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# ENVIRONMENTAL INFLUENCES ON AMPHIBIAN ASSEMBLAGES ACROSS SUBALPINE WET MEADOWS IN THE KLAMATH MOUNTAINS, CALIFORNIA

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Abstract: Many high-elevation regions in the western USA are protected public lands that remain relatively undisturbed by human impact. Over the last century, however, nonnative trout and cattle have been introduced to subalpine wetland habitats used by sensitive amphibian species. Our study compares the relative importance of cattle and trout impact on amphibian assemblages, abundance, and occupancy within a broader context of high-elevation environmental variables. We evaluated amphibian species richness and abundance across 89 subalpine wet meadow sites in the Klamath Mountains of Northern California, USA. At each wet meadow we also measured environmental characteristics including wilderness designation, elevation, meadow size, number of pools, distance to nearest lake, presence of nonnative trout, and impact of cattle. Cluster analysis found amphibian assemblages fell into three distinct groups, and ordination suggested the number of pools, elevation, and presence of nonnative trout are significant site variables associated with species groups in wet meadows. Individual species differed in population response to environmental characteristics. Regression trees and occupancy models indicated that the most-important variables associated with the population size and site occupancy of individual amphibian species are nonnative trout, wilderness area designation, the number of pools, and the distance to the nearest lake. While nonnative trout exhibited a strongly negative correlation with amphibian assemblages, abundance, and occupancy, cattle impact was only weakly associated with occupancy and abundance of some species.

*Key words*: Cattle; Nonmetric multidimensional scaling; Nonnative species; Occupancy; Trout; Wilderness area

Extinction and population declines of amphibian species have been significant and widespread (Stuart et al., 2004). Effective conservation efforts hinge upon identification and ranking of the environmental variables associated with population dynamics. Natural variation in abiotic habitat attributes (Skelly et al., 1999; Snodgrass et al., 2000; Urban, 2004; Welsh et al., 2006), native species interactions (Gustafson, 1994; Bailey et al., 2004), and habitat patch isolation (Sjogren, 1991) are often associated with amphibian assemblages and population status. Amphibian population declines can be caused by new or anthropogenic forms of disturbance including rapid climate change, land-use change, emerging diseases, environmental pollution, nonnative species, increases in UV-B irradiation, and exploitation for food, medicine, and the pet trade (Blaustein and Kiesecker, 2002; Beebee and Griffiths, 2005). Few studies have placed anthropogenic drivers of population decline within a broader context of natural environmental variability.

High elevation environments contain native and introduced environmental factors that influence amphibian population dynamics. High-elevation amphibians in the western United States have suffered population declines attributed to *Batrachochytrium dendrobatidis* fungal infections and stocking of nonnative trout in lakes (Knapp et al., 2003; Welsh et al., 2006; Morgan et al., 2007; Piovia-Scott et al., 2011). Many high-elevation amphibians use both lake and wet meadow habitat for foraging and breeding. However, the hydrological, geological, and ecological dynamics of high-elevation wet meadows differ markedly from lakes. Wet meadows can contain both permanent and temporary pools and are characterized by herbaceous vegetation. Fens are peat-forming wet meadows supported by nearly constant groundwater inflow (Bedford and Godwin, 2003) while other wet meadows can be snow-fed and aerobic. Wet meadows can enhance the landscape connectivity for amphibian dispers-

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al (Semlitsch, 2000), but they can also be highly productive (Moreno-Mateos et al., 2012) and provide complex refuge habitat for aquatic organisms (Chapman et al., 1996). Two nonnative vertebrate species, trout and cattle, potentially heavily affect wet meadows.

The negative impact of nonnative trout introductions on native amphibian populations in wetlands is well established (Bradford et al., 1993; Gillespie, 2001; Knapp et al., 2003; Pope, 2008). Most high-elevation lakes and wet meadows in the western United States were historically fishless because passage was obstructed by downstream barriers, but over the last century nonnative trout (Family Salmonidae) have been widely introduced to these aquatic habitats (Pister, 2001). Surveys of lakes in the Sierra Nevada Mountains and of lakes, ponds, and wet meadows in the Klamath Mountains of California, USA, showed that amphibian site occupancy is negatively correlated with native amphibian species palatable to nonnative trout (Knapp et al., 2003; Welsh et al., 2006). Nonnative trout are present in wet meadows through dispersal from stocked lakes.

Compared to that of trout, the impact of cattle grazing on amphibian populations is less clear, varying across species and habitat types. Cattle grazing can be negatively associated with amphibian abundance (Fleischner, 1994; Jansen and Healey, 2003; Riedel et al., 2008) and related to an increased incidence of ranavirus infection (Hoverman et al., 2012) and parasite abundance (McKenzie, 2007). In other cases, however, cattle grazing is positively associated with amphibian abundance or has no impact (Pyke and Marty, 2005; Roche et al., 2012). Experimental manipulation and simulation models indicate that, in the face of climate change, cattle grazing maintains hydrologic dynamics in vernal pools that support the endangered California Tiger Salamander (*Ambystoma californiense*; Pyke and Marty, 2005). In the Sierra Nevada Mountains, Roche et al. (2012) found no short-term impacts of cattle grazing on the persistence of Yosemite Toad (*Anaxyrus canorus*) in high-elevation wet meadows.

The Klamath–Siskiyou region supports the highest diversity of subalpine, lentic breeding amphibians in western North America, is located in an area of low human density, and is impacted by the presence of both cattle and trout. Building on work by Welsh et al. (2006) and Roche et al. (2012), our objectives were to (1) identify species assemblages of amphibians; (2) quantify habitat conditions associated with species abundance; and (3) determine how environmental drivers influence amphibian occupancy across wet meadows in the Klamath Mountains. We evaluated the degree to which anthropogenic (presence of introduced trout, cattle grazing impact) and natural environmental variability (elevation, meadow area, number of pools, and distance to permanent breeding bodies of water) influence amphibian assemblages and abundance. We predicted that the presence of both nonnative species would have a greater impact on amphibian abundance and diversity than other measured variables and that amphibian abundance and diversity would be higher at sites less impacted by trout and cattle. Although cattle grazing can mimic the effect of native ungulates (Collins et al., 1998; Maestas et al., 2003), we hypothesized that the localized and intense effects of cattle grazing in wet meadows would more heavily affect amphibians than would the Roosevelt Elk (*Cervus elaphus*) and Mule Deer (*Odocoileus hemionus*) native to the Klamath Mountains.

## Materials and Methods

### *Study Sites*

Study sites were located in subalpine wet meadows and fens in the Klamath Mountains of northwestern California, with many sample sites located within the Marble Mountain, Russian, Castle Crags, and Trinity Alps wilderness areas (Fig. 1). The climate is Mediterranean, consisting of warm, dry summers and moderately cold winters with heavy snowfall (peak average annual snow depth 1–4 m; California Department of Water Resources, 2014). The proximity of the Klamath Mountains to the Pacific Ocean produces strong west to east moisture and temperature gradients across the range (Skinner et al., 2006). Sample sites are generally snow covered from late October through mid-May. The geology of the region is varied and includes

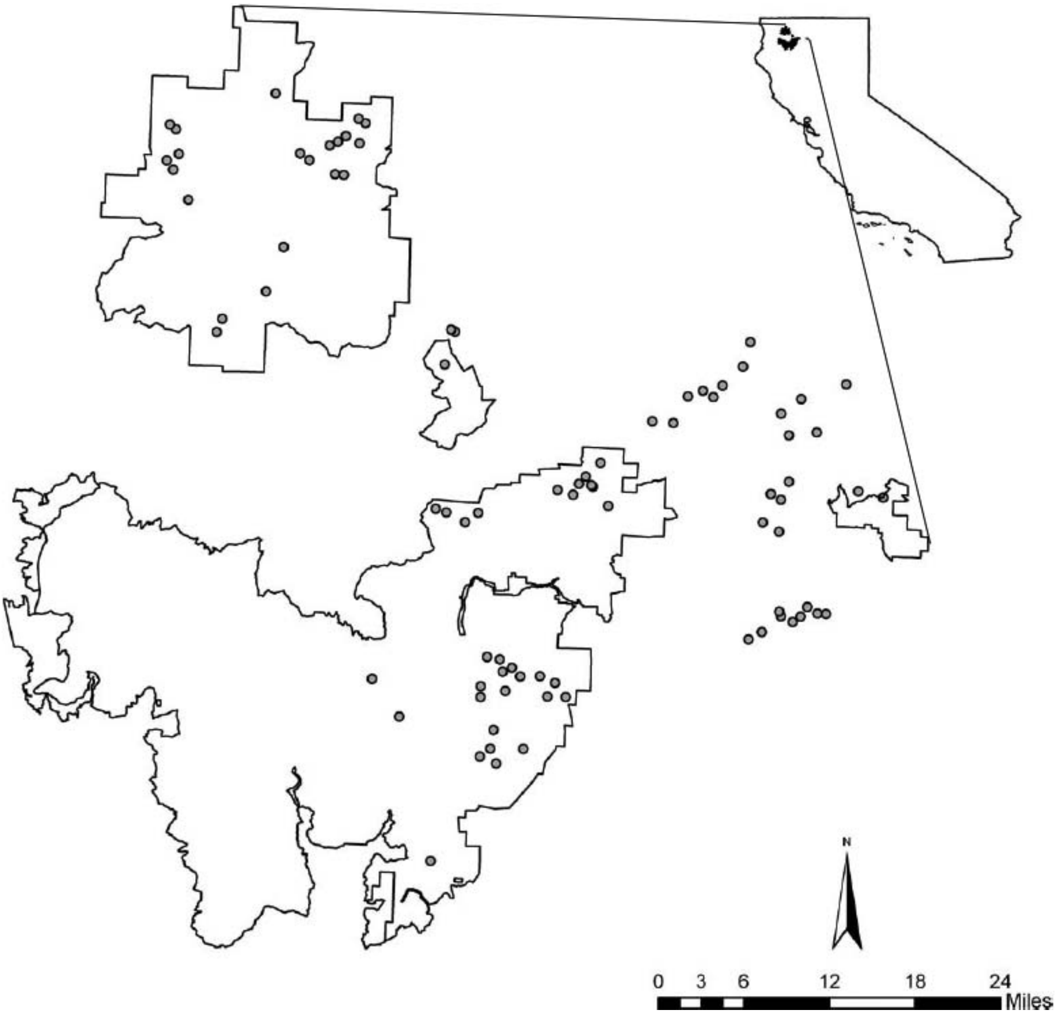



FIG. 1.—Location of wetland sites in the Klamath Mountains of Northern California (inset upper-right) with notation of wilderness area boundaries surrounding the Marble Mountain Wilderness Area (upper-left polygon), Russian Wilderness Area (middle polygon), Trinity Alps Wilderness Area (lower-left polygon), and Castle Crags Wilderness Area (lower-right polygon).

areas of metamorphic, ultramafic, and granitic rock types. Because of their diverse soil types and the geographical link between the Coast and Cascade Mountain Ranges, the mountains harbor a unique floristic region known as the Klamath–Siskiyou that supports high levels of biodiversity and endemism (Coleman and Kruckeberg, 1999; DellaSala et al., 1999).

The Klamath–Siskiyou supports the highest diversity of herpetofauna in the Pacific Northwest and includes several endemic species (Bury and Pearl, 1999). The amphibian fauna includes five lentic breeders (Cascades Frog [*Rana cascadae*], Northern Pacific Treefrog [*Pseudacris regilla*], Western Toad [*Anaxyrus boreas*], Long-toed Salamander [*Ambystoma macrodactylum*], and Rough-skinned Newt [*Taricha granulosa*]) and two stream breeders (Coastal Tailed Frog [*Ascaphus truei*] and Pacific Giant Salamander [*Dicamptodon tenebrosus*]). *Rana cascadae*, *P. regilla*, and *A. boreas* complete their development from egg to subadult over the course of a single summer season (May–

November). The native amphibian species co-occur with several nonnative species.

Trout and cattle, the focal nonnative species in our study, have a relatively long history in the region. Humans introduced cattle and trout to the Klamath Mountains over 70 yr ago. Records of cattle grazing within the Trinity Alps Mountains date back to 1911. Even after wilderness areas were established (Marble Mountain Wilderness Area [MMWA] in 1964 and Trinity Alps Wilderness Area [TAWA] in 1984), cattle grazing persisted within the Klamath–Siskiyou. Although the number of grazing allotments and cattle density was reduced by the 1970s, cattle are still granted access to over half of the ecoregion. The California Department of Fish and Wildlife started stocking trout (*Oncorhynchus mykiss*, *Salmo trutta*, and *Salvelinus fontinalis*) in the Klamath Mountains in the 1930s and the practice continues today. Although most lakes are no longer stocked, self-sustaining trout populations persist in most of the lakes and streams in the region. Cattle, trout, and native amphibian species occur syntopically across the wet meadow sites included in our study.

We surveyed 89 wet meadows, spanning elevations from 1602–2396 m, three times over the course of 2 yrs (once each between 22 June and 10 September 2010 and twice between 29 June 2011 and 16 September 2011). Over the course of each sampling period, we surveyed wet meadows in the same sequence based upon the site's elevation and aspect. Remote sensing images of the region indicate the Klamath Mountains are composed of a heterogeneous network of habitat patches comprised of coniferous forest, dry meadows, wet meadows, boulder or talus fields, lakes, and ponds (Google Earth 7.1.1.1580). To ensure that sample sites were distinct habitat units, we defined wet meadows as areas greater than 1000 $m^2$ in which the vegetation consists of a mixture of grasses, perennial herbs, rushes, and sedges and in which aquatic habitat was present. Pools were ephemeral or permanent and fed by groundwater and snowmelt inputs. We considered lakes to be water bodies larger than 1200 $m^2$ in area or 2 m in depth and did not include them in the analysis. In an effort to increase statistical independence of sites, we selected only one meadow from each natural basin. We defined basins as single drainages into major streams isolated from other such basins by well-defined ridgelines. We initially selected potential sample sites using remote sensing images (US Forest Service, 2009) and then made our final selection following field inspection to ensure that the wet meadow met the criteria described above.

### *Field Sampling*

At each wet meadow site, we evaluated amphibian species abundance (number of adult and juvenile individuals) using visual encounter surveys (VES; Crump and Scott, 1994) of linear transects across all meadow habitat. We conducted VES surveys during peak periods of amphibian activity; between 1000 and 1800 h. We recorded search time during VES and corrected the raw data to detections per hour for each species prior to analyses. Biases related to detection error are likely present in our analyses. To achieve our goal of generating a large sample size covering a broad range of sites over a large area, we compromised some of the accuracy associated with more-intensive surveys completed in a smaller number of wet meadows.

At each wet meadow, we collected data on topographic and meadow conditions that previous studies suggested might influence amphibian species assemblages including elevation, number of pools, meadow area, cattle impact, nonnative trout presence, and distance to nearest lake (Heyer, 1967; Cushman, 2006; Welsh et al., 2006; Riedel et al., 2008). We estimated the number of pools present in a meadow by counting distinct bodies of water greater than 0.10 m in depth and which persisted through all three sampling periods. We used fecal density rather than permitted number of cattle per acre to estimate the degree of cattle impact. Cattle use of grazing allotments can vary significantly with slope, season, and proximity to water sources (Tate et al., 2003) while fecal density may be a more-direct measure of local use. Because of the slow decomposition rates in high-elevation systems, fecal density in mountain meadows represents an aggregate assessment of the impact by cattle over the last 5–10 yrs (Roche et al., 2012). We evaluated fecal density (fecal pats/m$^2$) by counting fecal pats across transects spaced evenly across the entire measured meadow area. We assessed nonnative trout presence within meadows and associated bodies of water by using visual surveys and confirming with the California Department of Fish and Wildlife listings of stocked locations. We used the ruler tool on Google Earth's satellite images to determine the distance to the nearest lake.

### *Analyses*

To identify environmental variables that influence the occurrence of amphibian species in wet meadows, our analyses sought to identify potential aggregations of amphibian species, examine site factors associated with species groups across an environmental gradient, and quantify factors associated with abundance and occupancy of each of the most-common species. We first assessed normality and log-transformed values if skewness $>1$. For clustering and ordination analyses, we eliminated wet meadow sites where no amphibians were found and divided the remaining data into two sets: amphibian species abundance by site and environmental characteristics by site.

To analyze how amphibian species aggregated in groups across meadow sites, we used hierarchical clustering using Euclidean distance measures and Ward's linkage method (McCune and Grace, 2002) on the amphibian species abundance data. We inspected the cluster dendrogram and parsed it into three groups that retained over 65% of the data information. The cluster analysis suggests general patterns but does not imply statistically significant differences between groups.

Using both the amphibian species and environmental data sets, we used nonmetric multidimensional scaling (NMS) analysis to investigate how site conditions may influence amphibian species distributions. Because we measured site variables at different scales, we relativized each predictor variable by adjusting values to the standard deviation of each variable's mean value. We ran an NMS analysis using Euclidean distance measure, six starting axes, and 30 iterations. We determined the dimensionality of the data through a Monte Carlo test using random starting configurations and a scree plot indicating reduction in stress with two axes. Stress, in this case, is a measure of the poorness of fit between the species ordination and ecological distances of meadow site variables (McCune and Grace, 2002). We completed the final analysis with a single run with real data and 100 iterations using two axes and based upon Euclidean distance measures. The NMS uses the secondary data matrix to overlay a joint plot of significant site variables on the ordination of amphibian species data. The NMS analysis allowed us to determine which environmental variables are more universally important to the abundance of all the species we evaluated.

We used other analytical techniques to identify environmental variables associated with individual species. We used regression tree analysis to identify a hierarchy of significant site variables associated with abundance of the four common amphibian species. We pruned regression trees using a range of minimum deviations (0.01–0.35) and minimum node size of 10 depending on sample depth of the different species. We used PCORD (McCune and Mefford, 2006) for the clustering and NMS analyses and S-Plus (8.0) for the regression tree analysis.

Occupancy models allowed us to evaluate the environmental variables that affect abundance to such an extent that they contribute to complete exclusion of species in wet meadows. We constructed occupancy models of *R. cascadae*, *T. granulosa*, and *P. regilla* spanning the three sampling periods (once each between 22 June and 10 September 2010 and twice between 29 June 2011 and 16 September 2011) using the program PRESENCE (Hines, 2006). Setting the probability of colonization and extinction to zero, we were able to estimate the probability of detection and evaluate the importance of environmental site variables. We included nonnative trout and wilderness area as categorical covariates and elevation, number of pools, cattle impact, distance to nearest lake, and meadow area as continuous covariates of occupancy. We evaluated 125 models for each species; each model contained one to seven covariates of occupancy in every combination of environmental site variables. We used Akaike's information criterion criteria and model likelihood calculations to select the top models.

## Results

### Amphibian Species Assemblages

We found all seven species in wet meadow sites but found *Ambystoma macrodactylum* and *Ascaphus truei* at one site only and *D. tenebrosus* at two sites only. We omitted these three species from further analyses. We used the four most-common species—*R. cascadae* (present at 73 sites), *P. regilla* (55 sites), *T. granulosa* (19 sites), and *Anaxyrus boreas* (8 sites)—to perform analyses of species assemblages and single species presence and abundance across 89 wet meadow sites. We excluded *A. boreas* from regression tree analyses and occupancy modeling because of the low incidence of presence among wet meadow sites.

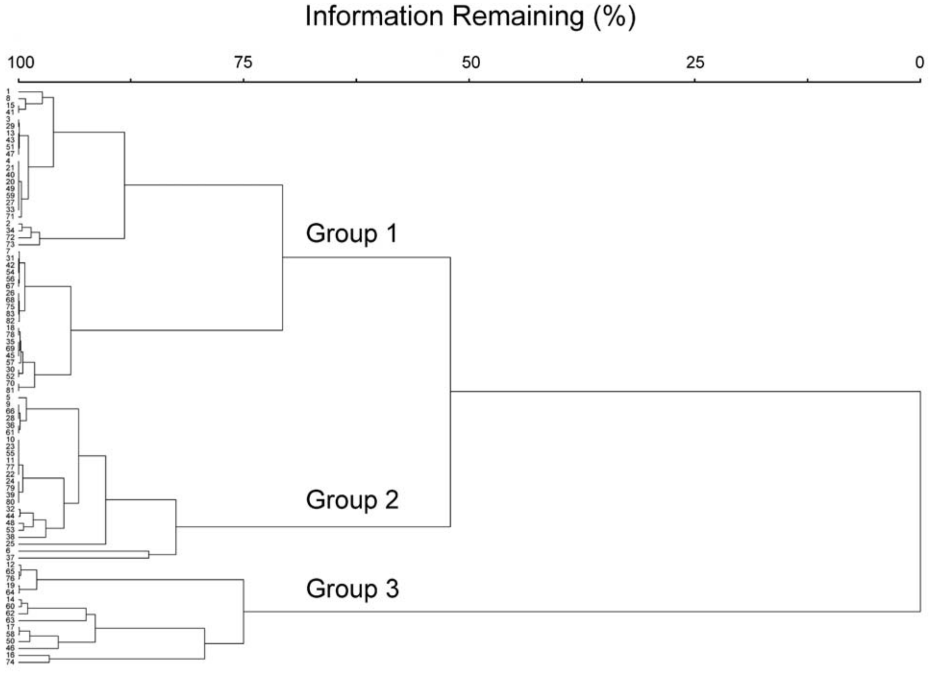
Comparing between sampling years, detections per hour did not differ for any of the four species, (*R. cascadae*, $P = 0.18$; *T. granulosa*, $P = 0.08$; *P. regilla*, $P = 0.81$; *A. boreas*, $P = 0.23$). *Pseudacris regilla* and *A. boreas* adults generally arrive at wetland sites early in the season, as snow begins to melt, and then leave shortly after breeding (Welsh et al., 2006). Comparing between sampling sessions in 2011, only *P. regilla* had higher detections per hour during the early sampling session ($P < 0.01$). As a result, we averaged detections per hour for *R. cascadae*, *T. granulosa*, and *A. boreas* across all visits and used only early season sampling for *P. regilla* for estimations of abundance in cluster, NMS, and regression tree analyses.

In the cluster analysis, classifying species assemblages into three groups explained over 60% of the variation among amphibian assemblages (Fig. 2). A relatively diverse species assemblage made up group one (the most common assemblage, at $n = 45$ sites), with *R. cascadae*, *T. granulosa*, *P. regilla*, and *A. boreas* all present in moderate abundance. *Rana cascadae*, with *A. boreas* at their highest levels of abundance, dominated group two ($n = 23$). *Taricha granulosa*, with *A. boreas* absent, dominated group three ($n = 15$).

### Environmental Variables Associated with Species Assemblages and Abundance

For the NMS ordination, we achieved the best fit between species abundance and environmental data across space using two axes (final stress = 7.15335, final instability = 0.00005). The proportion of variance (the fit between distance in the ordination and the original space) represented by the first and second axes is 0.80 and 0.18, respectively. The ordination shows a general grouping of wet meadows by the species assemblage groups identified by the cluster analysis (Fig. 3). The Bi joint analysis indicates that the elevation, number of pools, and presence of nonnative trout were important variables associated with differences in amphibian species assemblages and abundance. Group two assemblages, dominated by *R. cascadae*, tended to occur at higher elevations where the number of pools was high and nonnative trout were absent. Group three assemblages, dominated by *T. granulosa*, tended to occur in wet meadows at lower elevations where trout were present. Group one, the species assemblage with the highest diversity, occurred across the spectrum of environmental variables we measured but tended to occur most often in mid-elevation wet meadows with fewer pools where nonnative trout were absent.

When we analyzed site variables against the abundance of each of the four dominant amphibian species using regression tree analysis, each species displayed a different hierarchy of associated influences (Fig. 4). Wilderness area designation, distance to the nearest lake, and the number of pools within wet meadow site influenced *R. cascadae* abundance at wet meadows. Adult and juvenile frogs were most abundant in wet meadows located in the TAWA or sites outside of wilderness areas that were <734 m away from a lake and contained >30 pools. *Rana cascadae* was the least abundant at sites where nonnative trout were present and the number of pools was <31. Wilderness area, the number of pools and, to a lesser extent, cattle impact influenced *T. granulosa* abundance. Of the 19 wet meadows where *T. granulosa* was present, 14 were located in the MMWA. Populations of *T. granulosa* were the largest at wet meadows with high numbers of pools in




| GROUP | *Rana cascadae* | *Taricha granulosa* | *Pseudacris regilla* | *Bufo boreas* | Number of Sites |
|---|---|---|---|---|---|
| 1 | 1.579 ± 1.491 | 0.030 ± 0.199 | 0.330 ± 0.907 | 0.036 ± 0.118 | 45 |
| 2 | 11.838 ± 17.701 | 0.120 ± 0.364 | 0.141 ± 0.295 | 0.406 ± 1.946 | 23 |
| 3 | 2.819 ± 4.172 | 18.267 ± 13.819 | 0.545 ± 0.865 | 0 | 15 |

FIG. 2.—Cluster analysis on detections per hour of *Rana cascadae*, *Taricha granulosa*, *Pseudacris regilla*, and *Anaxyrus boreas* across wet meadow sites indicating amphibian assemblage groupings. Three groups explain over 65% of the information.

MMWA. Wet meadows within the MMWA were at a lower elevation (mean ±1 SD = 1829 ± 143 m) than wet meadows within the TAWA (1971 ± 139 m). The number of pools and distance to the nearest lake affected *P. regilla* abundance. *Pseudacris regilla* was the most abundant when wet meadows had >12 pools and the nearest lake was <166 m away.

Across all environmental variables, nonnative trout and the number of pools were the most-important environmental factors structuring amphibian diversity and abundance in wet meadows in the Klamath Mountains. Despite being present at only 33 of the 89 sites, nonnative trout presence showed a negative relationship with amphibian assemblages dominated by *R. cascadae* and the individual abundance of *R. cascadae*. The number of pools displayed a positive relationship with species assemblages dominated by *T. granulosa* and *R. cascadae* and the individual abundances of *P. regilla* and *T. granulosa*.

### *Environmental Variables Associated with Amphibian Occupancy*

The top occupancy models had high detection probabilities for *R. cascadae* (0.79 ± 0.03), *T. granulosa* (0.94 ± 0.04), and *P. regilla* (0.58 ± 0.05). The top-ranked models showed that occupancy of wet meadows by *R. cascadae* was positively associated with cattle and the number of pools and negatively associated with nonnative trout and the distance to the nearest lake (Table 1). Wet meadow occupancy by *T. granulosa* was positively associated with the number of pools and negatively associated with the distance to the nearest lake, elevation, and meadow area (Table 1). The top-ranked occupancy models for *P. regilla* showed that species occupancy of

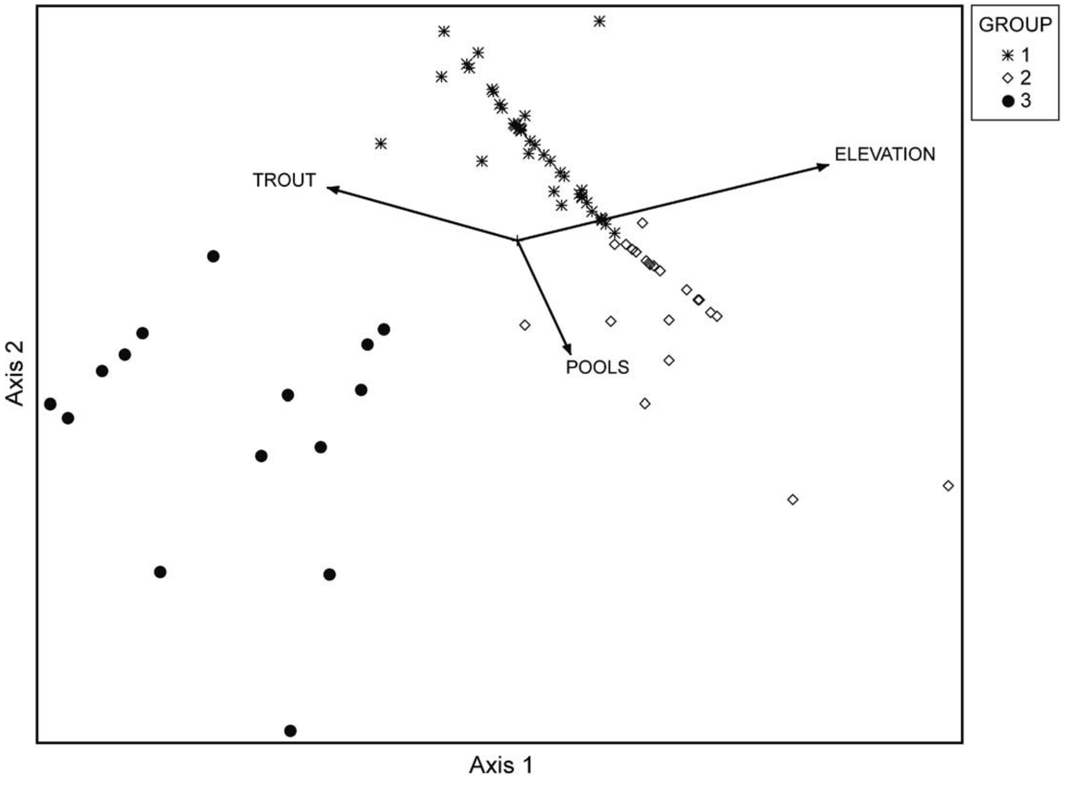



FIG. 3.—Joint plot based upon nonmetric dimensional scaling analysis indicating location of amphibian Group 1 (relatively high diversity sites where *Rana cascadae*, *Taricha granulosa*, *Pseudacris regilla*, and *Anaxyrus boreas* are present), Group 2 (dominated by *R. cascadae* with the highest abundance of *A. boreas*), and Group 3 (dominated by *T. granulosa* with the highest abundance of *P. regilla*). Bi-joint analysis indicates that elevation, presence of nonnative trout, and the number of pools are environmental variables related to amphibian assemblages in wet meadows.

wet meadows was positively associated with cattle impact, number of pools, and meadow area and negatively associated with nonnative trout and distance to the nearest lake (Table 1). Wilderness area identity influenced wet meadow occupancy by all three species; 81.7% of the wet meadows occupied by *R. cascadae* and 83.3% of the wet meadows occupied by *P. regilla* were found within the TAWA or outside wilderness areas. Of the wet meadows occupied by *T. granulosa*, most sites occurred within MMWA (75%).

## Discussion

Nonnative trout presence, the number of pools, wilderness area designation, and the distance to the nearest lake emerged as the most-important environmental factors to assemblages of subalpine amphibians in wet meadows. Contrary to our prediction that the presence of nonnative trout and degree of cattle impact would have the strongest influence on amphibian presence, diversity, and abundance, cattle impacts were only weakly associated with occupancy and abundance of some species. By contrast, nonnative trout exhibited a negative relationship with the assemblages, abundance, and occupancy of amphibian species.

Species groups were clearly delineated, and the observed patterns of species groups in wet meadows may be linked to shared species traits, in particular their palatability to nonnative trout (Welsh et al., 2006), thermal tolerance, and hydrological requirements. *Rana cascadae* (a palatable species) dominated one species assemblage while *T. granulosa* (an unpalatable species) dominated another

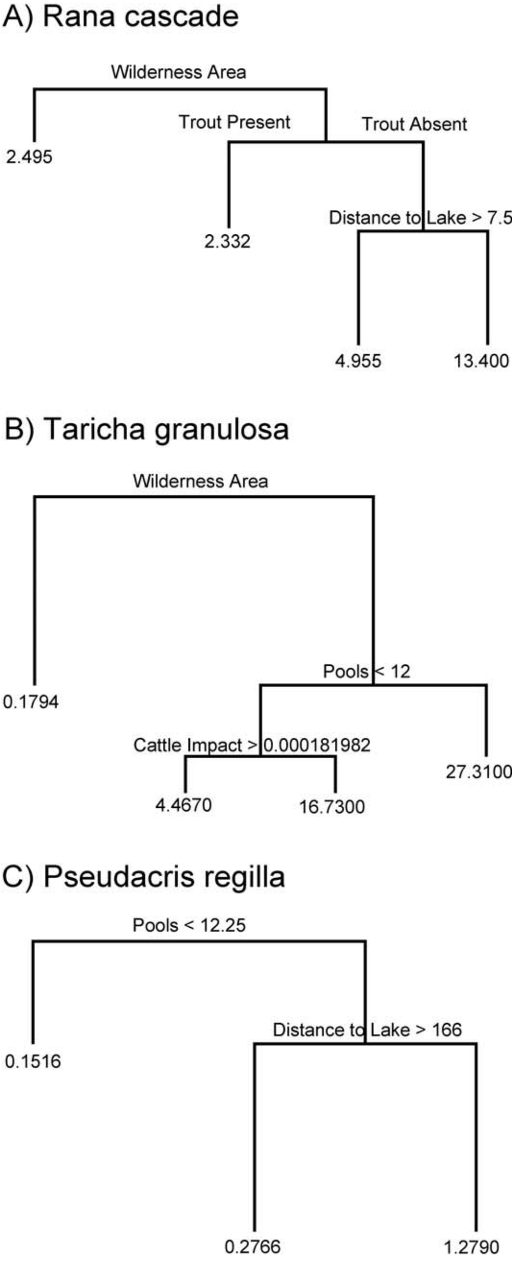



FIG. 4.—Classification and regression trees illustrating the environmental factors associated with detections per hour of individual amphibian species (A) *Rana cascadae*; (B) *Taricha granulosa*; and (C) *Pseudacris regilla*.

species group found in a different set of wet meadows. Ecological theory suggests that the range of environmental tolerances by individual species might explain the number of species found within a specific locality (Whittaker, 1960; Whittaker and Niering, 1965). Sites where more niches of particular species overlap might support higher diversity. By extension, wet meadow sites within the environmental tolerance limits of more amphibian species might be able to support higher diversity.

Within the bounds of the environmental gradient we evaluated, the species assemblage with the highest diversity occurred in wet meadows of mesic condition (mid-elevation, trout present and absent, and moderate numbers of pools). In contrast, the species groups dominated by *T. granulosa* and *R. cascadae* existed at the lower or upper range of the environmental gradient. The species group dominated by *T. granulosa* occurred at lower elevations in wet meadows with fewer pools where trout were often present, whereas the species group dominated by *R. cascadae* occurred at higher elevations in wet meadows where trout were typically absent. In general, the ordination analysis identified elevation, the presence of nonnative trout, and number of pools as the most significant variables structuring the distribution of amphibian species assemblages across subalpine wet meadows.

Some researchers have suggested that a more-focused examination of the geographic and ecological distribution of individual species, rather than species assemblages, provides a better understanding of the factors that determine species richness at local and regional scales (Heyer, 1967; Heatwole, 1982; Ricklefs, 2008). Indeed, our single species analyses of abundance and occupancy identified a greater number of important environmental variables, sometimes associated with only one species. Nonnative trout had a negative association exclusively with the abundance and occupancy of *R. cascadae*, and elevation and cattle impact had a negative association with *T. granulosa*. We identified distance to the nearest lake, wilderness area identity, and the number of pools as important environmental variables to all species.

Wet meadows with higher numbers of pools might be responsible for high abundance and occupancy in our study by providing both more overall aquatic habitat and more-isolat-

TABLE 1.—Multi-season occupancy models for *Rana cascadae*, *Taricha granulosa*, and *Pseudacris regilla* at wet meadow sites from 2010–2011. Models fixed extinction and colonization rates to zero, testing for the relative importance of environmental covariates associated with occupancy (ψ), and evaluating the probability of detection (p). Models with a likelihood greater than 50% are listed for each amphibian species.[a]

| | | Parameter estimates of covariates of occupancy (SD) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Model | Delta AIC | Wilderness area | | | Trout | Cattle | Pools | Distlake | Elevation | Area |
| | | TAWA | MMWA | Not wilderness | | | | | | |
| *R. cascadae* | | | X | | X | X | X | | | |
| Ψ(wilderness)p() | 0 | 26.01 (102191.75) | 0.84 (0.56) | 3.61 (2.51) | | | | | | |
| Ψ(wilderness + trout)p() | 0.3 | 26.01 (102191.75) | 0.84 (0.56) | 3.61 (2.51) | | | | | | |
| Ψ(wilderness + trout + cattle)p() | 0.9 | 27.64 (245074.34) | 1.46 (0.85) | 7.38 (90.52) | −1.18 (1.05) | | | | | |
| Ψ(wilderness + pools)p() | 1.1 | 26.33 (81838.63) | 2.37 (1.77) | 159.67 (10.00) | −1.94 (1.39) | 1.11 (1.38) | | | | |
| Ψ(wilderness + trout + distlake)p() | 1.1 | 25.461 (114117.45) | 1.205 (0.687) | 2.925 (1.243) | | | 1.19 (1.28) | | | |
| *T. granulosa* | | | X | | | | X | X | X | X |
| Ψ(wilderness + distlake + elev + area + pools)p() | 0 | −4.19 (1.25) | −0.18 (0.82) | −3.95 (1.22) | | | 1.51 (0.69) | −1.40 (1.00) | −1.51 (0.66) | −2.04 (1.37) |
| Ψ(wilderness + distlake + elev + pools)p() | 0.8 | −4.29 (1.29) | 0.16 (0.76) | −3.16 (0.96) | | | 1.17 (0.58) | 1.68 (1.04) | −1.09 (0.51) | |
| Ψ(wilderness + elev + area + pools)p() | 0.9 | −3.74 (1.09) | 0.30 (0.68) | −3.74 (1.13) | | | 1.13 (0.58) | | −1.44 (0.63) | −2.35 (1.34) |
| *P. regilla* | | | X | | X | X | | X | | X |
| Ψ(wilderness + distlake + cattle)p() | 0 | 11.89 (7.01) | 0.24 (1.77) | 26.47 (17.87) | | 9.57 (5.75) | | −7.14 (4.3) | | |
| Ψ(wilderness + distlake + area + cattle)p() | 0.6 | 11.17 (6.24) | 0.93 (1.84) | 23.18 (13.70) | | 9.18 (5.26) | | −6.57 (3.56) | | 1.82 (1.41) |
| Ψ(wilderness + distlake + pools + trout)p() | 1.2 | 4.19 (2.28) | 0.21 (0.96) | 11.91 (6.67) | −1.89 (1.40) | | 2.63 (1.60) | −3.64 (1.79) | | |

[a] AIC = Akaike's information criterion; TAWA = Trinity Alps Wilderness Area; MMWA = Marble Mountain Wilderness Area.

ed aquatic habitat, thereby relieving predation pressure and competitive stress. Even though nonnative trout exhibited a negative correlation with abundance and occupancy of *R. cascadae*, this predator did not completely exclude the palatable amphibian species from wet meadows where trout were present. Other studies have shown that pools provide breeding habitat, refuge from predators, and food resources—functions strongly linked to amphibian survival and persistence (Semlitsch, 2000).

Our findings are consistent with previous work that indicates the importance of habitat isolation and connectivity for amphibian patch occupancy and population size (Knapp et al., 2003; Cushman, 2006). *Taricha granulosa*, *R. cascadae*, and *P. regilla* were less likely to occur in wetland sites farther away from lakes, and the population sizes of *R. cascadae* and *P. regilla* were smaller at wetland sites farther away from lakes. Even for highly mobile species like *R. cascadae* and *P. regilla* (Reimchen, 1991; Garwood, 2009), spatial limitations influence population dynamics.

In most cases land use designations, especially the establishment of protected areas, affect the population status of native species (Chape et al., 2005). National forest wilderness areas offer habitat protection by prohibiting the maintenance of permanent roads and use of motorized vehicles. In our study, however, wet meadow occurrence inside or outside of wilderness area boundaries did not have an impact on amphibian abundance and occupancy overall. The identity of the wilderness area (i.e., MMWA vs. TAWA) was significant in many of our analyses, likely because some of the amphibian species were distributed unevenly across wilderness areas. Unequal distribution patterns may be associated with elevation and other environmental attributes. For example, *T. granulosa* occurred mostly in the MMWA, elevation was a significant predictor of *T. granulosa* occupancy, and the Marble Mountain range is generally not as high as the Trinity Alps mountain range. The importance of wilderness area identity is likely caused by amphibian responses to environmental differences inherent to each wilderness area rather than to legally designated boundaries within public lands.

Contrary to our prediction, cattle impact was not negatively associated with amphibian assemblages, abundance, or occupancy. Our results support another study reporting no association between cattle grazing and amphibians in wet meadows (Roche et al., 2012). In high-elevation meadows in the Sierra Nevada Mountains, overlapping use of meadow habitat by cattle and Yosemite Toad (*Anaxyrus canorus*) was minimized by differences in habitat preference, e.g., cattle preferring to forage in drier meadows while *A. canorus* was more abundant in wetter sites (Roche et al., 2012). In the Klamath Mountain sites, we observed temporal separation of meadow use. Ranchers did not release cattle into meadows to forage until after most amphibian eggs had hatched. Larval, juvenile, and adult amphibians are mobile and might be less vulnerable to habitat disturbance caused by cattle. Cattle feces may, in fact, increase meadow site productivity and the food resources available to amphibians. We observed *R. cascadae* larvae feeding on cattle feces (EMC, personal observation). Although we found cattle grazing impact did not influence population abundance or species assemblages, our research did not evaluate potential impacts over longer temporal scales.

Longer-term changes in habitat quality caused by climate change and cattle grazing might affect the status of amphibian populations in wet meadows in the future. Hydroperiod influences amphibian species richness and composition in wetland habitat (Pechmann et al., 1989; Skelly et al., 1999; Snodgrass et al., 2000). Cattle increase sedimentation and, over time, could eliminate pools important for amphibian breeding and larval survival. Climate change might also reduce hydroperiod length and the existence of wet meadow pools. Elimination of wet meadow pools with an appropriate hydroperiod might reduce wet meadow occupancy and the amount of habitat available to Klamath Mountain amphibians.

The potential to preserve the species richness of Klamath Mountain amphibians in wet meadows is time sensitive. *Rana cascadae* is listed as a species of special concern in

California and has experienced significant population declines in the southeast portion of its range (Fellers and Drost, 1993; Fellers et al., 2008). A growing body of literature has identified threats to the persistence of Klamath Mountain amphibians. In addition to nonnative trout, a fungal pathogen responsible for rapid population declines in amphibians threatens amphibians in the Klamath Mountains. *Batrachochytrium dendrobatidis* has been identified in all species and regions in the Klamath Mountains (Piovia-Scott et al., 2011).

Our research indicates that any conservation management plans for Klamath Mountain wet meadows should consider the amphibian species that live there and attempt to develop policies that focus on restoring and protecting wet meadows and fens that have high numbers of pools free of nonnative trout. Studies have shown there is rapid population expansion of native frog species following experimental removal of nonnative trout (Knapp et al., 2007; Pope, 2008). Extirpation of nonnative trout in wet meadows presents a formidable challenge because of the complexity of aquatic habitat. It might be best to invest limited resources in the protection of meadows with high-quality breeding habitat or by establishing artificial pools. Our ranking of the environmental variables associated with amphibian abundance and occupancy in wet meadows might help managers more effectively conserve a threatened group of species in the Klamath Mountains.

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## Literature Cited

Bailey, L.L., T.R. Simons, and K.H. Pollock. 2004. Estimating site occupancy and species detection probability parameters for terrestrial salamanders. Ecological Applications 14:692–702.

Bedford, B.L., and K.S. Godwin. 2003. Fens of the United States: Distribution, characteristics, and scientific connection versus legal isolation. Wetlands 23:608–629.

Beebee, T.J.C., and R.A. Griffiths. 2005. The amphibian decline crisis: a watershed for conservation biology? Biological Conservation 125:271–285.

Blaustein, A.R., and J.M. Kiesecker. 2002. Complexity in conservation: lessons from the global decline of amphibian populations. Ecology Letters 5:597–608.

Bradford, D.F., F. Tabatabai, and D.M. Graber. 1993. Isolation of remaining populations of the native frog, *Rana muscosa*, by introduced fishes in Sequoia and Kings Canyon National Parks, California. Conservation Biology 7:882–888.

Bury, R.B., and C.A. Pearl. 1999. The Klamath–Siskiyou herpetofauna: Biogeographic patterns and conservation strategies. Natural Areas Journal 19:341–348.

California Department of Water Resources. 2014. Available at http://cdec.water.ca.gov/. Archived by WebCite at http://www.webcitation.org/6MYGeEAeg on 11 January 2014.

Chape, S., J. Harrison, M. Spalding, and I. Lysenko. 2005. Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. Philosophical Transactions of the Royal Society – B Biological Sciences 360:443–455.

Chapman, L.J., C.A. Chapman, R. OgutuOhwayo, M. Chandler, L. Kaufman, and A.E. Keiter. 1996. Refugia for endangered fishes from an introduced predator in Lake Nabugabo, Uganda. Conservation Biology 10:554–561.

Coleman, R.G., and A.R. Kruckeberg. 1999. Geology and plant life of the Klamath–Siskiyou mountain region. Natural Areas Journal 19:320–340.

Collins, S.L., A.K. Knapp, J.M. Briggs, J.M. Blair, and E.M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280:745–747.

Crump, M.L., and N.J.J. Scott. 1994. Visual encounter surveys. Pp. 84–91 *In* W.R. Heyer, M.A. Donnelly, R.W. McDiarmid, L.A.C. Hayek, and M.S. Foster (Eds.), Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, USA.

Cushman, S.A. 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. Biological Conservation 128:231–240.

DellaSala, D.A., S.B. Reid, T.J. Frest, J.R. Strittholt, and D.M. Olson. 1999. A global perspective on the biodiversity of the Klamath–Siskiyou ecoregion. Natural Areas Journal 19:300–319.

Fellers, G.M., and C.A. Drost. 1993. Disappearance of the Cascades Frog *Rana cascadae* at the southern end of its range, California, USA. Biological Conservation 65:177–181.

Fellers, G.M., K.L. Pope, J.E. Stead, M.S. Koo, and H.H. Welsh. 2008. Turning population trend monitoring into active conservation: Can we save the Cascades Frog (*Rana cascadae*) in the Lassen region of California? Herpetological Conservation and Biology 3:28–39.

Fleischner, T.L. 1994. Ecological costs of livestock grazing in western North America. Conservation Biology 8:629–644.

Garwood, J. 2009. Spatial Ecology of the Cascades Frog: Identifying Dispersal, Migration, and Resource Uses at Multiple Spatial Scales. M.S. Thesis, Humboldt State University, California, USA.

Gillespie, G.R. 2001. The role of introduced trout in the decline of the spotted tree frog (*Litoria spenceri*) in south-eastern Australia. Biological Conservation 100:187–198.

Gustafson, M.P. 1994. Size-specific interactions among larvae of the plethodontid salamanders *Gyrinophilus porphyriticus* and *Eurycea cirrigera*. Journal of Herpetology 28:470–476.

Heatwole, H. 1982. A review of structuring in herpetofaunal assemblages. Pp. 1–19 *In* N.J. Scott, Jr. (Ed.), Herpetological Communities. U.S. Fish and Wildlife Service, Wildlife Research Report 13. U.S. Deptartment of the Interior, USA.

Heyer, W.R. 1967. A herpetofaunal study of ecological transect through the Cordillera de Tilaran, Costa Rica. Copeia 1967:259–271.

Hines, J.E. 2006. PRESENCE—Software to estimate patch occupancy and related parameters. Available at http://www.mbr-pwrc.usgs.gov/software/presence.html. USGS-PWRC. Archived by WebCite at http://www.webcitation.org/6HCglzh89 on 7 June 2013.

Hoverman, J.T., M.J. Gray, D.L. Miller, and N.A. Haislip. 2012. Widespread occurrence of ranavirus in pond-breeding amphibian populations. Ecohealth 9:36–48.

Jansen, A., and M. Healey. 2003. Frog communities and wetland condition: Relationships with grazing and domestic livestock along an Australian floodplain river. Biological Conservation 109:207–219.

Knapp, R.A., D. Bioano, and V.T. Vredenburg. 2007. Removal of nonnative fish results in population expansion of a declining amphibian (Mountain Yellow-legged Frog, *Rana muscosa*). Biological Conservation 135:11–20.

Knapp, R.A., K.R. Matthews, H.K. Preisler, and R. Jellison. 2003. Developing probabilistic models to predict amphibian site occupancy in a patchy landscape. Ecological Applications 13:1069–1082.

Maestas, J.D., R.L. Knight, and W.C. Gilgert. 2003. Biodiversity across a rural land-use gradient. Conservation Biology 17:1425–1434.

McCune, B., and J.B. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, USA.

McCune, B., and M.J. Mefford. 2006. PC-ORD. Multivariate Analysis of Ecological Data. Version 5.31. MjM Software, USA.

McKenzie, V.J. 2007. Human land use and patterns of parasitism in tropical amphibian hosts. Biological Conservation 137:102–116.

Moreno-Mateos, D., M.E. Power, F.A. Comin, and R. Yockteng. 2012. Structural and functional loss in restored wetland ecosystems. PLOS Biology 10:e1001247.

Morgan, J.A.T., V.T. Vredenburg, L.J. Rachowicz, R.A. Knapp, M.J. Stice, T. Tunstall, R.E. Bingham, J.M. Parker, J.E. Longcore, C. Mortitz, C.J. Briggs, and J.W. Taylor. 2007. Population genetics of the frog-killing fungus *Batrachochytrium dendrobatidis*. Proceedings of the National Academy of Sciences (USA) 104:13845–13850.

Pechmann, J.H.K., D.E. Scott, J.W. Gibbons, and R.D. Selitsch. 1989. Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. Wetlands Ecology and Management 1:3–11.

Piovia-Scott, J., K.L. Pope, S.P. Lawler, E.M. Cole, and J.E. Foley. 2011. Distribution of the fungal pathogen *Batrachochytrium dendrobatidis* in the Cascades Frog (*Rana cascadae*) and other amphibians in the Klamath Mountains. Biological Conservation 144:2913–2921.

Pister, E.P. 2001. Wilderness fish stocking: History and perspective. Ecosystems 4:279–286.

Pope, K.L. 2008. Assessing changes in amphibian population dynamics following experimental manipulations of introduced fish. Conservation Biology 22:1572–1581.

Pyke, C.R., and J. Marty. 2005. Cattle grazing mediates climate change impacts on ephemeral wetlands. Conservation Biology 19:1619–1625.

Reimchen, T.E. 1991. Introduction and dispersal of the Pacific Treefrog, *Hyla regilla*, on the Queen Charlotte Islands, British Columbia. Canadian Field Naturalist 105:288–290.

Ricklefs, R.E. 2008. Disintegration of the ecological community. American Naturalist 172:741–750.

Riedel, B.L., K.R. Russell, W.M. Ford, K.P. O'Neill, and H.W. Godwin. 2008. Habitat relationships of Eastern Red-backed Salamanders (*Plethodon cinereus*) in Appalachian agroforestry and grazing systems. Agriculture, Ecosystems and Environment 124:229–236.

Roche, L.M., A.M. Latimer, D.J. Eastburn, and K.W. Tate. 2012. Cattle grazing and conservation of a meadow-dependent amphibian species in the Sierra Nevada. PlosONE 7:1–11.

Semlitsch, R.D. 2000. Principles for management of aquatic-breeding amphibians. Journal of Wildlife Management 64:615–631.

Sjogren, P. 1991. Extinction and isolation gradients in metapopulations: The case of the Pool Frog (*Rana lessonae*). Biological Journal of Linnean Society 42:135–147.

Skelly, D.K., E.E. Werner, and S.A. Cortwright. 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. Ecology 80:2326–2337.

Skinner, C.N., A.H. Taylor, and J.K. Agee. 2006. Klamath Mountains bioregion. Pp. 170–194 *In* N.G. Sugihara, J.W. van Wagtendonk, J. Fites-Kaufman, K.E. Shaffer, and A.E. Thode (Eds.), Fire in California's Ecosystems. University of California Press, USA.

Snodgrass, J.W., M.J. Komoroski, A.L. Bryan, and J. Burger. 2000. Relationships among isolated wetland size, hydroperiod, and amphibian species richness: Implications for wetland regulations. Conservation Biology 14:414–419.

Stuart, S.N., J.S. Chanson, N.A. Cox, B.E. Young, A.S. Rodrigues, D.L. Fischman, and R.W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783–1786.

Tate, K.W., E.R. Atwill, N.K. McDougald, and M.R. George. 2003. Spatial and temporal patterns of cattle feces deposition on rangeland. Journal of Range Management 56:432–438.

Urban, M.C. 2004. Disturbance heterogeneity determines freshwater metacommunity structure. Ecology 85:2971–2978.

US Forest Service. 2009. Geodata Clearinghouse. Available at http://fsgeodata.fs.fed.us/index.php. Archived by WebCite at http://www.webcitation.org/6HChlqAOT on 7 June 2013.

Welsh, H.H., K.L. Pope, and D. Boiano. 2006. Sub-alpine amphibian distributions related to species palatability to nonnative salmonids in the Klamath Mountains of northern California. Diversity and Distributions 12:298–309.

Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30:280–338.

Whittaker, R.H., and W.A. Niering. 1965. Vegetation of the Santa Catalina Mountains, Arizona: A gradient analysis of the south slope. Ecology 46:429–452.

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