BIRD COMMUNITY RESPONSE TO PASSIVE VERSUS ACTIVE MANAGEMENT ON MOUNT ST. HELENS WASHINGTON

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A Thesis
Submitted in partial fulfillment of the requirements for the degree Master of Environmental Studies
The Evergreen State College
June 2016
This Thesis for the Master of Environmental Studies Degree

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Abstract

Bird community response to passive versus active management on Mount St. Helens Washington

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Post disturbance management, specifically salvage logging, is used regularly in Pacific Northwest forest ecosystems to off-set economic losses, reduce fire fuel loads and restore industrial timberlands. This practice also removes habitat components such as snags and downed wood which are important to many species of birds and other wildlife. The study of birds post-disturbance can provide information to managers on habitat components which have persisted and those which are lacking in the ecosystem, leading to more informed management decision-making. The body of knowledge regarding bird response to salvage logging continues to be sparse and studies lack the necessary longevity and comparison to a control to be conclusive. This study provides these necessary pieces by comparing study sites that are under long-term conservation for research (passively managed) and those that were salvage logged and replanted (actively managed) following the May 18, 1980 eruption of Mount St. Helens. We found a pattern where passively managed sites had greater bird abundance and diversity than noble fir plantations and significantly greater than Douglas-fir plantations. These results indicate a need for more understanding of the habitat components which are lacking in actively managed sites in order to develop best management practices for salvage logging.
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Acknowledgements

I wish to humbly thank some folks who have enriched my educational experience and enabled me to successfully complete this work. First and foremost thank you to my US Forest Service collaborator Charles M. Crisafulli for providing me with such an interesting dataset and guiding my analysis. Thank you Kevin Francis, MES Director, for guiding my thesis writing process and for providing me excellent feedback on my writing throughout the program. Thank you to all of my fellow 2014-2016 MES cohort who offered inspiration and commitment to learning over the past two years. I especially want to thank Rhianna Hruska and Hannah Trageser for their excellent feedback and motivation and Josh Carter for technical support. Thank you very much to my family who has always supported my ongoing educational and professional ambition, especially my parents Milo and Kay. Thank you Oliver for providing me with original images of birds for use in my thesis presentation. Thank you Anthony Saucier and Cash the labradoodle for unconditional love and support.
I. INTRODUCTION

The eruption of Mount St. Helens created a large-scale natural experiment useful for the study of volcanic ecosystems but also offers the opportunity to understand ecosystem succession following cataclysmic disturbance. It is the most vigorously studied eruption in history with long-term datasets monitoring plants, invertebrates, small mammals, birds, and volcanic processes (Dale, Swanson, and Crisafulli 2005). Disturbance is an important component of all ecosystems and must be understood and studied in the context of the natural disturbance regime of the area in question.

The eruption of Mount St. Helens constituted a natural part of the local disturbance regime, however a severe one which had not taken place for 123 years (Dale, Swanson, and Crisafulli 2005). The events of May 18, 1980 began with a 5.1 magnitude earthquake and the collapse of the entire northeast side of the mountain that became the largest landslide in recorded history (Lipman and Mullineaux 1981). The landslide released volcanic pressure in the form of magma and gases within the mountain triggering a supersonic blast which leveled a 500 square kilometer forested area (Lipman and Mullineaux 1981). The eruption also included a ‘hot, ash-charged gas shot’ which rose rapidly from the volcano to elevations of at least 23 km and proceeded to distribute ash throughout the northwest and Midwest United States (Lipman and Mullineaux 1981). The ash continued to circle the globe multiple times and most likely remained in the atmosphere for years (Lipman and Mullineaux 1981).

The culmination of the events of May 18, 1980 on Mount St. Helens was the total disruption of the ecosystem within the blast zone. Topography was leveled, lakes were relocated, and many large lifeforms such as deer, bear, and many birds were killed.
Smaller mammals such as mice as well as many plants, algae, and fungi were protected in micro-climates and survived the eruption (Dale, Swanson, and Crisafulli 2005). All life on Mount St. Helens, whether surviving or returning to the blast zone as colonizers, must adapt to an ecosystem recovering from cataclysmic change (See figure 1).

Figure 1: before and after images of Mount St. Helens, source: National Geographic

In 1982 the United States Federal Government set aside 44,550 hectares of the Mount St. Helens blast zone as a long-term study area. The Mount St. Helens National Volcanic Monument is an outdoor laboratory for the study of volcanism and natural succession following cataclysmic disturbance. The blast zone includes areas referred to as
the scorch zone, where magma and fires started from magma flows created conditions similar to forest fires, and the blowdown zone where the majority of trees were toppled by the blast (See figure 2). Other parts of the blast zone are outside of the Monument and are undergoing another type of experiment, in reforestation. After the eruption, Weyerhaeuser Corporation and the United States Forest Service collaborated to recover merchantable timber from the blast zone. This process included salvage logging, piling and burning of remaining material, scarification of soils, and planting of commercial tree species. Salvage logging has been a large part of the management regime on United States Forest Service lands for decades, however the ecological effects of this practice have not been well determined (McIver and Starr 2000).

Figure 2: blowdown zone of Mount St. Helens, source: J. Devine (USGS)
Measurements of bird abundance and diversity provide important insight for managers about the health of ecosystem processes and functions, especially following disturbance. This research compares bird communities in areas of the blowdown zone which were salvage logged and replanted (actively managed) with those in the Mount St. Helens National Volcanic Monument which were left to regenerate naturally (passively managed). Bird community response to these management regimes can help managers understand the effects of salvage logging and inform appropriate management decisions following disturbance. The protected portion of the blast zone within the Mount St. Helens National Volcanic Monument is a control which may lead to greater understanding of the long-term effects of management following natural disturbance. As human footprints on ecosystems continue to increase in size, a natural experiment such as this provides the opportunity to inform conservation biology and restoration ecology, two fields concerned with protecting ecosystems from threats such as climate change.

As the nature tourism industry has grown in the Pacific Northwest, birds have become cultural icons and important to local economies. Their story on Mount St. Helens, like the human one, begins with massive devastation and is just now beginning to make a comeback. From total annihilation in the blast zone, to slow colonizers, to drivers of succession, their progress has been well-documented since May 18, 1980. It is certain however, due to birds’ ease of identification and quantification and overall importance as ecosystem architects, that there will be more focus on their role as their numbers increase with continued succession on Mount St. Helens. Presence, or absence, of birds from a habitat provides important insight on the effects of disturbance, how an ecosystem is responding, and the ultimate path it will follow.
This document contains an introduction, a literature review, and a research manuscript. The introduction explains the context and setting of this research as well as the importance of understanding the effects of post-disturbance management on future biological communities. The research manuscript outlines our research, methods, and findings which seek to understand the differences between bird communities in areas that were salvage logged versus those that were not following the eruption of Mount St. Helens. It ends with a discussion of management implications of this research and recommendations for future research.

II. LITERATURE REVIEW

The following literature review will summarize the key lessons learned about succession of ecosystems after cataclysmic disturbance from 25 years of research on Mount St. Helens (MSH) and how the theoretical history of succession has shaped current ecological research on disturbance and management. It continues to define the differences between large and small disturbances, how they are studied, and how they shape the resulting landscape. It specifically reviews the processes of wind and fire disturbance, their importance to temperate ecosystems, and the role of salvage logging as a management tool in their wake. The literature review then explains colonization of plants and birds following disturbance, the unique interactions which shape future plant and animal communities, and why birds are appropriate indicators of habitat change. It ends with an exploration of salvage logging as a management technique, what is currently known about its effects, and questions about its impacts which still remain.
A. Impact of research at Mount St. Helens on successional theory

1. Conceptual foundations of disturbance and succession

Disturbance is an important component of all ecosystems, with the ability to increase heterogeneity over the landscape, providing opportunities for a greater diversity of organisms to thrive in a given environment (Wiens 1989). According to Picket and White (1985), “a disturbance is any relatively discrete event in time that disrupts ecosystems, community, or population structure and changes resources, substrate availability, or the physical environment”. This definition is the product of generations of research studying disturbance and the ensuing effects on the ecosystem, known as succession, which is one of the oldest and most central ecological theories. While Henry David Thoreau talked about his understanding of succession as early as 1859, Henry Cowles published formal works on the theory of succession beginning in 1899 describing how dune vegetation advanced through more or less formal stages as it matured (Cowles 1899). The theory evolved when Frederic Clements published Plant Succession (1916), introducing the idea of a climax community, a steady state which each ecosystem grows toward as it matures. Beginning in 1920, Henry Gleason began to publish his more complex and subtle version of succession which included chance events that could change the entire course of succession, opposing the idea of a climax community (Gleason 1939). More recently, research at MSH has offered deeper insight to some of the fundamental aspects of this complex and dynamic ecological process.

The magnitude, severity, and spatial distribution of a disturbance determines its effect on the surrounding ecosystem and ecological processes. Small-scale disturbances of high or low magnitude and large-scale disturbances of low to moderate magnitude are
studied relative to “patch dynamics” (Thompson 1978; Pickett and Thompson 1978; Pickett and White 1985). According to Pickett and White (1985),

1. “Patch” implies a relatively discrete spatial pattern, but does not establish any constraint on patch size, internal homogeneity, or discreteness.

2. “Patch implies a relationship of one patch to another in space and to the surrounding, unaffected or less affected matrix.


Disturbance events create patches across a landscape introducing heterogeneity with effects on the community of organisms it supports. The alteration of habitat structure and resource availability has unique effects on birds which can be negative or positive depending on a species’ specific adaptations.

Large-scale, high magnitude disturbances are studied in terms of succession because they affect the ecological processes supporting communities of species and require longer timeframes to recover (Pickett and White 1985). The study of ecosystem response to natural disturbance at MSH provides insights on important ecological questions about how succession proceeds on a large scale without human intervention. Dale, Swanson, and Crisafulli published the results of 20 years of research on MSH in *Ecological Responses to the 1980 Eruption of Mount St. Helens* (2005) and provided their own definition of succession.

Succession: The process of gradual replacement of one species or population by another over time and the concurrent change in ecosystem properties after a site has been disturbed. The concept can be extended to the replacement of one kind of community by another, the progressive change in vegetation and animal life
that may culminate in dominance by a community that is stable until the next disturbance. Succession refers to changes that occur over 1 to 500 years and not to seasonal changes in populations and communities (Dale, Swanson, and Crisafulli 2005).

This definition of succession was directly informed by research at MSH where succession did not proceed as a rapid march toward a climax community but instead in sporadic bursts and lags. (del Moral 1999). This is emphasized in the definition used by Dale, Swanson, and Crisafulli by use of the word “gradual” and clarification of long timeframes versus seasonal changes. The idea of a climax community is included but not guaranteed, while the inevitability of the next disturbance is emphasized. The following chapter reviews lessons learned about succession directly from study at MSH and situates them within the historical theoretical framework.

2. Lessons from Mount St. Helens: refugia provide the seeds of succession

One of the first surprises for biologists following the eruption did not consist of what was lost but what remained. Looking across the landscape after the events of May 18, 1980, it may have been hard to see anything more than total destruction. Not only did timber companies and the United States Forest Service (USFS) lose major investments in industrial timberlands but most wildlife within the blast zone were killed or driven away. However, small plants, insects, and even mammals were able to survive in refugia, locations where geographical features or natural structures (microsites) provided protection and stability for life to persist after the eruption (Dale, Swanson, and Crisafulli 2005). Microsite conditions protected intact fragments of the former ecosystem from which succession could build. Then, following the definition, succession proceeded with
species being added and changing ecosystem processes, creating niches to allow new
diversity, filling in new niches for colonization. For instance in the blowdown zone of MSH, the first wave of plant
colonization included late-successional species which emerged from under as much as a
meter of ash, pioneer species, and wind-dispersed plants from areas outside of the
impacted area (Crisafulli and Hawkins 1998). The wind-dispersed plant colonization
follows traditional successional theory while the late-successional species were
unexpected (Crisafulli and Hawkins 1998).

Late-successional species survived in refugia created by an array of site-specific
conditions.

Four factors appeared to increase the probability that individual plants would
survive in these locations: 1) patches of late-lying snow shielded some plants
from the blast; 2) plants living on the lee sides of ridges were not exposed to the
main force of the blast; 3) some plants survived in soils on the exposed rootwads
of large blown-down trees; and 4) some plants were able to resprout from
perennial root stock on steep slopes where erosion quickly cut through ash
deposits (Mac et al. 1998).

Some understory conifers survived within the blowdown zone and they demonstrated
rapid growth after the loss of shade and began producing cones by 1993 (Mac et al.
1998). This phenomena greatly accelerated the overall process of succession in the
blowdown zone providing habitat for colonizing species (See figure 3). Other survivors
in refugia who were more vulnerable understory plants, such as forbs, could not tolerate
new conditions created in the blowdown zone and did not survive to reproduce (Mac et
al. 1998).
The survival of understory conifers provided areas of the blowdown zone with a successional advantage due to the vertical structure gained by the trees’ rapid growth.

Ksudach, a volcano in Russia which erupted in 1907, was studied in the context of succession by extrapolating a successional theory from the relationships between vegetation and animal communities existing decades later. They noted that vertical structures such as dead standing trees left after the eruption may have attracted animal
seed dispersers including birds, acting as key drivers of succession. This work became the basis for further successional studies as well as ecological restoration work in the tropics (Thompson and Wilson 1979; McDonnell and Stiles 1983; Yarranton and Morrison 1974; McDonnell 1986). Vertical structure is now a known attractor of seed-dispersing animals, especially birds, who use the structures to move between areas of habitat and introduce colonizing plant species as they travel (McDonnell 1986).

Herbivores, especially arthropods initially, were as found to be as influential as plants themselves at dispersing seeds in the first wave of succession on MSH (Dale, Swanson, and Crisafulli 2005; Bishop 2002). Since insects are small they are able to take advantage of refugia to a larger degree than mammals, allowing them to function as the primary drivers of succession along with plants. As they emerged from volcanic soils they acted as tillers, bringing fertile soil buried by the eruption to the surface and creating a bed for dispersing seeds. These colonizing efforts are a mechanism of trophic interactions between species which allow them to gain the necessary resources for survival. As insects go about their business of decomposing items into soil they are inadvertently moving seeds and sowing future plant communities. These minute details of trophic interactions are often overlooked in healthy, intact climax ecosystems with glorious megafauna to distract; however they become crucial mechanisms of change when they are all that is left after cataclysmic disturbance.
3. Lessons from Mount St. Helens: succession is a series of chance events leading to structural change across an ecosystem

Another lesson learned from MSH is that succession does not proceed linearly toward the ecosystem which existed prior to disturbance, but on a novel route to an entirely different product (Dale, Swanson, and Crisafulli 2005). Not only are the flora and fauna existing on MSH today a product of a relict ecosystem spread by survivors after the eruption, but an ongoing series of smaller successions. Over time small trophic interactions between new immigrants to a disturbed area combine to create niches for other species to fill and provide opportunities for more trophic interactions. This process slowly changes the structure and dynamics of the vegetation and ecosystem processes eventually causing colonizing species to go locally extinct, a process MacArthur and Wilson (1963) defined as turnover. Eventually an equilibrium may be reached where immigration rates are equal to extinction rates and this is the theoretical ‘normal’ state of populations in insular (island-like) regions (Diamond 1969). These theories are the primary paradigm for conservation biologists who are engaged in answering the question of ‘how much is enough’ in reference to creating reserves to protect biological diversity (Quammen 1996).

While published in the late 1960s and early 1970s, MacArthur and Wilson’s theories on colonization and extinction have remained the quintessential models for ecologists, although some are beginning to build upon their work. Recent invasions of species such as the Barred Owl and Eurasian Collared-Dove have motivated biologists to think about colonization and extinction in less simplistic terms and take into account species-specific interactions and environmental change (Yackulic et al. 2015).
Researchers studying succession on MSH have not found general patterns across the disturbed landscape, but instead ‘chance colonization events’ which are the product of local conditions (del Moral and Bliss 1993; del Moral and Wood 1993; Turner et al. 1998). While disturbance is an intrinsic part of every ecosystem, it is extremely variable through space and time, imparting chance as a component of response (Wiens 1989).

B. Plant and bird colonization post-disturbance

1. Birds indicate response of ecosystem functions and processes to disturbance events

   Birds have long been recognized as effective tools for ecological monitoring of landscape change due to management or disturbance (Greenwood et al. 1993; Hutto 1998). There are three main reasons for their importance as indicators which are emphasized by Hutto (1998): 1) ease of identification and cost-effective survey methods; 2) allow for rapid collection of large amounts of data; 3) birds can be generalist or specialist, representing varied habitat needs and life-history traits. Wiens et al. (1986) and others have found that small to moderate severity disturbance to a stable ecosystem increases diversity by providing new opportunities for colonizers, while high severity disturbance may alter the habitat too much to sustain some species (Denslow 1985; Wiens 1985; Sousa 1979; Sousa 1984). While this phenomena has been well documented among many wildlife species, “there are no quantitative treatments of this relationship for bird communities” (Wiens 1989).

   Because large infrequent disturbances (LIDs) produce a diversity of vegetative types throughout the affected area, there may be many available niches for birds to re-colonize as succession progresses (Turner et al. 1998). As vegetation changes however,
assemblages of bird species in the community change as well, creating local extinction episodes (Kennedy et al. 2011). Most of the research concerning bird re-colonization of disturbed habitats has been completed in patches created by land management such as logging. One reason for this is that habitat destruction is the main threat to birds worldwide; another is that opportunities for this research are widespread in reference to management activities versus opportunities such as MSH to study large-scale disturbance in a natural experiment, which happen rarely.

This research compares bird communities in 2010, 30 years following the eruption, between sites which were passively managed and those which were actively managed, including salvage logging. Bird abundance and diversity are expected to be generally greater on the passively managed sites because debris was left onsite providing habitat for prey species, adding nutrients to the soil to support developing vegetation communities, and surviving plants on passively managed sites grew more quickly than planted trees species on actively managed sites. Salvage logging has rarely been looked at in an experimental study containing a control plot for comparison (USDA 2000). MSH offers this opportunity and therefore the results of this study may provide information which has remained elusive regarding long-term effects salvage logging has on ecosystem functions and processes as well as how managers can augment the practice to protect important wildlife habitat.

The recolonization of birds in the MSH blast zone has been studied with varying intensity since the May 18, 1980 eruption. Several species were documented in the blast zone during the summer of 1980, however observed species richness here was incredibly variable until 1984 showing no observable trends (Andersen and MacMahon 1986).
Recent studies show a correlated increase in species abundance and diversity on MSH as plant community complexity has increased (Crisafulli and Ronnenberg 2012). This confirms previous, classic studies of succession by Karr (1986) studying temperate forests in the Northeast United States and MacArthur et al. (1966) in the tropics relating disturbance and bird re-colonization. Andersen and MacMahon (1986) studied ground-nest predation on the pumice plain post-eruption and found that not only did birds die directly but also suffered from increased nest predation due to vegetation loss, a factor which may affect bird communities in the blowdown zone to a lesser degree. Factors affecting recolonization of birds on MSH are complicated, varied, and require further analysis to document how they are interacting to determine bird community structure.

2. Studies of bird functional groups provide broad analysis and generalization of results

For the study of re-colonization following a disturbance event, it is common to group bird species with similar life-histories into guilds. Members of a guild display similar patterns of foraging behavior as a functional group and will generally react in similar ways to disturbance. Analysis of guilds creates a more general picture of the effects of disturbance versus analyzing a species which produces more specific results. An analysis of guilds therefore can be generalized to a greater degree which is useful for management decision-making. A disturbed patch surrounded by extensive, intact habitat tends to exhibit higher rates of bird immigration while turnover (or extinction) lowers (Crooks et al. 2001; Boulinier et al. 2001; Hinsley et al. 1995; Schmiegelow et al. 1997; Mason 2001; Kraus et al. 2003). Extinction also generally happens at a higher rate the more isolated an intact patch is within a large disturbed area (Schiegelow et al. 1997;
Crooks et al. 2001; Kraus et al. 2003). Kraus et al. (2003) further tested these theories on butterflies, having similar life histories to birds, and found differences between various guilds of generalist species versus specialists. The study took place over two years and species richness and abundance was measured before and after a disturbance event. The total species richness and abundance was similar between years, but in larger patches of intact habitat generalists increased while specialists decreased in smaller patches (Kraus et al. 2003). These findings suggest that certain sizes of patches may provide a source of individuals to feed population growth while others may be creating a sink. This information is important for managers working with imperiled species whose populations are closely monitored.

There are serious limitations in existing studies of bird re-colonization of patches. The main limitation is that most bird studies in general are based on species abundance, diversity, and occupancy patterns without taking into account processes like colonization and extinction that may be affecting results (Fahrig 2003; Lampila et al. 2005; Kennedy 2011). In this case, long-term research on MSH could inform this gap by providing data about bird re-colonization alongside simultaneous studies of the larger processes at work. This study analyzes the effects of active management versus passive management in the context of large-scale natural disturbance, a truly rare opportunity. While few studies have examined bird communities in salvage logged stands compared to un-salvaged areas, none have compared them across forests recovering from large-scale disturbance. Within the context of natural succession on MSH, researchers may gain understanding of the larger processes driving bird community organization post-disturbance. This
understanding could lead to better management of industrial forests to maintain structural components that support greater biodiversity.

3. **Birds and plants exhibit highly specialized interactions which provide mechanisms for seed dispersal and drive succession following disturbance**

Birds and plants are two of the most dynamic mechanisms that drive succession consisting of specific interactions between species which change landscape conditions and provide opportunities for new species. There is no specific model for how birds and plants will interact to shape future communities on the landscape. This process represents elements of chance such as which species survive on a landscape following disturbance or who conditions following disturbance favor for re-colonization. Another level of complexity is found in the non-linear relationship which exists between birds and plants where each asserts influences over the other. There are certain bird species which are highly adapted to particular plant species or communities which are necessary for their existence and persistence on the landscape. As well, plants have adapted to attract avian seed dispersers and they depend on birds to spread their seeds and expand their ranges. On MSH these specific bird and plant (and vice versa) interactions are still developing and demand study for deeper understanding.

Colonization occurs after LIDs as species are introduced into habitats that they are able to exploit. The rate at which this occurs depends upon the species available in surrounding intact habitats to invade the disturbed area and to take advantage of remaining habitat niches (Clements 1915; Pickett et al. 1987a; Picket et al. 1987b; Turner et al. 1998). This process necessitates intricate relationships between various species of
plants and animals within and outside of the area (Jordano et al. 2007). In an area as thoroughly devastated as the MSH blast zone, the number of potential colonizers adjacent to the habitat to be colonized is limited. The extent of available niches is also limited by the complete lack of vegetation, therefore colonization may be slow, especially toward the interior of the blast zone (Turner et al. 1998). Multiple stages of succession may need to proceed before species with diverse habitat needs, such as birds, are able to successfully colonize. As birds are able to colonize however, they play important roles as seed dispersers and habitat architects driving succession. The following chapter will focus on the limited information available in the literature that refers to colonization of LIDs and the role that birds may play in succession.

4. Disturbance patch size determines available mechanisms of recolonization

LIDs differ from small-scale disturbances in the rate of processes and mechanisms of colonization. In smaller disturbances, colonizing plants recruited from outside of the affected area quickly exploit the newly exposed soils, dispersed by various mechanisms including wind and herbivores. In the wake of a LID such as MSH there exists a large interior area of disturbance which is far from the source of colonizing plants and animals, limiting the mechanisms of colonization. Multiple studies have shown that the number of species available to colonize a disturbed area decreases with distance from surrounding intact habitat (Aide and Cavalier 1994; da Silva et al. 1996; Nepstad et al. 1996; Turner et al. 1998). Events such as the eruption of MSH are important to the study of succession, teasing apart mechanisms which differ between large and small-scale disturbances and informing modern theory.
Patch size of disturbance also affects the colonizing herbivores, such as birds, who play a major role in spreading seeds creating unique biotic interactions and rates of colonization, many of which have yet to be determined on MSH (Lubchenco 1978; Mills 1986; Bowers 1993; Davidson 1993; Runkle 1985; Long et al. 1998; Turner et al. 1998). Keeping this pattern in mind it is easy to imagine how varying stages of succession may be taking place simultaneously across the landscape of MSH at a given time.

Turner et al. (1998) compiled research on various LIDs including MSH, describing current understanding about how varying degrees of disturbance regulate patch size and influence processes and mechanisms of succession:

Our analysis suggests that succession following LIDs will differ from smaller disturbances if biological legacies are minimal and colonization from surrounding undisturbed habitats is required; if new substrates are created, particularly if unique species assemblages can develop; or if bio-physical conditions or biotic interactions such as herbivory vary with patch size.

All of these limitations are a factor on MSH, although to varying degrees depending on where you are in the blast zone. In a managed setting, Diane De Steven (1993) found through studying abandoned agriculture fields that initial differences in seed dispersal based on the presence or absence of adjacent intact vegetation and visits by dispersers has a profound effect on succession. While the majority of studies on patch size have been carried out in managed landscapes, opportunities such as MSH offer an alternative view which adds to the complexity and relativity of successional theory.

Although study of patches does not directly correlate to large-scale, cataclysmic disturbance, lessons from this research can be used to inform how birds may be
colonizing MSH. Spatial organization of patches has been found to be important in how birds re-colonize habitats (Kennedy et al. 2011; Zamora et al. 2010). As with distance to surrounding intact habitat, distance between patches is important for colonizing birds because some birds refuse to fly in open areas to protect themselves from predation. The results vary on which elements of habitat diversity enable bird species to colonize and persist in a fragmented habitat. Kennedy et al. (2011), working in tropical rainforests, found that “the effect of vegetation structure on extinction probabilities was greater than the effect of patch area,” hinting at complex relationships existing in these habitats. This study further revealed that the quality of the intact habitat matrix surrounding a disturbed area may have the most effect on whether birds colonize an area and are eventually able to persist there.

This phenomenon could result in lower extinction rates in smaller patches embedded in a hospitable matrix than in larger patches embedded in an inhospitable matrix (Sisk et al. 1997; Estades 2001; Kennedy et al. 2011).

On MSH the forests surrounding the long-term study area are mostly Douglas-fir plantations managed intensely by Weyerhaeuser Corporation for wood production, potentially degrading habitat quality.

C. Mutualistic relationship between birds and plants increases biodiversity

1. Birds drive succession by aiding dispersal of plants

   Plant dispersal aided by birds depends on complicated interactions between seed ecology, plant locations, bird behavior and conditions at the site of deposition. These factors are all changed drastically following cataclysmic disturbance such as the eruption
of MSH. Some relationships between plants and their bird colonizers may be broken by a disturbance event and take long periods of time to re-establish. Disturbance also provides the opportunity for new and novel relationships to develop through chance interactions between colonizing species and subsequent adaptation. The following chapter provides a summary of the literature regarding how structural changes resulting from disturbance, natural or anthropogenic, influences bird colonization and succession.

Dispersal methods of plants are dependent on various factors, the most important of which is climate (Jordano et al. 2007). Dry and windy conditions favor plants that are wind-dispersed while animal dispersal is more successful in wet conditions (Howe and Smallwood 1982). Local ecology also plays a role in how plants disperse; for instance, plants time fruiting to coincide with migration patterns of frugivores (fruit-eating birds). These strategies have advantages for plants who want to spread their seeds long distances and for birds needing highly nutritious food sources for migration, overwintering, or breeding (Howe and Smallwood 1982). Competition may also play an important role in deciding which dispersal mechanisms a plant develops, especially regarding animal dispersal mechanisms. Researchers hypothesize that large fruit-bearing trees in the tropics are competing for bird species such as Parrots and Toucans who spread their seeds (Thompson and Wilson 1979). The abundance and preference of potential dispersers can affect the ability of a plant to reproduce successfully (Howe and Smallwood 1982). Different functional groups of birds disseminate seeds of plants in various ways depending on how many seeds they consume, where and how far they travel before depositing them (McAtee 1947; Jordano et al. 2007).
For some plant species the digestion process of birds may also contribute to the ability of a plant to sprout and ultimately survive, as some plant seeds need to be processed in order to germinate properly (McAtee 1947; Jordano et al. 2007). For other species seeds may be damaged by digestion in a bird’s stomach rendering them unable to reproduce successfully. Jordano et al. (2007) found in a thorough literature review of seed disperser studies, that small birds contribute a disproportionately large amount to seed dispersal than other frugivores, suggesting they are interacting with plant communities to play an important role in succession. This finding reinforces the importance of studying succession as an interaction between plant communities and dispersers, because they affect each other’s survival and the ultimate results of succession (Jordano et al. 2007).

Bird dispersal mechanisms utilized by plants have been well-documented in the tropics where both large, frugivorous birds and fruit-bearing trees are common (Thompson and Wilson 1979). McDonnell and Stiles (1983) studied recruitment of bird-dispersed plant species in abandoned agriculture fields in deciduous forests of eastern North America. They were looking to fill the gap of knowledge about temperate forest dispersal strategies by birds and the theory (also derived in the tropics) that patches of intact vegetation could recruit dispersers to the area. They found that not only do such patches function to recruit bird dispersers to potentially disperse seeds to adjacent areas but also individual trees act as important vectors (McDonnell and Stiles 1983; Yarranton and Morrison 1974). This effect has led to increased study on the effect of structure, especially height of vegetation, as a determinant of the rate of bird colonization after disturbance with the ability to affect vegetation communities.
2. **Avian role in plant dispersal enhanced during secondary succession**

Just as birds play a critical role in dispersing seeds throughout a disturbed area, the ability of birds to colonize a given area is highly dependent on the plant resources available. Primary succession is the initiation of development of soils and plant communities in conditions totally lacking organic matter (Grishin et al. 1996). Secondary succession takes place when soils are formed or were not completely destroyed. The blowdown zone of MSH is undergoing secondary succession (Grishin et al. 1996). Bird dispersers of plant seeds become more prominent during secondary succession when resources, such as berries and perch sites, are available to attract them to disturbed areas (McDonnell 1986).

Although birds generally contribute to later stages of succession to a greater degree, studies of natural succession following large, infrequent disturbances (LIDs) such as Ksudach and MSH have led to blurred lines between successional stages; reinforcing the new school of thought that each succession following a LID is a unique path toward a novel steady state (Grishin et al. 1996). Birds become architects of future plant community structure by depositing seeds in areas where they are foraging, nesting, or resting. As plant species diversify and more birds are attracted to a recovering habitat, both plant community and bird species diversity rise exponentially, creating a positive feedback loop of increasing biodiversity (Robinson and Handel 1993).

3. **Legacy structures attract bird dispersers to a disturbed area**

The geographic pattern and species diversity of seeds dispersed by birds during secondary succession may be heavily influenced by existing vegetation structure and
adjacent intact habitats. The mechanisms of the relationship between plants and birds that disperse them however are not well documented in the literature (McDonnell and Stiles 1983; McDonnell 1986). Results from work by Robinson and Handel (1993) on abandoned landfills produced strong evidence of the overwhelming effects animal dispersers have on succession after disturbance. Of nineteen species of colonizing plants on their study site only six were not dispersed by animals (Robinson and Handel 1993). Expanding his work on vegetation structure as vectors for bird dispersal, McDonnell (1986) created structures of various heights in abandoned agricultural fields to see which attracted more bird-disseminated seeds. Results were conclusive that the higher the structure, the more use it received from perching birds, and the more seeds were disseminated at the site (McDonnell 1986). He extrapolated from these findings; “it appears that saplings become more attractive perches and serve as recruitment foci for bird dispersed seeds after they project above the existing matrix of herbaceous vegetation.”

Differences between the heights of structures remaining post-disturbance in the blowdown zone may have played an important role in initiating succession driven by bird dispersal. The process of salvage logging removes dead standing and down wood which would have provided height structure across a disturbed area. On MSH, salvage logging removed surviving conifer saplings from actively managed sites which grew rapidly in the passively managed sites post-disturbance (Crisafulli and Hawkins 1998; Mac et al. 1998). Studies have shown that even minimal amounts of height structures left in a site post-disturbance attracts birds dispersers and can increase greatly the colonization of plants from outside sources (Robinson and Handel 1993; McDonnell 1986).
D. Disturbance enhances biodiversity in Pacific Northwest forests

1. *Birds respond to changes post-disturbance and species who colonize are adapted to survive in the new conditions*

   The disturbance regime of the PNW is diverse, varied in scale and helps to shape the available niches for bird species, increasing biodiversity in forest ecosystems (See figure 4). Coastal storms and weather slam into the Cascade Mountain Range, impacting forests on and surrounding MSH with wind and fire disturbance. These disturbances are normally small-scale, creating patchiness across the landscape resulting in a large-scale mosaic of different habitat niches with the ability to support complex communities of plant and animal species (Franklin and Dyrness 1973; Pickett and White 1985). Some of the effects of fire and wind disturbance include increased down and standing dead wood which attracts insects and other prey items for many wildlife species (Alexander et al. 2004; Rumbiatis del Rio 2006; Blake 1982). Dead and dying wood in a forest also creates cavities which provide many wildlife species with nesting habitat (Hutto and Gallo 2006; Clark et al. 2013; Schwab et al. 2006; Abbot et al. 2003). The patchiness created by small scale wind and fire disturbance opens up closed forest canopies, invigorating vegetation, leading to a greater diversity of understory niches, and increased bird abundance and diversity.
In the blowdown zone of MSH, disturbance mimicked closely large-scale fire and wind effects, with areas of total destruction interspersed with remnant vegetation and structure. Large-scale wind and fire disturbance are increasing in the PNW forest as climate change produces more extreme weather (IPCC 2014). Studies within MSH National Volcanic Monument, may produce results revealing long-term effects of these processes and providing insight for managers who are working to mimic local disturbance regimes and protect ecosystem resiliency.

Changes in bird communities post-disturbance reflect changes in habitat availability representing ecosystem structures and functions which remain or have
disappeared. While intense fire or wind removes opportunities for many bird species to inhabit a disturbed area, other species have adaptations allowing them to thrive post-disturbance. These behaviors, for instance boring by woodpeckers in search of insects, produce habitat structure for other species such as cavity nesters. Species such as woodpeckers function as ecosystem architects post-disturbance, and their occurrence due to structures remaining post-disturbance may greatly increase the rate of colonization of wildlife species. Salvage logging by definition removes some of these important resources and the effect that has on wildlife habitat must be understood to improve its use a management tool.

2. Fire suppression and salvage logging in Pacific Northwest forests may have unintended and unknown ecological consequences

While forest fires are an important component of PNW forest ecosystems, they also produce great risk to forestry resources and human structures leading to fire suppression and alteration of natural fire regimes (Agee 1993). Fire suppression is roundly blamed for recent increases in fuel loads leading to larger forest fires (Agee 2002). One product of this phenomenon is salvage logging which was implemented to produce economic gain post-disturbance on valuable industrial forest lands and decrease fuel loads (See figure 5). Initially integrated as post-fire logging, the practice was expanded to other lands impacted by wind and other disturbance after the passing of the so-called ‘salvage rider’ by the U.S. Congress in 1995 (McIver and Starr 2000). While green tree harvest on federal lands has declined recently to protect wildlife, salvage logging has not (McIver and Starr 2000). Salvage logging was introduced to the industry
rapidly to protect the economic interests of logging communities without the research in place to develop best management practices (McIver and Starr 2000; Foundation for Deep Ecology 2006). It is important to study the short- and long-term effects of salvage logging in order to improve the practice as its use continues to increase.

Figure 5: example of postfire salvage logging, source: John Muir Project

In 2000 the United States Department of Agriculture completed *Environmental Effects of Post-fire Logging: Literature Review and Annotated Bibliography* to assess the
need for more research to inform management of post disturbance forests. They found only 21 studies worldwide which consider the ecological effects of salvage logging, most of which did not include un-salvaged controls (McIver and Starr 2000). All of the studies documented took place on lands managed intensely for timber harvest pre and postfire disturbance. Franklin et al. (2000) stated that the rarest conditions on forest lands in the Pacific Northwest are those which have undergone natural disturbance where natural succession proceeded without management. This is the condition which is represented in this study, comparing post-eruption forests that were actively managed versus passively managed. The results of this study therefore will add significant knowledge to this field and can be expanded to gain further insight regarding long-term impacts of salvage logging on PNW forests, a current gap in the literature.

There are many ways in which salvage logging can create negative consequences for wildlife. Habitats is altered by removing dead and dying trees and other structural legacies and logging practices disturb sensitive soils. Hutto and Gallo (2006) found sites un-salvaged after forest fire had “significantly larger and taller trees, a higher density of trees, trees with more bark, higher live-tree density, and a higher proportion of intact snags than salvage logged plots.” Titus and Householder (2007) compared vegetation in plots on MSH that were salvage logged and replanted versus those that were not. They found an increased abundance of non-native species in salvage logged plots and limited nitrate and phosphorus in soils, potentially limiting the ability of native plants to thrive (Titus and Householder 2007). Un-salvaged plots contained more down woody debris, more tip-ups, fewer stumps and overall greater diversity and abundance of understory vegetation (Titus and Householder 2007). Studying wind disturbance in forests,
Rumbiatis del Rio (2006) found similar results and went further to say that from a landscape perspective “disturbance helps maintain understory diversity, whereas salvage logging does not.” When most or all of the remnant structures are removed from an area post-disturbance, colonization is reduced, providing surviving wildlife populations with limited to no resources (See figure 6).

![Habitat created by down wood and how they change with decay](source: USFS)

**Figure 6: depictions of habitat created by down wood and how they change with decay, source: USFS**

Birds specifically occupy a variety of niches within an ecosystem and their abundance and diversity increases as structural diversity increases (See figure 7). When structure is removed, prey items diminish and birds may be unable to inhabit an area until structural diversity develops. This in turn, affects colonization of plants as birds are not contributing to seed dispersal in the disturbed area. In the blowdown zone of MSH, structure was removed or maintained at varying levels depending on the severity of impact and the post disturbance management regime in a given area.
3. Increased knowledge of salvage logging impacts necessary for future implementation

Because birds and other wildlife are sensitive to changes in habitat structure and ecosystem function across a landscape, greater knowledge must be gained to guide managers as they work to balance habitat needs with harvest goals. Unlike the conclusive evidence for effects on forest vegetation, literature reviewed for this document found mixed impacts from salvage logging on bird species (Cahall and Hayes 2009; Rost et al. 2012; Greenberg et al. 1995; Azeria et al. 2011; Lain et al. 2008; Hutto and Gallo...
2006). For instance, Hutto and Gallo (2006) found salvage logging to be extremely detrimental to cavity-nesting species, who depend on snags created from fire and wind for nesting habitat. However, Cahall and Hayes (2009) found many species who prefer open habitats for berry production and insect foraging do not seem to be affected by salvage logging activities. Other species such as the Black-backed and American Three-toed woodpeckers are only found in recently, heavily burned forests where a large amount of dead and dying wood attracts their prey making them severely threatened by fire suppression and salvage logging (Hutto and Gallo 2006).

Other studies have questioned the ability of salvage logging as a post-disturbance management technique to meet its overall goals, adding to the urgency of conclusive research. One of the most controversial studies on salvage logging found that the practice did not meet some of its intended purposes: 1) to limit fuel loads lowering the chances of another forest fire; 2) clear space for reforestation (Cahall and Hayes 2009). Donato et al. (2006) found that salvage logging increased fine woody debris on the forest floor adding to fuel loads, and that damage to sensitive soils by large logging equipment reduced regeneration of conifers. Cahall and Hayes (2009) among others discuss the need for analyses of the effects of salvage logging on a larger scale and with greater use of un-salvaged controls.

This research offers the rare opportunity to study salvage logging within the context of large-scale disturbance with a control are that is protected for long-term research. Hutto (2006) and Beschta (2004) among others have attempted to recommend best management practices for salvage logging based on the research available. They
also acknowledge the need for more research on this issue and importance of control sites and long-term analysis.

III. RESEARCH MANUSCRIPT

A. Abstract

Post disturbance management, specifically salvage logging, is used regularly in Pacific Northwest forest ecosystems to off-set economic losses, reduce fire fuel loads and restore industrial timberlands. This practice also removes habitat components such as snags and downed wood which are important to many species of birds and other wildlife. The study of birds post-disturbance can provide information to managers on habitat components which have persisted and those which are lacking in the ecosystem, leading to more informed management decision-making. The body of knowledge regarding bird response to salvage logging continues to be sparse and studies lack the necessary longevity and comparison to a control to be conclusive. This study provides these necessary pieces by comparing study sites that are under long-term conservation for research (passively managed) and those that were salvage logged and replanted (actively managed) following the May 18, 1980 eruption of Mount St. Helens. We found a pattern where passively managed sites had greater bird abundance and diversity than noble fir plantations and significantly greater than Douglas-fir plantations. These results indicate a need for more understanding of the habitat components which are lacking in actively managed sites in order to develop best management practices for salvage logging.
B. Research setting

Mount St. Helens is an active stratovolcano situated in the Cascade Mountain Range of Washington State, USA. It is part of a larger string of volcanoes known as the ‘ring of fire’ which circle the Pacific Ocean and whose volcanism arises from the convergence zone of the North American Plate and the Juan De Fuca Plate (Swanson, Crisafulli, and Yamaguchi 2005). The Cascade Mountain Range runs north and south approximately 50 miles inland from the Pacific Ocean where it creates a barrier for moisture-laden coastal waters which shape the wet climate west of the mountains versus the dry climate to the east. Mount St. Helens has erupted at least 20 times in the past 4000 years, producing variable vegetation communities surrounding the volcano (Swanson, Crisafulli, and Yamaguchi 2005). Prior to the May 18, 1980 eruption specific portions of the volcano had undergone the impacts of volcanic processes including tephra fall, pyroclastic flow, lava flow, dome growth, mudflow, and lateral blasts at varying spatial and temporal scales (Swanson, Crisafulli, and Yamaguchi 2005). Other non-volcanic processes also at work on and around Mount St. Helens include glacial, river, landslide, anthropogenic resource management, and local climate events.

C. Climate and ecology

The climate of Western Washington in the vicinity of Mount St. Helens is most strongly affected by the Cascade Mountain Range interactions with marine air. Moisture-laden marine air masses move east from the west coast of the Pacific Ocean where they encounter the Cascades. As they move east and upward in elevation, they drop their moisture in the form of snow and rain along the Cascade crest creating a rain shadow
effect. The effect produces a wet, mild climate on the west side of the mountains and a
drier side with more extreme temperature range, on the east. Wind is an important factor
in the creation of the rain shadow and also drives wildfires in the summer months when it
is north-northeast prevailing. During winter, winds mostly come from the ocean, are
southwest prevailing, and bring with them storms and other weather phenomena.

The west side of the Cascade Mountains experiences mild temperatures in the
summer (mean maximum=22.3°C, mean minimum=7.3°C) as well as winter months
(mean maximum=0.4°C, mean minimum=-4.4°C) (Dale, Swanson, and Crisafulli, 2005).
The climate is also very wet with mean annual precipitation at Spirit Lake, located at 988
m elevation on Mount St. Helens, totaling 2372 mm from 1932-1962 (Dale, Swanson,
and Crisafulli). The climate supports a diverse conifer-dominant temperate forest in
various stages of succession across the landscape due to management and local
disturbance regimes including wind and fire. While the local Pacific Northwest climate
sets the stage for the development of the ecosystem surrounding Mount St. Helens, the
large volcano also has a significant effect on the local climate and ecology.

D. Recent volcanic history

The most recent eruption of MSH consisted of multiple volcanic processes that
disturbed a large area with heat, gases, and various types of flows. Beginning on March
15, 1980 after 123 peaceful years, a series of small earthquakes began which indicated
the intrusion of magma into the volcano. This activity continued for 2 months and
included outward signs such as swelling of the north side of the mountain and steam-
driven explosions from the top. After this initial awakening, the north side of the
mountain collapsed on the morning of May 18, 1980 resulting in the largest landslide in recorded history (See figure 8). Almost simultaneously, a 5.1 magnitude earthquake took place below the volcano (Dale, Swanson, and Crisafulli 2005). The 2.5 km$^3$ debris avalanche split into 3 parts; one deposited into Spirit Lake, creating a 260 meter seiche (a large, contained wave), permanently raising the water level of the lake 60 meters; another jumped Johnston Ridge 7 km north; while the majority of the debris traveled west through the North Fork Toutle River Valley. All structures including glaciers, forest, and plants were scoured in the wake of the debris avalanche, leaving hot (70-100$^\circ$ C) deposits of rock and debris mostly devoid of organic material (Dale, Swanson, and Crisafulli 2005).

Figure 8: time lapse photo series of the initial events of May 18, 1980 on Mount St. Helens, source: Gary Rosenquist
Pressure was released as the north side of the mountain collapsed creating a pyroclastic density current (blast surge) of hot gas, rock, and ash which shot north of MSH. The blast was pushing a 0.2 km³ cloud of hot rock debris which caught up with the landslide, proceeding to scorch and level vegetation ahead of it for a 570 km² area (Swanson and Major 2005). The area impacted by the eruption is known as the blast zone and it is subdivided into three separate zones (blowdown, scorch, and mudflow) based on severity of impact from the eruption due to distance from the blast origin (Swanson and Major 2005) (See figure 9). Deposits resulting from the eruption contained smaller particles, lower temperatures (100-300° C), and more organic matter as distance from the blast origin increased (Swanson and Major 2005). Approximately 1.1 km³ of volcanic material was ejected and areas of the blast zone were buried under a layer from 0.01 to 1.5 meters in depth. Areas closer to the volcano received deposits of hot tephra while deposits beyond the blast zone had sufficiently cooled.
A large, vertical tephra plume initiated minutes after the eruption and continued for nine hours (See figure 10). This material was carried by prevailing winds to the east-northeast, and eventually ultra-fine material circled the globe (Swanson and Major 2005).
Figure 10: map of Mount St. Helens ash fallout, source: USGS

Hot, pyroclastic flows from 300-850° C began next and continued for five hours, leaving a trail of sterile rock in its wake (Swanson and Major 2005). The resulting area is called the pumice plain because the majority of material deposited was pumice, leaving a smooth, barren surface. Thickness of flows varied from 0.25 to 10 meters and covered 15 km² north of the volcano (Swanson and Major 2005).

Lahars (mud flows) were created by various methods during the events of May 18, 1980 on MSH, carrying with them debris as they flowed down the major drainages of the volcano. Mechanisms included liquefaction of soils from shaking, water-saturated avalanche material, pumice melted glacier ice, and snow which combined as they moved.
rapidly downhill (Swanson and Major 2005). Downstream riparian areas were stripped of vegetation, streambeds were scoured, and infrastructure was carried away as lahars moved through. Depth of lahars varied from about 0.1 to more than 10 meters and the largest traveled from the North Fork Toutle River Valley and continued 120 km to the Columbia River (Swanson and Major 2005).

The eruption left in its wake a diverse matrix of habitats varying from total devastation of vegetation and soils to patches with legacy structures protecting some life, useful for the study of natural succession following cataclysmic disturbance. All birds and most wildlife present in the blast zone during the eruption were immediately killed (Swanson, Crisafulli, and Yamaguchi 2005). Numerous studies were initiated by researchers across the disturbance zone to document the short- and long-term ecological impacts of the eruption and response of local ecosystem components and processes.

E. Forest composition prior to May 18, 1980

Prior to the May 18, 1980 eruption, vegetation on Mount St. Helens consisted of mature temperate forest and managed industrial timberlands. The Western hemlock zone (Tsuga heterophylla) dominates the lowlands and gives way to the pacific silver fir zone (Abies amabilis) at higher elevations (Franklin and Dyrness 1973). Both zones contain similar understories of hardwood trees, ferns and flowering shrubs, however their climax forest conditions differ significantly. Dominant shrubs in both zones include vine maple (Acer circinatum), salal (Gaultheria shallon), red huckleberry (Vaccinium parviflorum) and trailing blackberry (Rubus ursinus) (Franklin and Dyrness 1973). These forest types
provide important habitat niches for the bird communities of the PNW throughout their various successional stages.

The Western hemlock zone extends from sea level to approximately 1000 m and its climax species thrive in the wet climate producing some of the greatest biomass in the world, an important natural resource central to the economy of the Pacific Northwest (Franklin and Dyrness 1973). While the climax conifer is Western hemlock, Douglas-fir (*Pseudotsuga menziessi*) is its fast-growing counterpart and sub-climax conifer and dominates many forest stands in this zone. Other sub-dominant tree species include a third conifer, Western red-cedar (*Thuja plicata*), and hardwoods including red alder (*Alnus rubra*), big-leaf maple (*Acer macrophyllum*) and Giant chinkapin (*Castanopsis chrysophylla*) (Franklin and Dyrness 1973). Hardwoods are rare but make up a significant portion of riparian vegetation where black cottonwood (*Populus trichocarpa*) and Oregon ash (*Fraxinus latifolia*) accompany red alder and big-leaf maple (Franklin and Dyrness 1973). The vast majority of this forest type had been converted from a mosaic of climax forest to managed timberland before 1980, creating conservation issues for bird species such as the Northern Spotted Owl.

The pacific silver fir zone exists above the Western hemlock zone up to 1,300 m where precipitation increases and temperatures cool producing more snowfall. Winter snowpack accumulates from 1-3 m while biomass and organic matter on the forest floor are shallower than the Western hemlock zone (Franklin and Dyrness 1973). Some conifer species span both zones including Western hemlock, Douglas-fir, Western red-cedar with pacific silver fir (*Abies amabilis*) the climax conifer (Franklin and Dyrness 1973). Other co-dominant conifers include noble fir (*Abies procera*) and Western white
pine (*Pinus monticola*) with mountain hemlock (*Tsuga mertensiana*) and Alaska yellow-cedar (*Chamaecyparis nootkatensis*) joining at higher elevations (Franklin and Dyrness 1973). Riparian areas contain a similar mix of hardwood and conifer species as the Western Hemlock zone. This zone has remained more intact than lower elevations being less accessible to logging operations, however some areas experience intense forest management as well.

**F. Methods: study sites**

All six study sites used in this analysis are from the blowdown zone of MSH (See figure 11, table 1). Two study sites representing passive management are located within the 44,550 ha Mount St. Helens National Volcanic Monument which was set aside in 1982 for the long-term monitoring of successional processes post-eruption (Titus and Householder 2007). These study sites are in long-term conservation status and received no treatment; no salvage logging, no post-logging burning, no replanting.
Figure 11: map of study site locations on Mount St. Helens. See table 1 for site names, source: USFS
<table>
<thead>
<tr>
<th>Site Code</th>
<th>Site Name</th>
<th>Management</th>
<th>Treatment</th>
<th>Coordinates</th>
</tr>
</thead>
<tbody>
<tr>
<td>BDCC</td>
<td>Smith Creek Blowdown Natural Succession</td>
<td>Passive</td>
<td>No salvage logging, no re-planting</td>
<td>Start: 557068, 5129262</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>End: 556773, 5129081</td>
</tr>
<tr>
<td>GRFOR</td>
<td>Blowdown Forest Natural Succession</td>
<td>Passive</td>
<td>No salvage logging, no re-planting</td>
<td>Start: 0570456, 5129115</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>End: 0570596, 5130088</td>
</tr>
<tr>
<td>BDNF</td>
<td>Blowdown noble fir Plantation</td>
<td>Active</td>
<td>Salvage logging, re-planting with noble fir</td>
<td>Start: 0575300, 5121111</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>End: 0575311, 5122057</td>
</tr>
<tr>
<td>CWRPLN</td>
<td>Coldwater Ridge noble fir Plantation</td>
<td>Active</td>
<td>Salvage logging, re-planting with noble fir</td>
<td>Start: 0557068, 5129081</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>End: 0556773, 5129081</td>
</tr>
<tr>
<td>CWRDFP</td>
<td>Clearwater Douglas-fir Plantation South</td>
<td>Active</td>
<td>Salvage logging, re-planting with Douglas-fir</td>
<td>Start: 555924, 5128198</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>End: 0555729, 5128824</td>
</tr>
<tr>
<td>CWPLNS</td>
<td>Coldwater Ridge Douglas-fir Plantation</td>
<td>Active</td>
<td>Salvage logging, re-planting with Douglas-fir</td>
<td>Start: 0576153, 5124234</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>End: 0575818, 5125156</td>
</tr>
</tbody>
</table>

*Table 1: table representing site codes, names, treatment and coordinates of locations on Mount St. Helens*

The other four study sites exist outside of the monument and have been actively managed by Weyerhaeuser and the USFS to rehabilitate industrial timberlands (Swanson and Major 2005). These four sites were all salvage logged and remaining debris post-
logging was burned on-site (Crisafulli 2016). On some actively managed sites, soils were scarified with large machinery to reach more fertile soils less impacted by volcanic activity to increase re-planting success (Crisafulli 2016). Actively managed sites were then replanted with commercial species, in a uniform spatial pattern with eight foot spacing (Crisafulli 2016). Most trees were planted using an auger or hoe on steep ground to access mineral soils beneath the volcanic remains for fear that trees would not survive in surface soils (Crisafulli 2016). Below 1000 m Douglas-fir was the primary species planted and above 1000 m noble fir was the primary species planted, with lodgepole pine, Engelmann spruce and western white pine representing a small minority of planting across sites (Crisafulli 2016). The names of the two passively managed sites are Smith Creek Blowdown Natural Succession (BDCC) and Blowdown Forest Natural Succession (GRFOR). The names of the two noble fir plantation actively managed sites are Blowdown noble fir plantation (BDNF) and Coldwater Ridge noble fir Plantation (CWRPLN). The names of the two Douglas-fir plantation actively managed sites are Clearwater Douglas-fir Plantation South (CWPLNS) and Coldwater Ridge Douglas-fir Plantation (CWRDFP).

G. Methods: bird data collection

Long-term bird data was collected at six sites within the blowdown zone, four representing active management and two representing passive management. These sites represent two separate management regimes: 1) passively managed and 2) actively managed. The actively managed sites are further subdivided based on the dominant tree species planted, noble fir or Douglas-fir. The six sites are analyzed by three treatments:
1) passively managed 2) actively managed noble fir plantation; 3) actively managed Douglas-fir plantation. Surveys sampling the local bird community were performed using a modified line transect method (Emlen 1977). Distance-sampling method entails walking transects and counting all birds observed within 100 meters of the transect line by sight and sound (Emlen 1977). Surveys were performed by trained technicians who rotated through sites to correct for observer inconsistency. Sites were surveyed in June, July, and August 2010 with varying effort. BDNF, CWPLNS, CWRPLN and CWRDFP were all surveyed four times while BDCC was surveyed five times and GRFOR was surveyed three times.

**H. Methods: data trimming**

A data trimming exercise was completed to correct for differences in detectability among individual bird species and differing site characteristics which may affect detectability. The frequency distribution of bird observations were plotted for a set of perpendicular distance categories from transects for each species and at each study site to determine a threshold beyond which the frequency of detection declined markedly (See figure 12). For this analysis, we decided not to trim any detections because of the focus on descriptive and qualitative methods.
I. **Methods: bird guild structure analysis**

Bird data was analyzed qualitatively by defining the foraging guild for each species according to the protocol used by the USFS specifically for the Bird Master List for MSH (USFS 2015). MSH researchers assigned guilds which include seasonal foraging guilds for breeding, non-breeding and year-round resident bird species. Some species who exhibit multiple foraging patterns depending on the season were assigned multiple guilds in the Bird Master List for MSH. We condensed the multiple assignments into one which represents a more general foraging guild or the most commonly used by the species according to life history information from Cornell Laboratory of Ornithology’s *The Birds of North America* (online) (Jackson, Ouellet, and Jackson 2002). Foraging guilds consist of three letter codes which represent specific
attributes of a bird’s foraging behavior; 1) food type, 2) foraging substrate, and 3) foraging technique (See appendix 1). Species are designated a code which pertains to the three foraging descriptions and when combined create one 9-letter code indicating foraging guild (See table 2).

<table>
<thead>
<tr>
<th>Species Code</th>
<th>Species</th>
<th>Guild</th>
<th>Definition</th>
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<td>INRBOGLE</td>
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<td>Omnivore, Ground, Forager</td>
</tr>
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<td>Omnivore, Ground, Forager</td>
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<td>Habitat</td>
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<td>Subdivision 1</td>
<td>Description</td>
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<td>Insect, Air, Sallier</td>
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<td>OMUCAFOR</td>
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<td>OMBAREXC</td>
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<tr>
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<td>Red Crossbill</td>
<td>OMUCAFOR</td>
<td>Omnivore, Upper Canopy, Forager</td>
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<td>OMFLOHOG</td>
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<td>Spotted Towhee</td>
<td>OMGROFOR</td>
<td>Omnivore, Ground, Forager</td>
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<td>Steller’s Jay</td>
<td>OMGROFOR</td>
<td>Omnivore, Ground, Forager</td>
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<td>SWTH</td>
<td>Swainson’s Thrush</td>
<td>OMLCAFOR</td>
<td>Omnivore, Lower Canopy/Shrub, Forager</td>
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<td>Townsend’s Warbler</td>
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<tr>
<td>TRES</td>
<td>Tree Swallow</td>
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<td>Varied Thrush</td>
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<td>Guild Definition</td>
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<td>------------</td>
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<td>Insect, Air, Screener</td>
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<td>Warbling Vireo</td>
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<td>Willow Flycatcher</td>
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<td>Insect, Air, Sallier</td>
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<td>Omnivore, Lower Canopy/Shrub, Gleaner</td>
</tr>
<tr>
<td>YWAR</td>
<td>Yellow Warbler</td>
<td>INLCAGLE</td>
<td>Insect, Lower Canopy/Shrub, Gleaner</td>
</tr>
</tbody>
</table>

Table 2: table of bird species codes, common names, guilds and guild definitions

J. Methods: bird data analysis

Bird data was summarized by treatments and analyzed to determine differences between bird abundance and species richness. Bird abundance was corrected for differences in survey effort by averaging detections per species before statistical analysis was completed. In order to represent the total number of species for diversity and richness analysis, detections per species were averaged by the days surveyed for the abundance comparison. Data was organized and summary statistics were compiled as indicators of bird abundance and species richness.
Relative abundance was analyzed with a one-way analysis of variance (ANOVA) on the number of detections per species compared across treatments (Nur, Jones, and Geupel 1999). The Shannon’s diversity index was applied to compare species richness across treatments. Shannon’s diversity index is the most widely used diversity index because it reflects both species richness and evenness of distribution among species. It uses natural logarithms (ln) and is calculated using the equation below, where $S$=number of species in the sample and $p_i$=proportion of individuals belonging to the $i$th species:

$$H' = \sum_{i=1}^{S} (p_i)(\ln p_i), \quad i=1, 2, \ldots, S$$  

(Nur, Jones, and Geupel 1999)

$H_{\text{max}}$ is also reported, a calculation related to Shannon’s diversity index, which is a measurement of the diversity potential of the dataset given a fixed number of species and is calculated using the formula:

$$-\ln \left( \frac{1}{S} \right) = \ln(S)$$  

(Nur, Jones, and Geupel 1999)

The ratio of observed diversity to maximum diversity is reported as evenness according to the following equation where $H' = \ln S$:

$$E = H'/H_{\text{max}}$$  

(Nur, Jones, and Geupel 1999)

Species richness was also compared by applying two measurements of community similarities which utilize presence/absence data. Jaccard similarity coefficient and Sorenson index are simplistic calculations used to bolster more sophisticated quantitative results. They are calculated using the following formulas,
where \( j \) = the number of species found at both site A and B, \( a \) = the number of species in site A, and \( b \) = the number of species found in site B.

\[
\text{Jaccard similarity coefficient } C_j = \frac{\text{\( j \)}}{a + b - \text{\( j \)}} \quad \text{(Nur, Jones, and Geupel 1999)}
\]

\[
\text{Sorenson index } C_s = \frac{2\text{\( j \)}}{a + b}
\]

The indices both equal 1 when the species from the two compared sites are equal and 0 if they have no species in common. The results from these indices can be used to show how species richness varies with environmental indicators such as vegetation measurements.

Jaccard similarity coefficient and Sorenson’s index do not account for species abundance within the community so we also used the Renkonen similarity index or percentage similarity index, where \( p^A_i \) = percentage of species \( i \) in sample A and \( p^B_i \) = percentage of species \( i \) in sample B, and \( S \) = number of species found in either sample:

\[
P = \sum_{i=1}^{i=S} \min(p^A_i, p^B_i) \quad \text{(Nur, Jones, and Geupel 1999)}
\]

The index delivers 0 when there is no overlap between species in the samples and 100 percent with complete overlap.

**K. Results: bird abundance and diversity among sites**

A total of 50 bird species were detected on 6 separate sites during 24 visits in 2010 for a total of 1,323 total detections (See table 3). Passively managed sites overall had higher bird abundance and species diversity, while one actively managed site had
similarly high abundance and diversity. Smith Creek Blowdown Natural Succession Site (BDCC) had the second highest bird abundance and the highest bird diversity. Blowdown Forest Natural Succession Site (GRFOR) had the highest bird abundance and the third highest bird diversity. The actively managed Blowdown Noble Fir Plantation Site (BDNF) had a much lower bird abundance but the second highest bird diversity. The remaining three sites were all actively managed and had lower bird abundance and diversity. Coldwater Noble Fir Plantation Site (CWRPLN) had lower bird abundance and lower number of bird diversity. Coldwater Ridge Douglas-fir Plantation Site (CWRDFP) had a slightly higher number of bird abundance and lower bird diversity. The site with the lowest bird abundance but the same bird diversity as other actively managed sites was Clearwater Douglas-fir Plantation South (CWPLNS).

<table>
<thead>
<tr>
<th>Bird Species Code</th>
<th>BDCC</th>
<th>BDNF</th>
<th>CWPLNS</th>
<th>CWRDFP</th>
<th>CWRPLN</th>
<th>GRFOR</th>
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*Table 3: table with bird species abundance per site with summary statistics. Species highlighted in green were detected on only one site, species highlighted in blue were detected on all sites*
L. Results: bird guild analysis

Seventeen different foraging guilds of birds were identified in this study, with all study sites representing at least half of them (See figure 12, 13). Both passively managed sites (BDCC, GRFOR) represented the highest number of guilds (13). One of the actively managed sites (BDNF) also represented 13 guilds of birds with the other three slightly lower. CWPLNS and CWRDFP both represented 11 guilds and CWRPLN represented ten. Four guilds were only represented on a single site; three of them were detected on passively managed sites (OMBAREXC on BDCC, INUCAFOR on GRFOR and INRBOGLE on GRFOR) and one was detected on an actively managed site (CAGROHAW on CWRDFP). Actively managed sites planted with Douglas-fir represented a lower number of guilds (10, 11) than actively managed sites planted with noble fir (11, 13).

![Figure 12: bar graph depicting mean species per guild between sites with standard deviation (SD) error bars](image-url)
Analysis of variance (One-way ANOVA) returned no significant difference between the guild structures of the sites nor treatments (p-value<0.05), however there are some interesting and significant qualitative differences between bird guild structure between treatments. Four separate guilds were only represented in one treatment. Prairie Falcon, the only species found in this study representing the CAGROHAW guild (carnivore, ground, hawker) was only detected in Douglas-fir plantation treatment. The guild analysis clearly shows a lack of insect and bark foragers on actively managed sites. The 3 guilds only detected on passively managed sites are INRBOGLE (insect, riparian bottom, gleaner), INUCAFOR (insect, upper canopy, Forager) and OMBAREXC (omnivore, bark, excavator). These guilds represent three different foraging areas and three different foraging techniques, but they all have the target in common. Insects are
the common factor within these guilds and the fact that they are only found on passively managed sights reinforces what other studies have found linking dead and dying wood to larger insect populations (Kroll et al. 2010).

**M. Results: bird abundance and diversity by treatment**

Quantitative analysis of bird data was carried out with regard to treatment type; passive, Douglas-fir plantation and noble fir plantation. The results of the bird analysis by treatment type show an overall pattern with passive management treatment producing the highest bird abundance, diversity and species richness followed by noble fir treatment and finally Douglas-fir treatment (See table 4).

<table>
<thead>
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<th>Treatment</th>
<th>Passive</th>
<th>Noble fir</th>
<th>Douglas-fir</th>
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<tr>
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<td>177</td>
<td>96</td>
<td>74</td>
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<td>Cumulative Species</td>
<td>39</td>
<td>36</td>
<td>24</td>
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<tr>
<td>Cumulative Guilds</td>
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<td>12</td>
<td>14</td>
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</tbody>
</table>

*Table 4: indicators of bird abundance and diversity by treatment*

Relative abundance, a measure of abundance of one species in relation to community abundance, was measured with ANOVA. We found a significant difference between passive and Douglas-fir plantation treatments (p-value=0.041). Comparison of relative abundance between all three sites was nearly significant (p-value=0.066) There was also no statistically significant difference between the passive treatment and noble fir
plantation treatments nor between Douglas-fir plantation and noble fir plantation treatments, however the results followed the established trend (See figure 14, table 5).

![MEAN AVIAN ABUNDANCE](image)

*Figure 14: bar graph of mean avian abundance per treatment with standard deviation error bars*

<table>
<thead>
<tr>
<th>Comparison</th>
<th>P-Value (ANOVA)</th>
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</tr>
<tr>
<td>Passive vs Douglas-fir</td>
<td><strong>0.041</strong></td>
</tr>
<tr>
<td>noble fir vs Douglas-fir</td>
<td>0.506</td>
</tr>
</tbody>
</table>

*Table 5: p-values obtained with a One-way Analysis of Variance Test of bird abundance compared between treatments, significant p-value indicated in red*

One method used to evaluate species richness in this study is Shannon’s diversity index which increases as species richness and evenness increase in the community.

Values of the index normally range from 1.5-3.6 with 4 being among the highest possible
outputs (Magurran 2004). The passive treatment reported the highest among sites, followed by noble fir plantation and finally Douglas-fir plantation (See table 6). Evenness did not vary significantly between treatments, indicating more variation in species richness between treatments (See table 6).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Average Detections</th>
<th>Species Richness</th>
<th>Shannon’s Index</th>
<th>Evenness</th>
<th>Hmax</th>
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</thead>
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<tr>
<td>Douglas-fir</td>
<td>73.75</td>
<td>24</td>
<td>2.64</td>
<td>1.21</td>
<td>3.18</td>
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<tr>
<td>Noble fir</td>
<td>96.25</td>
<td>36</td>
<td>2.84</td>
<td>1.26</td>
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<tr>
<td>Passive</td>
<td>177.06</td>
<td>39</td>
<td>2.9</td>
<td>1.26</td>
<td>3.66</td>
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Table 6: table of results of Shannon’s Index and related calculations which describe species diversity

Species richness was also evaluated using the Jaccard similarity coefficient calculation (Cj=1 when species richness of communities is the same and Cj=0 when communities have no species in common). Jaccard similarity coefficient calculated for passive treatment versus noble fir plantation treatment produced the highest number, followed by passive treatment versus Douglas-fir treatment and finally noble fir treatment versus Douglas-fir treatment (See table 7). The Sorenson index was calculated to compare with Jaccard similarity coefficient (Cs=1 when species richness of communities is the same and Cs=0 when communities have no species in common). Sorenson index calculated for passive treatment versus noble fir plantation produced the highest result, followed by noble fir treatment versus Douglas-fir treatment and finally passive versus Douglas-fir treatment (See table 7). Both indices show differences between all three
treatments with regard to species richness with the greatest difference between passive and Douglas-fir plantation treatments.

The Renkonen similarity index differs from the Jaccard similarity coefficient and Sorenson index because it also takes into account abundance of species within the community. Results equal 0 when there are no species in common amongst the compared communities and 100% when they are the same. The Renkonen similarity index shows the greatest similarity between passive treatment versus noble fir plantation treatment, followed by passive treatment versus Douglas-fir plantation treatment, and finally noble fir plantation treatment versus Douglas-fir plantation treatment (See table 7). In other words the greatest similarity of species richness with respect to within-community species abundance is between noble fir plantation treatment versus Douglas-fir plantation treatment and the least similarity between Douglas-fir plantation treatment versus passive treatment.

<table>
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<th>Treatments Compared</th>
<th>Jaccard</th>
<th>Sorenson</th>
<th>Renkonen</th>
</tr>
</thead>
<tbody>
<tr>
<td>Noble fir vs Passive</td>
<td>0.59</td>
<td>0.75</td>
<td>56%</td>
</tr>
<tr>
<td>Douglas-fir vs Noble fir</td>
<td>0.5</td>
<td>0.67</td>
<td>57%</td>
</tr>
<tr>
<td>Douglas-fir vs Passive</td>
<td>0.44</td>
<td>0.6</td>
<td>46%</td>
</tr>
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</table>

Table 7: table comparing results of three different calculations comparing species richness, Jaccard similarity coefficient, Sorenson index and Renkonen similarity index
**N. Discussion**

The results of this study produce a pattern where passively managed sites produced higher abundance and diversity of bird species as well as foraging guilds than actively managed sites which were salvage logged and replanted. Among actively managed sites, noble fir plantations had higher bird abundance and diversity than Douglas-fir plantations. This pattern was consistent throughout the study, however not all differences were statistically significant (p-value<0.05). Based on the well-documented ecology of PNW forests, two factors may explain these patterns: 1) Salvage logging removes down and standing dead wood on the site that provide habitat for some bird species and their prey; 2) Plant communities left to naturally regenerate may be more diverse in species and age, providing varied structure and increased habitat niches. In addition, the removal of wood in salvage logging might decrease nutrients available to developing plant communities, thus limiting the diversity of both flora and fauna.

Salvage logging also removes dead standing trees (snags) which are very important for many bird species. As they decay, snags attract a wide variety of insects and provide foraging opportunities for many species. Snags also contain cavities which provide nesting habitat for many bird species.

Open areas which support low shrubs, forbs, and grasses in the passive treatment may also provide habitat components necessary to support a different set of bird species, increasing abundance and species richness. Breaks in the forest canopy allow increased light to reach the forest floor, producing a more varied vegetation community dominated by flowering and fruiting shrubs which increase fruit and other prey items. Dense planting of commercial tree species blocks light from the understory and may decrease
the diversity of the forest plant community. A forest representing a more complex mosaic with this open component as well as closed-canopy conifer stands provides a larger number of habitat components. With more niches to fill, bird diversity increases, representing larger numbers of foraging guilds across the landscape. Passively managed sites are more likely to contain these varied components because they are derived from a mixture of surviving conifer saplings some of which grew rapidly after disturbance, and colonizing plant species (Mac et al. 1998). While the lack of vegetation data to compare with bird data limits the ability to answer questions about how habitat has responded, results of this study reflect documented effects of anthropogenic forest management.

The species used in the plantation also appears to have a significant impact on bird abundance and diversity. Noble fir plantations consistently produced higher bird abundance and diversity than Douglas-fir plantations. The scope of this research limits our ability to explain these intriguing results. One possible contributor to this result is that higher elevation plantation (noble fir) were younger because they were salvage logged and replanted at a later date than lower elevation (Douglas-fir) plantations (Franklin 2016). Similarly, noble fir plantations do not grow as quickly or vigorously as Douglas-fir, partly because they grow at higher elevations and have a shorter growing season (Franklin 1981). This means that their canopy may have been more open at the time, producing a more structurally complex understory with greater food resources to support bird abundance and diversity (Crisafulli 2016).

Our results also follow what Mac et al. (1998) found on MSH where surviving understory trees in the blowdown zone were invigorated by the loss of canopy and demonstrated vigorous growth (Mac et al. 1998). According to their results surviving
understory trees in the passively managed sites started with an age and height advantage over salvage logged sites. The rapid increase in height structure may have attracted a greater number of bird seed dispersers, advancing plant community diversity in passively managed sites faster than actively managed sites. This fact also helps to explain the difference between noble fir and Douglas-fir stands because noble fir was planted at higher elevations (~1300 meters) versus Douglas-fir (~750-950 meters) where snow created microsites that protected further protected young trees, creating the same advantage (Mac et al. 1998; Crisafulli 2016).

We researched the conservation status of all birds represented in this study with reference to the United States Endangered Species List and the Washington State Endangered Species List. The only species to occur on either list is the Prairie Falcon which was listed by Washington as State Monitored. The lack of rare or listed species may be indicative of the fact that the habitat is young for PNW temperate forest and has not yet developed the structural complexity to support a more varied community. Commonly, species of conservation concern are those that are specialized and appear rarely across the ecosystem and are therefore more subject to the mechanisms of scarcity (Quammen 1996). It is certain that many exciting changes will be occurring soon on Mount St. Helens and studying bird communities is an important way to understand them.

The results of this study point to significant differences in bird abundance and diversity between areas that were salvage logged and planted in the blowdown zone of MSH and those that were left to naturally regenerate. This analysis is limited however due to the lack of data describing vegetation communities within the stands which are
responding to the post-disturbance treatments. This type of analysis should be carried out with regard to this dataset in order to point to the specific habitat components which differ between treatments that are responsible for the differences in bird abundance and diversity between the treatments. Also we recommend continuing this research as it provides the unique opportunity to compare lands heavily managed for timber production versus those naturally recovering from cataclysmic disturbance. This research represents a rare and meaningful opportunity to learn how post-disturbance management can be augmented to protect important habitat for birds and other wildlife.


Crisafulli, C.M. Email message to author. June 6, 2016.


Franklin, Jerry F.  Email message to author.  June 5-8, 2016.


USFS-United States Forest Service. Map of study sites on Mount St. Helens provided by Charlie Chrisafulli via email.


Appendices

Appendix 1: List of guilds, guild codes and descriptions used for this analysis. Guilds not represented in this study were removed from this list.

<table>
<thead>
<tr>
<th>FOOD TYPE</th>
<th>CODE</th>
<th>DESCRIPTION</th>
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<tbody>
<tr>
<td>Carnivore</td>
<td>CA</td>
<td>Eats vertebrates</td>
</tr>
<tr>
<td>Insectivore</td>
<td>IN</td>
<td>Eats insects</td>
</tr>
<tr>
<td>Omnivore</td>
<td>OM</td>
<td>Eats a variety of foods including plants and animals</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>SUBSTRATE</th>
<th>CODE</th>
<th>DESCRIPTION</th>
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<tbody>
<tr>
<td>Air</td>
<td>AIR</td>
<td>Catches food in air</td>
</tr>
<tr>
<td>Bark</td>
<td>BAR</td>
<td>Forages on, in or under bark of trees</td>
</tr>
<tr>
<td>Floral</td>
<td>FLO</td>
<td>Forages on or in flowers</td>
</tr>
<tr>
<td>Ground</td>
<td>GRO</td>
<td>Forages on the ground or on very low, weedy vegetation</td>
</tr>
<tr>
<td>Lower Canopy/Shrub</td>
<td>LCA</td>
<td>Forages on leaves, twigs and branches of shrubs, saplings and lower crowns of trees</td>
</tr>
<tr>
<td>Riparian Bottom</td>
<td>RBO</td>
<td>Forages on bottoms of rivers and streams</td>
</tr>
<tr>
<td>Upper Canopy</td>
<td>UCA</td>
<td>Forages on leaves, twigs and branches of tress in main canopy</td>
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</table>

<table>
<thead>
<tr>
<th>TECHNIQUE</th>
<th>CODE</th>
<th>DESCRIPTION</th>
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<tbody>
<tr>
<td>Excavator</td>
<td>EXC</td>
<td>Locates food in bark by drilling holes</td>
</tr>
<tr>
<td>Forager</td>
<td>FOR</td>
<td>Takes almost any food items encountered upon the substrate</td>
</tr>
<tr>
<td>Gleaner</td>
<td>GLE</td>
<td>Feeds on grasses, sedges or grains in fields or meadows</td>
</tr>
<tr>
<td>Hawker</td>
<td>HAW</td>
<td>Flies after prey and captures it either in air or on ground</td>
</tr>
<tr>
<td>Sallier</td>
<td>SAL</td>
<td>Perches on exposed branch of twig, waits for</td>
</tr>
</tbody>
</table>


insect to fly by then pursues and catches in air

<table>
<thead>
<tr>
<th>Scavenger</th>
<th>SCV</th>
<th>Takes a variety of items, including refuse or carrion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Screener</td>
<td>SCR</td>
<td>Flies with bill open and screens prey from air</td>
</tr>
</tbody>
</table>

Appendix 2: Complete list of dataset used in this analysis including four-letter bird codes and number of detections per study site and summary statistics.

<table>
<thead>
<tr>
<th>Species</th>
<th>BDCC</th>
<th>BDNF</th>
<th>CWPLNS</th>
<th>CWRDFP</th>
<th>CWRPLN</th>
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<td>19</td>
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<td>21</td>
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<td>% Total Species</td>
<td>0.68</td>
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<td>0.38</td>
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