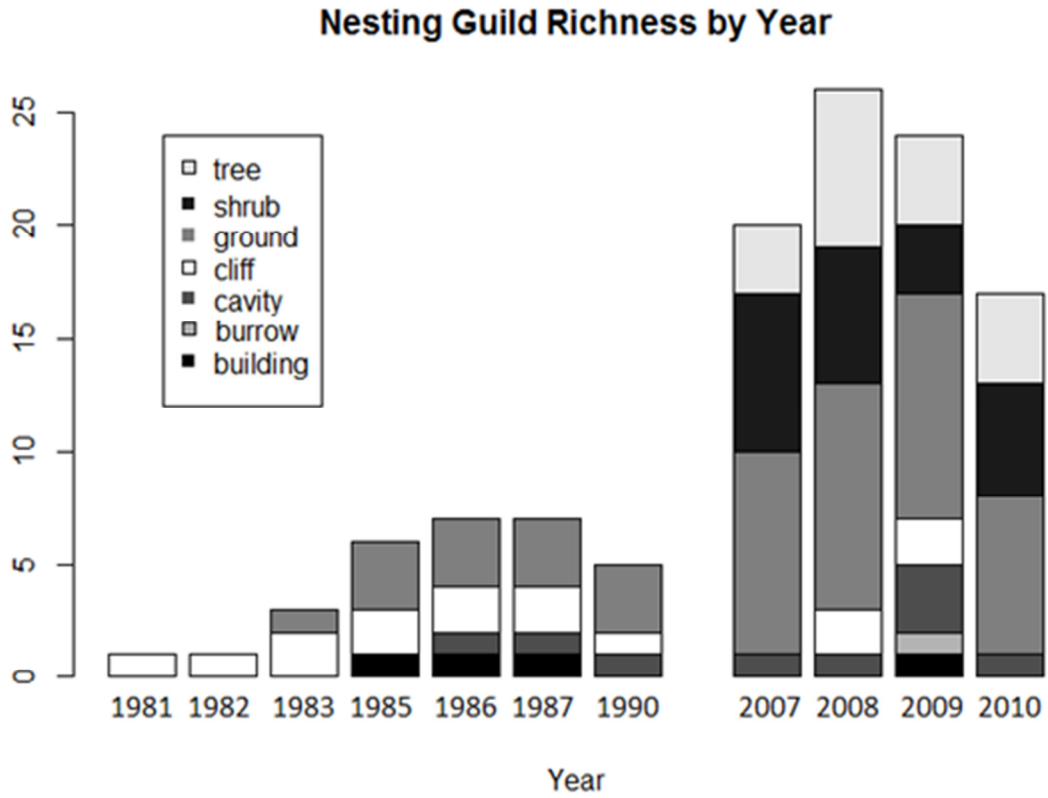


Figure 3-7. Observed richness of avian nesting guilds on the Pumice Plain.

Observed species richness of avian nesting guilds present on the Pumice Plain, 1981-1990 and 2007-2010.



Chapter 4 : Avian nesting success in primary successional habitat of Mount St. Helens, WA

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Abstract

The persistence of species within a local community relies on local recruitment and/or colonization from outside the local community. In this study I examined nest success as one component of local recruitment, a specific mechanism of maintaining populations of birds that have colonized a primary successional habitat at Mount St. Helens, WA. I found no significant difference in nest success of ground nesters, which included early colonist species, and shrub nesters who have colonized more recently, following establishment of more complex vegetation. Through monitoring local breeding attempts, I found that observed nest success for several locally common species was lower than recorded in other systems. I propose that in the absence of adequate local recruitment, repeated colonization events from the surrounding region may contribute to the persistence of some species in the local community.

Introduction

The assembly of local communities following extirpation from disturbance events requires colonization and survival of immigrating individuals from source populations. Each species' population may be maintained through some combination of colonization and extinction processes and repeated colonizations may "rescue" a population that would otherwise not survive (Brown & Kondric-Brown 1977). Successful reproduction is generally required for persistence of species within a

community. Population declines recorded for many species have been attributed to reproductive failure (Winter & Faaborg 1999, Herkert et al. 2003, Stephens et al. 2004), and can lead to extirpation from the local community. Reproduction allows for local recruitment within the community, potentially stabilizing the species composition and limiting species turnover. Thus, reproductive success is critical for determining not only the inter-annual and long-term occupancy of a species, but also the trajectory of community dynamics (Van Horne 1983, Martin 1988).

Communities in early-successional habitats are of particular interest due to their ephemeral and dynamic nature (Swanson et al. 2010). Natural disturbance regimes are important drivers of spatial and temporal heterogeneity of habitats, maintaining some portion of land in early-successional states (Turner 1987). Many disturbance-dependent bird species are declining as land management limit the scope, intensity, and frequency of natural disturbances (Brawn et al. 2001, Degraaf & Yamasaki 2003) and numerous bird species attain their highest densities under early seral conditions though this does not necessarily indicate habitat quality, as the reasons for high densities may be complex (Betts et al. 2010). Consequently, understanding the interaction of changing disturbance regimes and local dynamics of disturbed habitats is integral to predicting future changes in bird communities at local and regional scales.

In many regions of the world, volcanism is an important agent of natural disturbance (del Moral & Grishin 1999). Explosive eruptions involve complex geophysical processes that typically create several zones of different disturbance intensities and thus, a range of successional starting points (Dale et al. 2005). These areas of disturbance contribute to the patchwork of successional seres within a region.

Eruptions may be of varying intensity, but often consist of high intensity disturbances separated by long intervals, hundreds of years or more. The Mount St. Helens landscape, created by the May 18, 1980 eruption, provides a test bed for researching the effects of a high intensity, low frequency disturbance on the successional development and assembly of local communities. While previous studies have addressed the effects of volcanic eruption on breeding birds, few studies have directly addressed nesting success and those that have were conducted in island systems and focused on effects on waterbirds within 5 years of eruption (e.g., Ganter and Boyd 2000, Dalsgaard et al. 2007, Drew et al. 2010, Williams et al. 2010, Bond et al. 2012). Previous work at Mount St. Helens examined the prevalence of nest predation across the disturbance zones created by the 1980 eruption using artificial nests (Andersen and MacMahon 1986). However, to our knowledge no other study has examined avian nesting success across a community during ecological recovery following eruption in a mainland context.

In this study, we examined evidence of breeding and quantified reproductive success for colonizing bird species in an area undergoing primary successional recovery following volcanic disturbance. In the first study of avian nest success at Mount St. Helens following the 1980 eruption, we observed what bird species are utilizing this environment for reproduction, and examined how reproductive patterns in this early successional sere follow patterns seen in other contexts. We estimated nest success for ground-nesting and shrub-nesting birds, taking into account both the influence of nest location and the surrounding vegetation. For the most common species observed, we also compared the nest success in the early-successional habitat to published data so as

to better understand how local recruitment may contribute to the trajectory of bird community development in primary successional habitat at Mount St. Helens.

Methods

Study area

Our study area was on the Pumice Plain of Mount St. Helens in Skamania County, Washington state (Figure A1-1 map), an area of approximately 600 hectares which has been undergoing primary succession since 1980. The Pumice Plain sits immediately to the north of Mount St. Helens, has a northerly aspect and ranges in elevation from 1030 to 1310 meters. Mount St. Helens is an active volcano which erupted in May 1980; during the eruption, the Pumice Plain was buried first by the landslide caused by the collapse of the north face of the volcano, then by a deposit of pumice from the eruption's directed blast, and finally by pyroclastic flows. Additional pyroclastic deposits on the Pumice Plain in 1980 formed deposits over 40 m thick (Swanson and Major, 2005). Few migratory birds would have been present in the area at the time of the eruption, and any birds present were destroyed in the blast. All life on the Pumice Plain was destroyed by the eruption, though plants and animals survived the blast in nearby refugia (Adams et al. 1987).

Our study was conducted between 2007 and 2009, after 27 years of primary successional recovery following the 1980 eruption. At the time of the study, over 90% of the Pumice Plain consisted of relatively xeric 'upland' areas, much of which has sparse plant cover and some expanses of which is entirely barren. The upland areas generally supported herbaceous plant communities with 22-78% plant cover dominated by

Lupinus lepidus and mosses alone with other herbaceous cover (forbs and graminoids), with sparse woody plants (del Moral & Lacher 2005). The most common woody plants were *Penstemon cardwellii*, *Alnus sinuate*, *Salix sp.* and *Abies procera*. Conifer density was low, roughly 41 trees per hectare, with few trees reaching 2m or taller (Birchfield 2012). Shrub density was more variable but overall sparse. Bird densities were very low in upland areas of the Pumice Plain. Less than five percent of the Pumice Plain consisted of wetland areas and narrow (<10m width) riparian corridors. These areas were characterized with much higher density of woody plants, particularly *Alnus sinuate* and *Salix sp.* These wetland and riparian areas contain much higher density of breeding birds (Larsen & Crisafulli, unpublished).

Nest monitoring

Nests were located through opportunistic observation, systematic searches (2009-2010) and by observing behavioral cues of adult birds (e.g., carrying nesting material or food, alarm calls). Nest searches targeted both upland, riparian, and wetland areas, though we excluded 100 ha of the western Pumice Plain which was primarily barren of vegetation. Nests were marked with flagging tape 10 m from the nest and GPS locations were recorded. Nests were characterized by nest structure and materials, height off ground, and nest substrate. Nests were monitored every 2–5 days with few exceptions while active, following Martin and Geupel (1993) to limit disturbance caused by monitoring efforts. Nests were considered active until (1) all nestlings fledged, (2) all nest contents disappeared, or (3) no parental activity or change to nest contents was observed for at least 14 days (Cottam et al. 2009). Each nest that fledged at least one

chick was considered successful (Gentry et al. 2006, Rahmig et al. 2009). Nests were classified as successful based on recommendations in Martin and Geupel (1993) and Martin et al. (1997), as follows. Nests found empty on or after the expected fledge date were classified as successful unless there were direct indications of predation (e.g., nestling body parts, destroyed nest). For nests observed empty less than three days prior to the expected fledging date, if observations included fecal sacs in or near nests, fledglings nearby, or an adult bird carrying food near the nest, and if there were no compelling indications of predation, the nest was classified as successful. Empty nests found three or more days before the expected fledge date were classified as successful and right-censored at the last date of observation only if a fledgling was observed at or near the nest. Nests were aged using species-specific phenology from published sources (e.g., Poole 2005) and either known dates for the nest (date of egg laying, hatching, or fledging) or from visual estimation of nestling age. Indications of failed or predated nests included dead nestlings, disappearance of eggs or nestlings too young to fledge, fragments of eggshell, and physical damage to the nest.

Vegetation

The vegetation around nests was characterized in August of each year, after nests were no longer active. Foliage height diversity (FHD) was used as an index of the vegetation structure and complexity across several vertical strata. FHD was measured around each nest using a 3.5m polyvinyl chloride (PVC) pole marked at heights (10cm, 20cm, 40cm, 60cm, 80cm, 100cm, 125cm, 150cm, 175cm, 200cm, 225cm, 250cm, 300cm, and 350cm). For each height interval (0-10cm, 10-20cm, etc.), the presence or

absence of vegetation within a 12.5 cm radius of the PVC pole was recorded. These FHD data were collected at the nest location and at each meter along 5-meter transects to the North, South, East and West of the nest. For analyses, we considered both the maximum height interval in which foliage was present at the site of the nest, and FHD within five meters of the nest. FHD was calculated following MacArthur et al. (1966).

Analysis

We examined individual nest-site covariates for nest location and vegetation around the nest on daily survival rates and overall nest success. Although evidence of vegetation effects on nest success has been ambiguous (Stauffer et al. 2011), we predicted that nests with greater vegetative cover would have greater daily survival (Vukovich & Ritchison 2006) due to increased protection from nest predators. Nest success was estimated using a log-exposure model (Shaffer 2004) of survival probability (s) according to model covariates (x):

$$s(x_1) = \frac{e^{\beta_0 + \beta_1 x_1}}{1 + e^{\beta_0 + \beta_1 x_1}}.$$

We did not consider the effect of nest age on daily survival rates because of uncertainty in aging nests, although we suspected an effect of nest age on daily survival rates because of its significance in other studies (Dinsmore et al. 2002, Davis 2005). Nests that failed during the egg stage could not be accurately aged, and removing them from analyses would bias the resulting survival estimates and restricting sample sizes. Instead, we modeled a stage effect, characterizing nests by whether they contained eggs or nestlings. The best model was determined using Akaike's Information Criterion (Burnham & Anderson 2002).

For all covariate analyses, nests were aggregated into ground nests and shrub nests. Because of small sample sizes, we pooled data across species, as has been done in previous analyses of nest success (e.g., Rogers 1994). Year was considered a random effect. The simplest model estimated overall nest survival across the period of observation, providing separate nest success estimates for ground nests and shrub nests. Separate analyses were run for selected common species for which data from 20 or more nests were available; this threshold is required for accurate estimation of species-specific nest success rates (Hensler and Nichols 1981). Nest density was estimated across the Pumice Plain and nearest neighbor distances were calculated for each sample year. All analyses were conducted in R (version 3.0.0).

Results

Nests were observed for 19 species including 14 passerines, three shorebirds, one duck, and one nighthawk (Table 4-1). A total of 149 nests were observed over the three breeding seasons. Of these, 24 nests were either inactive throughout the monitoring period or already predated when found, leaving 125 nests known to be active and monitored. The majority of these nests ($n = 71$) were observed in 2010, with fewer nests observed in 2008 ($n=20$) and 2009 ($n=34$). Observed nest density across the Pumice Plain study area was 0.14 nests/ha in 2010, the year with the most observed nests. Though there was great variation in the nearest neighbor distance to another observed nest, ground nests were significantly farther from other nests than shrub nests ($p = 0.025$ in 2010). In 2010, ground nests were 125 ± 88 m from the closest nest of any type (mean \pm standard deviation) while shrub nests were 84 ± 115 m from the closest nest.

Average overall nest success (\pm s.d.) for ground nests (n=72) was 0.475 ± 0.074 (mean \pm s.d.), while average success for shrub nests (n=53) was 0.464 ± 0.076 (Table 4-2; survival curves in Figure 4-1). Willow Flycatchers (*Empidonax traillii*) and Yellow Warblers (*Setophaga petechia*) were the dominant shrub nesters, while most ground nests belonged to White-crowned Sparrows (*Zonotrichia leucophrys*) and Horned Larks (*Eremophila alpestris*). The best model as determined by AIC for overall nest success included nest stage, FHD, vegetation height at the nest, and a random effect of year (Table 4-3). Only FHD and year explained significant variance in the data, and their effects were small. As predicted, we observed increased nest success for nests with greater FHD and vegetation height at the nest, which we consider to be surrogates for nest concealment. Ground nests and shrub nests did not differ in overall nest success with or without the model covariates described above.

Species-specific nest success rates were calculated for the three most commonly observed species across all years: Yellow Warblers, White-crowned Sparrows, and Horned Larks (Table 4-2). White-crowned Sparrows averaged 3.5 eggs (range 2-5) per nesting attempt, with 38.0% nest success. Successful nests fledged an average of 2.9 young. Horned Lark nests averaged 3.9 eggs (range 3-5), and had 42.1% nest success, with successful nests fledging an average of 3.6 young. Yellow Warblers averaged 3.2 eggs per nesting attempt (range 2-5), and successful nests fledged an average of 2.8 young. Nest success for Yellow Warblers was 30.3%. Only one instance of nest parasitism was observed; a brown-headed cowbird egg in a Yellow Warbler nest.

Discussion

Our results identified the bird species breeding on the Pumice Plain at Mount St. Helens during early primary succession, and quantified their reproductive success. Low nest density was observed across the study site, due primarily to very low nest densities in the upland areas which make up the majority of the Pumice Plain. However, nest density was much higher in the riparian and wetland areas of the Pumice Plain which acted as concentrators of biological activity and where both ground and shrub nests were observed. While these highly vegetated areas account for less than five percent of the Pumice Plain area, 62% of observed nests were in these areas. Ground nesters including Horned Larks, Dark-eyed Juncos, and Common Nighthawks were common in upland areas while shrub nesters such as Yellow Warblers and Willow Flycatchers were common in wetland areas, as well as ground nesters such as Spotted Sandpipers. White-crowned sparrows were observed in both upland and wetland habitats. Overall nest densities for upland and wetland areas corresponded to low bird densities in upland areas and higher densities in wetland areas.

Our best model supported our expectation that vegetation at and around the nest location would improve nest concealment and lead to higher nest success. Overall nest success for breeding birds on the Pumice Plain was slightly less than 50% (Table 4-2). We found that though the effect was small, vegetation around a nest benefitted nest success, in results similar to other studies of avian nest success (e.g. Norment 1993, Stauffer et al. 2011). However, the most common breeding birds also showed lower nest success than the community as a whole. Published estimates of nest success for Yellow Warblers ranged from 47% to 72% (Poole 2005), while nest success on the Pumice Plain

was substantially lower at roughly 30%. Similarly, White-crowned Sparrow nest success in the published literature ranged from 40% to 75%, higher than the 38% observed on the Pumice Plain in 2008-2010. Finally, the published literature for nest success in Horned Larks ranged from 53% to 76%, whereas we found nest success of 42% for the species. For each of these common inhabitants of Pumice Plain, estimates of nest success on the Pumice Plain were lower than their respective published ranges. Further work may allow published studies to be further restricted according to location and habitat, to provide a better comparison to the study site. These results suggest local recruitment within these populations was limited and may have negative consequences for the local population. The low reproductive success observed for these species at Mount St. Helens was unexpected considering their local abundance. Because overall nest densities were still low, it is unlikely that intraspecific competition was a main driver of nest failure. In the context of successional change and community assembly, species with low local recruitment may rely more heavily on immigration from the surrounding region, decline in local population size, or experience local extinction. The local abundance of species experiencing low local recruitment may be supported by repeated colonization from regional populations. Thus, colonization processes and the rescue effect may continue to be important in the development of the bird community in the MSH primary successional habitat.

We observed no difference in nest success between ground & shrub nests. However, small sample sizes may have limited our ability to detect small differences. Further investigation would better elucidate whether there are consistent differences in the nest success of certain species on the Pumice Plain, and how the variation in local

recruitment may contribute to the dynamics of community assembly. This study did not examine the survival of fledglings nor their return rates as adults. Neither did it address immigration to this community from the surrounding region. Tracking individuals between years would provide greater insight into the relative roles of local processes and immigration/emigration for the population dynamics of birds on the Pumice Plain.

In this study, nest success increased slightly with both height of vegetation at the nest site and foliage height diversity near the nest. Both of these contributed to nest concealment, an important factor for limiting discovery by nest predators. While we did not specifically model causes of nest failure, nest predation is the most common cause of nest failure for passerine birds (Martin 1992), and most failed nests in this study showed clear signs of predation. Also, 15 ground nests were found after being depredated; these nests were excluded from analysis because there the history of the nest was unknown. We speculated that nest predators may develop search images and strategies based on common species, which would result in higher predation on nests similar to those commonly found by nest predators, and allowing some less common nesting species on the Pumice Plain to experience lower predation pressure. Although we did not identify nest predators in this study, several small mammals and some avian predators are likely. A predation study using artificial nests in the Mount St. Helens area immediately following the eruption (1981-1984) suggested that at the time, nest predators were relatively rare in the more disturbed areas of Mount St. Helens but predicted increasing levels of nest predation as nest predators recolonized these areas following the eruption (Andersen and MacMahon 1986). The study identified the Common Raven (*Corvus corax*) and Gray Jay (*Perisoreus canadensis*) as likely avian nest predators; of these

only the Common Raven was regularly observed in the study site. Separate surveys in the same habitats on the Pumice Plain indicated that the most likely nest predators are small mammals, such as the Cascades Golden-mantled Ground Squirrel (*Spermophilus saturatus*), Yellow-pine Chipmunk (*Tamias amoenus*), Pacific Jumping Mouse (*Zapus trinotatus*), and several other possible small mammal species (see Crisafulli et al. 2005), and other bird species, such as the Common Raven.

This study considered community-wide avian nesting success in the context of ecological recovery following volcanic disturbance in a mainland system. We demonstrated what birds are using the Pumice Plain of Mount St. Helens as breeding habitat, and that the most commonly observed species exhibited low reproductive success relative to species-specific expectations, suggesting that colonization may play an important role in the maintenance of local populations on the Pumice Plain. Differential reproductive success may contribute to the overall trajectory of community assembly on the Pumice Plain. Specifically from this work, higher nest success of less common species on the Pumice Plain could be a mechanism that leads to changing relative abundances of species in the community. However, further analysis considering species groups likely to compete for resources would be needed to determine if this is occurring. We saw no significant difference between ground nests and shrub nests to suggest that differences in local recruitment were affecting the dynamics between ground-nesting and shrub-nesting species at this time. Nest densities were low across upland areas and concentrated in riparian and wetland areas with more complex vegetation. Because biological activity was concentrated in these small vegetated areas,

nests may have been at an increased risk of predation from small mammal and avian nest predators.

Tables and Figures

Table 4-1. Species with active nests observed on the Pumice Plain.

Species	# Nests
Common Nighthawk (<i>Chordeiles minor</i>)	7
Dark-eyed Junco (<i>Junco hyemalis</i>)	6
Green-winged Teal (<i>Anas crecca</i>)	1
Horned Lark (<i>Eremophila alpestris</i>)	21
Killdeer (<i>Charadrius vociferous</i>)	2
Lazuli Bunting (<i>Passerina amoena</i>)	1
Lincoln's Sparrow (<i>Melospiza lincolni</i>)	4
Mountain Bluebird (<i>Sialia currucoides</i>)	1
Northern Rough-winged Swallow (<i>Stelgidopteryx serripennis</i>)	1
Savannah Sparrow (<i>Passerculus sandwichensis</i>)	1
Song Sparrow (<i>Melospiza melodia</i>)	1
Spotted Sandpiper (<i>Actitis macularius</i>)	3
Swainson's Thrush (<i>Catharus ustulatus</i>)	4
Violet-green Swallow (<i>Tachycineta thalassina</i>)	1
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	22
Western Meadowlark (<i>Sturnella neglecta</i>)	3
Willow Flycatcher (<i>Empidonax traillii</i>)	13
Wilson's Snipe (<i>Gallinago delicata</i>)	2
Yellow Warbler (<i>Setophaga petechial</i>)	33

Table 4-2. Estimated nest success

Nest success estimates from log-exposure model (Shaffer 2004), for the four most commonly observed bird species and for ground nests and shrub nests overall, aggregating across all years (2008-2010).

Species	n	Nest Success Estimate (%)	Mean Height (m)	Mean FHD
Yellow Warbler	33	30.3	1.52 ± 0.79	2.55 ± 0.13
White-crowned Sparrow	22	38.0	0.02 ± 0.11	2.21 ± 0.28
Horned Lark	21	42.1	0	1.27 ± 0.20
All Ground nests	72	47.5	0	1.77 ± 0.45
All Shrub nests	53	46.4	1.32 ± 0.75	2.54 ± 0.19

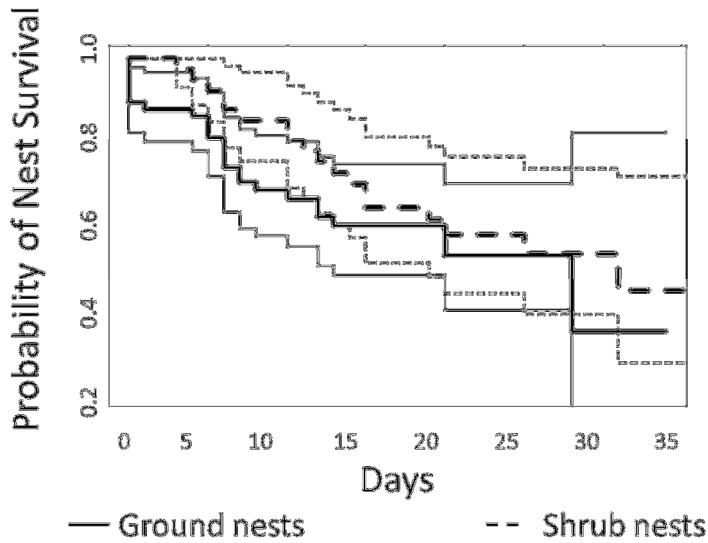
Table 4-3. Model selection criteria for nest survival models

Model selection criteria for nest survival models for all nests on the Mount St. Helens Pumice Plain in 2008-2010.

Model	AIC_c	ΔAIC_c
Stage + FHD + Nest Vegetation Height + Year	204.72	0
Stage + FHD + Nest Vegetation Height + Year + Nest Height	206.17	1.45
Stage + FHD + Year + Nest Height + Substrate	206.48	1.76
Stage + FHD + Nest Vegetation Height + Year + Nest Height + Substrate	206.61	1.89
Stage + Nest Vegetation Height + Year + Nest Height	206.88	2.16

Figure 4-1. Nest failure curves

Nest failure curves for ground and shrub nests on the Mount St. Helens Pumice Plain between 2007 and 2009. Thick black step-functions represent ground nests, whereas thick dotted step-functions represent shrub nests. Corresponding thin lines give upper and lower 95% confidence estimates on the means.



Appendices

Appendix 1: Mount St. Helens study site.

Figure A1-1. Map of Mount St. Helens disturbance zones.

Map of Mount St. Helens showing the Pumice Plain (study site) and other disturbance zones created by the 1980 Mount St. Helens Eruptions. Inset: Washington State showing position of Mount St. Helens (triangle). From Sugg and Edwards 1998.

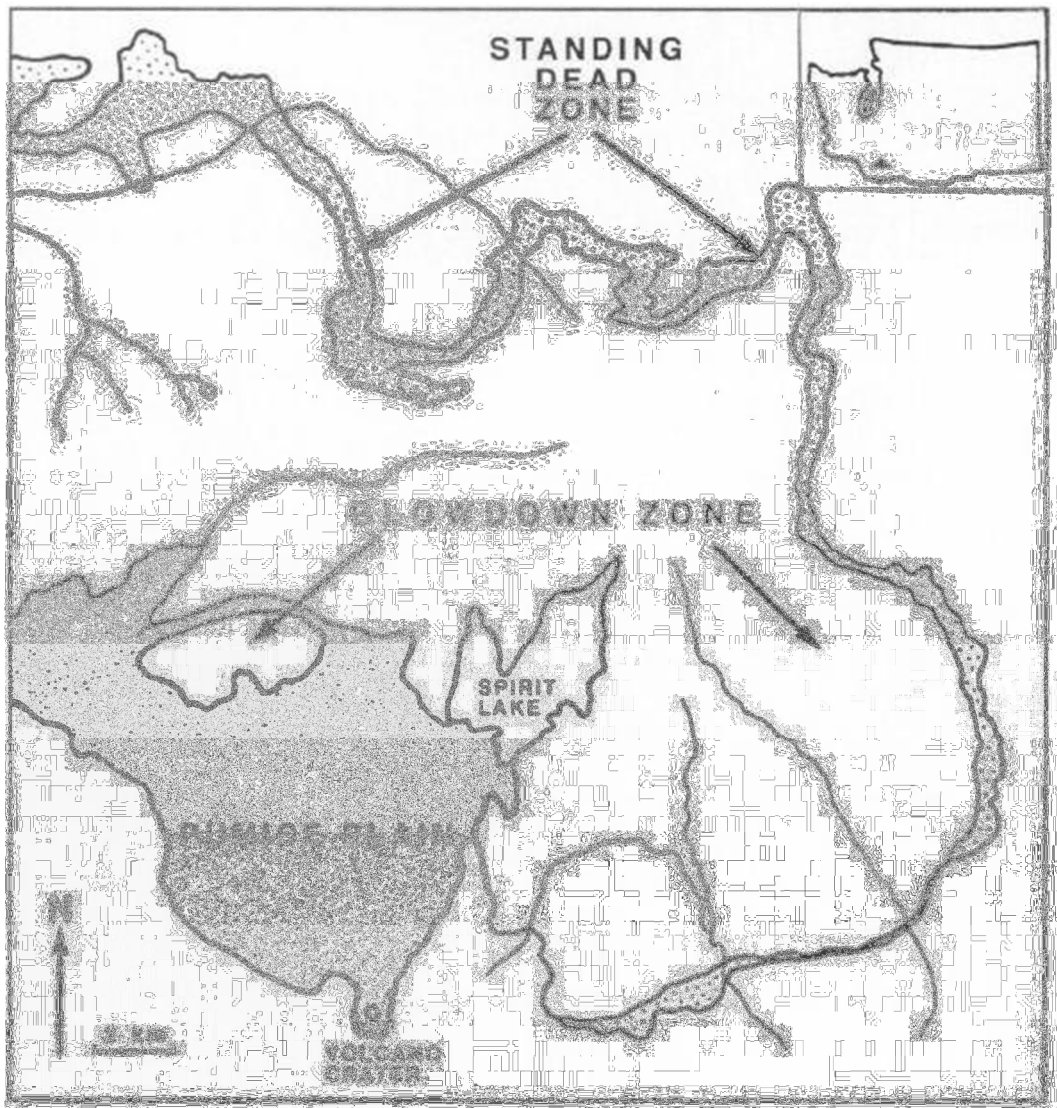


Figure A1-2. Satellite image of Mount St. Helens study site, transect locations, and surroundings.

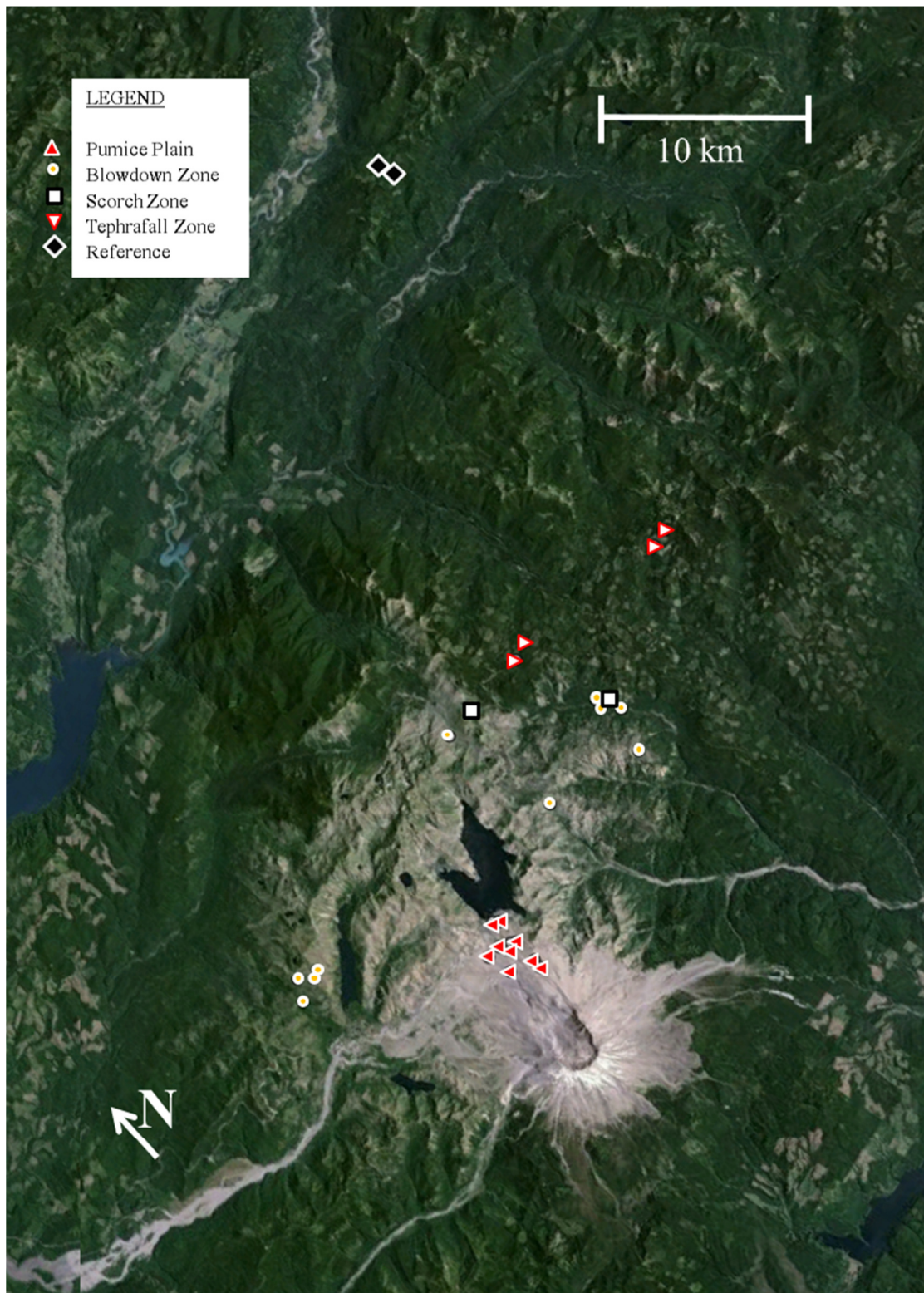


Table A1-1. Disturbance zones of Mount St. Helens.

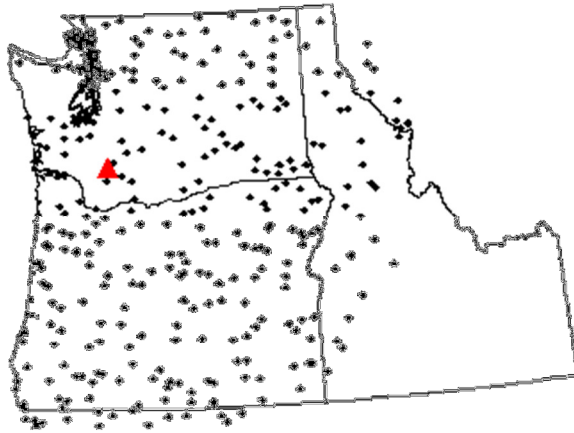
Zone	Disturbance Level	1980 Eruption Processes	Impact on Birds
Pumice Plain	High	Buried by debris avalanche Lateral Blast Buried by Pyroclastic Flows	No survival All new colonization
Blowdown	Moderate - High	Lateral Blast Trees scorched and knocked over	No survival All new colonization
Scorch	Moderate	Edge of Lateral Blast area Trees scorched but remained standing	No survival All new colonization
Tephra Fall	Low	Beyond Lateral Blast Aerial deposits of tephra, varying depth	Possible survival
Reference	None – Low	Outside of disturbed area Minor ash (tephra) fall possible	Expected survival

Appendix 2: Regional Source Pools and Minimum Source Regions

Figure A2-1. Distribution of regional observation within 600 km of Mount St. Helens, WA.

Maps of U.S. North American Breeding Bird Survey (BBS) routes (Panel A) and Monitoring Avian Productivity and Survivorship (MAPS) Program sites (Panel B) within 600 km of Mount St. Helens, WA. BBS routes are mapped by start location, demonstrating their relatively uniform distribution, while MAPS sites have a clumped distribution. Triangle indicates Mount St. Helens field site.

A.



B.

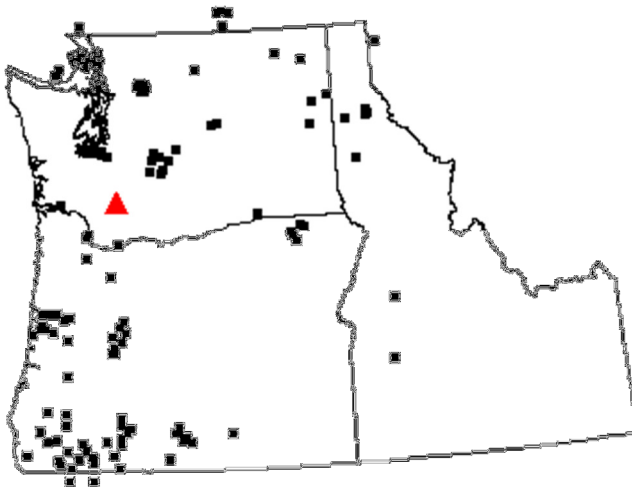


Figure A2-2. Patterns in proxy dispersal distances (to ‘nearest neighbor’ locations) across species.

Panel A combines all Mount St. Helens zones to show temporal pattern. Panel B combines all years to show differences across disturbance zones.

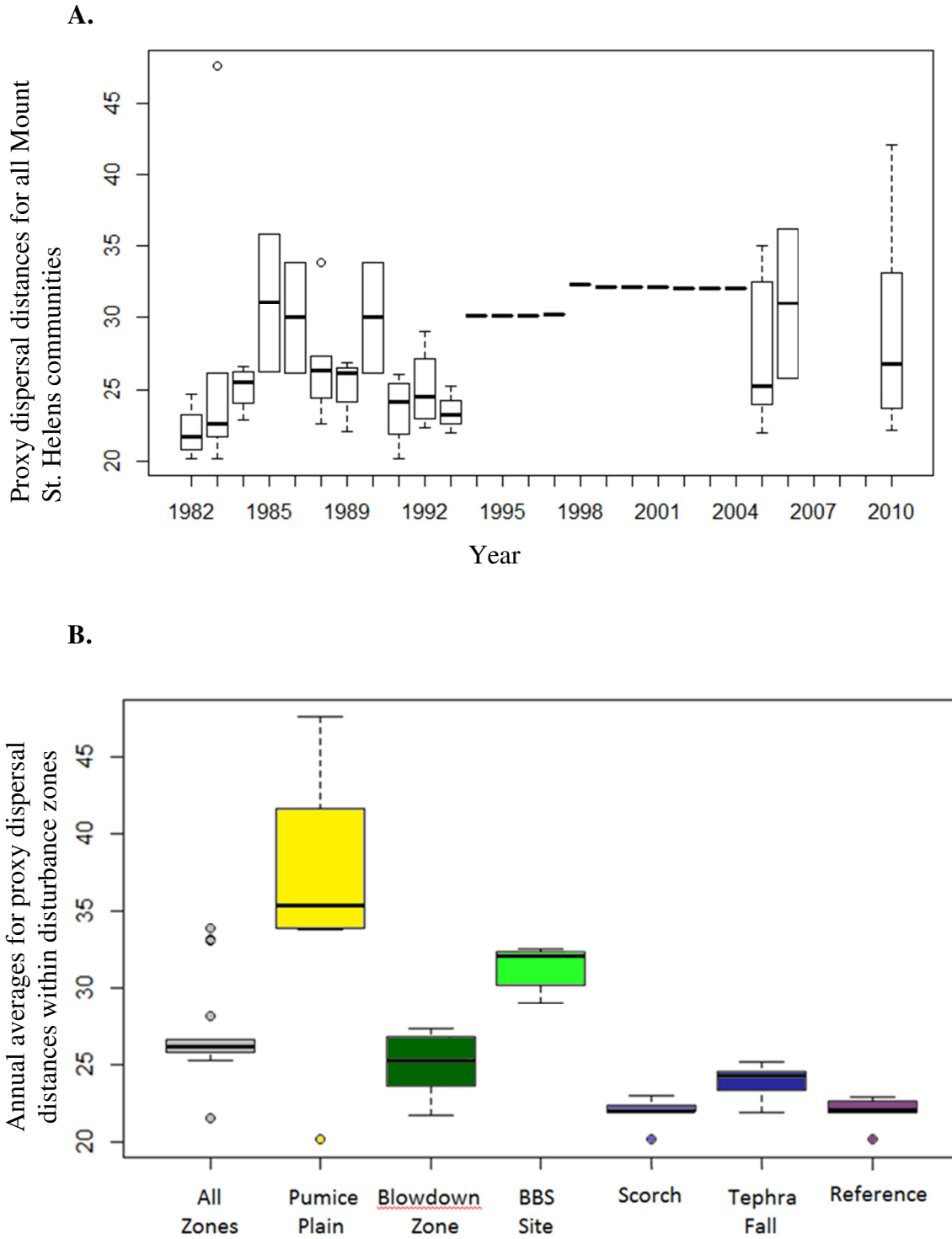


Table A2-1. Combined species list for Mount St. Helens RSPs.

List of all species included in any RSP with ‘1’ indicating presence in a given dataset. Species complexes are used following data sources (eg for difficult to distinguish species). The Mount Rainier species are included in the Spatial (combined datasets) column but not included in either the BBS or MAPS RSP dataset columns unless they were present in another regional observation site within the RSP.

Species	MSH	Atlas	Range Map	BBS	MAPS	Spatial (Combined)
NON-PASSERINES						
Acorn Woodpecker		1			1	
Allen's Hummingbird					1	
American Avocet		1		1		
American Bittern		1	1	1	1	1
American Black Duck		1				
American Coot		1	1	1		1
American Golden-Plover			1			
American Kestrel	1	1	1	1	1	1
American Three-toed		1	1	1	1	1
American White Pelican		1	1	1	1	
American Wigeon		1	1	1	1	1
Ancient Murrelet		1				
Anna's Hummingbird		1	1		1	
Arctic Tern		1				
Bald Eagle	1	1	1	1	1	1
Band-tailed Pigeon	1	1	1	1	1	1
Barn Owl		1	1	1	1	1
Barred Owl		1	1	1	1	1
Barrow's Goldeneye		1	1	1	1	1
Belted Kingfisher		1	1	1	1	1
Black Oystercatcher		1				1
Black Swift		1	1	1	1	1
Black Tern		1	1	1		1
Black-backed Woodpecker	1	1	1	1	1	1
Black-bellied Plover			1			
Black-chinned Hummingbird		1	1	1	1	1
Black-crowned Night-Heron		1	1	1		
Black-necked Stilt		1		1		
Blue Grouse (Dusky or Sooty)	1	1	1	1	1	1
Blue-winged Teal		1	1	1		1
Bonaparte's Gull			1			
Boreal Owl		1	1			

Table A2-1 continued

Species	MSH	Atlas	Range Map	BBS	MAPS	Spatial (Combined)
Brandt's Cormorant		1				
Broad-tailed Hummingbird					1	
Bufflehead		1	1	1		1
Burrowing Owl		1		1		
Cackling Goose			1			
California Condor			1			
California Gull		1	1	1	1	1
California Quail		1	1	1	1	1
Calliope Hummingbird		1	1	1	1	1
Canada Goose	1	1	1	1	1	1
Canvasback		1	1	1	1	1
Caspian Tern		1		1	1	1
Cassin's Auklet		1				
Cattle Egret			1			
Chukar		1		1		1
Cinnamon Teal		1	1	1		1
Clark's Grebe		1				
Clay-colored Sparrow		1			1	1
Common Goldeneye		1	1	1		
Common Loon	1	1	1	1	1	1
Common Merganser		1	1	1	1	1
Common Murre		1				1
Common Nighthawk	1	1	1	1	1	1
Common Poorwill		1		1	1	1
Common Tern			1			
Cooper's Hawk		1	1	1	1	1
Double-crested Cormorant		1	1	1	1	1
Downy Woodpecker		1	1	1	1	1
Dunlin			1		1	
Eared Grebe		1	1	1		
Eurasian Collared-Dove						1
Eurasian Wigeon			1			
Ferruginous Hawk				1		
Flammulated Owl		1	1			
Fork-tailed Storm-Petrel		1				
Forster's Tern		1	1			
Gadwall		1	1	1	1	1
Glaucous-winged Gull		1	1	1	1	1
Golden Eagle	1		1	1	1	1
Gray Partridge		1	1	1		
Great Blue Heron	1	1	1	1	1	1

Table A2-1 continued

Species	MSH	Atlas	Range Map	BBS	MAPS	Spatial (Combined)
Great Egret		1				
Great Gray Owl		1			1	
Great Horned Owl	1	1	1	1	1	1
Greater Sage-Grouse		1				
Greater White-fronted Goose			1			
Greater Yellowlegs	1		1	1		
Green Heron		1	1	1	1	1
Green-winged Teal	1	1	1	1	1	1
Gyr Falcon			1			
Hairy Woodpecker	1	1	1	1	1	1
Harlequin Duck		1	1	1	1	1
Herring Gull			1			
Hooded Merganser		1	1	1	1	1
Horned Grebe		1	1	1		
Killdeer	1	1	1	1	1	1
Leach's Storm-Petrel		1				
Least Sandpiper			1			
Lesser Scaup		1	1	1		1
Lesser Yellowlegs			1			
Lewis's Woodpecker	1	1	1	1	1	1
Long-billed Curlew		1		1		
Long-billed Dowitcher			1			
Long-eared Owl		1			1	
Mallard	1	1	1	1	1	1
Marbled Murrelet		1	1			1
Merlin		1	1			1
Mountain Quail		1	1	1	1	1
Mourning Dove	1	1	1	1	1	1
Northern Flicker	1	1	1	1	1	1
Northern Goshawk	1		1	1	1	1
Northern Harrier	1	1	1	1	1	1
Northern Long-eared Owl			1			
Northern Pintail		1	1	1		
Northern Pygmy-Owl		1	1	1	1	1
Northern Saw-whet Owl		1	1	1	1	1
Northern Shoveler		1	1	1		1
Nuttall's Woodpecker					1	
Osprey		1	1	1	1	1
Pacific Golden-Plover			1			
Pelagic Cormorant		1				1
Peregrine Falcon			1	1	1	1

Table A2-1 continued

Species	MSH	Atlas	Range Map	BBS	MAPS	Spatial (Combined)
Pied-billed Grebe		1	1	1	1	1
Pigeon Guillemot		1				1
Pileated Woodpecker	1	1	1	1	1	1
Prairie Falcon	1		1	1	1	1
Red Knot			1			
Red-breasted Merganser			1			
Red-breasted Sapsucker	1	1	1	1	1	1
Redhead		1	1	1		
Red-naped Sapsucker	1	1		1	1	1
Red-necked Grebe		1		1		
Red-necked Phalarope			1		1	1
Red-shouldered Hawk					1	
Red-tailed Hawk	1	1	1	1	1	1
Rhinoceros Auklet		1				1
Ring-billed Gull		1	1	1	1	1
Ring-necked Duck		1	1	1		1
Ring-necked Pheasant		1	1	1	1	1
Rock Pigeon		1	1	1	1	1
Rock Sandpiper			1			
Rough-legged Hawk			1			
Ruddy Duck		1	1	1		1
Ruffed Grouse		1	1	1	1	1
Rufous Hummingbird	1	1	1	1	1	1
Sanderling			1			
Sandhill Crane		1	1		1	
Semipalmated Plover			1			
Semipalmated Sandpiper			1			
Sharp-shinned Hawk	1	1	1	1	1	1
Sharp-tailed Grouse		1				
Short-billed Dowitcher			1			
Short-eared Owl		1	1	1		
Snow Goose			1			
Snowy Owl			1			
Snowy Plover		1				
Sora		1	1	1	1	1
Spotted Owl			1	1		1
Spotted Sandpiper	1	1	1	1	1	1
Spruce Grouse		1	1	1		
Surfbird			1			
Swainson's Hawk		1	1	1	1	1
Thayer's Gull			1			

Table A2-1 continued

Species	MSH	Atlas	Range Map	BBS	MAPS	Spatial (Combined)
Trumpeter Swan		1	1			
Tufted Puffin		1				
Tundra Swan			1			
Turkey Vulture		1	1	1	1	1
Upland Sandpiper		1				
Vaux's Swift	1	1	1	1	1	1
Virginia Rail		1	1	1	1	1
Wandering Tattler			1			
Western Grebe		1	1	1		
Western Gull		1				
Western Sandpiper			1			
Western Screech-Owl		1	1	1	1	1
Whimbrel			1			
White-headed Woodpecker		1	1	1	1	1
White-tailed Kite		1	1			
White-tailed Ptarmigan		1	1			1
White-throated Swift		1		1	1	1
Wild Turkey		1	1	1	1	1
Williamson's Sapsucker		1	1	1	1	1
Wilson's Phalarope		1	1	1		
Wilson's Snipe	1	1	1	1	1	1
Wood Duck		1	1	1	1	1
PASSERINES						
Alder Flycatcher					1	1
American Crow	1	1	1	1	1	1
American Dipper	1	1	1	1	1	1
American Goldfinch		1	1	1	1	1
American Pipit	1	1	1			1
American Redstart		1		1	1	1
American Robin	1	1	1	1	1	1
American Tree Sparrow			1			
Ash-throated Flycatcher		1			1	
Audubon's Warbler					1	1
Bank Swallow		1	1	1	1	1
Barn Swallow	1	1	1	1	1	1
Bewick's Wren		1	1	1	1	1
Black Phoebe					1	
Black-and-white Warbler					1	1
Black-billed Magpie		1	1	1	1	1
Black-capped Chickadee	1	1	1	1	1	1

Table A2-1 continued

Species	MSH	Atlas	Range Map	BBS	MAPS	Spatial (Combined)
Black-headed Grosbeak	1	1	1	1	1	1
Black-throated Gray Warbler	1	1	1	1	1	1
Black-throated Sparrow		1				
Bobolink		1				
Bohemian Waxwing		1	1			
Boreal Chickadee		1				
Brewer's Blackbird		1		1	1	1
Brewer's Sparrow	1	1	1	1	1	1
Brown Creeper	1	1	1	1	1	1
Brown-headed Cowbird	1	1	1	1	1	1
Bullock's Oriole	1	1	1	1	1	1
Bushtit		1	1	1	1	1
California Thrasher					1	
California Towhee					1	
Canyon Wren		1	1	1	1	1
Cassin's Finch	1	1	1	1	1	1
Cassin's Vireo		1	1	1	1	1
Cedar Waxwing	1	1	1	1	1	1
Chestnut-backed Chickadee	1	1	1	1	1	1
Chestnut-sided Warbler					1	
Chipping Sparrow	1	1	1	1	1	1
Clark's Nutcracker		1	1	1	1	1
Cliff Swallow		1	1	1	1	1
Common Raven	1	1	1	1	1	1
Common Yellowthroat	1	1	1	1	1	1
Dark-eyed Junco	1	1	1	1	1	1
Dusky Flycatcher		1	1	1	1	1
Eastern Kingbird		1		1	1	1
European Starling	1	1	1	1	1	1
Evening Grosbeak	1	1	1	1	1	1
Fox Sparrow	1	1	1	1	1	1
Golden-crowned Kinglet	1	1	1	1	1	1
Golden-crowned Sparrow	1	1	1	1	1	1
Grasshopper Sparrow		1	1	1		1
Gray Catbird		1		1		1
Gray Flycatcher		1		1	1	1
Gray Jay	1	1	1	1	1	1
Gray-crowned Rosy-Finch	1	1	1		1	1
Green-tailed Towhee		1	1	1	1	1
Hammond's Flycatcher		1	1	1	1	1
Hermit Thrush	1	1	1	1	1	1

Table A2-1 continued

Species	MSH	Atlas	Range Map	BBS	MAPS	Spatial (Combined)
Hermit Warbler	1	1	1	1	1	1
Hoary Redpoll			1			
Horned Lark	1	1	1	1		1
House Finch		1	1	1	1	1
House Sparrow		1	1	1		1
House Wren	1	1	1	1	1	1
Hutton's Vireo		1	1	1	1	1
Lapland Longspur			1			
Lark Sparrow		1		1		1
Lazuli Bunting		1	1	1	1	1
Least Flycatcher		1		1	1	
Lesser Goldfinch		1	1		1	
Lincoln's Sparrow	1	1	1	1	1	1
Loggerhead Shrike		1	1	1		1
MacGillivray's Warbler	1	1	1	1	1	1
Magnolia Warbler					1	
Marsh Wren		1	1	1	1	1
Mountain Bluebird	1	1		1	1	1
Mountain Chickadee		1	1	1	1	1
Nashville Warbler		1	1	1	1	1
Northern Bobwhite		1		1	1	1
Northern Mockingbird		1	1			
Northern Rough-winged	1	1	1	1	1	1
Northern Shrike			1			
Northern Waterthrush		1		1	1	1
Northwestern Crow			1	1		1
Olive-sided Flycatcher	1	1	1	1	1	1
Orange-crowned Warbler	1	1	1	1	1	1
Ovenbird					1	
Pine Grosbeak		1		1	1	1
Pine Siskin	1	1	1	1	1	1
Purple Finch		1	1	1	1	1
Purple Martin		1	1	1	1	1
Pygmy Nuthatch		1	1	1	1	1
Red Crossbill	1	1	1	1	1	1
Red-breasted Nuthatch	1	1	1	1	1	1
Red-eyed Vireo		1	1	1	1	1
Red-winged Blackbird	1	1	1	1	1	1
Rock Wren	1	1	1	1	1	1
Ruby-crowned Kinglet	1	1	1	1	1	1
Sage Sparrow		1		1		1

Table A2-1 continued

Species	MSH	Atlas	Range Map	BBS	MAPS	Spatial (Combined)
Sage Thrasher		1	1	1		1
Savannah Sparrow	1	1	1	1	1	1
Say's Phoebe		1	1	1		1
Sky Lark		1				
Snow Bunting			1			
Song Sparrow	1	1	1	1	1	1
Spotted Towhee	1	1	1	1	1	1
Steller's Jay	1	1	1	1	1	1
Swainson's Thrush	1	1	1	1	1	1
Townsend's Solitaire	1	1	1	1	1	1
Townsend's Warbler	1	1	1	1	1	1
Tree Swallow	1	1	1	1	1	1
Tricolored Blackbird			1			
Varied Thrush	1	1	1	1	1	1
Veery		1	1	1	1	1
Vesper Sparrow		1	1	1	1	1
Violet-green Swallow	1	1	1	1	1	1
Warbling Vireo	1	1	1	1	1	1
Western Bluebird		1	1	1	1	1
Western Flycatcher (Cordilleran or Pacific-slope)	1	1	1	1	1	1
Western Kingbird		1	1	1	1	1
Western Meadowlark	1	1	1	1	1	1
Western Scrub-Jay		1	1	1	1	1
Western Tanager	1	1	1	1	1	1
Western Wood-Pewee	1	1	1	1	1	1
White-breasted Nuthatch		1	1	1	1	1
White-crowned Sparrow	1	1	1	1	1	1
White-winged Crossbill		1	1			
Willow Flycatcher	1	1	1	1	1	1
Wilson's Warbler	1	1	1	1	1	1
Winter Wren		1	1	1	1	1
Wrentit					1	
Yellow Warbler	1	1	1	1	1	1
Yellow-breasted Chat		1	1	1	1	1
Yellow-headed Blackbird		1	1	1	1	1
Yellow-rumped Warbler	1	1	1	1	1	1

Table A2-2. Summary statistics of Mount St. Helens minimum source regions.

Summary statistics of minimum source regions for the entire Mount St. Helens bird community, the Blowdown Zone community, the Pumice Plain community, and the BBS site in the Tephra Fall Zone of Mounts St. Helens – table data for Figure 3. Only years in which the minimum source region changed for given Mount St. Helens bird communities are shown. Across-species mean and maximum proxy dispersal distances and total area of the minimum source region are given.

Community Sample	Year	Mean Distance (km)	Maximum Distance (km)	Area (km²)
MSH – All Zones	1982	22	52	1376
MSH – All Zones	1983	25	75	3618
MSH – All Zones	1984	31	134	5534
MSH – All Zones	1987	30	134	5645
MSH – All Zones	2007	30	134	8984
MSH – All Zones	2008	35	445	12996
MSH – Blowdown Zone	1982	25	34	1256
MSH – Blowdown Zone	1983	26	75	1376
MSH – Blowdown Zone	1984	29	75	2616
MSH – Blowdown Zone	1987	30	75	2982
MSH – Blowdown Zone	2005	24	75	4231
MSH – Blowdown Zone	2010	28	134	8984
MSH – Pumice Plain	1982	20	20	1256
MSH – Pumice Plain	1983	48	75	2170
MSH – Pumice Plain	2005	34	75	4231
MSH – Pumice Plain	2007	33	134	7164
MSH – Pumice Plain	2008	41	445	11175
MSH BBS Route	1992	29	33	473
MSH BBS Route	1994	30	61	1049
MSH BBS Route	1998	32	61	2559

Appendix 3: Pumice Plain Occupancy and Detection.

Table A3-1. Species occupancy and detection estimates.

Species occupancy and detection estimates from community occupancy model for the Pumice Plain 2007-2010 avifauna. Predicted occupancy identifies the proportion of sites within each habitat predicted to be occupied by a given species and the associated standard deviation. Detection identifies the probability of detection given occupancy for a species within a given habitat with associated standard deviation. Note this includes pathological cases of species where the model fits high occupancy and low detection.

Habitat	Species	Occupancy		Detection	
Upland	American Pipit	0.93	± 0.15	0.03	± 0.02
Upland	American Robin	0.88	± 0.24	0.01	± 0.01
Upland	Common Raven	0.96	± 0.08	0.08	± 0.03
Upland	Dark-eyed Junco	0.79	± 0.21	0.22	± 0.06
Upland	European Starling	0.87	± 0.25	0.01	± 0.02
Upland	Gray-crowned Rosy Finch	0.87	± 0.21	0.05	± 0.04
Upland	Horned Lark	0.93	± 0.07	0.73	± 0.03
Upland	Lincoln's Sparrow	0.71	± 0.38	0.15	± 0.17
Upland	Northern Rough-winged	0.90	± 0.20	0.01	± 0.01
Upland	Rock Wren	0.90	± 0.19	0.05	± 0.03
Upland	Rufous Hummingbird	0.78	± 0.30	0.06	± 0.04
Upland	Savannah Sparrow	0.79	± 0.28	0.11	± 0.05
Upland	Song Sparrow	0.88	± 0.23	0.01	± 0.02
Upland	Vaux's Swift	0.87	± 0.22	0.02	± 0.02
Upland	White-crowned Sparrow	0.52	± 0.16	0.38	± 0.05
Upland	Western Meadowlark	0.91	± 0.15	0.06	± 0.03
Wetland	American Crow	0.88	± 0.22	0.02	± 0.02
Wetland	American Robin	0.43	± 0.18	0.38	± 0.09
Wetland	Barn Swallow	0.50	± 0.44	0.03	± 0.05
Wetland	Brown-headed Cowbird	0.80	± 0.27	0.07	± 0.06
Wetland	Black-headed Grosbeak	0.92	± 0.16	0.04	± 0.03
Wetland	Brewer's Sparrow	0.38	± 0.43	0.07	± 0.23
Wetland	Bullock's Oriole	0.83	± 0.27	0.02	± 0.03
Wetland	Common Raven	0.35	± 0.42	0.05	± 0.05
Wetland	Common Yellowthroat	0.83	± 0.26	0.02	± 0.02
Wetland	Dark-eyed Junco	0.28	± 0.16	0.38	± 0.08
Wetland	Fox Sparrow	0.22	± 0.36	0.21	± 0.12

Table A3-1 continued.

Wetland	Hermit Thrush	0.64 ± 0.33	0.13 ± 0.10
Wetland	Lincoln's Sparrow	0.50 ± 0.17	0.86 ± 0.04
Wetland	Northern Flicker	0.54 ± 0.44	0.03 ± 0.05
Wetland	Orange-crowned Warbler	0.86 ± 0.24	0.02 ± 0.03
Wetland	Rufous Hummingbird	0.73 ± 0.22	0.22 ± 0.06
Wetland	Red-winged Blackbird	0.81 ± 0.26	0.09 ± 0.06
Wetland	Savannah Sparrow	0.53 ± 0.18	0.44 ± 0.08
Wetland	Song Sparrow	0.74 ± 0.34	0.06 ± 0.09
Wetland	Swainson's Thrush	0.26 ± 0.14	0.44 ± 0.09
Wetland	Violet-green Swallow	0.83 ± 0.27	0.02 ± 0.03
Wetland	Warbling Vireo	0.14 ± 0.12	0.40 ± 0.12
Wetland	White-crowned Sparrow	0.89 ± 0.11	0.59 ± 0.05
Wetland	Western Meadowlark	0.61 ± 0.32	0.15 ± 0.07
Wetland	Willow Flycatcher	0.86 ± 0.11	0.83 ± 0.04
Wetland	Yellow Warbler	0.97 ± 0.05	0.84 ± 0.03

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doi: 10.1002/9780470015902.a0022549

Curriculum Vita, Elise Larsen

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EDUCATION

Ph.D., Biology, University of Maryland (UMD) 2013

- Advisor: Bill Fagan
- Dissertation: Avian community responses to ecological disturbance and recovery at Mount St. Helens

M.S., Biology, College of William and Mary (W&M) 2008

- Advisor: Bryan Watts, Center for Conservation Biology
- Thesis: Effects of Urban Development on Breeding Bird Diversity: the role of diet and migration

B.S., Zoology, Concentration in Environmental Biology, Michigan State University (MSU) 2001

- Research Topic: Characterization of sinking particles through Carbon and Nitrogen elemental abundances in Grand Traverse Bay, Lake Michigan
- Phi Beta Kappa, Golden Key, Honors College

PUBLICATIONS (*co-first authors)

Bewick, S., Y. Pearson, E.A. Larsen, C. Şekercioğlu, E. Goldberg, S. Goldstein and W.F. Fagan. Predicting the maximum per capita rate of population growth for shorebirds – a phylogenetic comparative analysis. **In Prep.**

K. Olson, E.A. Larsen, T. Mueller, P. Leimgruber, T. Fuller, G. Schaller and WF Fagan. Survival probabilities of adult mongolian gazelles using continuous-time telemetry-based survival analyses. **Accepted at Journal of Wildlife Management.**

K.R.B. Schmitt*, E.A. Larsen*, M.W. Miller, A. Andrew, A.H.A. Badaway, M. Dougherty, K. Hrapczynski, B. Robertson, A. Taylor, A. Williams, S. Kramer, and S. Benson. A survey tool for assessing student expectations early in a semester. **In press at Journal of Microbiology and Biology Education.**

W.F. Fagan, Y. Pearson, E. Larsen, J.B. Turner, H.J. Lynch, H. Staver, J. Turner, A. E. Noble, S. Bewick, and E. Goldberg. 2013. Phylogenetic prediction of the maximum per capita rate of population growth. **Proceedings of the Royal Society, Series B.** 280: 20130523

K.R.B. Schmitt, A.H.A. Badaway, S. Kramer, K. Hrapczynski, E. Larsen, A. Andrew, A. Taylor, A. Williams, S. Benson, M. Dougherty, M. Miller, and B. Robertson. 2013. Student expectations from CS and other stem courses: they aren't like CS- majors! or (CS !=Stem-CS). *J. Comput. Sci. Coll.* **28(6): 100-108.**

E.A. Larsen, W.F. Fagan, J.M. Calabrese and M. Rhains. 2013. Female mating failure in nonautonomous spatial population models with protandry. *Entomologia Experimentalis et Applicata* **146: 130-140. #Invited Paper**

W.F. Fagan, C. Cosner, E.A. Larsen and J.M. Calabrese. 2010. Reproductive Asynchrony in Spatial Population Models: How Mating Behavior Can Modulate Allee Effects Arising from Isolation in Both Space and Time. *The American Naturalist* **175: 362-373.**

RESEARCH EXPERIENCE

Graduate Student and Research Assistant, Fagan Lab, UMD 2007-Present

- Successional dynamics and bird community composition at Mount St. Helens
- Phylogenetic analysis of maximum population growth rate [RA 2010-2012]
- Theoretical modeling of populations with reproductive asynchrony

Researcher, Oceanites Inc. 2008-2013

- Surveying penguin & seabird colonies in the Antarctic Peninsula region
- Biologist ambassador to Antarctic tourists including research lectures
- Outreach to local K-12 students

Graduate Student, Center for Conservation Biology, W&M 2005-2007

- Spatial analysis of the effects of landscape and human population on avian diversity, using data from the U.S. Census, U.S.G.S. National Land Cover Dataset, and North American Breeding Bird Survey

Volunteer, Fairfax County Stream Monitoring Program 2004-2005

- Stream health monitoring using benthic macro-invertebrates as indicators

Volunteer/Contract Employee, Patuxent Wildlife Research Center, USGS 1999-2001

- Nest monitoring, sample collection and sample preparation for field studies on contaminant exposure and effects of Opsrey
- Development of protocols, template and help files; data collection and entry for the Contaminant Exposure and Effects – Terrestrial Vertebrates (CEE-TV) database (<http://www.pwrc.usgs.gov/CEETV/>)

TEACHING EXPERIENCE

TA, Calculus for Life Sciences I & II, UMD 2008-2010, Fall 2012

- Prepared teaching materials including biology modules and quizzes.
- Instructed students in calculus and its applications in biology.
- Facilitated student review sessions, tutoring. Graded coursework and exams.

- GA, Calculus for Life Sciences I & II, UMD** 2007-2008
- Developed course materials for biological applications of math skills
- Guest Lecturer, Integrative Biology II, W&M** 2007
- Topic: Embryogenesis in Plants. Wrote corresponding exam material.
- TA, Integrative Biology I and II, W&M** 2005-2007
- Prepared teaching materials including handouts, question sets, and quizzes.
 - Instructed and supervised animal identification, dissections, and other course material.
 - Responsible for course content and student evaluation for 40-50 students.
 - Facilitated student review sessions, tutoring. Graded coursework and exams.
- Small group and individual instruction, BEACON Program** 2003-2005
- Taught G.E.D. material [science, math, history], English as a second language

OTHER PROFESSIONAL EXPERIENCE

-
- AIMS Coordinator, American Bird Conservancy** 2002-2005
- Supervised the Avian Pesticide Incident Network trial, which tested for pesticide residues and cholinesterase activity in birds from wildlife rehabilitation centers.
 - Constructed and managed the Avian Incident Monitoring System (AIMS) database of pesticide poisonings in wild birds in the U.S. (<http://www.abcbirds.org/aims>).
 - Managed USEPA cooperative agreement; prepared reports; built collaborative relationships with federal and state agencies, accessing previously unavailable data.

GRANT, AWARDS, AND FELLOWSHIPS (awarded to E. Larsen unless otherwise stated)

-
- Jacob K. Goldhaber Travel Grant**, UMD Graduate School. 2012
- Graduate Lilly Fellowship**, UMD Center for Teaching Excellence. 2011-12
- DC Lilly Conference Grant**, UMD Center for Teaching Excellence. 2011
- Exploration and Field Research Grant**, Explorers Club Washington Group. For: Bird Community Responses to Disturbance and Succession at Mount St. Helens. \$2400. 2010
- Departmental Excellence & Innovation in Undergraduate Teaching Award**, UMD Center for Teaching Excellence. Awarded to the Interdisciplinary Math 130/131 Team. 2008-2009
- Graduate Student Summer Research Fellowship**, UMD. 2009
- Eloise Gerry Fellowship**, UMD Biology Dept. 2007
- Honorable Mention for Excellence in Scholarship**, W&M Graduate Research Symposium - Natural and Computational Sciences. 2007
- Bill Sheehan Ornithology Research Grant**, Williamsburg Bird Club. For: The impacts of urbanizing landscapes on avian diversity in the Mid-Atlantic 2007

Coastal Plain: the role of avian dietary guild. \$500.
Student Conference Travel Grant, W&M Graduate Student Association. 2007
 For: Travel to the 2007 Southeastern Ecology and Evolution Conference.
 \$200.
Outstanding Teaching Assistant Award, W&M Biology Dept. 2006
Graduate Student Travel Grant, W&M Reves Center for International 2006
 Studies. For: Travel to the 4th North American Ornithological Conference,
 October 2006. \$500
U.S. Environmental Protection Agency Cooperative Agreement. 2005
 Awarded to American Bird Conservancy, Avian Incident Monitoring
 System. \$61,104.
U.S. Environmental Protection Agency Cooperative Agreement. 2004
 Awarded to American Bird Conservancy, Avian Incident Monitoring
 System. \$50,000.

PRESENTATIONS AND INVITED TALKS (* indicates presenter)

Larsen, E.A.*, A.H. Badaway*. "The Student-Faculty Chasm: Looking at where 2013
 student and faculty expectations meet and diverge". DC Lilly Conference,
 Bethesda, MD.
Larsen, E.A.*, C. Crisafulli, and W.F. Fagan. "Avian community assembly 2012
 processes during primary succession". Talk, ESA Annual Meeting, Portland, OR.
Larsen, E.*, K. Schmitt*, A. Andrew, A.H. Badawy, M. Dougherty, K.M. 2012
Hrapczynski, M. Walker Miller, B. Robertson, A. Taylor, A. Williams, S.
Kramer, S. Benson. "From seed to STEM: Cultivating understanding of student
 and faculty classroom expectations" Invited Talk, UMD Center for Teaching
 Excellence Lilly Showcase, College Park, MD.
Schmitt, K.*, A.H. Badawy*, B. Robertson*, A. Andrew, M. Dougherty, 2012
K.M. Hrapczynski, E. Larsen, M. Walker Miller, A. Taylor Sharma, S.
Benson, S. Kramer, A. Williams. "What do students expect? Assessment of
 Student Expectations in the classroom and applications for faculty" Talk,
 Innovation in Teaching and Learning Conference, College Park, MD
Andrew, A., A.H. Badawy, M. Dougherty*, K.M. Hrapczynski*, E. Larsen*, 2012
M. Walker Miller, B. Robertson, K. Schmitt, A. Taylor, A. Williams, S.
Kramer, S. Benson. "Building a Tool for Pre-assessing Student Expectations"
 Poster, UMD Graduate Research Interaction Day, College Park, MD. [Best Poster
 Award]
Larsen, E.A.*"What we can learn from birds at Mount St. Helens?" Invited Talk, 2011
 Explorer's Club Washington Group, Washington, D.C.
E.A. Larsen*, W.F. Fagan, C. Cosner, and J.M. Calabrese. "Reproductive 2009
 Asynchrony and Allee Effects in Spatial Population Models." Poster, Biology

Graduate Student Research Day, UMD.

E.A. Larsen* and W.F. Fagan. "Voltinism and the population dynamics of the pipevine swallowtail (Battus philenor).” Poster, Biology Graduate Student Research Day, UMD. 2008

E.A. Larsen* and B.D. Watts. "The impacts of urbanizing landscapes on bird diversity in the Mid-Atlantic Coastal Plain: the role of dietary guild." Poster, ESA Annual Meeting, San Jose, CA. 2007

E.A. Larsen* and B.D. Watts. "The impacts of urbanizing landscapes on bird diversity in the Mid-Atlantic Coastal Plain: the role of dietary guild." Talk, VA Academy of Science, Harrisonburg, VA. 2007

E.A. Larsen* and B.D. Watts. "Do birds like McDonalds? How diet affects bird diversity in the city." Talk, College of William and Mary Graduate Research Symposium, Williamsburg, VA. 2007

E.A. Larsen* and P. Ostrom. "Characterization of sinking particles through Carbon and Nitrogen elemental abundances in Grand Traverse Bay, Lake Michigan." Poster, MSU Undergraduate Research Forum, East Lansing, MI. 2001

PROFESSIONAL SERVICE

Webmaster, Fagan Lab, University of Maryland 2007 - 2013
Graduate Student Panelist, TA Training, University of Maryland 2012
Representative, Graduate Student Government, UMD 2008 - 2010
Graduate Student Representative, Conservation Biologist Search Committee, W&M 2007
Treasurer, Graduate Student Association, W&M 2006 - 2007
Representative, Graduate Student Association, W&M 2005 - 2006

PROFESSIONAL DEVELOPMENT

Ontologies for Evolutionary Biology, NESCent Workshop (Attendee) 2013
University Teaching and Learning Program, UMD Center for Teaching Excellence 2011 - 2013
Lilly Conference on College and University Teaching – D.C. (Attendee) 2011, 2013

MEMBERSHIPS

Ecological Society of America
American Ornithological Union