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ORIGINAL ARTICLE

Mammalian community response to historic volcanic eruptions

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Abstract

It is clear that ecosystems are devastated after a volcanic eruption coats the landscape with a layer of ash; however, the ecological recovery of mammalian communities after eruptions is poorly understood. Volcanic eruptions vary with magnitude and type and only a fraction of them have been analysed for effects on mammalian communities. To better understand mammalian community recovery, I investigated how species richness, evenness, and similarity change across volcanic boundaries in the 1980 Mount Saint Helens (MSH), Washington, and 1914–1917 Mount Lassen, California, eruptions. I compared these eruptions to Mount Rainier, Washington and Mount Shasta, California as controls for regional changes in the fauna. Richness and evenness remain relatively unchanged in Lassen. MSH saw an immediate drop in richness, followed by an increase over 5 years to pre-eruptive levels. Chord distance analysis suggests no long-term change in the Lassen fauna. The pre- and post-MSH fauna are different from one another. The post-eruptive fauna was more similar to neighbouring regions. It is clear from my results that larger eruptions tend to have a greater impact on mammalian community recovery than smaller eruptions, but ultimately, mammalian populations are robust and the presence of neighbouring communities is important for recolonizing devastated areas.

Keywords Volcano ecology · Disturbance ecology · Historical data · Mount Saint Helens · Mount Lassen

Introduction

While it seems obvious that ecosystems will be devastated after a volcanic eruption coats the landscape with a layer of ash, the ecological recovery of mammalian communities after eruptions is poorly understood. To date, the response of mammalian communities to eruptions has only been studied in one study system, a problematic situation which limits the effectiveness of land management policies in disturbed areas. Modern ecosystems disrupted by recent volcanism (since 1914), e.g. the 1980 Mount St. Helens (MSH) eruption in southern Washington, have been studied on short timescales with a primary focus on plant, fish, bird, and limited mammal communities (Bisson et al. 1988; Crisafulli et al. 2015; del Moral and Wood 1988; Franklin et al. 2000). Mammalian ecosystem recovery from volcanic eruptions has only been investigated in two study systems, one modern and one fossil [MSH and the 77–69 ka Toba super-eruption, Indonesia (Louys 2007)]. Modern mammalian studies have only focused on the impacts of MSH; however, volcanic perturbations are highly variable in their effects on ecosystems, necessitating investigation of additional eruptions to elucidate a more complete picture of ecological processes in volcanic reassembly in diverse ecosystems (Crisafulli et al. 2015). What research has been done using the fossil record is plagued by poor sampling and preservation before and after the eruption, leaving little chance to detect changes in faunal composition. To understand how volcanic events impact mammalian ecosystems, the modern records of continental eruptions in North America can be used to create predictions of how mammalian communities can reassemble after eruptions which can then be applied to other study systems. The information gleaned from this analysis can be used to

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understand whether and, if so, how volcanic events impact local mammalian communities.

The impacts of volcanism on ecosystems are either minor and short term or profound and enduring in tested study systems [e.g. birds, fish, and plants; Crisafulli et al. (2015)]. These biota are rarely annihilated after eruptions and either most taxa survive in a devastated area or endemic taxa survive in small refuge populations (Crisafulli et al. 2015). The tempo and mode of reassembly is often driven by the presence of the surviving population, characteristics of the new deposits, climate, and biotic interactions (Crisafulli et al. 2015). Of course, these predictions are primarily informed by volcanic events which occurred after the 1980 eruption of MSH and can only give predictions of recovery after, at most, 37 years.

MSH produced geologic results that mimic aridity with no long-term climate change, called ‘mock aridity’ by Harris and Van Couvering (1995), and altered the local soil chemistry through pyroclastic flows, mudflows, and avalanches (Dale et al. 2005). The non-mammalian fauna appears to be robust to these environmental changes (Bisson et al. 1988; del Moral and Wood 1988; Franklin et al. 2000). Many small bodied mammals survived the eruption, likely because many of them were fossorial and were protected by seeking shelter in burrows while all large bodied mammals were eradicated from a 600 km^2 area (Crisafulli et al. 2015). Small mammals were the first mammalian colonists to reclaim the devastated area after the eruption (Crisafulli et al. 2015; Dale et al. 2005). In the fossil record associated with Toba, long-term effects on mammal communities (102–103 years) were not observed after the eruption, an event which deposited large quantities of ash over the region (“Global Volcanism Program” 2013; Louys 2007; Williams 2012). As a result of poor sampling after the Toba eruption, we still do not know whether the ecosystem of the devastated area returned to a pre-eruption composition on larger timescales (e.g. 100 years). The 1914–1917 Mount Lassen eruption differs from these other eruptions by impacting the ecosystem exclusively through mudflows, though only impacts on plant communities have been studied there (Dale et al. 2005).

Study systems for volcano ecology will need to have a rich record of field-collected specimens before and after an eruption if long-term effects are to be investigated, as it is difficult to predict where and when eruptions will occur, or the magnitude of eruptions with enough time to properly sample an ecosystem before an eruption occurs. Museums hold a wealth of important data through vouchered specimens that tended to be difficult to get at before the digital mobilization of “dark data” began (Constable et al. 2010; Guralnick and Constable 2010; Marshall et al. 2018). The historic record preserved within museum data provides the best solution to open up more historic volcanic eruptions for ecological study. The historic record around the 1980 eruption of MSH in southern Washington and the 1914–1917 eruption of Mount Lassen in northern California are both rich in field-collected specimens. MSH offers a glimpse at short-term recovery, while Mount Lassen’s record can elucidate recovery on the century scale. Additionally, the ways in which museum mammalogy collections are treated in statistical analysis are similar to how museum paleontological collections are treated, allowing for more comparable results when additional biases are considered.

Eruptive history and climatic differences

It is important to understand the differences in the eruptive history of the volcanic systems if proper predictions are to be drawn regarding mammalian community recovery. The 1980 eruption of MSH and the 1914–1917 eruption of Mount Lassen are different in character, and these differences may impact the communities around them differently. Of the seven selected eruptions from the past two million years, these two eruptions are relatively small. From smallest to largest with volume ranges, these eruptions are: 1914–1917 eruption of Mount Lassen (0.001–0.01 km^3), 1980 eruption of MSH (0.1–1 km^3), 1991 eruption of Pinatubo (1–10 km^3), 1.3 Ma eruption of Yellowstone Mesa Falls (100–1000 km^3), 2.1 Ma eruption of Yellowstone Huckleberry Ridge (> 1000 km^3), and 74 ka eruption of Toba (> 1000 km^3) (“Global Volcanism Program” 2013).

Mount Saint Helens

MSH has erupted 44 times in the Holocene, with this first eruption beginning in 2340 BCE, of which only 13 have historical observations going back to 1831 (“Global Volcanism Program” 2013). The May 1980 eruption of MSH was by far the largest of those historically observed eruptions and one of the largest ever recorded at the site (“Global Volcanism Program” 2013). This eruption was characterized by steam blasts, landslides, ashfall, pyroclastic flows, and lahars (Christiansen and Peterson 1981). About 600 km^2 of the devastated area was blanketed by hot debris from this dacitic eruption (Christiansen and Peterson 1981). A great deal of water was incorporated into the landslides from the Toutle River, Spirit Lake, and the melting glaciers on the flanks of the volcano to produce large mudslides eventually deposited into the Cowlitz River (Christiansen and Peterson 1981). The additional water likely caused the landslides and mudflows to be larger than expected. The initial part of the eruption, which consisted of landslides, initial blast, and mudflows, caused the most loss of life. The subsequent Plinian eruption column (with a column of gas and ash) spread about 200 km from the volcano and produced lightning which started several fires over this wide area (Christiansen and Peterson 1981). The eruption continued to produce toxic gas and ash for 2 weeks following the eruption (Christiansen and Peterson 1981). This eruption did impact Mount Adams being within the area of impact, but did not impact nearby Mount Rainier, allowing it to serve as a control for regional faunal changes.

Mount Lassen

Mount Lassen has erupted six times in the Holocene with the first eruption in the year 800 and the two largest, equally sized events beginning in 1666 and 1914 ("Global Volcanism Program" 2013). These two eruptions also happen to be the last two confirmed at the site. The last eruption of Mount Lassen occurred between May 1914 and May 1917, with the strongest event occurring on May 22, 1915 (Clynne et al. 2012). The eruption covered 0.107 km^2 and produced 0.007 km^3 of proximal volcanic material with lahars and pyroclastic flows covering an additional 8 km^2 (Clynne et al. 2012). The eruption was andesitic to dacitic in composition and included intermittent steam expositions prior to the May 1915 eruption (Clynne et al. 2012). It is important to note here that the 1914–1915 winter included unusually high snowfall which likely added to the volume of lahars (Clynne et al. 2012). This eruption did not impact nearby Mount Shasta allowing it to serve as a control for regional faunal changes.

Collecting history

Field notes and field reports are the key to validating collection methods and identifying biases for the historical collections used in this study. Museum data are available at Mount Lassen from 1915 to 2011 (Fig. 1). The Lassen Transect was originally surveyed by Joseph Grinnell and Museum of Vertebrate Zoology (MVZ) crews between 1911 and 1934 and was resurveyed between 2003 and 2010 by the MVZ (Grinnell et al. 1930; Rowe et al. 2015). Mount Lassen was included in the Lassen Transect which was a 3000 square mile swath of northern California between the Sacramento River and the Nevada border. Both of these surveys were aimed at discovering the general fauna in the area, but the resurvey did differ from the original survey by using pitfall traps, no guns, and not trapping in rough terrain where pika tend to live (Rowe et al. 2015). The resurvey also relied on student crews from mammalogy classes to trap mammals, unlike the original survey which relied on professional

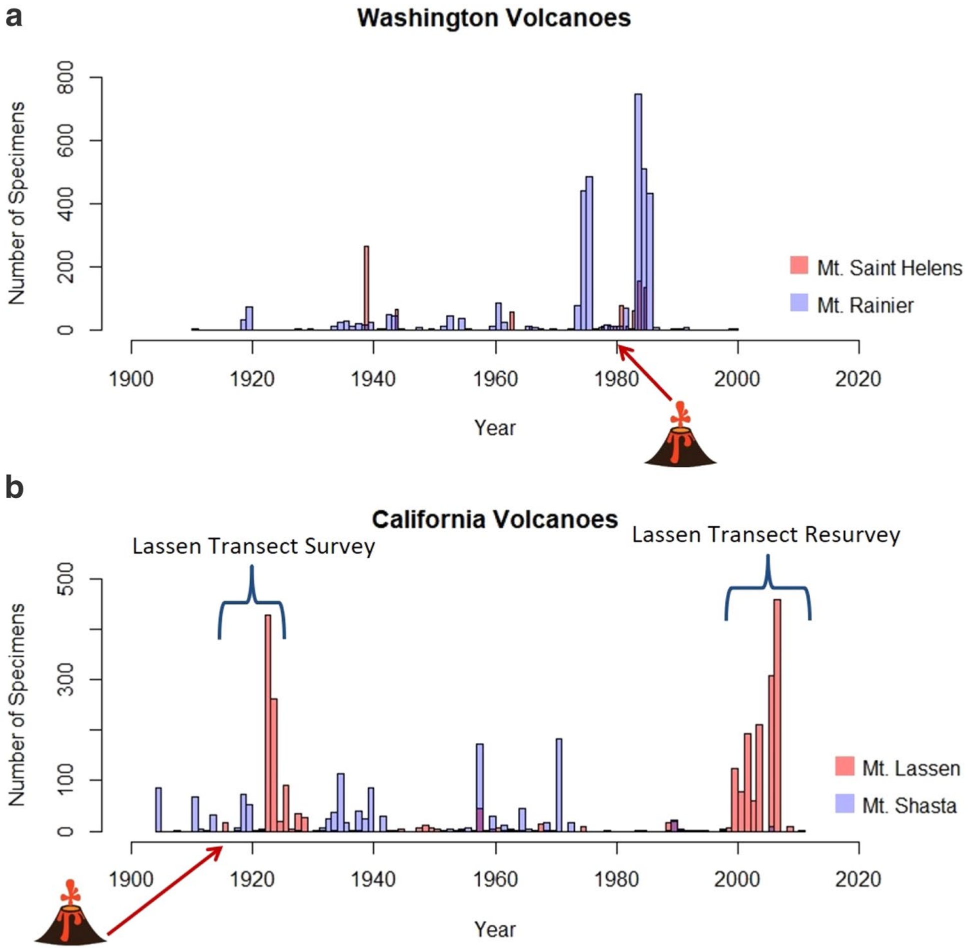

Fig. 1 Distribution of mammalian occurrence data. **a** Distribution around Mount Saint Helens and Mount Rainier. **b** Distribution around Mount Lassen and Mount Shasta. Red indicates the study system and blue indicates the control system. Volcano symbol represents the eruptive event

trappers. The field notes also indicated that the intervening years between the two surveys saw several taxon-specific expeditions to collect bats, gophers, chipmunks, or other small mammals (e.g. Sutton and Patterson 2000). At Mount Shasta, the collecting intensity was much more consistent over the past 100 years, so we do not see the same peaks in collecting like we see with Mount Lassen. The collecting around Mount Shasta (1893–2006; Fig. 1), like Mount Lassen, involved several mammalogy classes collecting around the mountain. Collections around Mount Lassen and Mount Shasta also included several roadkill and hunted specimens from throughout the collecting history. These isolated collections represent a random sample of taxa from the ecosystem and were not collected with standard methods like the transect samples.

Collecting around MSH (1929–1999; Fig. 1) was not nearly as systematic as the collections around Mount Lassen. Several of the specimens were collected by mammalogy classes both before and after the eruption. By far, the most prolific collector was the University of Washington College of Forest Resources, which was conducting small mammal biodiversity surveys in the area. Mount Rainier has museum data available from 1910 to 2000 (Fig. 1). The US Forest Service and US National Park Service also conducted several collecting expeditions in the area around both Mount Rainier and MSH. These collections were intended to be surveys. The common general small mammal surveys at both Mount Rainier and MSH utilized guns, live traps, and snap traps, while little to no specimens were collected from pitfall traps. As expected, there were also various salvaged roadkill specimens and hunter-donated specimens. Some specimens were even confiscated poached specimens. There were some taxon-specific collections such as charred specimens collected after the eruption as part of a deer survey to evaluate the effects of the MSH eruption (Lyman 1989). These taxon-specific collections were not common at either MSH or Mount Rainier.

Although fish, bird, and plant community recovery has been extensively studied as well as cursory observations about small mammal recovery after modern eruptions, no one has studied mammalian community recovery from volcanic eruptions holistically or with quantitative methods. I attempt to address this gap in knowledge by investigating ecological diversity metrics in multiple study systems. MSH can tell us about short-term recovery (less than 10 years) at high temporal resolution (annual estimates of mammal diversity are available) for an eruption of its magnitude (0.1–1 km^3) while Mount Lassen can tell us about longer-term recovery from an eruption of its magnitude (0.001–0.01 km^3). Since little is known about the length of time necessary for a mammalian community to ecologically recover and stabilize, the degree to which peripheral source populations play in mammalian recovery, and the degree to which eruption size plays in ecological recovery, it is necessary to explore the data using exploratory ecological methods.

Material and methods

I must establish how modern mammal communities have reassembled after well-documented eruptions. I focused on the large historical collection of mammals associated with the 1980 MSH eruption and the 1914–15 Mount Lassen eruption. To account for regional climate changes that may be responsible for any changes in the fauna, I used the coeval communities from two ecologically-analogous volcanoes as control systems: Mount Rainier (last erupted 1894; $n=3413$ specimens) in west-central Washington and Mount Shasta (last erupted 1786; $n=1180$ specimens) in northern California. Control systems are necessary to evaluate the role of climate in post-volcanic reassembly. Both control ecosystems had time to recover from their previous eruptions at the time of the MSH and Mount Lassen eruptions. The sample associated with MSH ($n=636$ specimens) was collected between 1929 and 1999, allowing an investigation of the pre- and post-eruption faunal relationship (Fig. 1). The sample associated with Mount Lassen ($n=2520$ specimens) records a relatively continuous 96-year record (1915–2011) of the mammal community, providing insight into longer-term impacts (Fig. 1). I used occurrence data from within a 30 km radius of the peak of each of these volcanoes, because this is approximately the area that was devastated by the eruption of MSH. I kept this area consistent among all study sites to control for potential species area effect where larger areas would be expected to have more species represented (Barnosky et al. 2005; Godron 1971; Rosenzweig 1995). Mammal occurrence data associated with these volcanoes were downloaded from the VertNet portal (https://vertnet.org/) on April 27, 2015 and represent 18 museum collections (Supplemental Data 1); institutional abbreviations are in Supplemental Data 2. Human observations were excluded from this study, leaving only vouchered museum specimens.

Data were subdivided into bins based on the timing of volcanic eruptions and the distribution of those data. MSH and Mount Lassen were binned independently. Test systems and their controls were subdivided in the same way.

I read over field notes related to the specimens downloaded from VertNet to account for any collection bias (e.g. a field expedition collecting only ground squirrels yielding a disproportionately large sample relative to the actual population in the system). Historic notes and field catalogues have important information regarding the collecting techniques that can help determine if there were collecting biases. This information helps inform interpretations of the data and may help to explain aberrant results from data analysis if collecting biases are present. In most cases, periodic small collections from donation, salvage, or taxon-specific collecting were interspersed with many small mammal surveys. It is worth noting that in the intervening period between the original MVZ Lassen survey and the MVZ Lassen resurvey, there is a majority of taxon-specific survives which warrants the separation of this period of time into a separate time bin. That said, all bins (except the before mentioned intervening period at Mount Lassen) have very similar collecting histories and that supports that these bins have similar biases and are directly comparable.

To determine whether the number and abundance of species change after eruptions, I calculated the ecological metrics of richness (number of species) and evenness (the percentage of the community belonging to each species). Richness is measured with Chao richness which uses sample size to estimate the number of species that should be represented if the entire population was gathered (Chao et al. 2009) as opposed to raw richness which is simply the number of species observed in a sample. Chao richness will be greater than the raw richness and also calculates standard error. This type of metric helps to produce a standardized result despite variable or uneven sample sizes and helps account for collecting biases. Evenness is measured using the Hurlburt Index, or unbiased Simpson Index, which measures how unequal the abundances of species in a community are while incorporating rarefaction subsampling (Hurlbert 1971) as well as the classic Shannon Diversity Index which uses both richness and abundance based on the natural log (Poole 1974). Pielou's Evenness Index is derived from the Shannon Index to remove the effects of species richness (Pielou 1966). Multiple evenness indices were calculated as each method sheds light onto different aspects of this ecological character (Smith and Wilson 1996). In all indices, larger numbers indicate greater evenness or diversity, while lower numbers indicate lower evenness or diversity. Another way to account for the uneven samples compare richness based on effective number of species (Hill numbers) using coverage-base rarefaction/extrapolation following Chao et al. (2014).

To describe the similarity of the pre- and post-eruption communities, I used a chord distance analysis which is a measure of the number of species shared between populations (Calede et al. 2011; Faith et al. 1987). Larger values indicate greater dissimilarity between the two sites. Nonmetric multidimensional scaling (NMDS), which uses rank orders to collapse information from multiple dimensions or axes (representing species) into two dimensional space to allow for visualization, was also computed on abundance data to visualize the distance between the different communities (Kruskal 1964). All data will be analysed together in both the chord distance analysis and the NMDS to avoid statistical fishing and to directly examine patterns. All statistical methods were performed using the vegan package version 2.3-5 (Oksanen et al. 2016), except for the Hill numbers calculated using coverage-base rarefaction/extrapolation which was performed using the iNEXT package version 2.0.20 (Hsieh et al. 2016). Both were implemented in R version 3.2.3 (R Core Team 2015) and can be found in Supplemental Data 3.

Results

The pre- and post-eruption communities at MSH [high temporal resolution and short-term recovery and larger magnitude (0.1–1 km^3)] were extremely disparate according to the chord distance analysis (cd = 1.24). The richness was lower after the eruption and there were more unequally distributed abundances of species (Table 1). The Hills numbers with coverage-base rarefaction/extrapolation show that the pre- and post-eruption communities at both MSH and Mount Rainier are distinctly different from one another (Fig. 2). When the 5 years after the MSH are investigated each year at a time, we see that richness is low for the first 3 years and after 5 years returns to a level comparable to the pre-eruption level (Table 2, Fig. 3). When I calculate Hill numbers (diversity) using coverage-base rarefaction/extrapolation for the 5 years after the MSH eruption and compare it to that of Mount Rainier, I find that the result of the Chao richness holds true for MSH, but Rainier is not statistically different through that time period (Fig. 4).

Over the 100 years after the eruption of Mount Lassen [long-term recovery and smaller magnitude (0.001–0.01 km^3)], the community is relatively stable (Fig. 5, Tables 3,

Table 1 Ecological statistics for Washington

	n	Raw richness	Chao richness	Chao *SE*	Shannon Index	Hurlburt Index	Pielou's evenness
Saint Helens pre-eruption	167	28	37.33	8.84	2.95	0.94	0.88
Saint Helens post-eruption	450	25	26.00	1.58	2.16	0.82	0.67
Rainier pre-eruption	1597	76	84.75	6.04	2.98	0.90	0.69
Rainier post-eruption	1816	47	53.43	5.46	2.47	0.87	0.64

n sample size (number of museum specimens), *SE* standard error

Fig. 2 Plots of Hills numbers with coverage-base rarefaction/extrapolation for time bins. **a** Richness in Washington volcanoes. **b** Richness in California volcanoes. The shaded area around each line is the 95% confidence interval

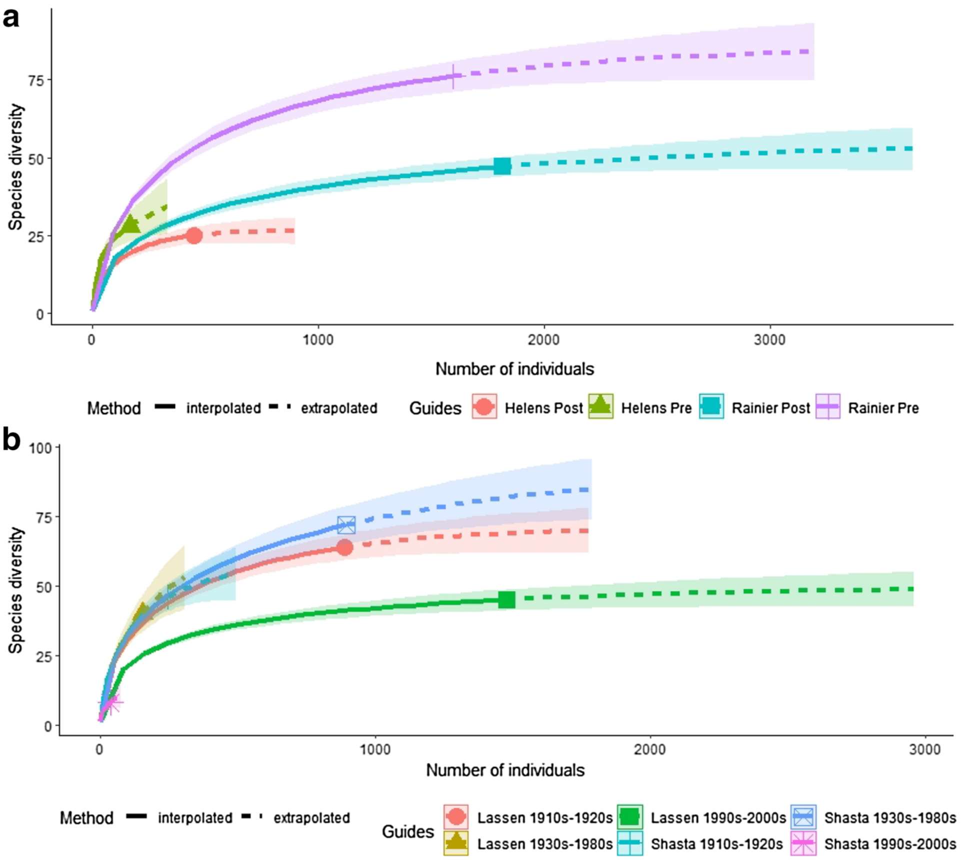

Table 2 Yearly ecological statistics for post-eruption Washington

Year	System	*n*	Raw richness	Chao richness	Chao *SE*	Shannon Index	Hurlburt Index	Pielou's evenness
1980	Helens	33	11	14.30	4.10	0.56	0.50	0.81
1981	Helens	33	11	13.50	3.14	0.30	0.16	0.43
1982	Helens	32	10	17.50	8.09	0.29	0.17	0.41
1983	Helens	32	12	26.00	13.13	1.92	0.82	0.8
1984	Helens	32	10	20.00	10.17	1.64	0.66	0.58
1985	Helens	32	11	32.00	17.26	1.95	0.81	0.72
1999	Helens	32	12	17.50	5.35	1.05	0.80	0.96
1980	Rainier	12	9	37.00	21.22	2.02	0.91	0.92
1981	Rainier	12	9	12.75	4.18	2.14	0.95	0.97
1982	Rainier	69	9	10.00	1.80	1.38	0.62	0.63
1983	Rainier	6	5	8.00	4.09	1.56	0.93	0.97
1984	Rainier	747	23	23.14	0.49	1.92	0.78	0.61
1985	Rainier	509	20	20.25	0.73	2.44	0.90	0.815
1999	Rainier	NA	NA	NA	NA	NA	NA	NA

Specimens were collected after the May 18, 1980 eruption

SE standard error, *n* sample size (number of museum specimens), *NA* data not available

4). Richness and evenness do decrease at Mount Lassen and Mount Shasta to a similar degree. The Hills numbers with coverage-base rarefaction/extrapolation show that the community from the 1910s to 1920s at both Mount Lassen and Mount Shasta are distinctly different from community from the 1990s to 2000s (Fig. 2). Chord distance analysis suggests no long-term change in the Lassen fauna (Fig. 5). It is clear that the Mount Lassen 1930–1980 time bin is quite

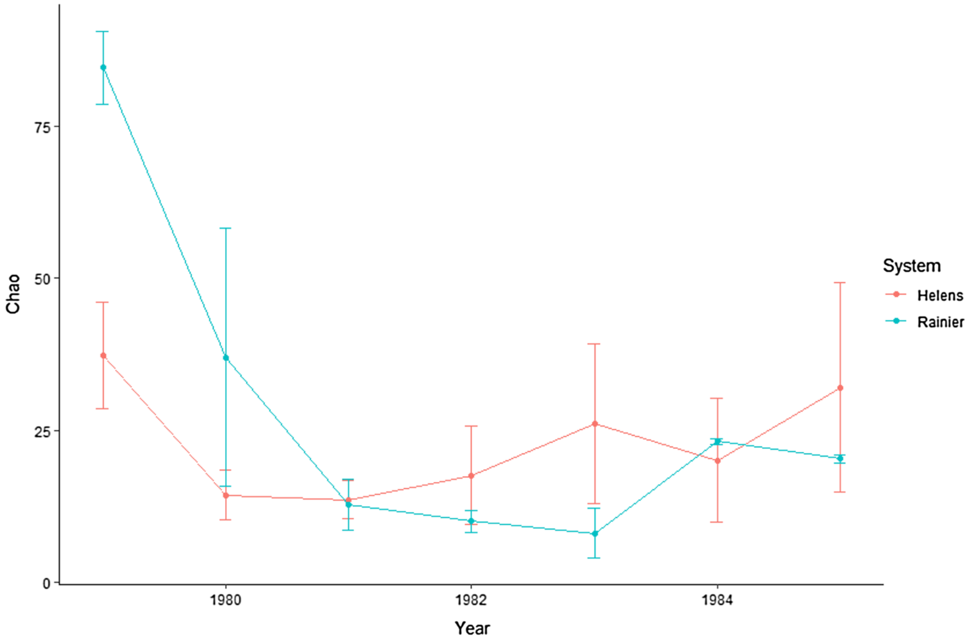

Fig. 3 Plot of calculated Chao richness for 5 years after the 1980 Mount Saint Helens eruption. The plot shows the relationship between the control system (Mount Rainier) compared to Mount Saint Helens. The datum prior to 1980 is the pre-eruption bin. Error bars are standard errors calculated from the Chao richness. In general, there is an increase in the number of species present after the eruption for 3–5 years at Mount Saint Helens

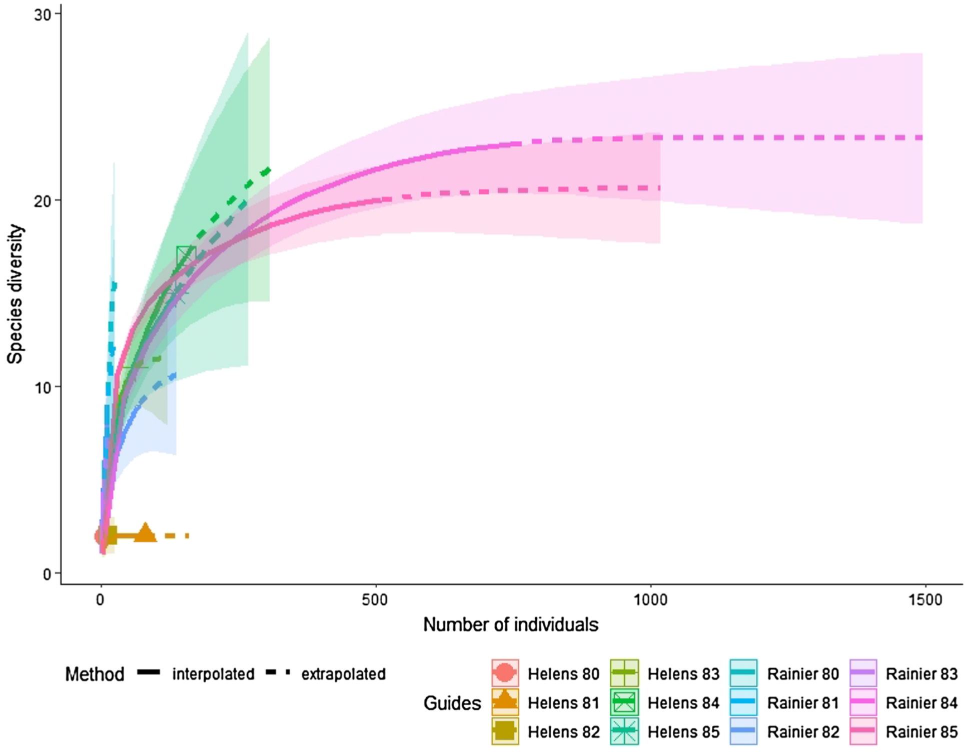

Fig. 4 Plots of Hills numbers with coverage-base rarefaction/extrapolation for the 5-year period after the eruption of Mount Saint Helens. Plot includes both Mount Saint Helens and Mount Rainier

disparate from the other time bins (Fig. 3, Table 4) but this is likely from collection bias determined from field notes. There are fewer species and more unevenness, but the community immediately after the eruption and 100 years later is not nearly as different as the pre- and post-MSH-eruption communities.

Discussion

The diversity metrics calculated from historical occurrence data show unique patterns between the two study areas, suggesting that the magnitude of eruption matters to mammalian community recovery. The data also suggest

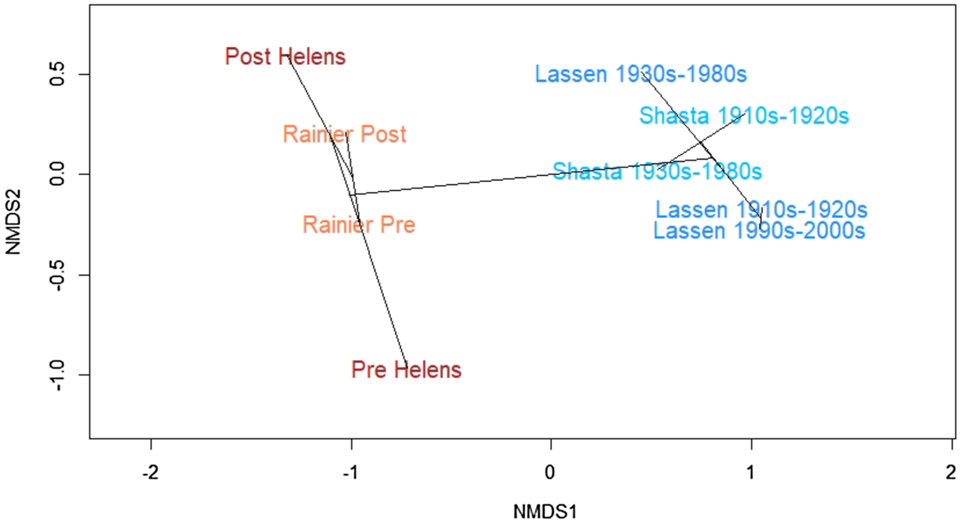

Fig. 5 NMDS of all volcanoes and bins based on abundance data. The length of the lines represents the degree of similarity. The longer the line connecting the points, the more different are the bins. The obvious major difference is between California and Washington sites. All of the California bins are very similar to each other than Lassen 1930–1980, which was biased by several taxon-specific field collections. The pre-Saint Helens bin is very different from the other Washington bins, indicating that the pre- and post-eruption faunas at Saint Helens are different from one another. The post-eruption fauna at St. Helens is more similar to the fauna at Rainer. Stress = 0.00009573504 and R^2 (level of dissimilarity as a percent) = 1

Table 3 Ecological statistics for California

	n	Raw richness	Chao richness	Chao *SE*	Shannon Index	Hurlburt Index	Pielou's evenness
Lassen 1910–1920s	888	64	70.00	4.54	3.31	0.95	0.80
Lassen 1930–1980s	154	40	61.90	13.88	3.20	0.95	0.87
Lassen 1990–2000s	1478	45	48.50	3.66	2.63	0.87	0.69
Shasta 1910–1920s	248	46	56.10	7.19	3.22	0.94	0.84
Shasta 1930–1980s	894	72	89.50	10.11	3.40	0.95	0.79
Shasta 1990–2000s	38	8	14.00	7.10	1.72	0.82	0.82

n sample size (number of museum specimens), and *SE* standard error

some flow of populations from source populations into regions impacted by eruptions.

The NMDS shows that there is a strong regional effect separating the Washington and California study areas, as expected (Fig. 5). The two regions are separated by approximately 500 km in the N–S direction. The two study areas would not be expected to have the same fauna because they represent different environments.

With regard to Mount Lassen [long-term recovery and smaller magnitude (0.001–0.01 km^3)], there appears to be no noticeable change in the mammalian fauna on the longer-term timescale when looking at the NMDS (Fig. 5) caused by the eruption. Although the ecological statistics (Table 3, Fig. 2) show a decline, the same decline can be seen in the control system, suggesting that this is a climate or regional signal rather than one driven by the community recovery post-eruption. Additionally, the Mount Lassen 1930–1980 time bin does appear to be aberrant from the other two bins in the NMDS (Fig. 5). A small sample size given the large temporal component to this bin and its disparity are likely the result of differing collecting methods from other time bins (Fig. 1). From reviewing field notes at the MVZ, it is clear that a majority of the collecting trips that were done in the Mount Lassen 1930–1980 time bin were for specific taxa (e.g. bats or gophers) and not for general faunal diversity studies. However, Chao richness of this bin is within the error of the other two bins, suggesting that the sample size standardization has accounted for this collecting bias.

Overall, the fauna at Mount Lassen is not very different from the fauna seen at Mount Shasta (Fig. 5), suggesting that the smaller Mount Lassen eruption had a minor impact on the local fauna and the devastated areas were able to

Table 4 Chord distance for all volcanoes and bins

	Post-Helens	Lassen 1910s–1920s	Lassen 1930s–1980s	Lassen 1990s–2000s	Rainier pre	Rainier post	Shasta 1910s–1920s	Shasta 1930s–1980s	Shasta 1990s–2000s
Pre-Helens	1.24	1.41	1.40	1.41	1.03	1.15	1.41	1.39	1.39
Post-Helens	–	1.41	1.41	1.41	0.83	0.78	1.41	1.41	1.41
Lassen 1910s–1920s	–	–	1.15	0.90	1.41	1.41	0.83	0.94	1.23
Lassen 1930s–1980s	–	–	–	1.22	1.39	1.40	1.23	1.20	1.39
Lassen 1990s–2000s	–	–	–	–	1.41	1.41	0.86	1.12	1.37
Rainier pre	–	–	–	–	–	0.58	1.41	1.38	1.39
Rainier post	–	–	–	–	–	–	1.41	1.39	1.38
Shasta 1910s–1920s	–	–	–	–	–	–	–	0.98	1.28
Shasta 1930s–1980s	–	–	–	–	–	–	–	–	1.25

repopulate quickly with local taxa. Mount Lassen only produced mudflows and disturbed a relatively small area (Dale et al. 2005). Mount Lassen does not have pre-eruption data, making it impossible to truly gauge the full impact of the eruption on the existing fauna; however, the historical record at Mount Lassen does allow for an in-depth examination of the long-term assembly of the recovery fauna. The assembly of the recovery fauna cannot be seen with the resolution of the time bins used in the study, but it likely occurred between the end of the eruption (1916) and the end of the first time bin (1929).

The pattern seen at MSH suggests that the fauna around the volcano prior to the eruption was different from the fauna after the eruption, and we can therefore reject the null hypothesis of no change post-eruption. This is in contrast with the plant community which appears to have been similar pre- and post-eruption (del Moral and Wood 1988). The richness does appear to decease at both the MSH and Mount Rainier (Fig. 2), suggesting that climate still plays a role in recovery. The NMDS (Fig. 5) suggests that the fauna at MSH after the eruption was more similar to the fauna seen at Mount Rainer both before and after the eruption (Fig. 5, Table 1). Field collections from the pre-eruptive fauna appear to have been collected through standard biodiversity field trips. The eruption of MSH was much more powerful than that of Mount Lassen, covering a larger area with pyroclastic flows, mudflows, and avalanches (Dale et al. 2005).

The yearly data after the MSH eruption [high temporal resolution and short-term recovery and larger magnitude (0.1–1 km^3)] shows that the first 5 years after the eruption are very disparate, but eventually stabilize. The Chao richness steeply drops after the eruption, but has returned to a level similar to the pre-eruption landscape by 1985 (Table 2, Fig. 3). Although the Chao richness at Rainier appears to drop more steeply than MSH, the Hills numbers show that this is not the case (Fig. 4), ruling out the signal at MSH only being a climate signal. However, the fauna is more uneven than the pre-fauna until 1983 (Table 2). As with richness, we see a fast recovery in evenness within about 5 years post-eruption. The lack of museum data in the 2000s prohibits the investigation of long-term recovery post-eruption, but the data can give insight into the short-term faunal recovery, an area that could not be studied with the Mount Lassen eruption.

It would be worth continuing field work in any area that has been volcanically disturbed or to begin in areas with the potential to be disturbed. Field collections present direct and reproducible evidence of ecological change, especially with modern field note methods. A good sample both before and after the eruption is imperative to understanding mammalian ecological response to volcanism.

The differences in size of the devastated areas and general eruptive behaviour between these two eruptions may also explain the mammalian community responses. The relatively quick recovery and stabilization time after the Mount Lassen eruption may result from simply less perturbation and destruction of habitat. It would have presumably been easier for taxa in surrounding areas to return to the devastated areas. It is also likely that local fauna would have survived the eruption at similar sites nearby and could quickly recover the population. MSH' larger devastated area would have made it more difficult for recovery taxa to be introduced and likely would have seen the extirpation of some local fauna, potentially explaining the similarity between the Mount Rainier and MSH recovery faunas.

It is important to note here that the museum collections used in this study do not represent the complete fauna of either area, but rather can be characterized as a faunal assemblage similar to the fossil record. This similarity makes it possible to apply the predictions of the modern record to the fossil record and gain access to an entirely new set of volcanic study systems. The fossil record has the added benefit of including larger scale eruptions than the modern record, thus elucidating a more complete picture of mammalian community response to volcanism.

It is also worth noting that the frequency and volume of volcanic eruptions at these two sites are vastly different ("Global Volcanism Program" 2013). As Mount Lassen has had far fewer and smaller eruptions through its history, it would be less likely that the mammalian community here would be robust to changes from evolving alongside these eruptions It would be more likely that neighbouring point populations of the same species repopulated the devastated areas. Conversely, MSH has erupted much more frequently during the Holocene and the volume has been far greater. Of the 44 Holocene eruptions, 8 were similar in volume or larger than the 1980 eruption. It is more likely that the mammalian community at MSH would be more robust to eruptions than the community at Mount Lassen, as it would have evolved with far more and greater-sized eruptions. It would appear that the frequency of eruptions at the two sites did not have as great of an impact as expected. These two eruptions are only a small sample of the volumes and types of eruptions that have occurred through Earth history and it would be interesting to look at more examples of the larger eruptions (e.g. "super-volcanos") from the fossil record.

The data in the Mount Lassen dataset suggest that robust communities fully recover after the eruption. The data in the MSH dataset suggest destabilization through the elimination of local communities and recolonization of non-native species from other regions, namely Mount Rainier. These data also show that there was a decrease in the total number of species for the 5 years post-eruption which could be explained by increased aridity, rather than 'mock aridity' (Harris and Van Couvering 1995), or a reduction in available resources, among other hypotheses. The support of different methods of community restructuring in each study system is likely the result of the eruptive behaviour and size of the two systems. Again, every volcanic eruption has different characteristics, making it necessary to investigate as many as possible. MSH had a larger eruption than Mount Lassen, suggesting that scale may play an important role in the mammalian ecological recovery in volcanically disturbed area.

The data presented here are exploratory, but hypothesis testing could be performed. A permutational multivariate analysis of variance (PerMANOVA) can be used to calculate statistical differences in community composition (Anderson 2001). Additional hypotheses can be derived from the work presented here that can be tested with a PerMANOVA given additional variables that were not available for this study.

Though it may seem obvious that larger eruptions will have a greater impact on the mammalian community, a 5- to 10-year period of recovery can now be established for a MSH sized eruption. Larger volcanoes may cause longer recovery times, but additional field collections in these study systems will be needed to shed light on the relationship. It is also evident that volcanic eruptions create a more arid environment from the pre-eruptive one given sufficient scale through eliminating local populations and thus permitted recolonization by neighbouring communities.

In the end, all of the bins in the study, with the exception of Mount Lassen 1930–1980, have very similar collecting histories. They were dominated by small mammal surveys with periodic small collections from donation, salvage, or taxon-specific collecting. The similar collecting histories mean that these bins have similar biases and are directly comparable.

Conclusions

The mammalian communities at Mount Lassen and MSH provide an excellent opportunity to examine the impacts of different magnitudes of eruptions on differing timescales. Mammal communities at MSH are very disparate 1–5 years after the eruption compared to the pre-eruption fauna, but eventually stabilize. The fauna in the volcanically devastated regions may never fully return to the pre-eruption community, but after 5–10 years the community appears to stabilize. The mammal community at Mount Lassen persisted on the longer scale after the initial stabilization. The eruption of MSH appears to have fundamentally changed the surrounding ecosystem, resulting in a different fauna that may have been introduced from refugia like Mount Rainier. The smaller scale of the Mount Lassen eruption clearly had little to no long-term effect compared to the larger MSH eruption on the mammalian communities. Climate also plays a role. It is clear that the larger the eruption, the longer it takes for mammalian communities to recover. Not only are the eruptions larger, but they open the door for arid adapted taxa and refuge taxa from nearby regions to recolonize the devastated area. Land managers might encourage arid adapted colonizing species to help stabilize the devastated area after an eruption if it is similar in size to MSH. However, if the eruption is more similar in size to Mount Lassen, less management may be necessary.

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