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Genetic structure among coastal tailed frog populations at Mount St. Helens is moderated by post-disturbance management

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Abstract. Catastrophic disturbances often provide "natural laboratories" that allow for greater understanding of ecological processes and response of natural populations. The 1980 eruption of the Mount St. Helens volcano in Washington, USA, provided a unique opportunity to test biotic effects of a large-scale stochastic disturbance, as well as the influence of post-disturbance management. Despite severe alteration of nearly 600 km^2 of habitat, coastal tailed frogs (*Ascaphus truei*) were found within a portion of the blast area five years after eruption. We investigated the genetic source of recolonization within the blast area and tested whether post-eruption salvage logging and subsequent tree planting influenced tailed frog movement patterns. Our results support widespread recolonization across the blast area from multiple sources, as all sites are grouped into one genetic cluster. Landscape genetic models suggest that gene flow through the unmanaged portion of the blast area is influenced only by distance between sites and the frost-free period ($r^2 = 0.74$). In contrast, gene flow pathways within the blast area where salvage logging and replanting occurred post-eruption are strongly limited ($r^2 = 0.83$) by the physiologically important variables of heat load and precipitation. These data suggest that the lack of understory and coarse wood (downed and standing dead tree boles) refugia in salvaged areas may leave frogs more susceptible to desiccation and mortality than those frogs moving through the naturally regenerated area. Simulated populations based on the landscape genetic models show an increase in the inbreeding coefficient in the managed area relative to the unmanaged blast area. In sum, we show surprising resilience of an amphibian species to a catastrophic disturbance, and we suggest that, at least for this species, naturally regenerating habitat may better maintain long-term genetic diversity of populations than actively managed habitat.

Key words: amphibians; Ascaphus truei; *coastal tailed frog; disturbance; inbreeding; landscape genetics; Mount St. Helens, Washington, USA; natural regeneration vs. management; recolonization; salvage logging.*

INTRODUCTION

Large, infrequent disturbances, such as fires, floods, hurricanes, and volcanic eruptions, have a strong impact on affected biotic communities, but have received less attention than smaller, more frequent disturbances (Turner and Dale 1998). However, large disturbances merit current research attention because they provide "natural laboratories" in which to test theories of ecological response and succession. Such disturbances often lead to "ecological surprises," or long-term changes in community state, when combined with other disturbances (Paine et al. 1998, Franklin and MacMahon 2000, Turner et al. 2003). Broadscale disturbances can create a heterogeneous landscape composed of several disturbance types, some of which may be applicable to understanding the effects of more common disturbances at smaller spatial scales (Foster et al. 1998, Romme et al. 1998).

The 1980 eruption of Mount St. Helens, Washington, USA provided a unique opportunity to test biotic responses to rapid environmental change, and it has consequently contributed a great deal toward ecological theory, such as a better understanding of patterns of succession (Franklin and MacMahon 2000, Dale et al. 2005*a*). In the aftermath of the eruption, there was a complex disturbance gradient classified into the following broadly defined zones: (1) the debris avalanche/pyroclastic flow (DAPF) zone, within a 75-km^2 area north and west of the volcano, where new landforms were created and there was little to no organismal survival; (2) blowdown/scorch (BDSC) zone, a 480-km^2 area where trees were killed but remained as biological legacies and the understory was buried beneath a deposit of blast material and tephra; (3) live standing forest within a zone of tephra-fall deposits (thousands of km^2); and (4) undisturbed forest (Swanson and Major 2005).

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The BDSC zone has been subject to two different management treatments since the eruption. One portion of this area was designated as Mount St. Helens National Volcanic Monument and was left to develop via natural processes. As a result, the monument retains all biological legacies (e.g., downed logs, snags, and surviving vegetation) remaining after the eruption. The remainder of the BDSC zone was designated for active management, where dead trees were salvaged for commercial use and young trees were replanted to create conifer plantations (Dale et al. 2005*b*). As such, the managed area had a significant canopy overstory (density of 19 trees/200 m^2), but little coarse woody debris, understory, and litter depth at the time of our study (Titus and Householder 2007). The presence of these two post-disturbance management strategies provides a rare opportunity to test population responses in an actively managed vs. a naturally recovering landscape.

We studied the population genetic response of coastal tailed frogs (*Ascaphus truei*) across the range of disturbed habitats in the vicinity of Mount St. Helens to test the biotic response of a potentially highly sensitive indicator of environmental degradation. Amphibians are in a global decline, and they are highly susceptible to habitat alteration (Collins and Storfer 2003, Stuart et al. 2004). Tailed frogs are a niche-limited amphibian species in the Pacific Northwest; they breed in forest streams and inhabit forested areas, and have among the lowest desiccation and thermal tolerances documented for amphibians (Claussen 1973, Brown 1975). As a result, they are expected to be highly susceptible to disturbance that reduces canopy cover and shade (Welsh 1990). Larvae typically spend 2–3 years in streams before metamorphosing, and therefore the species has a generation time of several years. The eruption probably extirpated all tailed frog larvae in streams in both the DAPF and BDSC zones (Hawkins et al. 1988, Crisafulli and Hawkins 1998). Tailed frog adults and tadpoles were found just five years after eruption and currently persist in numerous streams in the BDSC zone. Tailed frogs were present and breeding in 8 of 10 BDSC zone sites surveyed between 1985 and 1987, and in 26 of 28 sites surveyed from 1995–1998. Current population sizes are unknown, but tadpole densities reached high levels from 1988 to 1992 ($>10/m^2$), before decreasing to $<5/m^2$ by 1995 (Hawkins et al. 1988, Crisafulli and Hawkins 1998). Despite the apparent suitable breeding habitat within the DAPF zone for at least 10 years, there is currently no documented presence of any stream-breeding amphibian (Crisafulli et al. 2005*b*).

In contrast, pond-breeding amphibians have colonized several new ponds in the DAPF zone (Karlstrom 1986, Crisafulli et al. 2005*b*). Bakkegard (2008) studied the genetic structure of two pond-breeding amphibians, the rough-skinned newt (*Taricha granulosa*) and the northwestern salamander (*Ambystoma gracile*). Neither species had any degree of genetic subdivision across the DAPF or BDSC zones, a result attributed to long-distance dispersal through open terrain. However, tailed frogs are unlikely to have long-distance movements across the open blast area due to their comparatively high desiccation sensitivity, and therefore we predict a more apparent genetic structure post-eruption.

Using a landscape genetics approach, we test three alternative hypotheses regarding the source of the tailed frog populations currently residing in the BDSC zone: (1) a small number of isolated blast area residents survived the eruption; (2) recolonization occurred entirely through a few source populations adjacent to the blast area (i.e., tephra-fall sites); or, (3) there has been extensive gene flow into and within the blast area. Under the first scenario, we predict high genetic structuring and signatures of bottlenecks. In contrast, support for the second hypothesis would come from clustering algorithms that group immigrants with one or a few surrounding sites. Support for the third hypothesis would be evidence of a high degree of gene flow throughout the blast area and surrounding areas with little to no apparent loss of genetic diversity. In addition, we discriminate among landscape genetic models to test whether topography, climate, and vegetation have differentially influenced genetic connectivity within the unmanaged blast area, the actively managed blast area, and surrounding tephra and undisturbed forests. Such models can provide key insights into how post-disturbance management strategies can affect population connectivity, and thus genetic diversity and structuring.

Materials and Methods

Sampling design

During the summers of 2007–2008, we collected samples from 30 sites ($n = 844$; Table 1) across four disturbance zones surrounding Mount St. Helens. These zones included: (1) the portion of the 1980 BDSC zone that was designated as unmanaged national monument and primarily consisted of blown-down trees (six sites); (2) the portion of the 1980 BDSC zone that was salvage-logged immediately after the eruption and had trees replanted manually (seven sites); (3) intact forest that was outside the 1980 blast area, but received 10–20 cm of tephra deposits (seven sites), and; (4) intact forest not disturbed by the 1980 eruption (hereafter referred to as "undisturbed") (10 sites). Sites in disturbance categories 1–2 were previously identified and surveyed by Crisafulli et al. (2005*b*) and represent almost all known areas with tailed frogs in the blast area (Fig. 1). All sampling sites were within either the Mount St. Helens National Volcanic Monument or Gifford Pinchot National Forest. At each site, individuals were sampled from a 50-m stretch of stream using kick-sampling and a net, with all samples gathered during one site visit. In all but three sampling sites, we collected tissue samples from at least 20–30 individuals. We sampled larval individuals

TABLE 1. Sites (grouped by category) and genetic diversity measures of coastal tailed frogs (*Ascaphus truei*) for each disturbance category around Mount St. Helens, Washington, USA.

Site no.	Category	N	Avg. no. alleles	H_e	H_o	F_{IS}	Bottleneck P	Shifted mode?
1	1	29	16	0.87	0.82	0.059	0.89697	no
2	1	30	17.09	0.893	0.863	0.034	0.0105	no
3	1	30	18.64	0.893	0.866	0.03	0.369	no
4	1	31	16.36	0.855	0.818	0.044	0.55078	no
5	1	19	13	0.876	0.834	0.049	0.28857	no
6	1	30	16.45	0.876	0.862	0.016	0.28857	no
Average		28.17	16.26	0.877	0.844	0.039		
7	2	22	14.64	0.851	0.855	−0.005	0.68115	no
8	2	31	17.64	0.872	0.87	0.003	0.79346	no
9	2	7	8.55	0.889	0.831	0.07	0.55078	no
10	2	30	17.64	0.873	0.86	0.016	0.0415	no
11	2	32	16.73	0.865	0.853	0.013	0.38232	no
12	2	32	18	0.871	0.836	0.04	0.83984	no
13	2	28	16.45	0.882	0.84	0.049	0.10303	no
Average		26	15.66	0.872	0.849	0.027		
14	3	27	16.18	0.877	0.862	0.017	0.0415	no
15	3	31	16.45	0.874	0.856	0.021	0.48291	no
16	3	31	16.55	0.876	0.848	0.032	0.0415	no
17	3	32	17.09	0.867	0.84	0.032	0.48291	no
18	3	30	16.55	0.886	0.89	−0.005	0.0105	no
19	3	32	17.64	0.885	0.845	0.046	0.94922	no
20	3	28	16.64	0.88	0.862	0.021	0.12012	no
Average		30.14	16.73	0.878	0.858	0.023		
21	4	31	17.64	0.884	0.857	0.031	0.55078	no
22	4	32	16.82	0.863	0.832	0.037	0.6499	no
23	4	23	15.36	0.87	0.854	0.019	0.68115	no
24	4	29	16.82	0.873	0.829	0.052	0.87988	no
25	4	20	13.36	0.86	0.852	0.01	0.55078	no
26	4	31	17.09	0.871	0.848	0.027	0.9126	no
27	4	31	16.27	0.852	0.844	0.01	0.23242	no
28	4	7	8	0.852	0.831	0.028	0.48291	no
29	4	35	17.73	0.872	0.865	0.009	0.76758	no
30	4	29	17.36	0.889	0.864	0.028	0.68115	no
Average		26.8	15.65	0.869	0.848	0.025		

Notes: Category represents the disturbance type (1, unmanaged blast zone; 2, managed blast zone; 3, tephra-fall; 4, undisturbed forest); "Average" rows are the average of sites within a category. N is the sample size (after removal of full siblings). Genetic measures include the average number of alleles per locus at each site, expected heterozygosity (H_e), observed heterozygosity (H_o), and inbreeding coefficient (F_{IS}). The bottleneck P value represents the P value for the heterozygosity excess test, and "shifted mode" indicates a shift in allele frequency distributions.

by removing a small tail clip placed in 100% ethanol, and we collected saliva samples from adults using buccal swabs, which were immediately placed in lysis buffer (Goldberg et al. 2003). However, the vast majority of individuals encountered were larvae (only eight adults were sampled, in total).

Microsatellite genotyping methods

We extracted DNA from all samples using the Qiagen DNEasy 96 well plate kit (Qiagen, Valencia, California, USA). We used polymerase chain reaction (PCR) to amplify 13 microsatellite DNA loci developed for coastal tailed frogs (Spear et al. 2008). We ran all PCR reactions divided into three multiplexed panels using the Qiagen Multiplex PCR kit, with a negative control included in each run. We submitted all microsatellite products to be run on an ABI 3730 automated sequencer (Applied Biosystems, Foster City, California, USA) at the Washington State University LBB1 core facility. We used GeneMapper 3.7 software (Applied Biosystems 2004) to genotype all samples. Finally, because a large number of larval individuals were sampled, we used the software COLONY (Wang 2004) to identify full siblings using a maximum likelihood algorithm. This algorithm runs until there have been a sufficient number of iterations to lead to convergence; the specific number of iterations can vary dependent on the dataset. If full siblings were detected, we removed all but one sibling from the analysis, as this has been shown to give a better representation of the genetic structure of the adult population in amphibians (Goldberg and Waits 2010).

Identification of source areas for colonization

We used Genepop version 3.4 (Raymond and Rousset 1995) to test whether loci and sites were in Hardy-Weinberg equilibrium and linkage equilibrium. If any loci were out of Hardy-Weinberg equilibrium at multiple

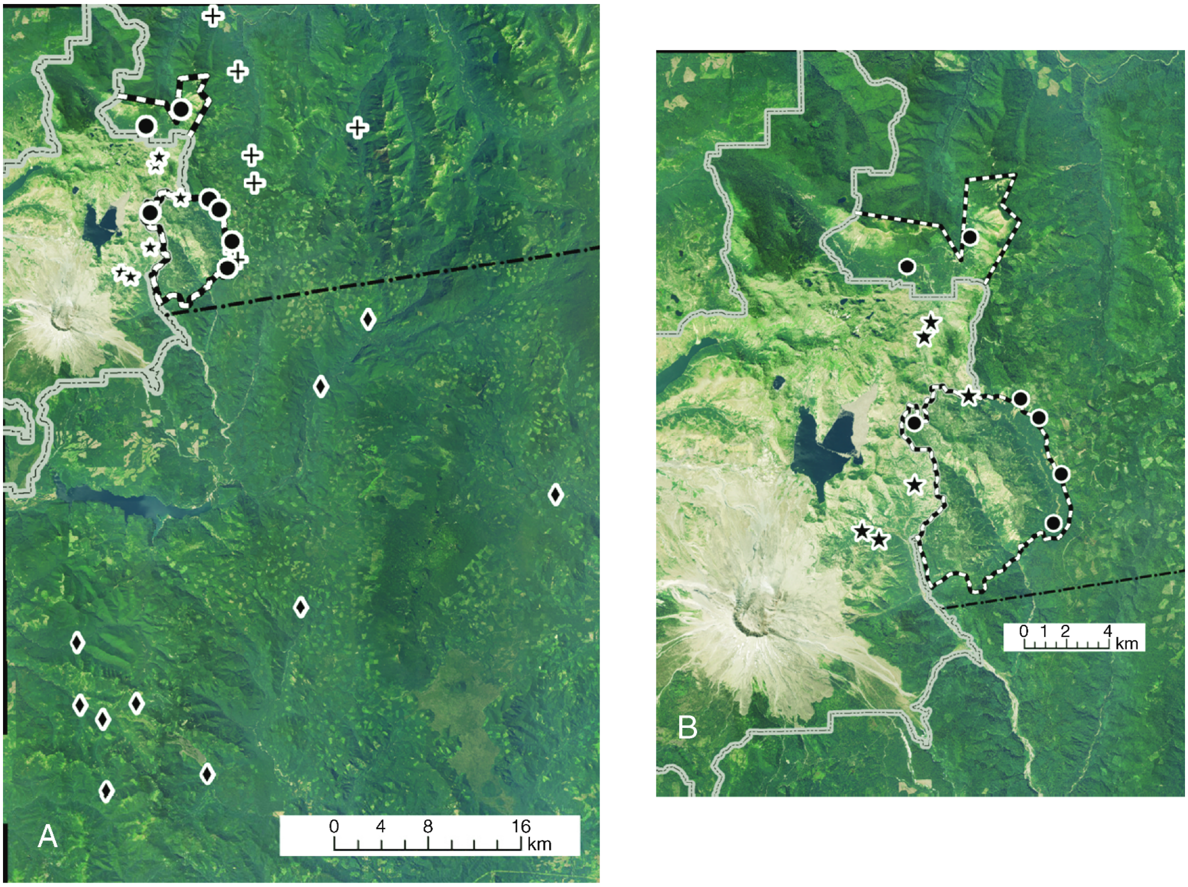

FIG. 1. (A) Overview map of sites in Mount St. Helens, Washington, USA, study area. The background is a digital ortho aerial photograph of the region. Stars represent unmanaged sites in the blast area, circles represent managed sites in the blast area, crosses represent sites in forests with tephra-fall, and diamonds represent undisturbed sites. The gray line represents the Mount St. Helens National Volcanic Monument boundary, the black and white line represents the managed blast area, and the dot-dashed line represents the approximate boundary between tephra ash-fall and undisturbed forest. (B) Close-up map of the blast area showing more clearly the distribution of blast area sites and blast area boundaries.

sites, we tested if null alleles were likely to be present using the software FreeNA (Chapuis and Estoup 2007), which estimates the proportion of null alleles using the expectation maximization (EM) algorithm developed by Dempster et al. (1977). We excluded from further analysis any loci with >10% of null alleles. We estimated measures of observed and expected heterozygosity and inbreeding coefficient (F_{IS}) with GDA version 1.1 (Lewis and Zaykin 2001). To examine whether population genetic parameters such as observed heterozygosity, allelic richness, and inbreeding coefficient differed based on the four disturbance regimes, we used FSTAT 2.9.3 (Goudet 2001), with significant differences determined based on 10 000 permutations.

We tested for genetic clustering among sites using the Bayesian clustering program STRUCTURE 2.3.1 (Pritchard et al. 2000). We ran five iterations for each proposed number of clusters (K), up to $K = 6$. Each iteration was run for 1 000 000 cycles with a burn-in of 100 000. To determine the most likely value of K, we used the method advocated by Evanno et al. (2005), which selects the value of K with the highest second-order rate of change in log-likelihood. However, because this method cannot identify situations in which $K = 1$, we assumed one cluster if this had the greatest log-likelihood. We also calculated G'_{ST}, a standardized measure of genetic differentiation (Hedrick 2005) using both FSTAT and Recode Data version 0.1 (Meirmans 2006).

Finally, we tested for signatures of hypothesized severe population size declines through the use of heterozygosity excess tests (Cornuet and Luikart 1996), and shifted allele distributions (Luikart et al. 1998). An excess of heterozygotes relative to equilibrium expectations is an ephemeral signature of severe declines within the past few generations (Cornuet and Luikart 1996). We assumed a stepwise mutation model and used the Wilcoxon signed rank test with a Bonferroni correction to account for population comparisons to determine if a population exhibited significant heterozygosity excess. The shifted allele distribution test describes the distribution of allele frequencies, with the normal expectation that most alleles will be of low frequency. A shifted distribution in which the majority of alleles are of intermediate frequency is characteristic of populations that have experienced declines due to initial loss of rare alleles.

Landscape effects on colonization

We used regression analysis and two different potential paths of gene flow to model landscape influence across all sites and then separately for each disturbance grouping. We used a hierarchical approach to detect if environmental explanatory variables differed based on spatial scale and disturbance type (Murphy et al. 2010). Specifically, we divided spatial analyses into four different sets of sites (Fig. 1). First, we tested a global model (all sites in all categories). The second model included sites within the BDSC zone (regardless of current management history). The third model included sites within the tephra-fall area. Finally, we divided the BDSC zone into separate models for the unmanaged area and the managed, replanted area.

We examined movement paths based on forest (i.e., canopy cover) and stream corridors. The two potential movement paths that we tested were straight-line paths among sites and a least-cost path that was based on forest and stream presence, with any open area that was not part of a stream corridor considered to be unsuitable (Appendix A). We constructed this path because the primary large, open areas in the region are due to the Mount St. Helens eruption, and thus we could test whether tailed frogs only followed stream corridors when moving through the blast area. We assigned all forested or stream areas a cost of 1, whereas we assigned all open, non-stream areas with a cost of 1000. These costs were chosen to simulate open regions as extreme barriers, to reflect the hypothesis that frogs would not successfully move through areas without canopy cover. We created the cost surface using the "cost distance" function and built the least-cost path with the "cost path" function in ArcGIS 9.3 (ESRI 2008). Along both path types, we calculated values for several independent variables, including total topographical distance, distance through non-forest, average canopy cover, average heat load index, average slope, average frost-free period, and average growing-season precipitation. The values of independent variables along the two potential movement paths were identified using the "intersect" function in ArcGIS 9.3. All sources and calculations for each of these variables are listed in Appendix A. We used two different measures of genetic differentiation as the dependent variable. These included G'_{ST} and the proportion of shared alleles, D_{ps} (Bowcock et al. 1994). The two measures of genetic distance are different in how they represent genetic diversity, as G'_{ST} is based on heterozygosity and reflects equilibrium assumptions, whereas D_{ps} is based on allelic similarities and is not subject to equilibrium assumptions.

We used geographically weighted regression (GWR; Fotheringham et al. 2002) or multiple linear regression to test the influence of the landscape and climatic variables along each path on D_{ps} or G'_{ST}. GWR is a type of spatial regression analysis that accounts for spatial autocorrelation across the entire study area. The analysis is performed by estimating regression parameters at each data point using only data points within a specified bandwidth of the focal point and parameter estimation based on a spatial weight, defined by a spatial weighting matrix. We created a spatial weighting matrix based on the distance between the midpoints of each pairwise site comparison. Specifically, we used a bi-square weighting function in which the weight (W_{ij}) = 1 − $(d_{ij}/b)^2$, where d represents the distance between the two midpoints I and j, and b is the bandwidth. We included 10–15% of neighboring sites as the bandwidth, with the exact percentage determined by greatest AIC support (Rangel et al. 2006).

Ordinary least squares (OLS) multiple linear regression may be more appropriate in cases when there is not strong spatial autocorrelation or local differences in D_{ps} or G'_{ST}. Therefore, for each model, we tested whether model support (based on AIC) was greater for OLS regression than for GWR, and used the specific regression analysis that had the highest support. Regardless of the regression method used, we chose the best-supported model(s) based on AIC weight. All regression analyses were run in SAM (Spatial Analysis in Macroecology; Rangel et al. 2006).

Our landscape genetic results indicated that different environmental processes influenced genetic structure in the monument blast area and managed blast area. To assess whether these differences would lead to differences in genetic diversity in the two areas, we used the spatially explicit genetic simulation model CDPOP version 1.0 (Landguth and Cushman 2010). CDPOP simulates mating and reproduction of individuals with dispersal and mating distances dictated by a resistance surface input by the user. The individual locations on the landscape are determined by the user and are fixed throughout the simulation. That is, the same locations are also occupied from generation to generation, although the individuals that occur in that location may or may not be offspring of the individual at that location in the previous generation. Our simulation area was created based on a minimum convex polygon that contained all of our sampling sites in the monument, managed, and tephra disturbance categories. The best-supported resistance surface for the monument disturbance category was simple isolation by distance, and the forest/stream resistance surface was best for the managed and tephra-fall areas. Therefore, our simulation resistance surface combined the isolation by distance surface in the monument boundary with the forest/stream resistance surface for the remaining area. We also ran a second simulation on a surface that was entirely isolation by distance to provide a comparison of genetic diversity in the managed area without the restrictions of the resistance surface.

Because streams are required for successful reproduction, we restricted all individual locations to streams. We randomly placed 250 individuals across the simulation area. Because the monument area was smaller than the managed/tephra area, there were 105 individuals in the monument and 145 individuals outside the monument. Our main interest was to understand how genetic diversity might change on a timescale relevant to management, and therefore we ran each simulation for 10 generations, which equals 50–100 years, assuming an average generation time of 5–10 years for tailed frogs. For each of the two simulation scenarios, we ran 10 replicate runs. We assumed nonoverlapping generations and constant population size. The number of offspring are modeled as a Poisson distribution with a mean of 62 (an average value for tailed frog clutch size based on Adams and Pearl (2005)). However, because population size is constant, juvenile mortality is extremely high, as is the case in actual amphibian populations (Wilbur 1980). Dispersal and mating movement distances were chosen based on an inverse square function, with a maximum movement distance of 5000 cost distance units (equivalent to a frog moving 5 km in ideal habitat). Sex ratio at birth was equal. Males were allowed to mate with replacement, whereas females mated without replacement. For each generation 0–10, we averaged the F_{IS} and F_{ST} values separately for the monument and managed areas for both simulations.

RESULTS

Genetic diversity and differentiation across disturbance types

Two of the 13 microsatellite loci (A14 and A29) were out of Hardy-Weinberg equilibrium at multiple sampling sites and had high estimated proportions of null alleles. Thus, we removed loci A14 and A29 from all genetic analyses. There was no consistent pattern of linkage disequilibrium among loci, with only seven (of 78) locus pairs out of linkage equilibrium among all sites and each pair occurring at one site each. Most sites had zero or only one full sibling pair of larvae, with the latter evenly distributed across the disturbance categories.

Genetic diversity was generally high and consistent among disturbance types (Table 1): the range in average number of alleles was 15.56–16.26, H_e (expected heterozygosity) ranged from 0.869 to 0.878, H_o (observed heterozygosity) from 0.844 to 0.858, and F_{IS} from 0.023 to 0.039. No comparisons of genetic diversity among disturbance types were significantly different. Furthermore, there was no evidence of widespread bottlenecks, as would be indicated by heterozygosity excess or shifted allele distributions at any sampled site, although two sites in the blast area and three sites in the tephra-fall area had values of $P < 0.05$ but were not significant after Bonferroni correction (Table 1). Clustering analysis determined that the greatest likelihood was $K = 1$, detecting no population substructure across the entire sampling region (Fig. 2), and the global value of G'_{ST} was 0.028. Combined, this indicates widespread recolonization that has resulted in low genetic differentiation and high genetic diversity.

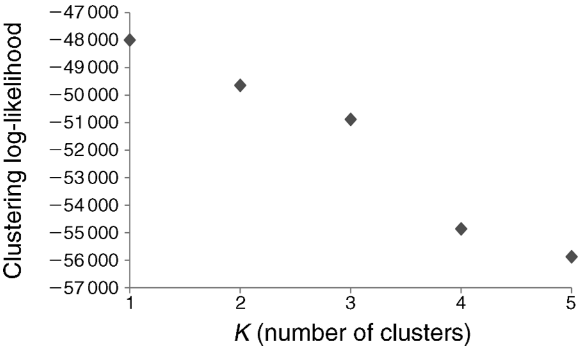

FIG. 2. Plot of the genetic clustering log-likelihood values from the Bayesian STRUCTURE program (Pritchard et al. 2000) for each potential value of K (number of genetic clusters).

Landscape genetic patterns across disturbance types

The hierarchical regression analysis showed that there were different environmental factors influencing gene flow dependent on the disturbance types. Additionally, models based on the two genetic distances were generally similar, although D_{ps} had a consistently stronger correlation based on r^2 (Tables 2 and 3). The best-supported global model came from a GWR based on the least-cost forest/stream path and D_{ps}, which included total topographic distance, growing-season precipitation, and slope ($r^2 = 0.660$; AIC weight $= 0.55$) (Table 2). Distance was positively correlated with D_{ps}, whereas slope had a negative correlation. Growing-season precipitation was both positively and negatively correlated across the different local regressions that comprise GWR, and thus a consistent relationship was not apparent. The major difference in the G'_{ST} top model was that frost-free period was included instead of growing-season precipitation, and non-forest distance was included instead of total distance; r^2 (0.392) was much lower (Table 3). The remaining global models with some AIC support were similar for both genetic distances, as slope and some measure of distance (either topographic or non-forest) were included in every model (Appendices B and C). Frost-free period also was included in secondary D_{ps} models.

The next hierarchical division, between blast area sites and tephra-fall sites, produced different models, but explained relatively little differentiation across both genetic distances ($r^2 = 0.226$–0.363) (Tables 2 and 3). The best-supported regression model across the blast area (an OLS model with D_{ps}) followed the least-cost path and contained four variables: distance through non-forest, canopy cover, slope, and growing-season precipitation (Table 2). Distance through non-forest and growing-season precipitation were both positively correlated with D_{ps}, whereas canopy and slope were negatively correlated. The G'_{ST} model with the highest

TABLE 2. Best-supported D_{ps} model results from geographically weighted regression (GWR) or ordinary least squares (OLS) analysis for all hierarchical models in different disturbance categories surrounding Mount St. Helens.

Disturbance category, path, (analysis)	Variable	Direction	r^2	AIC	AIC weight
Global, LC forest/stream (GWR)	total distance	+	0.66	−1523.23	0.55
	slope	−			
	gsp	+/−			
Blast area, LC forest/stream (OLS)	non-forest distance	+	0.347	−221.286	0.47
	canopy	−			
	slope	−			
	gsp	+			
Tephra, LC forest/stream (OLS)	non-forest distance	+	0.363	−123.257	0.69
National Volcanic Monument, straight line (OLS)	non-forest distance	+	0.738	−82.35	0.47
	ffp	+			
Managed blast area, LC forest/stream (OLS)	non-forest dist	+	0.83	−56.357	0.48
	hli	+			
	slope	−			
	ffp	+			
	gsp	+			

Notes: The global model includes all sites in all categories. Path is the least-cost (LC) path upon which the model is based. Variables are the independent variables included in the model, and direction refers to the correlation with D_{ps} (genetic distance, as proportion of shared alleles). Variable abbreviations are: gsp, growing-season precipitation; ffp, frost-free period; hli, heat load index. For the GWR analysis, + or − symbols indicate the direction in which correlation varies across the local regressions.

support was based on the same least-cost path, but was more simplistic, including only non-forest distance and frost-free period (Table 3). Other models that had some support based on AIC weight were largely similar, including a distance variable, slope, and growing-season precipitation (Appendices B and C). The best model describing the geographic distribution of genetic differentiation across the tephra-fall zone was very simplistic, following the least-cost path and only influenced by distance through non-forest based on D_{ps} and following a straight-line path and including frost-free period for G'_{ST} (Tables 2 and 3). This was the only instance in which the model path differed between D_{ps} and G'_{ST} models.

Finally, separate OLS models describing the unmanaged and replanted portions of the blast area produced differing results, and the top models in both portions explained more variation than did any of the other hierarchical models ($r^2 = 0.612$–0.83) (Tables 2 and 3), with the highest proportion of variation again explained using D_{ps} models. Differentiation among the sites within the unmanaged blast zone was based on a straight-line path and only included two variables: distance and frost-free period for D_{ps} and distance through non-forest and slope for G'_{ST} (Fig. 3, Tables 2 and 3). All were positively correlated with genetic distance. In contrast, the managed, replanted blast area sites were best described by gene flow models following the forest/stream least-cost path, with multiple independent variables that included distance through non-forest, growing-season precipitation, slope, frost-free period, and heat load index (Fig. 3, Tables 2 and 3). Slope was negatively correlated with genetic distance across the managed blast area, whereas all of the remaining independent variables included in the managed blast area model were positively correlated with genetic distance. Secondarily supported models were extremely similar as well, with

TABLE 3. Best-supported G'_{ST} model results from geographically weighted regression (GWR) or ordinary least squares (OLS) analysis for all hierarchical models in different disturbance categories surrounding Mount St. Helens.

Disturbance category, path, (analysis)	Variable	Direction	r^2	AIC	AIC weight
Global, LC forest/stream (GWR)	non-forest distance	+	0.392	−1771	0.83
	ffp	−			
	slope	−			
Blast area, LC forest/stream (OLS)	non-forest distance	+	0.226	−298	0.41
	ffp	−			
Tephra, straight line (OLS)	ffp	−	0.328	−107	0.57
National Volcanic Monument, straight line (OLS)	non-forest dist	+	0.638	−67	0.31
	slope	+			
Managed blast area, LC forest/stream (OLS)	non-forest dist	+	0.612	−70	0.23
	gsp	+			
	slope	−			
	hli	+			

Notes: Path is the least-cost (LC) path upon which the model is based. Variables are the independent variables included in the model, and direction represents the positive (+) or negative (−) correlation with G'_{ST}. Variable abbreviations are: gsp, growing-season precipitation; ffp, frost-free period; hli, heat load index.

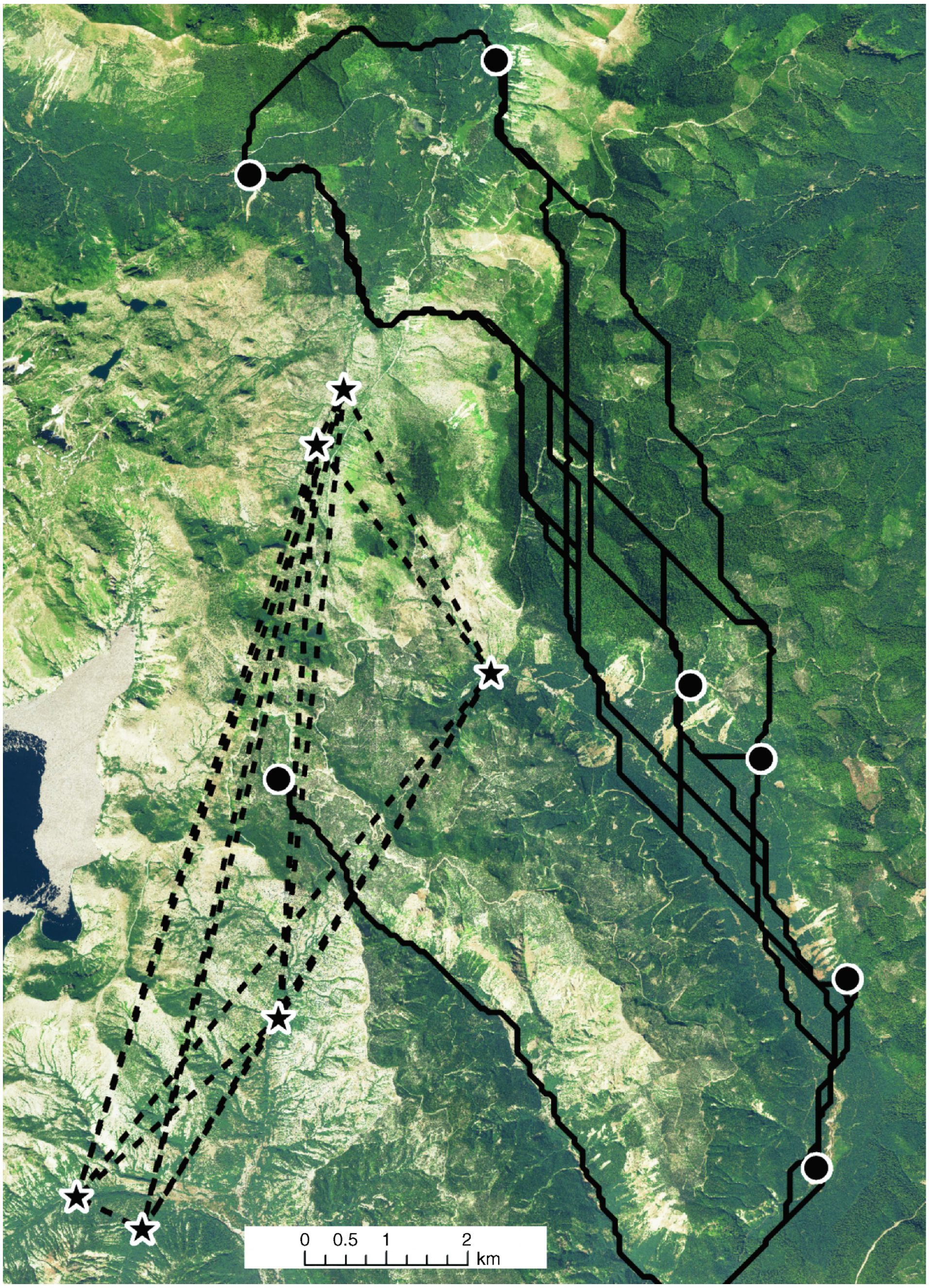

FIG. 3. Map of blast area sites depicting least-cost paths among both unmanaged and managed blast area sites. Dashed lines represent the best-supported path for unmanaged sites (stars), and solid lines represent the best-supported path for managed sites (circles).

all models with any support containing 3–5 variables (Appendices B and C).

The post hoc simulations demonstrated that F_{IS} is generally higher in the managed area relative to monument populations, especially from generation 7–10 (Fig. 4A). Similarly, F_{IS} was greater for the managed populations under the scenario of the resistance surface as compared to managed populations under IBD (Fig. 4B). Interestingly, F_{ST} was greater for the monument populations than the managed populations (Fig. 4C). However, F_{ST} was greater for managed populations simulated on the resistance surface relative to the IBD scenario (Fig. 4D). Thus, population differentiation is increased due to the more restrictive landscape conditions in which the current managed populations exist.

DISCUSSION

The eruption of Mount St. Helens provided a rare opportunity to study the ecological effects of a catastrophic event, and our study suggests surprising resiliency of tailed frogs to such dramatic and rapid landscape alterations. Our genetic data suggest rapid recolonization from outside source populations within one generation. Additionally, our landscape genetic analyses show that post-eruption management, in the form of salvage logging and replanting, has the potential to limit future tailed frog genetic diversity and gene flow relative to naturally regenerated areas, especially in response to future environmental change.

Colonization and genetic diversity across disturbance zones

Based on previous research (Crisafulli et al. 2005*b*), we addressed the hypothesis that residual adults would be the primary population founders in the unmanaged blast area. Although residual adults probably contributed to populations in the current blast area, evidence suggests that gene flow has been widespread across the blast area, as well as within the surrounding tephra-fall and undisturbed forest. A high overall rate of gene flow is most clearly supported by the lack of any detectable genetic structure across the entire sampled area. High gene flow and recolonization across the volcanic area is supported from two further lines of evidence.

First, there were no significant differences in genetic diversity measures in the blast area compared to the intact forest, and the levels of genetic diversity were consistent with those of other undisturbed populations on the Olympic Peninsula (Spear and Storfer 2008). Populations that have undergone severe reductions with subsequent isolation are expected to lose genetic diversity and increase inbreeding (Frankham et al. 2002), and this has been demonstrated in bottlenecked populations of birds and amphibians on isolated islands (Boessenkool et al. 2007, Lampert et al. 2007, Ewing et al. 2008). Whereas we might not expect to see immediate changes in heterozygosity (Keyghobadi et al. 2005), allelic diversity and inbreeding should differ in the post-bottlenecked population. However, our analysis showed no significant differences between allelic diversity and inbreeding between blast area populations and those in undisturbed forests. The average number of alleles was similar among undisturbed forest and sites affected to varying degrees by the blast. Although F_{IS} values were significantly greater than zero, there were no differences among disturbance categories, suggesting that estimated levels of inbreeding were not due to the volcanic eruption.

The lack of consistent heterozygosity excess or shifted allele distribution is a second indicator of widespread genetic exchange across the blast area. It is very likely that a number of adults survived in isolated refugia, but the eruption eliminated all larval individuals in streams (two-year classes). As a result, surviving adults would have had to persist in the blast area during early stages of plant succession (Crisafulli et al. 2005*b*). Therefore, scenarios in which the blast area populations did not suffer dramatic reductions in effective population size are unlikely. It follows, then, that the current genetic identity of recolonists has resulted from multiple dispersal events from populations outside the blast that created panmixis with blast area survivors, probably via movement through stream corridors that pass through both blast area and intact forest.

Surprisingly, the patterns of genetic diversity and structure are consistent with the few studies that have investigated genetic structure of other taxa at Mount St. Helens. Bakkegard (2008) observed similarly high levels of gene flow in rough-skinned newts (*Taricha granulosa*) and northwestern salamanders (*Ambystoma gracile*) and Yang et al. (2008) did not detect any founder effects and found low genetic structure in animal-dispersed black huckleberry (*Vaccinium membranaceum*). Although the results of the previous two studies were unexpected by the authors, *V. membranaceum* is dispersed by mammals and birds that can more easily move across barren terrain. With respect to the two salamander species, *T. granulosa* is known to sometimes occur in open areas, and *A. gracile* uses the extensive tunnel network created by northern pocket gophers (*Thomomys talpoides*) across the blast area (Crisafulli et al. 2005*b*). In addition, dispersal of salamanders up to 3.2 km across pyroclastic flow surfaces has been documented at Mount St. Helens (Crisafulli et al. 2005*b*). In contrast to these species, coastal tailed frogs are not known to cross extensive open areas or to use underground burrows, and a study on the Olympic Peninsula, Washington concluded that open alpine meadows strongly impeded tailed frog gene flow (Spear and Storfer 2008). Thus, our results suggest that some aspect of the Mount St. Helens landscape has facilitated genetic connectivity through a seemingly hostile matrix, which may include features such as seeps (Crisafulli et al. 2005*b*), hill-shading, regenerated vegetation, or coarse woody debris.

Landscape influences on gene flow across disturbance types

Landscape genetic analyses allow us to detect and identify specific variables that facilitate or inhibit gene flow (Storfer et al. 2007), in this case, through the apparently unsuitable post-eruption St. Helens landscape. Our hierarchical approach demonstrated that landscape influence on gene flow varied with both spatial scale and disturbance type, even between sets of sites separated by only a few kilometers. The global model indicated that most gene flow followed a least-cost route almost exclusively through forest, and if forest cover was lacking, along stream paths. Although topographical distance was positively correlated with genetic distance and frost-free period duration was negatively correlated, as expected, slope was surprisingly negatively correlated. In other words, as the degree of

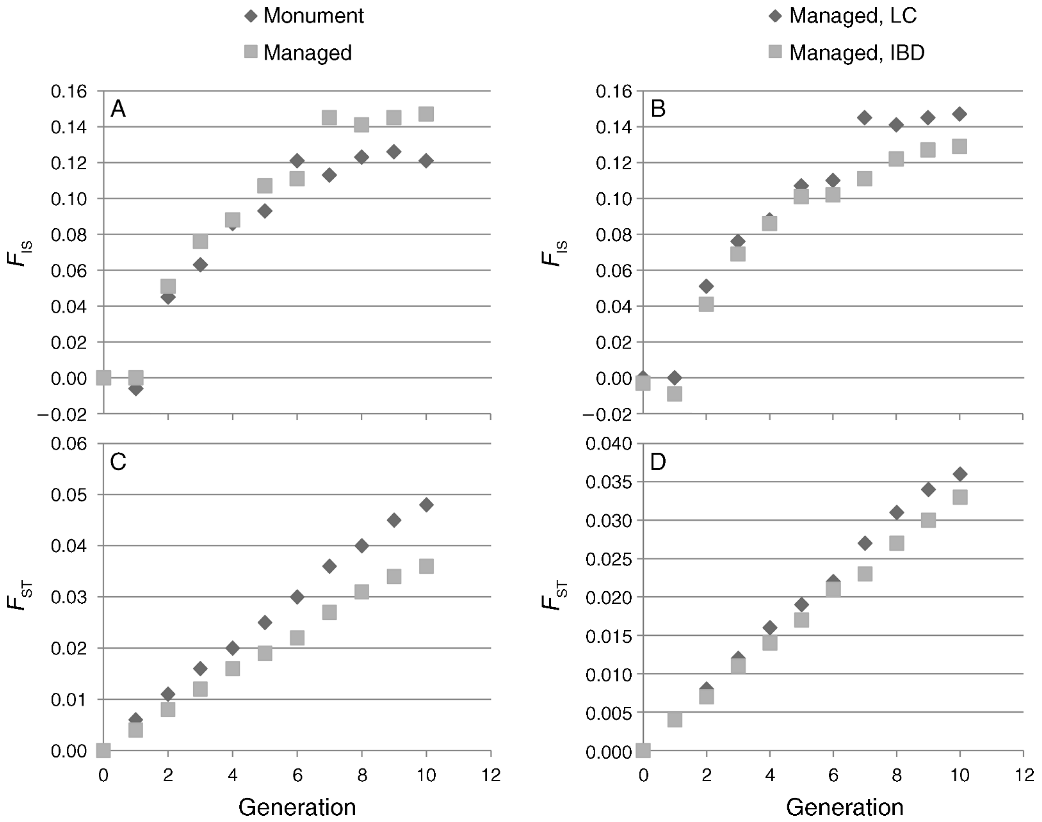

FIG. 4. (A, B) Plots of F_{IS} (genetic diversity and inbreeding within subpopulations) and (C, D) F_{ST} (amount of genetic differentiation among subpopulations due to drift) over 10 generations for simulated tailed frog populations in the Mount St. Helens blast area. The figure compares changes in (A) F_{IS} and (C) F_{ST} in monument (unmanaged) and managed-area populations using resistance surfaces suggested by landscape genetic models, as well as changes in (B) F_{IS} and (D) F_{ST} in managed populations simulated on the resistance surface (LC, least-cost path) and managed-area populations simulated under isolation by distance (IBD).

slope increased, so did gene flow. Interestingly, this same relationship with slope occurred across managed forests on the Olympic Peninsula (Spear and Storfer 2008). Adults may move up to high-gradient areas in late summer (Hayes et al. 2006), and if these movements facilitated dispersal, slope would be positively correlated with gene flow. The surprising relationship with slope also highlights the ability of landscape genetic analyses to identify nonintuitive results that can be the subject of further hypothesis testing (Spear et al. 2005, Storfer et al. 2010).

Our first hierarchical division, which created separate models for blast area (including managed and unmanaged together) and tephra-fall forest, demonstrated lowered support (based on r^2) for either of the two models as compared to the global model. The blast area model included variables similar to the global model, but with roughly half of the r^2 support. Across the tephra-fall forest, the amount of variation explained was similarly low, but the best model was relatively simplistic and only included distance (D_{ps}) or frost-free period (G'_{ST}); both had relatively low r^2 values. Tailed frogs, and amphibians in general, are not known to exhibit simple isolation by Euclidean distance (Funk et al. 2005, Spear et al. 2005, Giordano et al. 2007, Measey et al. 2007, Spear and Storfer 2008); thus, there are perhaps additional unsampled landscape variables that better explain genetic structure in the tephra-fall forest.

The second hierarchical division (separating managed vs. unmanaged blast area) strongly suggests that different processes are affecting gene flow in the blast area, dependent on management history after eruption. Contrary to our expectations that gene flow would follow a least-cost forest/stream path across the unmanaged blast area, the best-supported gene flow model followed a straight line, with topographic distance and length of frost-free period or slope as the only significant independent variables. In contrast, across the managed blast area, gene flow was best described by the least-cost path and several climatic variables, including heat load index, growing-season precipitation, and frost-free period. The positive relationship of frost-free period with genetic differentiation in both models differs from the global model and is somewhat unexpected. Frogs are not expected to move over frozen or snowbound ground, and therefore a longer frost-free period should increase gene flow, not decrease it. Instead, this relationship in the blast area may represent the pattern of survival within the BDSC zone, where some amphibians probably survived the blast under cover of ice and snow, as evidenced by occasional observations of adult amphibians in the blast area shortly after the eruption (Crisafulli et al. 2005*b*). The fact that such areas are correlated with increased connectivity is consistent with the observation that succession and recovery at Mount St. Helens have occurred from multiple foci within the blast area (Franklin and MacMahon 2000), and suggests that residual individuals have played an important role of population recovery.

The genetic support for a constrained least-cost path in the managed area indicates that connectivity will be reduced and therefore will lead to a reduction of genetic diversity relative to populations in the monument. Our simulation results supported this intuition, although seven generations were needed for differences to become apparent. This explains the lack of a difference in current levels of genetic diversity, as there has been at most only five generations since population recovery was initiated. The other insight from the simulations is that genetic diversity responds more strongly to landscape changes than genetic differentiation. The larger increase in F_{ST} in the monument area is probably related to the smaller monument area suitable for tailed frogs and a reduced density of stream habitat relative to the managed area. There is a greater degree of population differentiation in the managed area under the resistant landscape as opposed to the isolation by distance scenario. Thus, we predict that tailed frogs in the unmanaged monument will exhibit higher substructure simply due to distance, but loss of diversity within subpopulations will be less than that of frogs in the managed area. Furthermore, we can infer that the higher F_{IS} values in the managed area are due to landscape conditions because the hypothetical scenario of isolation by distance in the managed area did not lead to increased F_{IS} relative to the monument populations. We would also stress that the differences in genetic diversity in the managed area are likely to be conservative, as our simulations only used the resistance surface used to generate the least-cost paths, and did not incorporate the climatic constraints included in the managed model that would probably further decrease diversity. However, these basic simulations demonstrate that there are future genetic consequences for tailed frogs in the blast area, despite the current lack of genetic differences.

Given that both the managed and unmanaged portions of the blast area were subject to approximately the same degree of disturbance from the Mount St. Helens eruption, it is curious why the landscape models are so different. We suggest that the management history after eruption offers the most likely explanation, as this is the major difference between the two areas. Within the national monument, there is currently little forest cover, with primarily a shrub canopy and much coarse woody debris. Outside the national monument, in the managed blast area, nearly all large logs were salvaged and conifers were planted, such that the area now resembles a tree plantation with little understory (Crisafulli et al. 2005*a*, Titus and Householder 2007). Our results therefore imply a differential population response to salvage logging compared to natural regeneration, which we hypothesize is due to the importance of biological legacies for increasing gene flow in post-disturbance environments. The importance of biological legacies such as downed woody debris to ecosystem recovery has been suggested by several authors (Franklin and MacMahon 2000, Franklin et al. 2002, Lindenmayer and Noss 2006, Manning et al. 2006, Lindenmayer et al. 2008, Olson and Burnett 2009, Swanson et al. 2011), and this study indirectly supports the importance of legacy structures to amphibians.

Our previous research also supports the importance of biological legacies left after severe fire for Rocky Mountain tailed frogs, *Ascaphus montanus* (Spear and Storfer 2010). We suspect that the removal of coarse woody debris has led frogs to more closely follow forested and stream corridors. However, the most pertinent effect we see is that gene flow is influenced by several more variables in the salvaged blast area, such as heat load index and growing-season precipitation. As such, it is possible that climate changes in the future could disrupt population dynamics of amphibian populations that require the protective cover of understory structures. The importance of coarse woody debris for amphibian populations in disturbed areas is increasingly being appreciated (Waldick et al. 1999, Butts and McComb 2000, Thompson et al. 2003, Alkaslassy 2005, Spear et al. 2005, Rittenhouse et al. 2008; but see Aubry 2000). Our results suggest that coarse woody debris might help to create a stable microclimate that is more resistant to the impacts of the broader environment.

We acknowledge that the least-cost path used in this study is quite coarse (using only forest land cover and streams); there is likely to be more fine-scale heterogeneity that is influencing genetic connectivity across the blast area. Indeed, our hypothesis of the importance of coarse woody debris is fully dependent on the existence of such heterogeneity. We were unable to incorporate fine-scale features because the spatial data are currently unavailable, and therefore we had to rely on variables such as forest cover and canopy cover.

Conclusions

Our study has major findings relevant to both conservation and disturbance ecology. As amphibians are declining globally, our study gives hope that some amphibian populations initially decimated after large-scale disturbances may be able to recover and quickly repopulate once the habitat has stabilized and suitable terrestrial features exist to facilitate dispersal. We demonstrate the resilience of a (seemingly) environmentally sensitive species, the coastal tailed frog, to a broadscale and catastrophic disturbance. Specifically, we have documented high levels of genetic diversity shortly after disturbance. This resilience previously has been demonstrated for several species of pond-breeding amphibians across Mount St. Helens (Karlstrom 1986, Crisafulli et al. 2005*b*, Bakkegard 2008), but the response of the stream-breeding tailed frog is important, considering its low desiccation tolerance.

Despite overall high gene flow, landscape genetic models suggested that environmental variables influence genetic connectivity differently due to management type, a conclusion that also was recently supported for the closely related *Ascaphus montanus* (Spear and Storfer 2010). Management strategies after broadscale disturbances such as fire, windstorms, or volcanic eruptions are often difficult to evaluate and can be highly controversial (Lindenmayer et al. 2008). Post-disturbance salvage logging is often proposed due to economic concerns, to facilitate forest succession, to minimize the risk of pest outbreaks, and to reduce fuel load and potential future fire severity (Sessions et al. 2004). However, salvage logging can also be detrimental owing to loss of biological legacies, soil disturbance, or impaired natural regeneration (Lindenmayer and Noss 2006). In particular, our landscape genetic models strongly suggest that individuals in salvage-logged areas may be more affected by environmental factors such as heat load and climate relative to areas left to naturally regenerate. We expect that such constraints will lead to long-term differences in genetic diversity, and our simulations provide evidence that salvage logging can influence population genetic structure in ways that may not be apparent demographically for several generations. Finally, the fact that climatic factors were most prominent in the landscape genetic models implies that the interaction between habitat alteration and global climate change are likely to be critical for understanding population response to disturbance.

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SUPPLEMENTAL MATERIAL

Appendix A

Description of landscape variables used for least-cost path or regression analyses (*Ecological Archives* A022-047-A1).

Appendix B

All model results for landscape correlations with D_{ps} (*Ecological Archives* A022-047-A2).

Appendix C

All model results for landscape correlations with G'_{ST} (*Ecological Archives* A022-047-A3).