

Amphibians in the climate vise: loss and restoration of resilience of montane wetland ecosystems in the western US

Maureen E Ryan^{1,2*}, Wendy J Palen², Michael J Adams³, and Regina M Rochefort⁴

Wetlands in the remote mountains of the western US have undergone two massive ecological “experiments” spanning the 20th century. Beginning in the late 1800s and expanding after World War II, fish and wildlife managers intentionally introduced millions of predatory trout (primarily *Oncorhynchus* spp) into fishless mountain ponds and lakes across the western states. These new top predators, which now occupy 95% of large mountain lakes, have limited the habitat distributions of native frogs, salamanders, and wetland invertebrates to smaller, more ephemeral ponds where trout do not survive. Now a second “experiment” – anthropogenic climate change – threatens to eliminate many of these ephemeral habitats and shorten wetland hydroperiods. Caught between climate-induced habitat loss and predation from introduced fish, native mountain lake fauna of the western US – especially amphibians – are at risk of extirpation. Targeted fish removals, guided by models of how wetlands will change under future climate scenarios, provide innovative strategies for restoring resilience of wetland ecosystems to climate change.

Front Ecol Environ 2014; 12(4): 232–240, doi:10.1890/130145

Wetland ecosystems in the mountains of western North America are biologically rich and situated in some of the most culturally iconic and protected landscapes on Earth. Diverse in form (eg wet meadows, bogs, fens, snowmelt ponds, perennial ponds, deep lakes) and function, montane wetlands provide both habitat for a wide range of species and ecosystem services such as water storage, nutrient cycling, and carbon sequestration. Despite high levels of protection, wetland ecosystems in the western mountains have been subjected to two massive ecological “experiments” over the past 150 years: the widespread introduction of non-native fishes to formerly

fishless waterbodies and contemporary climate change (Bahls 1992; Knapp *et al.* 2001; Hamlet *et al.* 2007). For native amphibians and invertebrates that rely on montane wetlands as breeding and rearing habitat, the combined effect of these two forces is akin to a vise. In deep lakes, predation by non-native fishes excludes many native species from otherwise viable habitat. Meanwhile, new hydrologic models suggest that many shallow wetlands are likely to disappear or become unsuitable habitat for native amphibians and invertebrates in future climates (Lee *et al.* in review). Between these two pressures, amphibians, invertebrates, and other native species could be left without viable habitat (Lacan *et al.* 2008), resulting in extensive biodiversity loss and amplifying the overall pattern of heightened amphibian declines in protected areas (Adams *et al.* 2003, 2013; Stuart *et al.* 2004). In the face of these challenges, targeted climate adaptation efforts (ie management actions that help ecosystems adapt to a changing climate) offer a way to loosen the vise on wetland ecosystems that are otherwise likely to vanish.

The first “experiment” began in the late 1800s with the widespread introduction of predatory fish (primarily *Oncorhynchus* spp) throughout formerly fishless mountain landscapes (Bahls 1992; Knapp *et al.* 2001). Receding Pleistocene glaciers created mountain ponds and lakes that were isolated from natural recolonization by fish, and that came to be dominated by amphibians and other aquatic species that thrive in fishless habitats (Knapp *et al.* 2001). Introductions of fish from lower elevations began piecemeal with individual human settlers, who carried fingerling trout into the mountains in waterproof canvas packs and released them into high-elevation lakes and streams to create opportunities for fishing (Knapp *et al.* 2001). The geographic scope of these stocking efforts esca-

In a nutshell:

- Introduced fish (mostly trout and other salmonids) exclude amphibians and other native species from large “climate-resistant” ponds and lakes in mountainous areas of the western US
- Shallow fish-free wetlands used by native species are disproportionately vulnerable to climate-induced drying
- Interactions between climate change and introduced fish are an underappreciated source of native biodiversity loss in wetlands
- Targeted fish removals offer a proactive approach for restoring wetland ecosystem resilience to climate change in regions at high risk for extinctions
- Newly developed wetland modeling tools can improve climate adaptation action plans that help ecosystems maintain local and regional resilience in the face of a changing climate

¹School of Environment and Forest Sciences, University of Washington, Seattle, WA (*moryan@u.washington.edu); ²Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, Canada; ³US Geological Survey Forest and Rangeland Ecosystem Science Center, Corvallis, OR; ⁴North Cascades National Park Complex, Sedro-Woolley, WA

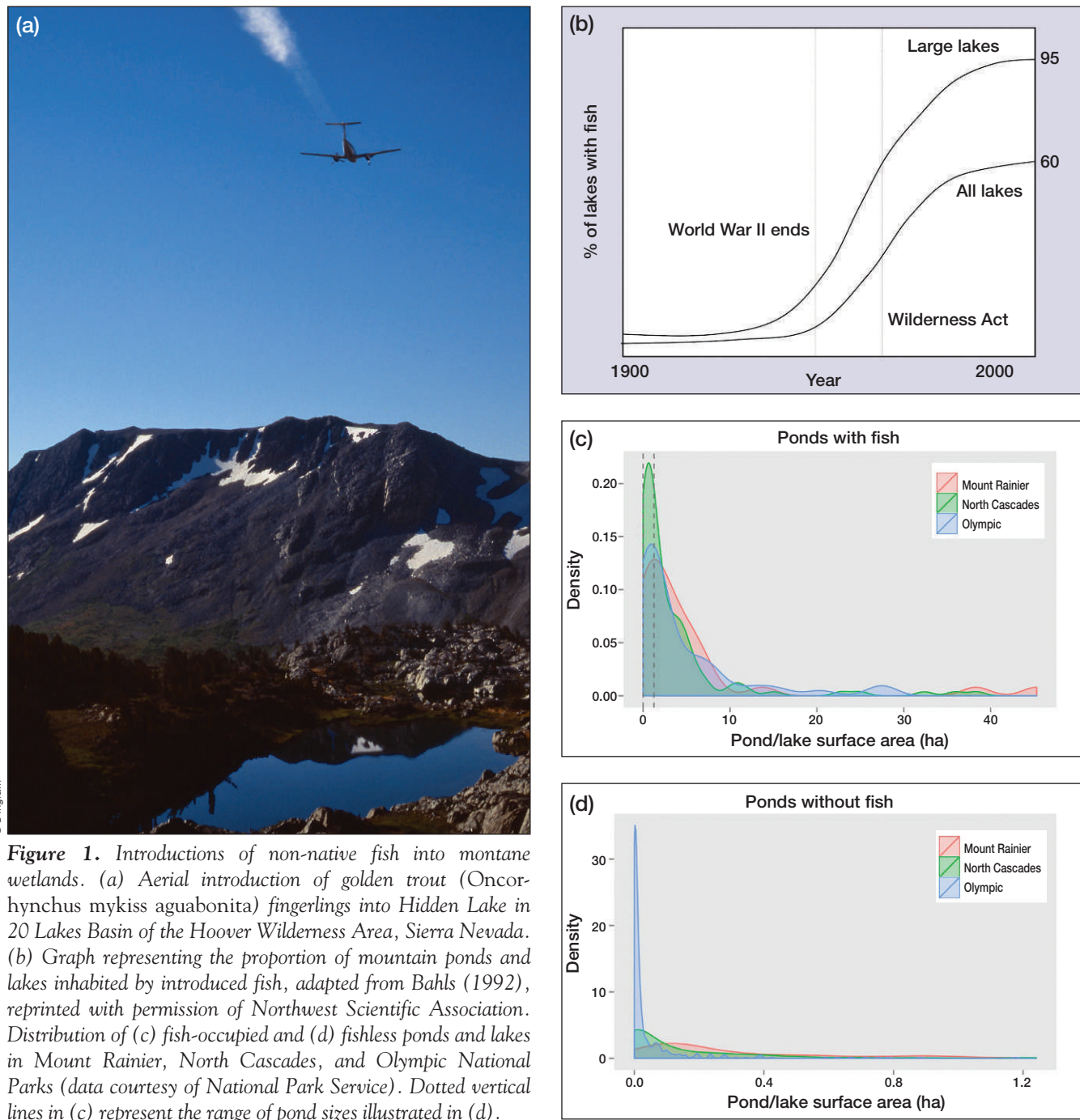


Figure 1. Introductions of non-native fish into montane wetlands. (a) Aerial introduction of golden trout (*Oncorhynchus mykiss aguabonita*) fingerlings into Hidden Lake in 20 Lakes Basin of the Hoover Wilderness Area, Sierra Nevada. (b) Graph representing the proportion of mountain ponds and lakes inhabited by introduced fish, adapted from Bahls (1992), reprinted with permission of Northwest Scientific Association. Distribution of (c) fish-occupied and (d) fishless ponds and lakes in Mount Rainier, North Cascades, and Olympic National Parks (data courtesy of National Park Service). Dotted vertical lines in (c) represent the range of pond sizes illustrated in (d).

lated dramatically in the 1940s with the beginning of government-agency-sponsored aerial fish stocking (Figure 1, a and b) to promote recreational fishing and use of back-country areas (Bahls 1992; Knapp *et al.* 2001). While many agencies ended stocking programs by the 1980s, it continues today in select regions.

The introduction of trout and other non-native fish species profoundly altered the biological structure and function of aquatic ecosystems through intense predation on native aquatic species, resulting in alterations to food web and nutrient dynamics (Knapp *et al.* 2001; Schindler *et al.* 2001; Kats and Ferrer 2003). The ascent and decline of agency-led fish stocking, followed by recent efforts to

remove introduced fish in some areas, provides an interesting case study, not only of the biological effects of species introductions but also of the evolving values that underlie environmental management and decision making.

The second “experiment” is anthropogenic climate change, which is imposing broad shifts in thermal environments and summer water availability. Montane wetlands are among the most sensitive ecosystems to an altered climate (Burkett and Kusler 2000), and predicted changes in temperature and precipitation regimes are expected to combine to alter the distribution and persistence of wetlands in alpine regions (Mote *et al.* 2005; IPCC 2007).

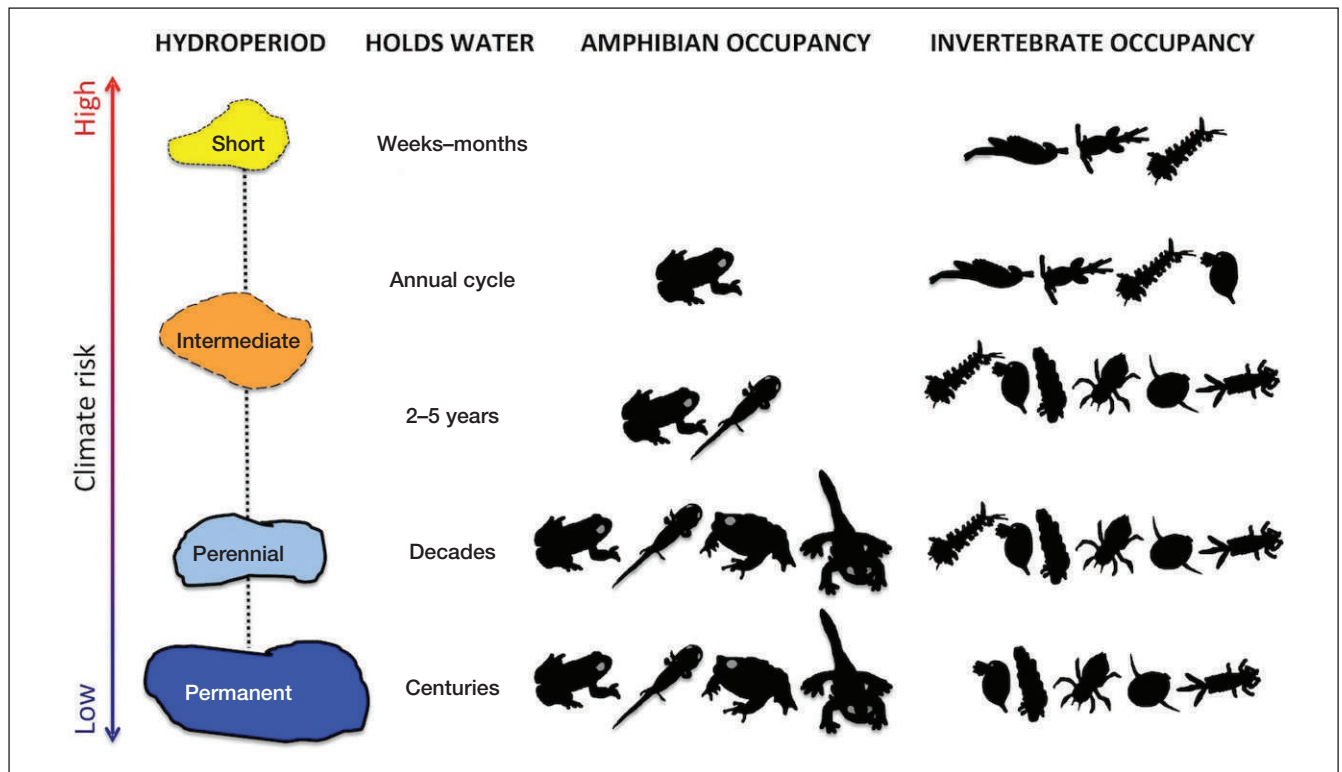


Figure 2. Projected climate risk and species occupancy across a gradient of hydroperiods in ponds and lakes without fish. Organism icons serve as examples of dominant species present in each pond type. Icons for perennial ponds represent (left to right): Cascades frog, long-toed salamander, western toad, northwestern salamander, mosquito larva, cladoceran, caddisfly larva, dragonfly larva, beetle, and mayfly larva. Shorter hydroperiod ponds also include icons for fairy shrimp and copepods.

The risk of habitat and biodiversity loss due to the combined effects of climate change and fish introductions may be overlooked because these remote ecosystems are understudied. In most montane landscapes, even the most basic information about locations and attributes of individual wetlands is sporadic at best. Even more uncommon are time series of the physical, chemical, and biological dynamics of montane wetlands (and in many cases, wetlands in general) that could be used to assess historical variability and forecast future impacts of a changing climate. As a result, few tools exist to support wetland management or to inform climate adaptation strategies. What is the magnitude and distribution of vulnerability of montane wetland ecosystems to climate change? Has the presence of introduced fish eroded the natural capacity of montane wetland ecosystems and species to persist or adapt? What are the associated consequences for biodiversity? Where are the risk hotspots located? And most importantly, what can be done to prevent ecological losses? Here we summarize risks, current research, and strategies for adaptation.

■ Patterns of biodiversity in montane wetlands of the western US

Due to recent glaciation, steep topography, and geographic barriers to upstream fish dispersal (Knapp *et al.* 2001), the majority of montane wetlands in the western

US were historically devoid of fishes. Native wetland communities in many areas of the region are therefore composed primarily of amphibians, aquatic macroinvertebrates, and zooplankton, with occasional use by waterfowl (eg dipper [*Cinclus mexicanus*], goldeneye [*Bucephala clangula*]), mammals (eg beaver [*Castor canadensis*], otter [*Lontra canadensis*], mink [*Neovison vison*], elk [*Cervus elaphus*], shrews [*Sorex* spp], coyote [*Canis latrans*]), and reptiles (eg garter snakes [*Thamnophis* spp]). Aquatic species and assemblages have historically sorted along a gradient of life histories that represent adaptations for coping with the highly dynamic nature of wetland depth, duration of inundation, and nutrient supply.

Wetlands in general are dynamic in a wide variety of ways, exhibiting periodic variations in the volume, temperature, dissolved chemistry, optical transparency, and permanency of water. Wetland hydroperiod – the timing and permanency of inundation – is among the strongest filters for species persistence relative to other attributes. In montane wetlands, water permanence and the periodicity of drying set important ecological thresholds that determine which species can breed or exist at a given site, based on their life history and developmental requirements (Wellborn *et al.* 1996). The commonalities among species life histories in the presence of these thresholds allow for classification of montane wetlands into semi-discrete ecological types (Figure 2). Similar ecological filters can be observed in lower elevation wetlands, but the

greater sensitivity of montane regions to climate change makes widespread ecological transitions likely at higher elevations (Lee *et al.* in review).

Ephemeral or seasonally available montane ponds provide habitat primarily for fast-developing species that metamorphose into terrestrial or aerial stages, or those with desiccation-resistant eggs (eg Culicidae, Branchiopoda, some hemipterans, copepods, cladocerans, Pacific chorus frog [*Pseudacris regilla*]). Hydrologically intermediate ponds that hold water in most years but may occasionally dry up support these same species, in addition to some ranid frogs (eg Cascades frog [*Rana cascadae*], Columbia spotted frog [*Rana luteiventris*]). Perennial ponds that nearly always remain inundated but the volume of which fluctuates widely allow for a broader range of species, including those with life histories that require multiple years to complete larval development in montane environments (eg perennial trichopterans, long-toed salamander [*Ambystoma macrodactylum*], rough-skinned newt [*Taricha granulosa*], mountain yellow-legged frogs [*Rana muscosa* and *Rana sierrae*]). Permanent ponds provide habitat for the broadest potential range of species, including those with obligate or facultative aquatic adult stages (eg northwestern salamander [*Ambystoma gracile*], tiger salamander [*Ambystoma tigrinum*], Gerridae, Corixidae, Notonectidae, Trichoptera). Gradients in predation are also associated with these hydrologic characteristics and co-determine the distribution of species across habitat types (Wellborn *et al.* 1996; Snodgrass *et al.* 2000). For example, the presence of large salamanders or predatory dragonfly larvae may reduce larval survival of smaller amphibians, resulting in avoidance of such habitats for breeding and rearing by these species (Adams *et al.* 2003; Hoffman *et al.* 2003).

Habitat diversity is a key factor in maintaining high levels of regional biodiversity (Chesson 2000; Whittaker *et al.* 2001). In addition, pond-breeding amphibians and invertebrates are adapted to fluctuating environments in ways that enhance their natural resilience (Hairston *et al.* 1996). Life history traits such as large clutch sizes (eg amphibians) and high rates of dispersal (eg invertebrates) allow for rapid recolonization of sites when local extinctions occur (Drake and Naiman 2000; Hanski and Gaggiotti 2004; Knapp *et al.* 2005). Long-lived adults and species with large clutch sizes (eg amphibians) or robust egg banks that can withstand cold or drought (eg invertebrates) also demographically buffer populations, allowing them to persist through poor years and rebound quickly when conditions improve (Hairston *et al.* 1996; Chesson 2000). The combination of habitat diversity and life histories adapted to high environmental variability has allowed mountain lake fauna to persist up to now.

■ Fish introductions erode natural resilience of wetlands

As a result of the government-sponsored drive to create recreational fishing opportunities in montane areas, trout and other salmonids now occupy roughly 95% of large

mountain lakes and 60% of smaller ponds and lakes in formerly fishless areas of the western US (Bahls 1992). Trout do not survive in warm, shallow wetlands that are subject to occasional or frequent drying but they do persist as self-sustaining populations in many deep permanent ponds and lakes, even after stocking has ceased (Figure 1c; Armstrong and Knapp 2004).

Trout are voracious predators of native wetland fauna such as amphibians, invertebrates, and plankton. Where trout or other introduced fish are present, many native species are excluded and entire ecosystems are dramatically altered (Knapp *et al.* 2001; Schindler *et al.* 2001). For amphibians, predation pressure by fish on all but the most toxic species (western toad [*Anaxyrus boreas*] and rough-skinned newt) is high in permanent ponds and lakes, which often leads to a marked absence of amphibians in ponds where fish occur (Knapp *et al.* 2001; Pilliod *et al.* 2010). In some cases, fish predation has contributed to endangered species listings (eg southern mountain yellow-legged frog [*R. muscosa*], Sierra Nevada yellow-legged frog [*R. sierrae*]).

Fish introductions often initiate trophic cascades – shifts in the relative abundance of organisms at different levels of the food web (eg fewer amphibians, aquatic insects, and large zooplankton; greater phytoplankton biomass). These changes affect primary productivity and ecosystem functions such as nutrient cycling and provisioning of food and habitat for wildlife (Schindler *et al.* 2001; Kats and Ferrer 2003). The effects of fish introductions also extend to terrestrial ecosystems since predation on aquatic invertebrates reduces food for alpine birds, such as rosy-finches (*Leucosticte* spp), that rely on invertebrate larvae in mountain lakes (Epanchin *et al.* 2010). Reduced numbers of amphibian metamorphs also limit food for mesopredators such as small mammals and snakes (Eby *et al.* 2006). Because of the efficiency with which fish are able to exploit aquatic prey in montane lakes and ponds that are relatively simple in structure, fish – even when present at low densities – can effectively exclude prey species (Knapp *et al.* 2001; Schindler *et al.* 2001). As a result, local distributions of native species have in many cases become restricted to shallower habitats where fish are unable to persist (Bahls 1992). Most montane wetland species have shown little capacity for adaptive response to introduced fish aside from avoidance (Knapp *et al.* 2001), suggesting limited capacity to evolve sufficient defenses if populations are forced by climate-induced habitat loss to use ponds and lakes co-occupied by fish.

■ Vulnerability of montane wetland species to the combined effects of climate change and fish

Globally, wetland ecosystems are among the most sensitive to climate change, and their vulnerability is amplified at high elevations (Carpenter *et al.* 1992; Burkett and Kusler 2000; IPCC 2007; Erwin 2009). Montane wetlands are sensitive to hydrologic drivers (such as snow-pack volume, runoff, direct precipitation, and evapotranspiration) that collectively determine the rate and

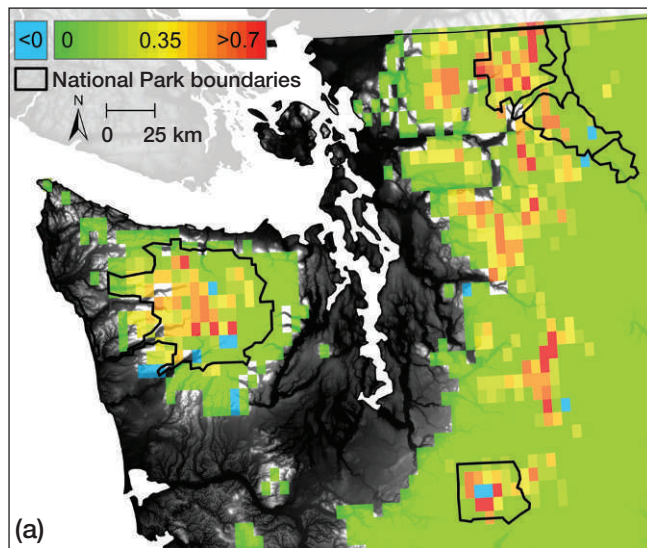
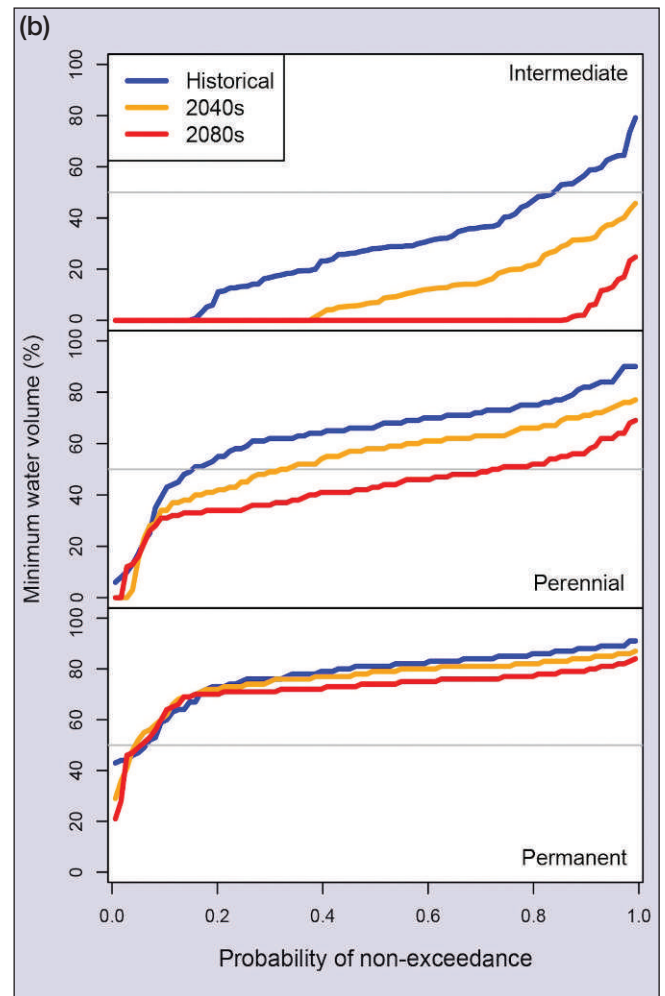


Figure 3. Hydrologic projections of climate impacts to wetlands. (a) Coarse-scale Variable Infiltration Capacity (VIC) model projection of change in the probability of drying for intermediate hydroperiod wetlands in Washington State. Areas below an elevation of 2000 ft (~610 m) are excluded from the color overlay. Red grid cells are those in which ponds have the greatest increase in likelihood of drying, which tend to be in watersheds characterized by transition in dominant precipitation from snow to rain. (b) Detailed projections of hydrologic change for an intermediate (top), perennial (middle), and permanent (bottom) wetland on Mazama Ridge in Mount Rainier National Park, Washington State. All projections in (a) are for the 2080s, based on averaged projections from ten General Circulation Models for the IPCC A1B scenario (projections courtesy of S Lee and A Hamlet).



balance of water inflow and seasonal fluctuations in pond levels (Figure 3; Lee *et al.* in review). In the western US, most of these factors are projected to change over the next century (Hamlet *et al.* 2005; IPCC 2007).

Signs of climate change are already evident in high-elevation ecosystems of the US (Hamlet *et al.* 2005; Mote *et al.* 2005; IPCC 2007). For instance, snowpack – an important water storage mechanism in mountain ecosystems – has declined by >50% in some regions over the past half-century due to the combined effects of warming and changes in precipitation patterns (Hamlet *et al.* 2005; Mote *et al.* 2005). Likewise, shifts toward earlier snowmelt runoff, peak water availability in spring, and soil moisture recession are already underway (Hamlet *et al.* 2007). Across the West, climate projections forecast these changes to continue, coincident with higher temperatures and longer and more frequent summer droughts (Hamlet *et al.* 2005; Mote *et al.* 2005; IPCC 2007). In each of the high-elevation landscapes where the effects of climate on mountain wetlands have been studied (Cascade Range, Washington State and Oregon; Olympic Range, Washington State; and Trinity Alps, California), these changes amount to earlier and faster rates of wetland drawdown, reduced overall water availability, increased frequency of complete drying, and a longer dry period in summer. Changes are forecast to be

greatest in intermediate hydroperiod ponds (those that currently dry late in the fall or dry out only in drought years) and in watersheds that shift from having the majority of annual precipitation fall as snow to those dominated by rain (Figure 3; Lee *et al.* in review).

Wetlands will continue to change in depth, hydroperiod, and thermal conditions (IPCC 2007; Lee *et al.* in review), affecting patterns of natural selection and ecological processes such as species interactions. For example, amphibians and invertebrates that require multiple years of permanent water to complete metamorphosis are likely to experience more frequent pond drying events that may increase larval mortality and reduce recruitment. Fast-developing species that use ephemeral or intermediate ponds will be affected when the rate of drying exceeds their developmental capacity (Amburgey *et al.* 2012). Increased larval growth rates in response to warmer temperatures may accelerate metamorphosis in ponds where basal food resources similarly shift (Winder and Schindler 2004). However, faster development in warmer ponds has been associated with reduced size at metamorphosis, which is linked to reduced survival and fitness at later stages (Scott *et al.* 2007). Higher water temperatures and shallower wetlands also increase the risk of mortality, and initial benefits of warming may turn into costs if thermal optima are exceeded (Duarte *et al.* 2012; Gerick *et al.*

al. 2014). In permanent ponds occupied by fish, reduced water levels may alter the amount of shallow littoral zone habitat that serves as a refugium from predators.

The consequences of climate-induced changes for wetland species will also depend on the spatial arrangement of wetlands and the degree of hydrological and biological connectivity (dispersal and movement) among them. Wetlands in many montane landscapes are spatially clustered on account of geological features that generate the topography suitable for surface waters to pool. In mountain valleys, wetland clustering, connectivity, and access by fish are also strongly influenced by beaver activity. These clusters determine the distribution and metapopulation structure of different species (Hanski and Gaggiotti 2004).

Under climate change, some shallow wetlands may not hold water at all in the future, some will transition to different hydroperiod types, and others will experience little change (Figure 3b). Climate impacts to wetland species at the scale of local landscapes (eg wetland clusters) will therefore depend on the relative abundance of wetland types and how they are transformed. Biological impacts will then depend on how these climate-induced hydrologic changes affect rates of local extinction and recolonization, as well as demography. The greatest impacts to wetland-reliant taxa will most likely occur when local landscapes: (1) primarily contain shallow wetlands that are highly vulnerable to climate-induced drying and (2) are composed of multiple wetland types but “climate-resistant”, deeper wetland habitats are made unsuitable by the presence of introduced fish (Lacan *et al.* 2008).

At local and landscape scales, changing hydrologic patterns may also affect whether the availability of water (eg pond depth, areal extent, connectivity) fluctuates in synchrony across wetlands. Synchronized variations in population size across the landscape can reduce metapopulation viability and elevate extinction risk (Hanski and Gaggiotti 2004; Liebhold *et al.* 2004). Estimates of synchrony and autocorrelation (similarities in population dynamics in time and space) among amphibian populations are often low (Trenham *et al.* 2003), and intrinsic variability of alpine weather, geology, and hydrologic flow is high at relatively small spatial and temporal scales. However, by definition, fish-induced habitat loss means that the range of available habitat is limited as compared with that which was available historically. If climate-induced changes further homogenize the types of wetlands available to native species, this will increase the likelihood of spatial synchrony in pond conditions and population dynamics.

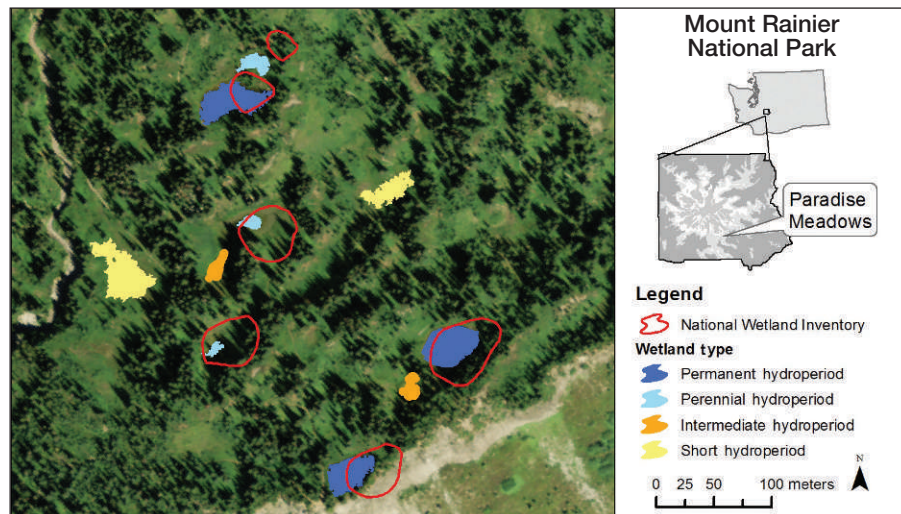


Figure 4. Ponds on Mazama Ridge in Mount Rainier National Park, delineated by Object-Based Image Analysis. The previously best available resource for wetland maps is the National Wetland Inventory (red polygons), which tends to include high offset errors and errors of omission, particularly for small or short hydroperiod wetlands, as evident here (map courtesy of M Halabisky).

Although the net consequences of these ecological processes are unknown, they serve as the motivation for the development of a series of new modeling tools (Figures 3 and 4). New object-based remote-sensing methods make it possible to identify and classify wetlands and to understand the distributions of different wetland types within and among regions (Figure 4). Empirically based, macroscale hydrologic modeling approaches such as the Variable Infiltration Capacity (VIC) model then make it possible to simulate historical wetland dynamics and forecast future hydrologic changes over broad geographic regions (Figure 3a) and for individual sites (Figure 3b). Used in combination with species occupancy data, these tools can be applied to evaluate vulnerability and metapopulation or landscape-scale resilience of both amphibian populations and wetland ecosystems.

It is thought that climate change will not only affect average temperature and precipitation values but also increase temperature and precipitation variability within and among years. Theory predicts that increased variability will tend to affect short-lived species more negatively than long-lived species, through both ecological and evolutionary mechanisms (Chesson 2000; Morris *et al.* 2008). From this we might infer, for instance, that as compared with long-lived amphibians, short-lived invertebrates could be affected more negatively by increasing climatic variation. Since invertebrates are an essential food source for larval and adult salamanders and for adult frogs, different responses among taxonomic groups create the potential to decouple predator–prey relationships in these systems. On the positive side, environmental variation can also buffer population growth rates and promote species coexistence (Chesson 2000). Multi-year, decadal, and longer correlations between environmental states (eg climate oscillations) can lead to long-term positive or negative effects on

population growth (Tuljapurkar and Haridas 2006; Schreiber and Ryan 2010). While the direction of outcome is uncertain, theoretical models indicate that the biggest effects of correlations occur in populations near the threshold of positive and negative growth rates, as would occur in populations in marginal habitats at the edge of species ranges or in populations experiencing rapid environmental changes (Schreiber and Ryan 2010).

Key uncertainties remain in how changes in temperature and hydrology will affect montane amphibian distributions and demography (eg reproduction, survival, growth). Regarding potential for responses of older life stages to exacerbate or compensate for lower recruitment, the evidence so far is equivocal, with both positive and negative effects of a warming climate on adult survival and fecundity (Reading 2007; Griffiths *et al.* 2010; McCaffery and Maxell 2010). Amphibian phenological shifts associated with temperature increases have been observed from a range of elevations (Gibbs and Breisch 2001; Carroll *et al.* 2009), but patterns are uneven among species (Carey and Alexander 2003). Population sizes and rates of gene flow influence the capacity of populations to genetically adapt to new climatic conditions (Lavergne *et al.* 2010), and both may be affected by shifting population demography and habitat distributions. Given the range of uncertainties, it may be most useful to focus questions on how to “buy some time” for both research and in situ biological adaptation to proceed (Hansen and Hoffman 2011).

■ Strategies for restoring resilience of montane wetland ecosystems

Removals of introduced fish are a viable approach for restoring resilience of native montane wetland ecosystems to climate change. Fish removals have consistently resulted in rapid amphibian and invertebrate recolonization of newly restored habitats (Drake and Naiman 2000; Knapp *et al.* 2005; Pope 2008), demonstrating that it is possible to restore habitats that are more likely to persist in future climates. Observations of natural recolonization are supported by studies showing that montane amphibians are capable of dispersing through seemingly hostile terrain such as dry mountain passes, boulder fields, and steep slopes (Garwood and Welsh 2007). For example, Cascades frogs have been observed to move distances >800 m and >230 m in elevation over land even during dry periods in the summer (Garwood and Welsh 2007). Long-toed salamander allozyme data reveal that populations within mountain basins are genetically well mixed, suggesting that individuals move across ridges (Tallmon *et al.* 2000). Anecdotal observations exist of salamanders moving across snow (D Pilliod pers comm; WJP pers obs). The capacity for natural recolonization therefore reduces the need for costly or otherwise problematic translocations following fish removals (Garwood and Welsh 2007).

In montane wetlands, introduced fish removal efforts (including planning and compliance) are labor intensive,

expensive, and often controversial, especially when chemical piscicides such as rotenone are involved. Gill netting has limited adverse effects on nontarget species but tends to be more expensive because eradication often requires annual netting for 2–8 years (eg \$15 000 per acre in Sequoia National Park or \$5000–10 000 per lake per year in North Cascades National Park) and is less successful in large (>3 ha) or deep (>10 m) lakes (Knapp and Matthews 1998; NPS 2013; R Glesne and A Rawhouser pers comm). Chemical piscicides are more effective on a wide range of lake sizes, in lakes with fish populations in inlets and outlets, or in lakes with abundant trout spawning habitat. Chemical treatments tend to be cheaper overall if successful in one application, although in terrain where helicopter access is required for transport of materials and personnel, costs can rapidly escalate for either chemical or gill netting treatments (~\$1000 hr⁻¹) (Knapp and Matthews 1998; R Glesne and A Rawhouser pers comm). The primary downside of chemical treatments is that rotenone is toxic to immature amphibians and invertebrates that use gills for respiration, with negative effects that can persist for several years (Knapp and Matthews 1998; Billman *et al.* 2012). Non-gill-breathing amphibian life stages may not be affected, however, and lakes were quickly repopulated by tadpoles at higher abundances following fish removals (Billman *et al.* 2012). Targeted fish removals therefore offer an opportunity for proactive conservation action in advance of future climate changes that are expected to reduce amphibian habitat availability.

From a practical standpoint, fish management is straightforward relative to efforts to reduce other threats to freshwater ecosystems, which may involve complex disease dynamics (eg *Batrachochytrium dendrobatidis*; Rohr and Raffel 2010), entrenched global systems (eg aerially deposited contaminants, pesticides, and industrial byproducts; Davidson 2004), or release of persistent organic pollutants from melting glaciers (Bizzotto *et al.* 2009). While these problems must also be addressed, in the short term, fish removals have already been successful and can be implemented through existing resource-management decision-making channels (eg within individual National Forests or National Parks) and therefore represent a feasible climate adaptation technique (Hansen and Hoffman 2011). A key element of a wetland climate adaptation strategy, given limited resources, is identifying priority sites for fish removals.

■ New tools for guiding climate-change adaptation in wetland ecosystems

Until recently, very limited capacity existed for modeling the effects of climate change on wetlands and prioritizing regions of highest risk. However, researchers have developed new wetland-specific climate projections using soil moisture simulated by the VIC hydrologic model (Figure 3), an empirically based model, implemented at 1/16th degree resolution (~5 km × 7 km), that simulates the

water balance in three soil layers comprising the first several meters of soil (Liang *et al.* 1994). The VIC model successfully reproduces historical summer drawdown for montane wetlands in the Pacific Northwest and has been applied in other contexts to assess the ecological effects of changing hydrologic flows associated with climate change (Mote *et al.* 2003; Lee *et al.* in review). The VIC model produces coarse-scale projections of hydrologic change (Figure 3a) and detailed hydrologic projections for individual ponds (eg shifts in drying date, changes in probability of drying, changes in minimum volume; Figure 3b) when empirical data on pond hydrology are available, and is being modified to include water temperature changes (Lee *et al.* in review). Already implemented across the western US and southern British Columbia, use of the VIC model can be extended to assess climate-change impacts on a wide range of wetland types. New remote-sensing techniques using Object-Based Image Analysis (OBIA) of existing aerial and satellite imagery also allow for fine-scale mapping of wetlands in remote and previously unsurveyed regions (Figure 4) with improved delineation accuracy down to ~ 0.02 ha, far smaller than that permitted by earlier approaches (Figure 4; Halabisky *et al.* 2011). Along with biological survey data, these tools can be combined to assess the vulnerability of native biodiversity to climate-induced changes. In the case of montane wetland fauna, they may identify regions where native species are most at risk from the combined effects of climate change and fish introductions. In these regions, fish removal from strategic sites can be used to restore resilience to a landscape where inaction might lead to species losses.

■ Conclusions

A shared goal of conservation biology and the emerging field of climate-change adaptation is to preserve existing biodiversity. Forecasting future threats, buying time for evolutionary responses, and building resilience ahead of losses are primary conservation goals in response to climate change (Hansen and Hoffman 2011). We propose that while the historical legacy of fish introductions may be setting the stage for sudden, major biodiversity losses, opportunities exist to mitigate these effects. The large-scale ecological “experiments” discussed here will have many consequences that will only be understood after the fact. However, we have the basic tools in place to make informed decisions that acknowledge imminent risks. The feasibility of fish removals creates real opportunities to build adaptive capacity and restore resilience through proactive management. Implementation requires collaboration between managers and stakeholder communities, including montane lakes fishermen, policy makers, biologists, and the public. This work is already underway in many regions, and represents the development of a foundation for a more forward-thinking and informed “experiment” in climate adaptation planning.

■ Acknowledgements

We thank A Hamlet, M Halabisky, S Lee, and R Munshaw for intellectual input, assistance with graphics, and helpful comments on drafts of this manuscript; N Steinweg, R Parks, M Healy, and R McIntyre for field assistance and great questions; and R Knapp, L Hansen, K Pope, and J Garwood for fruitful discussion of the topic. While writing this manuscript, MER was supported by a David H Smith Postdoctoral Fellowship and funding from the Northwest Climate Science Center; WJP was supported by the National Science and Engineering Research Council and the Canada Research Chairs Program. The Pacific Northwest Landscape Conservation Cooperative provided funding for development of hydrologic models. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement of the US Government. This is contribution number 460 of the Amphibian Research and Monitoring Initiative (ARMI).

■ References

- Adams MJ, Pearl CA, and Bury RB. 2003. Indirect facilitation of an anuran invasion by non-native fishes. *Ecol Lett* 6: 343–51.
- Adams MJ, Miller DAW, Muths E, *et al.* 2013. Trends in amphibian occupancy in the United States. *PLoS ONE*; doi:10.1371/journal.pone.0064347.
- Amburgey S, Funk WC, Murphy M, and Muths E. 2012. Effects of hydroperiod duration on survival, developmental rate, and size at metamorphosis in boreal chorus frog tadpoles (*Pseudacris maculata*). *Herpetologica* 68: 456–67.
- Armstrong TW and Knapp RA. 2004. Response by trout populations in alpine lakes to an experimental halt to stocking. *Can J Fish Aquat Sci* 61: 2025–37.
- Bahls P. 1992. The status of fish populations and management of high mountain lakes in the western United States. *Northwest Sci* 66: 183–93.
- Billman HG, Kruse CG, St-Hilaire S, *et al.* 2012. Effects of rotenone on Columbia spotted frogs *Rana luteiventris* during field applications in lentic habitats of southwestern Montana. *N Am J Fish Manage* 32: 781–89.
- Bizzotto EC, Villa S, Vaj C, *et al.* 2009. Comparison of glacial and non-glacial-fed streams to evaluate the loading of persistent organic pollutants through seasonal snow/ice melt. *Chemosphere* 74: 924–30.
- Burkett V and Kusler J. 2000. Climate change: potential impacts and interactions in wetlands of the United States. *J Am Water Resour As* 36: 313–20.
- Carey C and Alexander MA. 2003. Climate change and amphibian declines: is there a link? *Divers Distrib* 9: 111–21.
- Carpenter SR, Fisher SG, and Grimm NB. 1992. Global change and freshwater ecosystems. *Annu Rev Ecol Syst* 23: 119–39.
- Carroll EA, Sparks TH, Collinson N, *et al.* 2009. Influence of temperature on the spatial distribution of first spawning dates of the common frog (*Rana temporaria*) in the UK. *Glob Change Biol* 15: 467–73.
- Chesson P. 2000. General theory of competitive coexistence in spatially-varying environments. *Theor Popul Biol* 58: 211–37.
- Davidson C. 2004. Declining downwind: amphibian population declines in California and historical pesticide use. *Ecol Appl* 14: 1892–902.
- Drake DC and Naiman RJ. 2000. An evaluation of restoration efforts in fishless lakes stocked with exotic trout. *Conserv Biol* 6: 1807–20.

- Duarte H, Tejedo M, Katzenberger M, *et al.* 2012. Can amphibians take the heat? Vulnerability to climate warming in subtropical and temperate larval amphibian communities. *Glob Change Biol* **18**: 412–21.
- Eby LA, Roach WJ, Crowder LB, *et al.* 2006. Effects of stocking-up freshwater food webs. *Trends Ecol Evol* **21**: 576–84.
- Epanchin PN, Knapp RA, and Lawler SP. 2010. Nonnative trout impact an alpine-nesting bird by altering aquatic-insect subsidies. *Ecology* **91**: 2406–15.
- Erwin KL. 2009. Wetlands and global climate change: the role of wetland restoration in a changing world. *Wetl Ecol Manag* **17**: 71–84.
- Garwood JM and Welsh HH. 2007. Ecology of the Cascades frog (*Rana cascadae*) and interactions with garter snakes and nonnative trout in the Trinity Alps Wilderness, California. Arcata, CA: USDA Forest Service.
- Gerick AA, Munshaw RG, Palen WJ, *et al.* 2014. Thermal physiology and species distribution models reveal climate vulnerability of temperate amphibians. *J Biogeogr*; doi:10.1111/jbi.12261.
- Gibbs JP and Breisch AR. 2001. Climate warming and calling phenology of frogs near Ithaca, New York, 1900–1999. *Conserv Biol* **15**: 1175–78.
- Griffiths RA, Sewall D, and McCrea RS. 2010. Dynamics of a declining amphibian metapopulation: survival, dispersal and the impact of climate. *Biol Conserv* **143**: 485–91.
- Hairston Jr NG, Ellner S, and Kearns CM. 1996. Overlapping generations: the storage effect and the maintenance of biotic diversity. In: Rhodes JOE, Chesser RK, and Smith MH (Eds). Population dynamics in ecological space and time. Chicago, IL: University of Chicago Press.
- Halabisky M, Moskal LM, and Hall SA. 2011. Object-based classification of semi-arid wetlands. *J Appl Remote Sens* **5**: 053511.
- Hamlet AF, Mote PW, Clark MP, *et al.* 2005. Effects of temperature and precipitation variability on snowpack trends in the western US. *J Climate* **19**: 4545–61.
- Hamlet AF, Mote PW, Clark MP, *et al.* 2007. Twentieth-century trends in runoff, evapotranspiration, and soil moisture in the western United States. *J Climate* **20**: 1468–86.
- Hansen L and Hoffman J. 2011. Climate savvy. Washington, DC: Island Press.
- Hanski IA and Gaggiotti OE. 2004. Ecology, genetics, and evolution of metapopulations. Burlington, MA: Elsevier.
- Hoffman RL, Larson GL, and Brokes BJ. 2003. Habitat segregation of *Ambystoma gracile* and *Ambystoma macrodactylum* in mountain ponds and lakes, Mount Rainier National Park, Washington, USA. *J Herpetol* **37**: 24–34.
- IPCC (Intergovernmental Panel on Climate Change). 2007. Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland: IPCC.
- Kats LB and Ferrer RP. 2003. Alien predators and amphibian declines: review of two decades of science and the transition to conservation. *Divers Distrib* **9**: 99–110.
- Knapp R and Matthews K. 1998. Eradication of nonnative fish by gill netting from a small mountain lake in California. *Restor Ecol* **6**: 207–13.
- Knapp RA, Corn PS, and Schindler DE. 2001. The introduction of nonnative fish into wilderness lakes: good intentions, conflicting mandates, and unintended consequences. *Ecosystems* **4**: 275–78.
- Knapp RA, Hawkins CP, Ladau J, *et al.* 2005. Fauna of Yosemite National Park lakes has low resistance but high resilience to fish introductions. *Ecol Appl* **15**: 835–47.
- Lacan I, Matthews K, and Feldman K. 2008. Interaction of an introduced predator with future effects of climate change in the recruitment dynamics of the imperiled Sierra Nevada yellow-legged frog (*Rana sierrae*). *Herpetol Conserv Biol* **3**: 211–23.
- Lavergne S, Mouquet N, Thuiller W, *et al.* 2010. Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annu Rev Ecol Evol S* **41**: 321–50.
- Lee S, Ryan ME, Hamlet AF, *et al.* Forecasting climate change impacts on the hydrology of montane wetlands. *PLoS ONE*. In review.
- Liang X, Lettenmaier DP, Wood EF, *et al.* 1994. A simple hydrologically based model of land surface water and energy fluxes for GSMs. *J Geophys Res* **99**: 14415–28.
- Liebold A, Koenig WD, and Bjornstad ON. 2004. Spatial synchrony in population dynamics. *Annu Rev Ecol Evol S* **35**: 467–90.
- McCaffery RM and Maxell BA. 2010. Decreased winter severity increases viability of a montane frog population. *P Natl Acad Sci USA* **107**: 8644–49.
- Morris WF, Pfister CA, Tuljapurkar S, *et al.* 2008. Longevity can buffer plant and animal populations against changing climatic variability. *Ecology* **89**: 19–25.
- Mote PW, Parson EA, and Hamlet AF. 2003. Preparing for climatic change: the water, salmon, and forests of the Pacific Northwest. *Climatic Change* **61**: 45–88.
- Mote PW, Hamlet AF, Clark MP, *et al.* 2005. Declining mountain snowpack in western North America. *B Am Meteorol Soc* **86**: 39–49.
- NPS (National Park Service). 2013. Restoration of native species in high elevation aquatic ecosystems plan and draft environmental impact statement. Three Rivers, CA: Sequoia and Kings Canyon National Parks.
- Pilliod DS, Hossack BR, Bahls PF, *et al.* 2010. Non-native salmonids affect amphibian occupancy at multiple spatial scales. *Divers Distrib* **16**: 959–74.
- Pope KL. 2008. Assessing changes in amphibian population dynamics following experimental manipulations of introduced fish. *Conserv Biol* **22**: 1572–81.
- Reading CJ. 2007. Linking global warming to amphibian declines through its effects on female body condition and survivorship. *Oecologia* **151**: 125–31.
- Rohr JR and Raffel TR. 2010. Linking global climate and temperature variability to widespread amphibian declines putatively caused by disease. *P Natl Acad Sci USA* **107**: 8269–74.
- Schindler DE, Knapp RA, and Leavitt PR. 2001. Alteration of nutrient cycles and algal production resulting from fish introductions into mountain lakes. *Ecosystems* **4**: 308–21.
- Schreiber SJ and Ryan M. 2010. Invasion speeds for structured populations in fluctuating environments. *Theor Ecol* **4**: 423–34.
- Scott DE, Casey ED, Donovan MF, *et al.* 2007. Amphibian lipid levels at metamorphosis correlate to post-metamorphic terrestrial survival. *Oecologia* **153**: 521–32.
- Snodgrass JW, Komoroski MJ, Bryan Jr AL, *et al.* 2000. Relationships among isolated wetland size, hydroperiod, and amphibian species richness: implications for wetland regulation. *Conserv Biol* **14**: 414–19.
- Stuart SN, Chanson JS, Cox NA, *et al.* 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* **306**: 1783–86.
- Tallmon DA, Funk WC, Dunlap WW, *et al.* 2000. Genetic differentiation among long-toed salamander (*Ambystoma macrodactylum*) populations. *Copeia* **1**: 27–35.
- Trenham PC, Koenig WD, Mossman MJ, *et al.* 2003. Regional dynamics of wetland-breeding frogs and toads: turnover and synchrony. *Ecol Appl* **13**: 1522–32.
- Tuljapurkar S and Haridas CV. 2006. Temporal autocorrelation and stochastic population growth. *Ecol Lett* **9**: 327–37.
- Wellborn GA, Skelly DK, and Werner EE. 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annu Rev Ecol Syst* **27**: 337–63.
- Whittaker RJ, Willis KJ, and Field R. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. *J Biogeogr* **28**: 453–70.
- Winder M and Schindler DE. 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology* **85**: 2100–06.