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Metrics of disturbance in a redwood forest ecosystem: responses of stream amphibians to repeated sediment infusions

Hartwell H. Welsh Jr., Adam K. Cummings,† and Garth R. Hodgson

Pacific Southwest Research Station, Redwood Sciences Laboratory, USDA Forest Service, 1700 Bayview Drive, Arcata, California 95521 USA

Citation: Welsh Jr., H. H., A. K. Cummings, and G. R. Hodgson. 2019. Metrics of disturbance in a redwood forest ecosystem: responses of stream amphibians to repeated sediment infusions. Ecosphere 10(10):e02886. 10.1002/ecs2.2886

Abstract. Disturbances are part of the natural dynamics of Earth's ecosystems, with these events more common now in the Anthropocene. Yet metrics for calibrating these impacts and measuring an ecosystem's capacity to recover are lacking. Highway construction in 1989 to bypass Prairie Creek Redwoods State Park in California resulted in storm-driven infusion of exposed sediments into five streams; five nearby streams that were not intersected by the bypass construction were not affected by this event and served as controls for a natural experiment. A second large storm event in 1995 contributed sediment loads into all ten streams resulting in a disturbance gradient that allowed us to examine the effects of repeated sediment disturbances. We evaluated the impacts of these stresses on three resident stream amphibian species in 1990 and again in 1996. In 1990, the impacted streams had sixfold higher pool sediment loads and significantly lower larval tailed frog (*Ascaphus truei*) densities and lower densities of coastal giant salamanders (*Dicamptodon tenebrosus*) and southern torrent salamanders (*Rhyacotriton variegatus*) compared with the un-impacted streams. During the six years between these storm events, pool bowl sediment loads increased 14-fold in the previously un-impacted streams and threefold in the previously impacted streams. Larval tailed frogs and torrent salamanders further declined in both sets of streams in 1996 although non-significantly. In contrast, giant salamander densities increased in both stream sets. Of the three species, giant salamanders appeared the most resistant to the depositional events, while the other two species appeared to decline relative to the intensity of the sediment disturbances but still persist. We believe these results demonstrate the usefulness of these three amphibians as metrics for measuring the effects of this common disturbance type on the ecological resilience of stream networks in this and other temperate northwest forest ecosystems.

Key words: amphibians; *Ascaphus truei; Dicamptodon tenebrosus;* disturbance; ecological resilience; ecological stability; metrics of ecosystem status; old-growth redwood forest; *Rhyacotriton variegatus;* streambed sedimentation.

Received 28 May 2019; revised 18 July 2019; accepted 29 July 2019; final version received 28 August 2019. Corresponding Editor: George Middendorf.

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† **E-mail:** adamcummings@fs.fed.us

Introduction

Measuring the properties of stability in ecosystems is extremely challenging given the dynamic nature of plant and animal populations and the physical environments in which they evolve. Further, the application of these concepts is scale-dependent and highly variable in space and time (Levin 2000, O'Neill 2001). While these concepts are intended to encompass whole systems, measuring everything is impractical if not impossible, making the selection of truly informative system processes and/or elements essential. In a practical vein, ecosystem recovery from destabilizing perturbations has been characterized as the relative influence of disturbance on one or

more measurable aspects of structure or composition (DeRose and Long 2014), which seems like too general a definition to be useful. One proposal for measuring the relative impacts of, and the recovery from, disturbances is to use time series data to monitor change through time of multiple species as they respond to system perturbations (Ives 1995). However, collecting time series data is time consuming and expensive so efficiency and frugality require the choice of metrics is based on prior knowledge of the sensitivity of particular elements to potential system perturbations in order to select informative metrics (Fleishman and Murphy 2009).

We assert that a useful perspective on the ability of an ecosystem to recovery from disturbance (i.e., ecological resilience; Gunderson 2000) could come from examining the nature of relative stability in an ecosystem with an extended history of minimal disturbance, and that contained ancient taxa. Consequently, we chose a highly stable ecological assemblage and selected metrics from among the phylogenetically oldest endemic vertebrates (i.e., long-branch or early branching taxa; Grandcolas et al. 2014, Faith 2015) to examine responses to one of the most common system perturbations. This approach has the effect of fixing the property of stability both spatially and high on the temporal scale (i.e., long-term stability), allowing us to examine the response to disturbance of multiple long-associated taxa, those well-suited to inform the parameters of ecosystem stability (Scheffer et al. 2001).

As such, the ~2000-yr-old coastal redwood (*Sequoia sempervirens*) forests of northwest California are considered among the oldest, and by inference the most resilient, of the planet's ecological assemblages (Sawyer et al. 2000). Among the most frequent disturbances in redwood forests are seasonal storms that form over the Pacific Ocean, tracking eastward to pummel these forestlands with copious amounts of wind and rain (Lorimer et al. 2009). Along with localized or individual wind-driven tree fall, the influx of large amounts of precipitation often brings landslides and widespread flooding into redwood forest catchments (Lorimer et al. 2009). Huge old trees comprise the vast majority of biomass in redwood forests, and their great life spans indicate they are highly resistant to these perturbations. However, the trees are not the only biotic entities representing deep time (Axelrod 1976) and, given their high resistance to perturbations, perhaps not the best metric to examine long-term stability in the system.

As potential sentinel species, amphibian sensitivity to a wide range of ecosystem perturbations is unparalleled among the planet's vertebrates (Wake and Vredenburg 2008, Hof et al. 2011, Blaustein et al. 2011). Several amphibians occur in streams in redwood forests (Welsh et al. 2000); environments within these forests most immediately impacted by storm events (Reid et al. 2010). The tailed frog (*Ascaphus truei*), the southern torrent salamander (*Rhyacotriton variegatus*), and the coastal giant salamander (*Dicamptodon tenebrosus*) are members of endemic Pacific Northwest families. Given the origins of these families in the Jurassic (Ascaphidae and Rhyacotritonidae) and Early Cretaceous (Dicamptodontidae; Vieites et al. 2007), these taxa represent deep time, evidencing long-term associations with the ancient temperate rainforest ecosystems of the Pacific Northwest. Furthermore, the abundances of these species have been demonstrated to decline and remain suppressed over long periods in response to sediment disturbances in redwood forest (Ashton et al. 2006).

Headwater or low order streams comprise the majority of the lotic network within catchments (Meyer et al. 2001, Gomi et al. 2002), comprising 80% of total stream length (Dunne and Leopold 1978). As such, the headwater streams of a forest catchment are analogous to capillaries in a vertebrate circulatory system, comprising the interface between aquatic and terrestrial domains (Nakano and Murakami 2001, Wipfli 2005, Greene et al. 2008). Similarly, as measures of the status of forest catchments "…organisms are the integrators of all that happens in a watershed" (Karr and Chu 2006:10). In addition, the complex life histories of most amphibians include both aquatic and terrestrial environments (Wilbur 1980), such that perturbations in both domains can influence their populations (Clipp and Anderson 2014). The concept that amphibians in general are ecosystem integrators makes them good candidates as metrics of ecosystem health and stability (see Davic and Welsh 2004).

In this study, we employed natural events (i.e., a natural experiment) to examine the responses of larval tailed frogs, larval and adult southern

torrent salamanders, and larval and neotenic coastal giant salamanders (i.e., the native stream amphibian assemblage) to multiple sediment infusion disturbances within a watershed of a never-harvested, ancient redwood forest, Prairie Creek State Park, in Humboldt County, California, USA (Fig. 1). Our intent was to determine the status of these amphibians on this landscape following multiple sediment perturbations, thereby examining their applicability as metrics of stream network disturbance within this highly stable temperate rainforest ecological assemblage (Carpenter et al. 2001). We hypothesized that these amphibian populations would respond negatively to sediment disturbances, but that responses would differ among species given the unique niche attributes of each (Welsh 1993). The evidence of persistence of any of these species in the face of these strong perturbations over the relatively short duration of this study would constitute evidence of high long-term resistance in this network, especially given the Jurassic and early Cretaceous ages of these lineages and their association with this ancient temperate rainforest forest type.

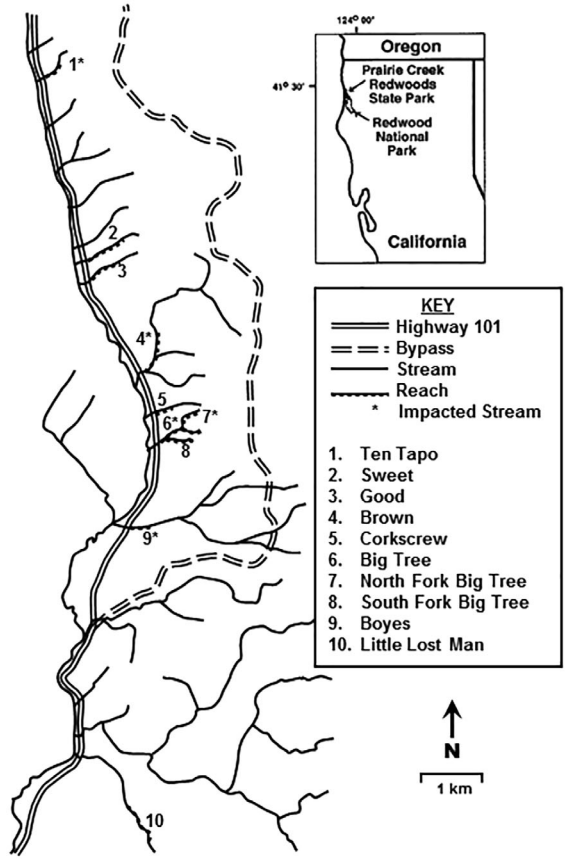

Fig. 1. Locations of the ten tributary streams sampled in this study at Prairie Creek State Redwoods and Redwood National Park, Del Norte County, California, USA. Amphibians were sampled in 1990 and 1996. All tributaries drain into Prairie Creek which drains into Prairie Creek drains into Redwood Creek.

Materials and Methods

Study design

We examined the responses of three stream amphibians to sediment perturbations in this forest ecosystem by comparing data collected twice in essentially the same manner from the same set of 10 streams following two system-wide disturbance events occurring seven years apart. The first disturbance consisted of a strong storm in October of 1989 that followed the exposure of large amounts of fine soil upslope of the stream network during a major road construction project. Large quantities of fine sediment washed into five of the ten streams, leaving five unaffected streams following this first event. Given the protected status of Prairie Creek State Park (est. 1925), general proximity of the streams, and similarities in slope, aspect, and geology, that constituted our study area, we made the assumption that both amphibian populations and sediment loads were similar in all 10 streams prior to this disturbance event (Welsh and Ollivier 1998). The infusion of large amounts of fine sediments into headwater streams is an extreme disturbance to resident aquatic biota and can cause ecological dysfunction throughout a lotic network (Waters 1995). Amphibians were sampled in the following summer of 1990 (first reported in Welsh and Ollivier 1998). The second disturbance, with much greater impacts, occurred during the winter of 1995–1996 (Fig. 2); the result of this second strong storm washed large quantities of fine sediments into all ten streams. This sequence of disturbance events provided us with five streams in each of four increasingly more intense disturbance categories: (1) five un-impacted control streams sampled in 1990; (2) five road-associated streams sampled in 1990; (3) five 1990 control streams sampled in 1996; and (4) five 1990 road-

associated streams sampled in 1996. Amphibians were sampled a second time in the summer of 1996 using the same protocols employed during the first sampling.

Sediment measurements

In each stream and every pool bowl, we calculated the average of three measurements (cm) across the deepest part of the pool bowl to derive a single value for pool bowl fine sediment depth. In addition, we made ocular estimates (%) of the pool tail cobbles and boulders that were embedded in fine sediments in these same pools (i.e., the average percentage of the cobbles and boulders at the pool tail that were partially obscured by sediment). Further, along with each cross-stream belt sample (see *Amphibian sampling*) ocular estimates of fine substrates and substrate embeddedness were recorded (Welsh and Ollivier 1998). Searchers calibrated their vision with laminated cards depicting a range of values for randomly shaded portions of cards from 10% to 100%.

Amphibian sampling

Studies of stream meso- and microhabitat use by the three target amphibians indicated specialization in physical niche attributes for each species (Welsh and Lind 1996, 2002); consequently, we employed a mesohabitat-based cross-stream sampling design comprised of 0.6-m wide belts placed with a random start and at 10-m intervals in mesohabitats >10 m in length. We sampled all available mesohabitat types in each stream in proportion to their occurrence (i.e., run, glide, riffle, pool, and step run; details in Welsh et al. 1997). This sampling strategy generated density estimates by mesohabitat type for each amphibian species, with density calculations based on the combined areas of the belts searched in each mesohabitat type used by each species regardless of their actual presence in a particular mesohabitat. Because sampling occurred before, during, and after the period of emergence of larval tailed frogs, we eliminated young of the year (<13 mm total length) prior to analysis to avoid biasing comparisons among streams. In the case of the southern torrent salamander, pool, glide, and run mesohabitats were eliminated from our calculations because this species was never found in these mesohabitat types. Search crews in 1990 did not use clear plastic view boxes whereas crews in 1996 did, which likely improved their ability to detect the target species, which could improve detections in the later sample period. However, these streams were small and shallow, and the water clear when we sampled such that any advantage provided by the view boxes would be minimal.

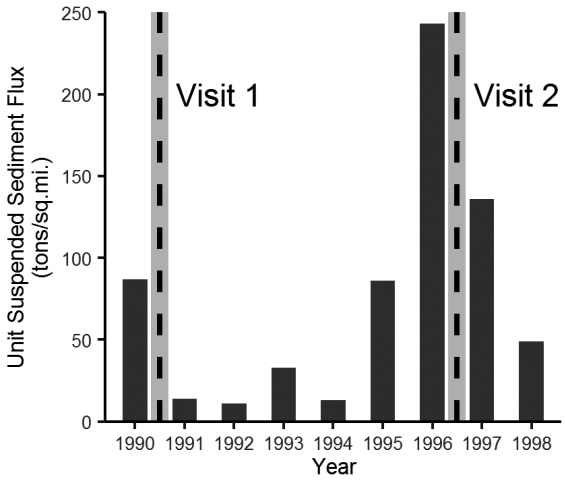

Fig. 2. Suspended sediment flux (tons/square mile) in Prairie Creek below Brown Creek for water years 1990–1998. Data from R. Klein, Hydrologist, Redwood National Park.

Analyses

We used generalized linear mixed-effects models (GLMM; Zuur et al. 2009) to model the occupancy and relative abundances of the three amphibian species in relation to the gradient of disturbances and habitat covariates. Generalized linear mixed-effects models allow for the inclusion of both fixed and random effects while modeling statistical errors using non-normal distributions with associated link functions. We also used zero-inflated GLMMs since we expect that zeroes in the dataset are generated in two distinct ways: (1) a binomial process and (2) a count process and consequently the data likely contain more zeros than would be expected in a traditional count distribution (i.e., Poisson or negative binomial).

To control for the variable search effort and stream size, models included area searched as an offset parameter. Repeated sampling events in 1990 and 1996 were controlled for by including Creek Id as a random effect. Pools were removed

from the tailed frog larvae and southern torrent salamander models to reduce zero inflation (116/124 and 124/124 mesohabitats were unoccupied, respectively). Glide/run mesohabitats were removed from southern torrent salamander models as well (47/48 mesohabitats unoccupied). For all models, we calculated Akaike's information criterion with a correction for small sample size (AIC_c) to determine which model had the best fit in each set (Burnham and Anderson 2002). If more than one model was within 2 AIC_c from the top model, the models were averaged and the full or unconditional model coefficients were used for inference (Burnham and Anderson 2002). We performed all analyses in the statistical software R ver. 3.2.1 (R Core Team 2015) using the supplemental packages glmmADMB (Skaug et al. 2011) and MuMin (Barton 2012).

Relative occupancy model.—If slower flowing mesohabitat types are heavily impacted by sedimentation events, they may become unsuitable, causing amphibian habitat associations to change. To test this, we modeled mesohabitat occupancy using binomial GLMM with a logit link with a species-specific binomial presence/absence value at the mesohabitat level as the response (Appendix S1). We lacked sufficient data to test changes in occupancy of each mesohabitat type so instead we modeled the total mesohabitat-level occupancy, which indicates how evenly dispersed animals are within the stream-mesohabitat continuum. The full model included StreamSet, Year, and the StreamSet × Year interaction as fixed factors. To account for uneven stream architecture across disturbance levels, we included Mesohabitat and Stream Id as categorical random effects. Furthermore, to control for over-dispersion the models include an observation-level random effect (Elston et al. 2001). Relative occupancy rates for each disturbance level were back calculated for each species using the inverse logit function.

The data were collected prior to the understanding of the importance of controlling for imperfect detection with sample design and so occupancy and detection rates could not be disentangled in the analysis (Mackenzie et al. 2002). We have several reasons to assume detection probabilities are high and consequently do not influence our general conclusions: (1) Detection probabilities for all three species have exceeded 0.85 using similar methods (Kroll et al. 2008), and (2) by using mesohabitat as the level of analysis, we extensively searched an area much larger than the home ranges of our target species.

Abundance model.—To measure whether the sediment disturbance continuum affected the overall density of stream-associated amphibians, we modeled species-specific abundance using a count GLMM with a logit link with counts of individual animals at the mesohabitat level as the response variable. The degree of over-dispersion and zero inflation of the count data varied by species so we took a two-stage modeling approach, first, a GLMM candidate model set fitting the full model with animal density at the mesohabitat scale as the response, but we varied the error distribution (Poisson, quasi-Poisson, or negative binomial) and whether zero inflation was included to determine which best fit for each species (Appendix S2). The model with the lowest AIC_c score was selected for each species. Secondly, using the error structure identified in the first step, we built a GLMM model set (Appendix S2) with amphibian count at the mesohabitat level as the dependent variable to assess the influence of two environmental covariates (percent embedded and percent fines) on amphibian abundance across the disturbance continuum (Appendix S1).

Results

Sedimentation

We sampled sediments in 549 pools over the course of the study, finding greater quantities in the road-associated streams compared with those not transected by the road in both sample periods (Fig. 3a). Pool tail embeddedness increased in the road-associated streams compared to control streams in 1990; however, embeddedness declined in both stream sets between sampling periods and the difference between the two sets seen in the initial comparison remained in the later sampling (Fig. 3b). These results indicated that the larger storm of 1995–1996 had a flushing effect on pool tail cobbles and boulders that removed fine sediments from the pool tails during the latter event.

Amphibians

In 1990, we sampled 86 belts in the five control streams and 93 belts in road-associated streams,

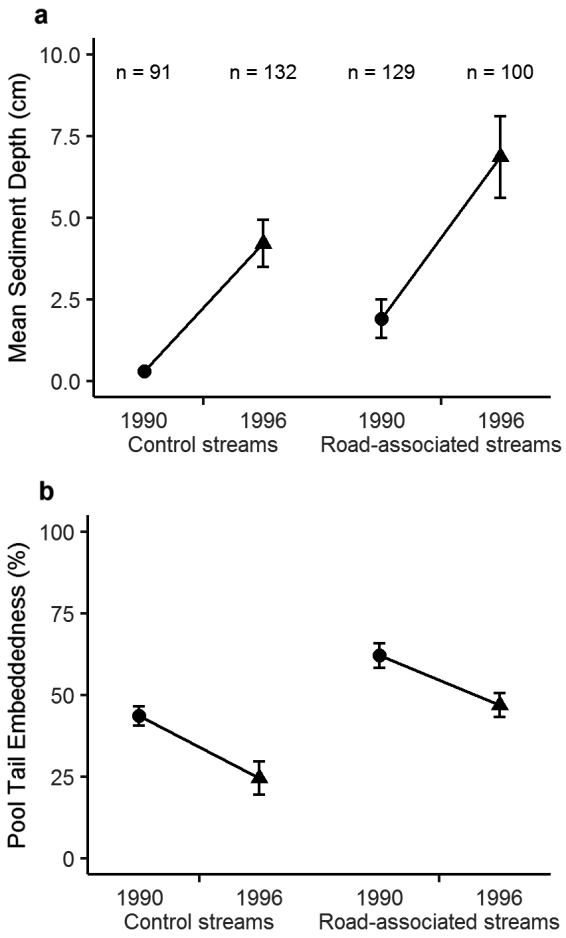

Fig. 3. Sediment measurements across disturbance continuum. (a) Mean pool bowl sediment depths (cm) for the four sets of streams. (b) Mean pool tail embeddedness (%) for the four sets of streams. Lines connect stream sets showing trend between two sample periods.

with samples distributed roughly equally among five mesohabitat types. We found 53 coastal giant salamanders, 33 larval tailed frogs, and 30 southern torrent salamanders in the five control streams (Table 1). We found 57 coastal giant salamanders, 26 larval tailed frogs, and nine southern torrent salamanders in the five road-associated streams. In 1996, we sampled 111 belts in the five control streams and 105 belts in the five road-associated streams. We found 102 coastal giant salamanders, 22 larval tailed frogs, and 21 southern torrent salamanders in the control streams. In the road-associated streams, we found 84 coastal giant salamanders, 18 larval tailed frogs, and 12 southern torrent salamanders. Densities per m^2 of the three amphibian species are reported for each of the four stream sets in Table 1. The 1989 storm event affected tailed frog densities most strongly in step-run mesohabitats and much less in riffle mesohabitats, likely due to the relatively distinct hydrodynamics in the two mesohabitats. The 1995 storm was associated with a decline in tailed frog densities in riffles (Fig. 4).

Occupancy models

We found two different patterns of mesohabitat occupancy across the disturbance continuum. Larval tailed frog occupancy rates ranged from 0.67 (confidence interval [CI]: 0.46–0.82) in 1990 control streams to 0.11 (CI: 0.05–0.24) in 1996 road-associated streams, displaying a pattern of decreasing occupancy within specific mesohabitats with increasing disturbance (Fig. 4). Similarly, southern torrent salamander occupancy declined in response to disturbance. There were three times more occupied mesohabitats in 1990 control streams than in the 1990 road-associated streams, but this difference was not statistically significant ($P = 0.22$). This discrepancy may be due to the relatively low overall occupancy of torrent salamanders, even in the undisturbed 1990 control streams (0.45 [CI: 0.19–0.74]). All three disturbance levels had similar occupancy rates ($P > 0.10$; 1990 road-associated, 0.10 [CI: 0.02–0.34]; 1996 control, 0.17 [CI: 0.05–0.42]; 1996 road-associated, 0.04 [CI: 0.01–0.17]; Fig. 5).

In contrast, coastal giant salamander occupancy was not as negatively influenced by the disturbance regime and was in fact considerably higher across treatments in comparison with the other two species. In treatment I streams, coastal giant salamanders had similar occupancy rates to tailed frogs (0.78 [CI: 0.63–0.88] and 0.67 [CI: 0.46–0.82], respectively). There is weak evidence that mesohabitat occupancy of giant salamanders increased after streams was impacted by the first disturbance (treatment II > treatment I, $P = 0.06$; Fig. 5).

Abundance models

The three amphibians responded differently to percent fine sediments and stream embeddedness. The inclusion of either embeddedness, percent fines, or both covariates in models of torrent salamander abundance did not improve model fit, and consequently, all models in the set had

Table 1. Number of belts, counts, and densities (/m^2) of coastal giant salamanders (*Dicamptodon tenebrosus*; DITE), tailed frog larvae (*Ascaphus truei*; ASTR), and southern torrent salamanders (*Rhyacotriton variegatus*; RHVA) in both stream sets and years, representing the disturbance continuum of increasing sedimentation in streams at Prairie Creek State Redwoods, California, USA.

Stream set and Creek	Total belts	DITE belts	DITE counts	DITE density	ASTR belts	ASTR counts	ASTR density	RHVA belts†	RHVA counts	RHVA density
Control set 1990										
Good Ck.	25	13	33	0.85	11	29	0.75	4 (18)	7	0.21
S. Fk. Big Tree Ck.	7	5	9	2.24	3	5	1.24	2 (4)	2	0.76
Sweet Ck.	24	14	35	1.5	8	20	0.85	7 (19)	12	0.59
Corkscrew Ck.	15	9	15	1.29	4	9	0.77	5 (10)	9	1.07
Little Lost Man Ck.	15	12	60	0.82	7	62	0.85	0 (10)	0	0
Total	86	53	152	1.01	33	125	0.83	18 (61)	30	0.23
Control set 1996										
Good Ck.	31	31	169	1.9	8	15	0.17	3 (24)	4	0.06
S. Fk. Big Tree Ck.	12	9	32	1.42	1	1	0.04	2 (9)	4	0.22
Sweet Ck.	25	25	193	2.43	2	2	0.03	4 (18)	7	0.11
Corkscrew Ck.	15	12	53	1.58	1	1	0.03	3 (11)	4	0.17
Little Lost Man Ck.	28	25	229	0.92	10	71	0.29	2 (19)	2	0.01
Total	111	102	676	1.43	22	90	0.19	14 (81)	21	0.06
Road-assoc. set 1990										
Brown Ck.	27	23	69	0.98	8	25	0.35	1 (16)	1	0.02
Big Tree Ck. (main)	25	16	45	0.91	14	32	0.65	2 (15)	4	0.11
N. Fk. Big Tree Ck.	17	7	17	0.69	2	2	0.08	2 (12)	3	0.19
Boyes Ck.	14	5	7	0.31	1	2	0.09	0 (9)	0	0
Ten Tapo Ck.	10	6	7	0.65	1	4	0.37	1 (7)	1	0.13
Total	93	57	145	0.81	26	65	0.37	6 (59)	9	0.07
Road-assoc. set 1996										
Brown Ck.	23	22	224	1.54	9	24	0.16	0 (14)	0	0
Big Tree Ck. (main)	41	34	185	1.17	5	8	0.05	4 (29)	4	0.04
N. Fk. Big Tree Ck.	18	17	110	1.61	3	3	0.04	4 (14)	8	0.15
Boyes Ck.	13	4	6	0.07	0	0	0	0 (7)	0	0
Ten Tapo Ck.	10	7	22	0.44	1	1	0.02	0 (6)	0	0
Total	105	84	547	1.07	18	36	0.07	8 (70)	12	0.04

† Total belts sampled in parentheses for RHVA after eliminating belts in mesohabitats (i.e., pools, glides, and runs) where RHVA were never detected.

AIC_c scores within two points of the top model (Fig. 6). Conversely, the inclusion of embeddedness improved model fit for both giant salamander and tailed frog (Table 2), indicating the negative influence of increased embeddedness on their numbers.

Giant salamander abundance was negatively influenced by both increasing embeddedness and percent fines (Table 2; Fig. 6). The averaged top model for giant salamander contains both environmental covariates. For every 10% increase in the embeddedness of a mesohabitat, giant salamander relative abundance decreases 11% per unit area (CI: 5–18%). Similarly, for every 10% increase in percent fines giant salamander relative abundance decreases three percent (CI: 5% increase to 12% decrease; Fig. 6). The degree of embeddedness of a habitat also negatively influenced tailed frog abundance. For every 10% increase in embeddedness, tailed frog abundance decreases 35% (CI: 18–52%; Table 2); however, percent fines did not appear in the top model (Appendix S1).

While tailed frog occupancy levels did not decrease following the 1990 event, density did decline (Figs. 5, 7). Following the 1996 event, tailed frog occupancy and density decreased in both sets of streams (Figs. 5, 7). The small number of torrent salamanders in the 1990 control streams was sufficient to estimate density; however, their numbers declined following both storm events such that detecting significant differences was not possible (Fig. 7). Giant

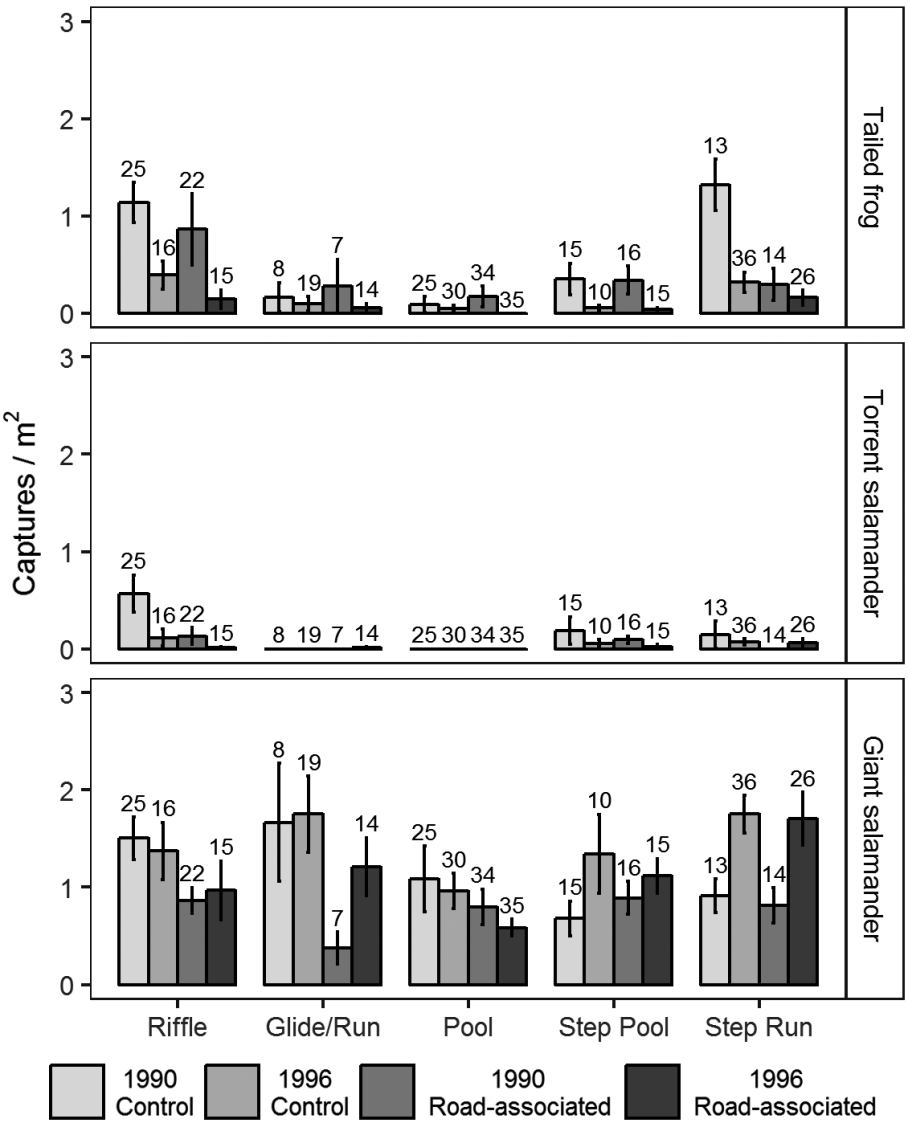

Fig. 4. Measured density of three amphibian species with respect to mesohabitat type in each of the four sets of streams. Bars represent weighted means (and weighted standard error). Numbers above bars are total mesohabitats sampled.

salamander densities were not significantly reduced in either stream set following the 1990 event, and appeared to increase in both stream sets following the 1996 event, however, only significantly so in control streams (Fig. 7).

Discussion

Under the paradigm of ecological resilience (Gunderson 2000), the concept of ecosystem stability is the long-term potential for system persistence (Curtin and Parker 2014). This view holds that the dynamic behavior of an ecosystem is understood to be the manifestation of two distinct but related properties: resilience and stability (or resistance); stability is the system's ability to return to an equilibrium state, while resilience is a measure of the system's ability to absorb changes in state variables while continuing to persist (Holling 1973). A system can be highly

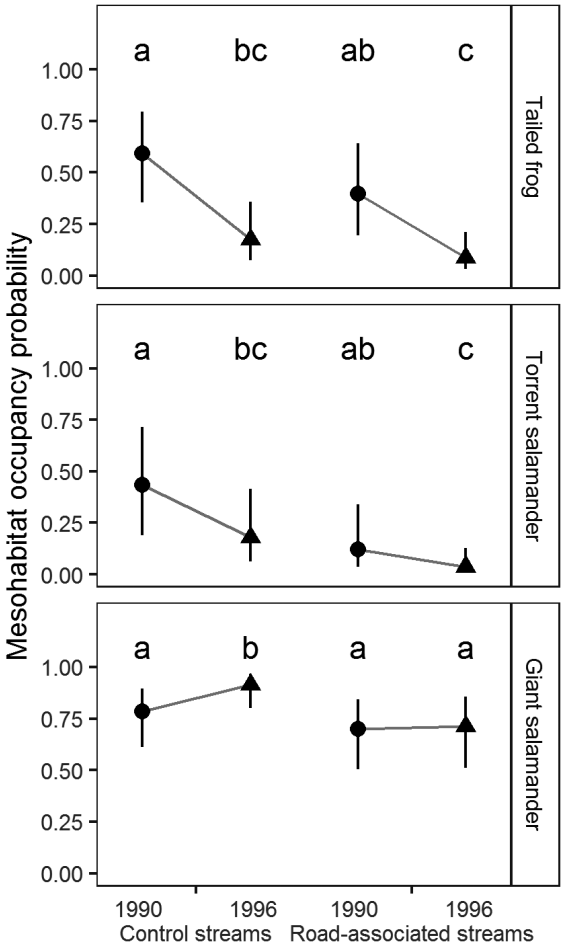

Fig. 5. Relative occupancy (estimated using binomial generalized linear mixed-effects model) for coastal giant salamanders (*Dicamptodon tenebrosus*), larval tailed frogs (*Ascaphus truei*), and southern torrent salamanders (*Rhyacotriton variegatus*) in the four sets of streams representing the fine sediment disturbance continuum. Probabilities calculated using the inverse link function of mixed-effects logistic models. Letters indicate significantly different post hoc group comparisons (Sidak, $\alpha = 0.10$).

resilient and still fluctuate greatly, that is, have low stability (Holling 1973). Regardless of these elegant definitions, actually determining key thresholds that pertain to these concepts remains problematic. The fact is that resilience can only truly be demonstrated over long time spans where resistance occurs over periods equating to decades and beyond. Stated more succinctly, resilience is nothing less than resistance and the ability to recover demonstrated over the long term. Thus, finding direct evidence of resilience by commonly conducted scientific study is all but impossible given the temporal and logistic constraints of such studies. Nonetheless, we submit that indirect evidence of resilience can be found by studying the contemporary responses of long-branch taxa (i.e., those that have been extant on Earth for eons) existing in ancient ecosystems. Both the redwood ecosystem and the resident amphibians we studied here meet these requirements.

Documenting ecological thresholds (i.e., tipping points in ecological systems where elements or functions are modified or lost) is a logical means to determine relative condition. Odum (1992) noted the first signs of environmental stress usually occur at the population level, affecting individuals of especially sensitive species. The use of amphibian assemblages as metrics of ecosystem status has been previously described (Welsh and Ollivier 1998, Hughes et al. 2004, Welsh and Hodgson 2008). Prior research has indicated that larval tailed frogs, southern torrent salamanders, and coastal giant salamanders each occupies a unique niche space along the ecological gradients of water temperature and fine sediment loads (Welsh and Hodgson 2008). These species-specific characteristics serve to establish a set of critical ecological thresholds for each species in headwater stream environments that provide important points along a resilience-resistance scale. Ecosystem stability may erode as more ecological threshold points are exceeded causing specific components and processes to be lost (With and Crist 1995, Huggett 2005, Groffman et al. 2006, Bryce et al. 2010). The results of our natural experiment illustrate the effects of a common disturbance on the resident amphibian assemblage in a relatively stable ecosystem. Their continued presence, despite fluctuations in abundance, provides insight into the status of a key system component, the stream network, and its relative ability to support the entire stream-dwelling community of organisms.

Results from the first storm in 1989 were previously published (Welsh and Ollivier 1998), with the current analysis expanding on the original effort. The original analysis concluded giant salamander abundance was negatively impacted by both the degree of embeddedness and percent

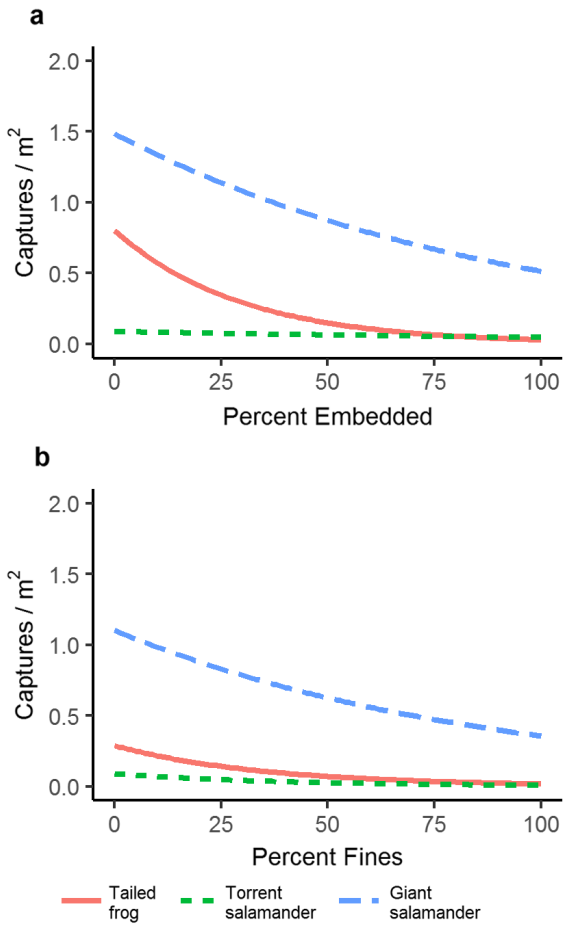

Fig. 6. Predicted response to environmental variables by three amphibian species as predicted by generalized mixed models. (a) Percent embedded, (b) percent fines.

fines associated with each mesohabitat (Welsh and Ollivier 1998). In this effort, we found giant salamanders, while showing sensitivity to these same environmental covariates (Fig. 6), were more resilient than the other two species, with both occupancy and density actually increasing in the control streams following the second storm (Figs. 5, 7). Tailed frog abundance was negatively impacted by embeddedness, even after controlling for mesohabitat preference (Welsh and Ollivier 1998). In this new study, they showed further declines in both occupancy and density following the additional disturbance in the road-associated steams (Figs. 5, 7). Tailed frog densities also declined relative to the amounts of embeddedness and percent fines in the current analysis (Fig. 6). Our results indicate tailed frog larvae experienced declines in both occupancy and density with increasing sediments along the disturbance continuum. This species was sufficiently abundant at our study site such that we were able to detect clear declines in their numbers in response to the increasing disturbance. This decline could be explained by the loss of non-filamentous algae due to scour by sediment during high flow events (Alabaster and Lloyd 1982). The influx of fine sediments can also reduce total periphyton biomass by reducing available sunlight and suitable microhabitat (Newcombe and MacDonald 1991, Welsh and Ollivier 1998). Larval tailed frogs have been shown to be sensitive to other large-scale ecosystem perturbations such as forest fires and timber harvest, and also to track positively with ecosystem recovery (Corn and Bury 1989, Hossack and Honeycutt 2017). Tailed frogs' sensitivity to fine sediments may be mitigated in watersheds with a less erodible dominant geology (Wilkins and Peterson, 2000).

Southern torrent salamander occupancy was negatively associated with the sediment-associated disturbance continuum (Fig. 5). Southern torrent salamanders are generally found in association with low flow seeps and extreme headwater environments, and are not especially abundant in the stream types in this study. The decline in occupancy suggests the marginally suitable habitat that was available became less common in response to the disturbance events. The niche specificity of southern torrent salamanders also likely explains why the southern torrent salamander count data were highly zero-inflated. The non-detection of torrent salamanders in many belts was likely caused by more than one process: Many mesohabitat types we sampled do not typically support torrent salamanders, and of those that could support torrent salamanders, only some were occupied while others not. Consequently, the paucity of capture data influenced the power of the analyses to detect an environmental covariate effect. In both analyses, torrent salamander abundance was not found to be significantly depressed by increases in the environmental covariates tested; a situation that is best explained by their low numbers and the resulting limited statistical power since their sensitivity to fine sedimentation is well established in other

Table 2. Top models describing relationship between environmental covariates and disturbance regime.

	Coastal tailed frog | Quasi-Poisson + Zero inflation				Coastal giant salamander | Negative binomial				Southern torrent salamander | Poisson + Zero inflation			
Model parameter	Est.	SE	*Z*	*P*	Est.	SE	*Z*	*P*	Est.	SE	*Z*	*P*
Intercept	0.55	0.60	0.92	0.36	0.48	0.34	1.40	0.16	−0.43	0.67	0.63	0.53
1990 road-assoc.	−0.20	0.43	−0.5	0.64	−0.44	0.43	1.01	0.31	−1.38	0.96	1.43	0.15
1996 control	−1.98	0.31	−6.4	<0.001	0.21	0.14	1.54	0.12	−1.02	0.37	2.72	0.006
1996 road-assoc.	−2.29	0.42	−5.5	<0.001	−0.43	0.42	1.03	0.30	−2.30	0.96	2.37	0.018
All pool	N/A				Intrcp				N/A			
Glide run	Intrcp				0.24	0.15	1.58	0.11	N/A			
Riffle	0.84	0.45	1.87	0.06	0.03	0.15	0.19	0.85	Intrcp			
Step pool	0.11	0.46	0.24	0.81	0.05	0.14	0.32	0.75	−0.42	0.39	1.06	0.29
Step run	0.82	0.42	1.94	0.05	0.36	0.13	2.79	0.005	−0.26	0.34	0.78	0.44
Embedded	−0.04	0.01	−3.9	<0.001	−0.01	0.003	3.46	0.001	−0.02	0.02	0.68	0.49
Fines	N/A				0.00	0.004	0.67	0.51	0.002	0.01	0.35	0.73
Creek Id (var.)	0.17	0.02			0.37	0.03			1.50	0.10		
Zero Inflation	0.14	0.09			N/A				0.41	0.10		
Over-dispersion	2.53	0.45			3.60	0.61			N/A			

Notes: Estimated coefficients and standard error from the top model or averaged top model of candidate model sets described in Appendix S1. Trt, treatment; Est., estimate; SE, standard error.

studies (Welsh and Lind 1996, Welsh and Hodgson 2008). Thus, their value as a sentinel species while clear is highly dependent on sufficient numbers being present to detect statistically significant differences.

The 1996 surveys of the control streams had a higher coastal giant salamander mesohabitat occupancy rate than the earlier surveys of the same streams and both survey periods of the road-associated streams. The giant salamanders appeared to be more tolerant of the sediment disturbance compared with the other two species (Welsh and Hodgson 2008), given that they did not decline noticeably and actually increased abundance following disturbance in the control streams. One highly speculative explanation for this trend comes from a trophic cascade perspective: Giant salamanders feed almost exclusively on benthic macroinvertebrates with grazer insects being their primary prey (Parker 1994). Tailed frog larvae can decrease grazer insect abundances by over 50% through exploitative and interference competitive interactions (Atwood and Richardson 2012, Kiffney and Richardson 2001, Lamberti et al. 1995). Possibly the reduction in tailed frog larvae in disturbed streams freed invertebrate grazers from competition, and consequently, they flourished, providing an enhanced food base which then supported greater giant salamander numbers. However, directed research with controlled experiments would be necessary to elucidate any trophic interactions between these amphibian species. Alternatively, the addition of clear plastic viewing buckets to the 1996 surveys (slightly improving our ability to detect all three target species) could further explain the relative increase in giant salamander detections in that year's control streams. However, this second explanation is not supported when examining the road-associated streams across years, which do not show the increased occupancy. Furthermore, we expected high detection probabilities in both years given the thorough survey methods applied. Larval spring salamanders (*Gyrinophilus porphyriticus*) in eastern North America exhibit higher tolerance to stream embeddedness than do adults (Lowe et al. 2004). If a similar pattern exists in giant salamanders, it could help clarify their population-level tolerance to sedimentation events.

The negative effects of fine sediments on headwater amphibian assemblages are well established (Welsh and Hodgson 2008, Kaufmann and Hughes 2006), with torrent salamanders exhibiting the greatest sensitivity, followed by larval tailed frogs, with coastal giant salamanders the least sensitive of the three. These results are to be expected given the highly specific aquatic habitat requirements of the torrent salamander (Welsh and Lind 1996) and larval tailed frog (Welsh and

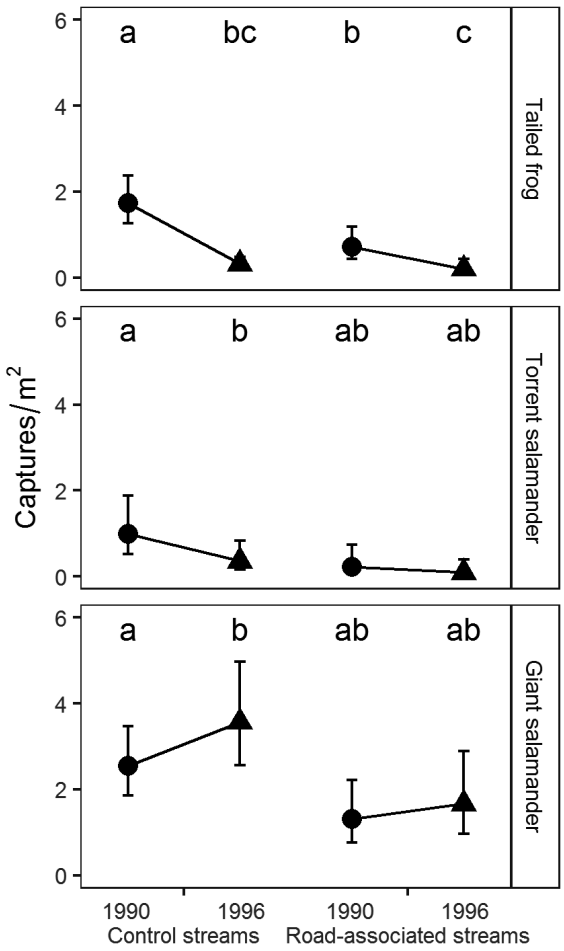

Fig. 7. Estimated density (±95% confidence interval) of three amphibian species across the disturbance continuum from generalized linear mixed-effects model estimates.

Lind 2002), whereas the aquatic giant salamander are more of an ecological generalist (Welsh and Lind 2002). Considering their complex roles in aquatic and terrestrial food webs, these species arguably represent more than the ecological subsystem where they reside, but rather are reasonable metrics for the status of the entire ecosystem (Davic and Welsh 2004).

The relative status of populations of these amphibians in headwater streams of redwood and other Pacific Northwest rainforests can indicate the stability and resistance/resilience of an entire catchment network (Welsh 2011). For example, their presence and relative numbers in streams can indicate whether appropriate conditions exist to support anadromous fish runs (Welsh et al. 2001, Welsh and Hodgson 2008). Pacific Northwest catchments host the largest anadromous salmonid runs in the continental United States, and these runs bring marine nutrients that facilitate tree growth and augment forest food webs (Groot and Margolis 1991, Willson et al. 1998, Wipfli and Baxter 2010). Furthermore, these marine-supplemented forests have an unusually high potential for facilitating the critical ecological service of sequestering atmospheric carbon (Hudiburg et al. 2009, Keith et al. 2009).

As humankind advances in the Anthropocene, it is evident that ecological assemblages across the planet are under stress (Vitousek et al. 1997). It is the loss of ecosystem resistance/resilience that usually paves the way for a switch to an alternative ecosystem state (Scheffer and Carpenter 2003). Therefore, it is imperative we understand stability and resilience in stable reference ecosystems and how they respond to stress such that in the future we have accurate metrics for restoration and maintenance (Stoddard et al. 2006, Pollock et al. 2012). Lacking such metrics makes us susceptible to the shifting baseline syndrome (Pauly 1995) and the compromised ecosystems that can result (Worm et al. 2009). Only by avoiding this pitfall can we maintain the productive and resilient ecosystems that will provide the vital ecological services that sustain a healthy vibrant planet and its biological wealth (Scheffer et al. 2000).

Acknowledgments

We would like to thank field crew members Don Ashton, Kary Schlick, Jennifer Bloeser, and Jeff Neumann. Comments from Lisa Ollivier, Karen Pope, Bret Harvey, Blake Hossack, and anonymous reviewers improved the manuscript. Statistical advice from Nels Johnson and Jim Baldwin also improved the manuscript. We also thank the staff of Prairie Creek State Park for facilitating this research.

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