Global Change Biology

Global Change Biology (2017) **23**, 77–93, doi: 10.1111/gcb.13437

Vulnerability of stream community composition and function to projected thermal warming and hydrologic change across ecoregions in the western United States

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Abstract

Shifts in biodiversity and ecological processes in stream ecosystems in response to rapid climate change will depend on how numerically and functionally dominant aquatic insect species respond to changes in stream temperature and hydrology. Across 253 minimally perturbed streams in eight ecoregions in the western USA, we modeled the distribution of 88 individual insect taxa in relation to existing combinations of maximum summer temperature, mean annual streamflow, and their interaction. We used a heat map approach along with downscaled general circulation model (GCM) projections of warming and streamflow change to estimate site-specific extirpation likelihood for each taxon, allowing estimation of whole-community change in streams across these ecoregions. Conservative climate change projections indicate a 30–40% loss of taxa in warmer, drier ecoregions and 10–20% loss in cooler, wetter ecoregions where taxa are relatively buffered from projected warming and hydrologic change. Differential vulnerability of taxa with key functional foraging roles in processing basal resources suggests that climate change has the potential to modify stream trophic structure and function (e.g., alter rates of detrital decomposition and algal consumption), particularly in warmer and drier ecoregions. We show that streamflow change is equally as important as warming in projected risk to stream community composition and that the relative threat posed by these two fundamental drivers varies across ecoregions according to projected gradients of temperature and hydrologic change. Results also suggest that direct human modification of streams through actions such as water abstraction is likely to further exacerbate loss of taxa and ecosystem alteration, especially in drying climates. Management actions to mitigate climate change impacts on stream ecosystems or to proactively adapt to them will require regional calibration, due to geographic variation in insect sensitivity and in exposure to projected thermal warming and hydrologic change.

Keywords: aquatic insects, climate change, ecoregion, streamflow, taxa distribution, thermal tolerance

Received 24 November 2015; revised version received 9 June 2016 and accepted 14 June 2016

Introduction

Understanding and predicting ecological responses to climate change is an urgent and significant challenge (Sala *et al*., 2000; Grimm *et al*., 2013). Many factors, both abiotic and biotic, interact to determine extinction risk of species to climate change, making a full accounting of vulnerability difficult (Cahill *et al*., 2013). Potential ecological change is commonly examined using species distribution models to estimate regional-scale patterns of species extinction vulnerability. However, for model predictions to be compelling, they should be 'mechanistically' couched in terms of climate-sensitive variables, such as temperature and precipitation, which are known to regulate species physiological performance and reproductive success (see Kearney & Porter, 2009). While much research has accumulated on species vulnerability across their geographic ranges (Urban, 2015), the vulnerability of traits linked to species' functional roles in ecosystems is less well known (Suding *et al*., 2008; Díaz *et al*., 2013). Additionally, little is known about how vulnerability of species traits and their effects on ecosystem function might covary geographically along gradients of temperature and precipitation. Understanding the spatial variation in species vulnerabilities to extinction, and then linking species deletions to changes in community composition, can provide insight into potential shifts in ecosystem processes and functions at local to regional scales.

Stream ecosystems are globally ubiquitous and considered highly sensitive to climate change (Meyer *et al*., 1999; Durance & Ormerod, 2007; Woodward *et al*., 2010; Poff *et al*., 2012). Temperature and precipitation-driven

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streamflow are factors that not only directly influence current distribution and abundance of species (Vannote & Sweeney, 1980; Poff *et al*., 1997) but that also respond directly to climate change (Buisson & Grenouillet, 2009; Woodward *et al*., 2010; Wenger *et al*., 2011). The role of warming in causing range shifts of freshwater species, especially fish (Ficke *et al*., 2007; Buisson & Grenouillet, 2009), is relatively well explored. However, very few studies have examined species' vulnerabilities to hydrologic change and how combined thermal and streamflow changes at regional scales will modify distributions of selected species (Wenger *et al*., 2011; Kuemmerlen *et al*., 2015). No previous studies have modeled changes for whole communities of species and potential shifts in ecosystem function across broad climatic gradients at regional scales.

Aquatic insects are the dominant fauna of small streams worldwide, comprising the majority of animal diversity and biomass while playing key functional roles in food webs and energy flow from detritus and algae to higher trophic levels (Covich *et al*., 1999). These taxa are also water quality indicators and widely incorporated in governmental stream monitoring programs (e.g., USEPA; Kenney *et al*., 2009). The distributions of insect taxa and local community composition can be well explained by spatial variation in local thermal and streamflow conditions, especially in 'reference' streams (Chinnayakanahalli *et al*., 2011), that is, those that are minimally impacted by numerous anthropogenic stressors including dams and land cover alteration such as agriculture or urbanization.

Here, we empirically model the geographic distribution of 88 insect taxa according to prevailing temperature and streamflow conditions across 253 reference streams in 12 states in the western USA, a geographic area roughly a third the size of Europe (Fig. 1). We identified *a priori* eight ecoregions, relatively homogeneous bioclimatic regions that span a broad diversity of climate (from cold to hot and from very dry to very wet; Fig. 2) and dominant vegetation types (ranging from desert scrub to arid grasslands to montane forests) that create different terrestrial catchment settings for our small study streams. The aims of this study were to: (i) model the occurrence of 88 stream insect taxa across the 253 sites based on current temperature and hydrologic conditions at each site, (ii) predict local extirpation of the taxa in response to site-specific sensitivity to projected exposure to altered temperature and hydrology from anthropogenic climate change, (iii) evaluate the impact of such extirpations on insect community composition within each of eight climatic ecoregions, and (iv) assess whether taxon vulnerability is associated with aquatic insect foraging modes and thus whether projected climate change might lead to geographic variation in alteration to stream trophic structure and ecosystem function.

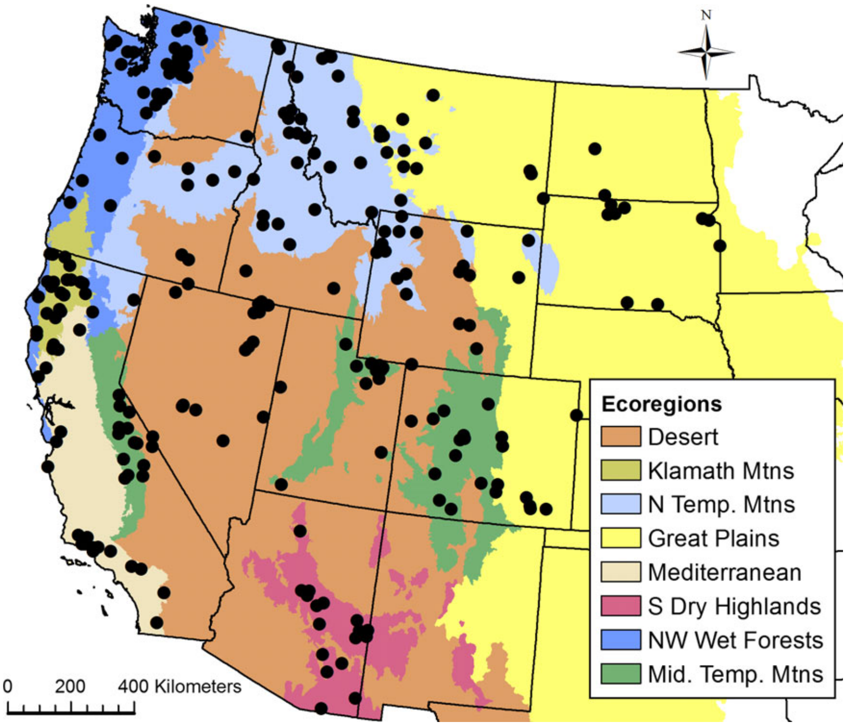


Fig. 1 Map showing eight a priori defined ecoregions (coded by color) and the location of 253 stream sites (black dots) in the western United States.

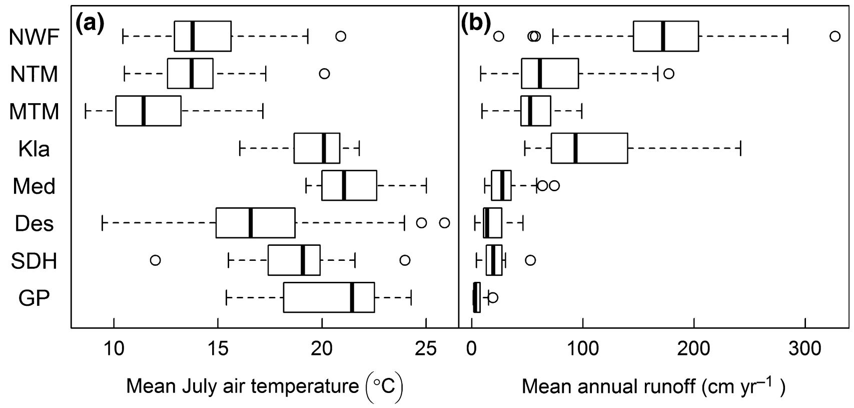


Fig. 2 The range of (a) July air temperatures and (b) mean annual runoff (a surrogate for streamflow volume and permanence) within each ecoregion. GP, Great Plains; SDH, Southern Dry Highlands; Des, Desert; Med, Mediterranean; Kla, Klamath; MTM, Middle Temperate Mountains; NTM, Northern Temperate Mountains; NWF, Northwestern Wet Forests.

Materials and methods

Dataset

Our aquatic insect dataset came from US Environmental Protection Agency's (USEPA) Environmental Monitoring and Assessment Program – Western Pilot Study (Stoddard *et al.*, 2005). Over 1300 sites in 12 western states were sampled in the WEMAP study, but we limited our analysis to 253 reference sites for two reasons. First, we wanted to focus on temperature and hydrology changes from climate change without needing to account for the confounding factors of other anthropogenic perturbations, such land cover change, which can also modify streamflow and thermal conditions but in complex ways (Allan, 2004; Kuemmerlen *et al.*, 2015). Second, the method used to calculate mean annual runoff from catchment characteristics could not be accurately estimated whether anthropogenic hydrologic alterations dominated catchment hydrology (Carlisle *et al.*, 2010). Stream insect samples were collected from riffle–pool habitats in small, wadeable streams by the USEPA and state agencies following the procedures in Peck *et al.* (2006). We performed the analyses in this study for the 88 aquatic insect taxa that occurred at 20 or more sites in our dataset, as suggested in Yuan (2006). Most taxa were designated at the genus level, but a few were reported at the level of subfamily (chironomids) or family (Capniidae, Leuctridae, and Taeniopterygidae). In the United States, identification of aquatic insects to species level is generally incomplete, and genus-level taxonomy is typically used for water quality assessments and ecological studies. The use of genus-level identification produces a conservative estimate of potential species extirpations, as some species within a genus will likely have a smaller geographic range and thus be more sensitive to thermal and streamflow changes.

The USEPA data included both occurrence (presence–absence) and abundance data. The use of occurrence has traditionally been used in modeling the effects of climate on species distributions (Liu *et al.*, 2005), but recent studies have advocated the use of abundance in species distribution models (Howard *et al.*, 2014). Analysis of abundance data can provide information about local population responses to climate change changes in abundance (Jarema *et al.*, 2009), can be effective in predicting clumped species distributions (Estrada & Arroyo, 2012) and can demonstrate the level of risk for extinction of each species (Durance & Ormerod, 2007), but most of these studies have used datasets that included intensive regional surveys or collected data over long periods of time. Our dataset included a single sampling event for stream sites dispersed across a large area, and we doubt our data could adequately reveal local population risk or show dispersal patterns. To test this assumption, we performed our distribution model analysis (described below) using both abundance data and occurrence data and measured their predictive ability using the AUC score. The occurrence model demonstrated a significantly better predictive ability (two-tailed t-test: $t_{188} = -5.83$, $P < 0.001$) than the abundance model, so we retained it for the remainder of the analysis.

Most biological data were collected during summer months (June–September) when water temperatures are near their annual maximum temperatures and flows are low. Maximum water temperature is a strong correlate of aquatic insect distributions (Vannote & Sweeney, 1980; Hawkins *et al.*, 1997; Haidekker & Hering, 2008), but measured water temperatures were not available at these sites. Mean summer water temperatures and air temperatures are strongly positively correlated, especially for reference sites at regional scales in the United States (Hill *et al.*, 2013), but deviations between maximum air temperature and actual water temperature can vary substantially at local scales due to factors such as shading, groundwater inputs, and topographic shading (e.g., Clews *et al.*, 2010; Isaak *et al.*, 2016). We used average July air temperature (model variable Temp) of the catchment, defined by the drainage area upstream of the site, as a surrogate for maximum water temperature. We calculated Temp from the 800-m-resolution Parameter-elevation Regressions on Independent Slopes Model (PRISM) database (30-year period of record from 1971 to 2000; PRISM Climate Group, Oregon State University, Corvallis, Oregon; http://www.prismclimate.org) using methods from Cuhaciyan (2006). Monthly July air temperature is a coarse surrogate for maximum water temperature, and because it is a standard output of general circulation models (GCMs), it is suitable for modeling future vulnerability of aquatic insect taxa at regional scales.

We modeled a coarse-grained streamflow metric that can be appropriately derived using monthly scale precipitation and surface runoff projections from GCMs. As a measure of streamflow, we used mean annual runoff (MAR; mean annual stream discharge/catchment area). From an analysis of hundreds of gauged US reference streams (see Poff, 1996), MAR is significantly positively correlated with daily mean streamflow, negatively correlated with variability in daily streamflow, and strongly declines across a gradient of streamflow permanence to streamflow intermittency (see also Fig. 2b). Thus, MAR represents a measure of stream size and degree of streamflow permanence, key environmental factors influencing species diversity and community trophic structure in streams (Sabo *et al*., 2010a; McHugh *et al*., 2015). MAR is a coarse grain variable that is appropriate for the monthly GCM precipitation and runoff predictions, while other natural flow regime elements (coefficient of variation, maximum or minimum daily flow, etc.) are too fine grain to be modeled confidently relative to the outputs from GCMs. MAR, which we also refer to generically as streamflow hereafter, was derived using a random forest technique that uses catchment-scale variables (e.g., precipitation, geology, soils, vegetative cover) to estimate long-term, average discharge at some ungauged site based on model calibration to regional, reference-quality US Geological Survey (USGS) stream gauges, as described in Carlisle *et al.* (2010). In that study, the mean values of MAR were calibrated within 3%, with a standard deviation of 27%, of the 1272 observed values from existing streamflow gauge data. In the statistical analysis that follows, the model variables for mean July air temperature are referred to Temp and for MAR as Flow. To better approximate a normal distribution, Temp was square root transformed and Flow was fourth root transformed. Both Temp and Flow were standardized by subtracting the mean and dividing by the standard deviation.

Models that comprehensively predict extirpation risk should be based on 'mechanistic' processes (*sensu* Kearney & Porter, 2009) that regulate species occurrences. At broad spatial extents, we were unable to incorporate important factors such as species interactions and local food resources (Durance & Ormerod, 2010; Woodward *et al*., 2010). By modeling extirpation risk only in terms of temperature and precipitation-driven streamflow, we limited our analysis to investigation of how geographically defined thermal and hydrologic niches of stream insects are likely to change across their distributional ranges, thereby causing taxa to experience spatially variable extinction risk. Given this goal, we deliberately restricted our predictor variables to simple descriptions of temperature and streamflow that are directly linked to taxa distribution and that are appropriately matched to the coarse temporal grain of GCM projections. Thus, we present our model predictions as 'first approximation' estimates of vulnerability of stream taxa and ecosystem function that are mechanistically based and realistically scaled, if not necessarily comprehensive.

Modeling geographic distributions of insect taxa

We developed 12 logistic general linear regression models (GLMs) to model the probability of occurrence of each taxon across its current geographic range as a function of currently prevailing conditions of Temp and Flow. We included all possible combinations of Temp, Flow, Temp^2, Flow^2, and Temp × Flow (actual models are shown in Table S1). Each model was fit using the glm function in R 3.10 software (R Development Core Team, 2014). Five taxa (*Dicosmoecus*, *Fallceon*, *Gumaga*, Orthocladiinae, Taeniopterygidae) were either rare (20–25 sites) or very common (>240 sites) and had perfect separation (i.e., the model separates all the test data into correct presence/absence classes) when the more complex models with quadratic terms and linear interactions were used (with $Y = \text{Temp} + \text{Flow} + \text{Temp}^2 + \text{Flow}^2 + \text{Temp} \times \text{Flow}$ being the most complicated model). Perfect separation is likely due to overfitting, the case of either too few presences (or absences in case of Orthocladiinae) and/or too many parameters. Overfitting often results in the maximum likelihood producing very large standard errors or failing to converge. To better model these five taxa, we used a penalized logistic general linear model, the brglm function in the brglm package for R (Kosmidis, 2013).

We compared the ability of each GLM to support the data by comparing the Akaike information criterion (AIC) between the 12 models for each species. Each taxon had different optimal models (according to AIC scores), so we averaged the coefficients from all 12 models for each taxon using the AIC weights to create a similarly structured GLM for all taxa. The AIC weight is the likelihood that a model is the best given the data and a set of candidate models (Johnson & Omland, 2004). The resulting ensemble distribution model for each taxon was used in our climate change predictions. The AIC weights for each of the 12 models are in Table S1, and coefficients for the ensemble models are in Table S2.

We calculated the area under the receiver operating characteristic curve (AUC) for each ensemble model to determine within-model fit. The AUC measures the ability of a model to discriminate between true positives and false positives, and an accepted rule for adequate model discrimination is 0.70 (Hosmer & Lemeshow, 2000). Additionally, we wanted to measure model predictive ability given new data. We did this by randomly separating our data into training (75% of observations) and testing (25% of observations) datasets 1,000 times, each time creating a new ensemble model for each taxon using the training dataset, and calculating the AUC for the testing dataset with the mean AUC representing the cross-validated predictability of our models. It is expected that cross-validated AUC would be lower than the within-model AUC, but a 5-point reduction in AUC is considered acceptable (Wenger *et al*., 2011). Sixty-eight of the 88 taxa had within-model AUC scores ≥0.70 and had cross-validated AUC scores <5 points lower than the within-model AUC scores (Table S2). Of the remainder, 11 scored between 0.65 and 0.70, while another nine had AUCs >0.70, but had cross-validated AUC scores >5 points lower than the within-model AUC score. We ran our climate prediction analyses with and without these 20 taxa and found that the results for the ecoregion-scale analysis were similar. Therefore, we present the results here for the entire community of 88 common taxa.

Defining climate ecoregions

We created climate ecoregions by *a priori* modifying Omernik's level I ecoregions (Omernik, 1987) to group sites in the context of existing temperature and precipitation that would reasonably capture thermal and hydrologic regional-scale change due to climate change. Our Desert (Des), Mediterranean (Med), and Great Plains (GP) ecoregion designations are the same as Omernik's. The Southern Dry Highlands (SDH), Middle Temperate Mountains (MTM), and Northern Temperate Mountains (NTM) ecoregions represent a gradient of continental mountainous regions. The Southern Dry Highlands ecoregion consists of the mountainous regions in Arizona with drier climatic conditions than other mountains to the north. The two remaining mountainous regions were divided according to latitude. The Middle Temperate Mountains ecoregion (consisting of the Sierra Nevadas, Wasatch and Uinta Mountains, and the southern Rockies of Colorado) is lower in latitude with warmer, longer summers compared to the Northern Temperate Mountains ecoregion (consisting of the northern and middle Rockies, eastern Cascades, and Blue Mountains) further north. The Northwestern Wet Forests (NWF) ecoregion captures the extremely wet conditions of the US Pacific northwest, with markedly different hydrologic and thermal regimes compared to other, drier mountainous areas. The Klamath Mountains (Kla) ecoregion (mountains named after the indigenous Klamath people of this region) in northern California and southern Oregon contains montane flora and fauna, but it has very dry, warm summers. Ecoregions and sites are shown in Fig. 1, and differences in maximum temperature and annual runoff are shown in Fig. 2.

Projecting future climate across sites and ecoregions

To assess how changes in climate may affect individual taxa and communities of taxa, we used two approaches to simulate climate change. First, we used a 'heat map' approach (Poff *et al.*, 2015) to portray a broad range of plausible future climate space. Presentation of an incremental heat map has the advantage over a traditional method of applying a single predictive value from a climate model in that an entire range of possibilities (response curve) can be observed. For individual taxa, modeled vulnerability under 'current' conditions (0 temperature increase and 0 change in flow) can have misclassification rates that fall within acceptable guidelines (Hosmer & Lemeshow, 2000), but most studies ignore these baseline losses when projecting losses of taxa from a community, apart from presenting a misclassification or validation statistic. Heat maps show misclassification given current conditions as well adjustments to Temp or Flow that might accompany future climate change, such as modifications to streamflow due to diversion or damming. We increased the mean annual July air temperature by increments of 0.05 °C up to a total of 5 °C for a total of 101 increments, encompassing the range of possible temperature increases predicted by the GLMs. We also changed mean annual runoff by the same number of increments as temperature, resulting in intervals of 1.9% from −80% to +110% at each site. Changes in flow from −50% to +110% encompass the range of flow changes predicted by the climate models, but we extended the drying magnitude range to −80%, to allow visualization of taxa responses to possible human-caused drying of streams (e.g., by water extraction from small streams), a plausible societal response to climate change, especially in relatively dry regions. Once changes in Temp or Flow crossed a taxon prevalence threshold, the taxon was removed from the site. For the taxon analyses, we calculated proportion of extirpated sites by tallying the number of sites that lost the once-present taxon and dividing by the initial number of sites where the taxon occurred. For community analysis, we calculated the proportion of taxa lost per site by summing the total number of taxa extirpated from each site and dividing by that site's initial number of common taxa.

A second approach to assess the effects of climate change on stream communities and taxa was to incorporate site-specific climate model projections of air temperature and hydrology using data from the World Climate Research Programme (WCRP). The WCRP developed the Coupled Model Intercomparison Project phase 5 (CMIP5) multimodel dataset. The previous version, CMIP3, has been used extensively for the last decade, so we included both dataset projections in the ecoregion analysis to determine whether the choice of climate dataset resulted in substantial differences in inferred vulnerability of stream systems to climate change. The two datasets use different methodologies and scenarios to estimate the future concentration of atmospheric CO_2. The CMIP3 dataset was derived using specific scenarios of greenhouse gas emissions while the CMIP5 dataset uses estimated concentrations of greenhouse gasses. The two methodologies are not completely compatible, but we attempted to compare them using the 'middle' climate scenario for each dataset, with CO_2 emissions leveling off in the mid-21st century (scenario A1b for CMIP3, RCP 4.5 for CMIP5; Brekke *et al.*, 2013). We note that our results are probably generally conservative given the low CO_2 emission storyline we adopted in this analysis (cf. Urban, 2015). For each database, we selected four climate change models that capture the extreme projections of both warming and precipitation change for each ecoregion, that is, warm-dry (mild increases in temperature and reduced streamflow), warm-wet (mild increases in temperature and increased streamflow), hot-dry (high increases in temperature and decreased streamflow), and hot-wet (high increases in temperature and increased streamflow). We averaged all climate model projections (not just the four extreme models) for a 5th climate model that represents the 'mean model' for both CMIP3 and CMIP5 datasets. Because individual taxa are not necessarily constrained to a particular ecoregion, we selected models that represented extremes for the entire dataset in the analyses for individual taxa. However, for the whole-community level ecoregion analyses, we selected the specific models that represented extremes within each individual ecoregion. The models used for each analysis are identified in Table S3 for the CMIP3 dataset and Table S4 for the CMIP5 dataset.

Modeling vulnerability of individual taxa and whole communities

For each taxon, we designated a threshold from the ensemble GLM where the taxon would be theoretically vulnerable to local extirpation due to future changes in either Temp, Flow, or their interaction. Multiple techniques have been used in the literature to designate thresholds, but the prevalence approach has been shown to be effective in making presence/absence predictions (Liu *et al.*, 2005; Santika, 2011), and it is relatively robust (Urban, 2015). If the predicted probability of occurrence for a given taxon at a site fell below its regional prevalence, we designated the taxon as being at risk of extirpation at that site. For example, the genus *Hexatoma* was found at 85 of our 253 sites (34%) and if the taxon's predicted probability of occurrence at a site fell below this 34% prevalence criterion under projected temperature and streamflow values, we designated it as being extirpated from that site. We modified this approach somewhat using the threshold cutoff of 0.5 for taxa with prevalence values >0.5; otherwise, a taxon could be designated as extirpated from a site even though its model may predict a high probability of occurrence. The use of a single, precise threshold per taxon as an extirpation cutoff implies an accurate understanding of each taxon's extirpation vulnerability, when, in reality, this is a poorly understood process. To account for uncertainty in our model, we performed a sensitivity analysis by increasing and decreasing the threshold by 5% and 10% of the threshold value and predicting the number of sites lost per taxon using the temperature and streamflow predictions from the mean climate change model and the newly adjusted thresholds.

Using the ensemble GLM and extirpation threshold for each taxon, we assessed how projected climate change may affect (i) the number of sites at which an individual taxon is likely to be extirpated and (ii) the number of taxa (from a maximum of the 88 common taxa) potentially lost from the current community at each site. To examine geographic variation in whole-community vulnerability, we averaged the total number of taxa extirpated per site across all sites within an ecoregion for each of the eight ecoregions.

For each site's upstream catchment, we used the mean July air temperature (Temp) and mean annual runoff (Flow) from 1971 to 2000 for each of the five models as a baseline climate value, calculated the mean July air temperature and annual runoff from 2041 to 2070 climate projections from five models as a future value, and calculated the difference between the two values. The difference was retained as a value (°C) for Temp and a proportional change for Flow. The climate model analyses were produced using ArcGIS™ 9.3 GIS software (ESRI, Redlands, CA, USA). We then applied the changes in Temp and Flow to the current mean July temperature and streamflow variables at each site and calculated the number of thresholds crossed for each site and taxon.

Exploring taxon buffering to thermal warming and stream drying

Extirpation vulnerability will depend on a taxon's tolerance limits relative to local climate change exposure. Deutsch *et al.* (2008) used the term 'warming tolerance' to describe how much warmer a species' environment could become before extirpation occurred. The magnitude of this tolerance will vary geographically, as populations near thermal range limits will be more sensitive to a unit increase in temperature than those far from the thermal limit. An analogous approach can be taken for streamflow change. If taxa occurrences are limited by minimum or maximum values of Flow across the geographic range, then the tolerance for a streamflow change at a site can be calculated as the difference between the projected local changes in streamflow relative to the minimum or maximum tolerable flow.

To calculate how well taxa are 'buffered' from warming and streamflow change across their entire geographic ranges in the eight ecoregions, we calculated how much of an increase in Temp and a change in Flow at each site would be needed to exceed each taxon's thermal maximum or streamflow minimum, based on the assumptions that the warmest site in the taxon's observed range in our dataset was set as its thermal limit and that the driest site was its streamflow limit. We performed two GLM analyses on each taxon's distribution, one for warming (using Temp) and the other using streamflow change (Flow) and we determined whether its probability of occurrence from the taxon-specific GLM declined with increasing Temp by 1 °C or decreasing Flow by −10% intervals. As we were primarily interested in the ability of stream communities to buffer against streamflow reduction, due to climate change, water withdrawals, or other anthropogenic activities, we only designated taxa as vulnerable to Flow reduction, labeled as 'drying tolerance'. Although some taxa may be vulnerable to streamflow increases, we did not include them in this analysis.

Our aim here was to evaluate the relative contribution of thermal vs. hydrologic change to taxon extirpation vulnerability. Within each ecoregion, we summed the number of taxa that would cross the extirpation threshold at 1 °C increments of warming and at 10% increments of streamflow reduction to determine ecoregion-scale vulnerability to thermal warming and to stream drying, treating these predictor variables independently.

Quantifying potential vulnerability of ecosystem function

Modification of ecosystem function can occur when taxa playing particular functional roles in ecosystems are differentially vulnerable to environmental change (Díaz *et al.*, 2013). We defined 'function' in terms of trophic structure of whole insect communities. Redundancy in functional roles played by species in a community can promote resilience of that function against species deletions (Yachi & Loreau, 1999), and accordingly, we calculated the proportional loss of total taxa across all sites within each ecoregion (under the mean CMIP5 scenario only) for each of five different foraging modes typically used in stream ecology. Each taxon (typically genus level) was assigned to one of five commonly used trophic designations (from Poff *et al.*, 2006). Filter-feeders capture suspended food particles in the water column; collector-gatherers feed on small detrital particles deposited on the streambed; grazers (or scrapers) consume algae and biofilm associated with hard substrata; predators consume animal prey; and shredders consume coarse particulate detritus mostly of terrestrial origin (e.g., leaves).

Results

Taxa vulnerability to warming and streamflow change

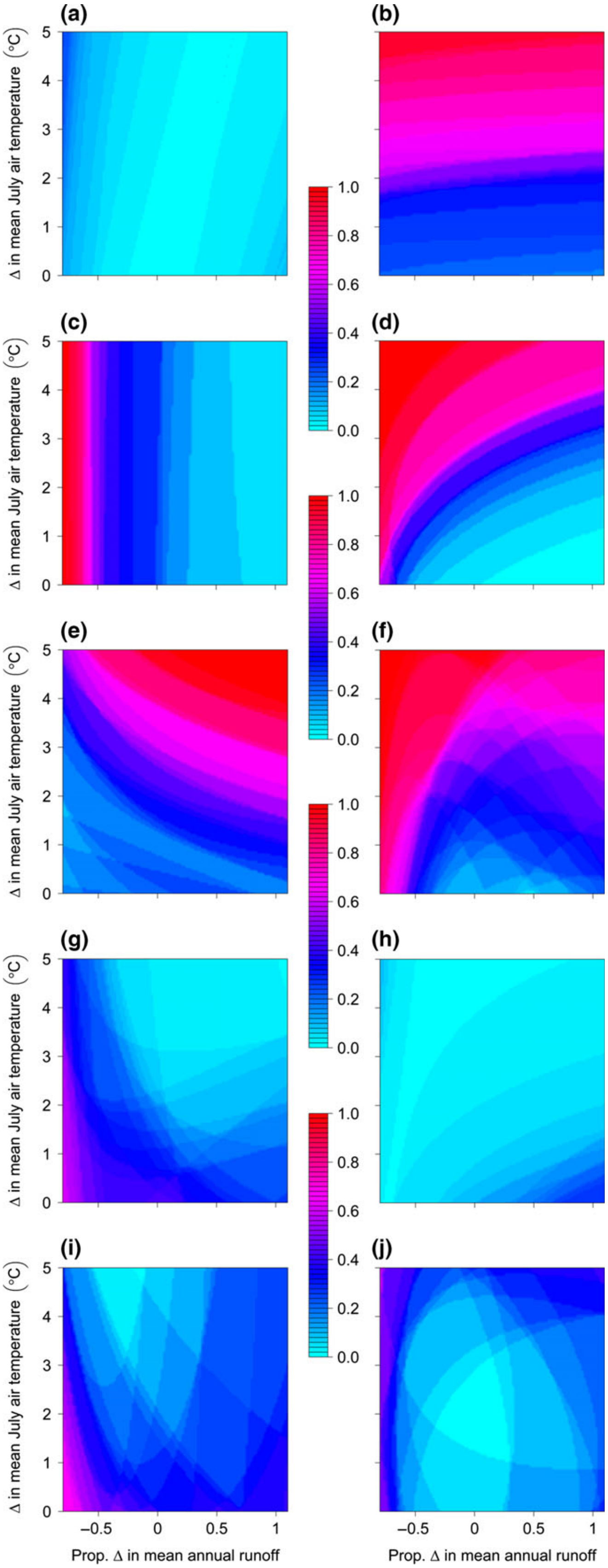
From the GLM projections for each of the 88 taxa (Table S2), we identified 10 qualitative types of vulnerability to simulated changes in temperature and streamflow (Fig. 3a–j). Responses included no vulnerability to either warming or streamflow changes (a), to warming alone (b), and to decreasing streamflow alone (c). Some taxa had a negative response to both warming and decreasing streamflow (d), to warming and increasing streamflow (e), or to warming and both increasing and decreasing flow (f). Interestingly, some taxa exhibited *decreasing* vulnerability as temperature increased, either in combination with increasing flow (g), with decreasing flow (h), or with some intermediate change in streamflow (i). One group's (j) vulnerability reflected a strong interactive effect between temperature and streamflow. Taxa membership in the 10 groups is given in Table 1. The predicted proportional loss of individual taxa from currently occupied sites ranged from 0.0% to 83.3% (Table 1), reflecting taxon-specific sensitivities to projected local change in Temp and Flow. For example, loss of the cranefly *Tipula* (Fig. 3b) varied from 16.7% of sites (warm-dry scenario) to 83.3% of sites (hot-wet scenario), whereas the mayfly *Centroptilum* (Fig. 3g) varied from 2.4% (hot-wet scenario) to 23.8% of sites (warm-dry scenario). The sensitivity analysis of the extirpation threshold showed some variability in extirpation predictions, but this variation was typically less that the variation across different climate change scenarios (Table 1). A 5% reduction in the threshold value resulted in a mean reduction of 1.9% of sites where extirpation occurred, with a range of 0–10.9%. A 10% reduction in each taxon's threshold resulted in a mean reduction of 3.6% of sites where extirpation occurred, with a range of 0–17.4%. With a few exceptions, these values fell within the range of extirpation predictions made across the five climate change models in Table 1, indicating that the range of extirpation loss represented by the five climate models adequately represents uncertainty in our predictions.

Community vulnerability in ecoregions

We found differences in community vulnerability between ecoregions (Fig. 4). Five ecoregions had relatively similar responses, showing increasing vulnerability along the streamflow reduction axis and increasing temperature axis, with about 15–30% loss of taxa falling within envelope of GCM model projections of Temp and Flow changes. The Klamath ecoregion (Fig. 4a) showed vulnerability to small increases in temperature, with flow reductions amplifying the vulnerability. The Mediterranean (Fig. 4b) and Southern Dry Highlands (Fig. 4c) ecoregions were less responsive to warming than the Klamath, showing about a 20% projected loss of taxa, but the Mediterranean ecoregion could lose up to 35% of taxa in a hot-dry future under our conservative CO_2 emission storyline. The Northern Temperate Forests (Fig. 4d) ecoregion could lose up to 20% of taxa under a hot-dry scenario where warming of 5 °C is projected. The Great Plains (Fig. 4e) are projected to get wetter and showed a relatively low proportion of total loss of taxa of about 15%.

Among the remaining three ecoregions, Desert (Fig. 4f) was highly vulnerable to decreased streamflow and had a moderate interaction with increased warming, with 25–40% loss of taxa projected under most GCMs. In contrast to other ecoregions, Northwestern Wet Forests (Fig. 4g) showed slight vulnerability to increased flow volumes but minimal vulnerability to projected warming. Even in the hot-wet climate scenario, only moderate loss of taxa (~20%) was projected. The Middle Temperate Mountains (Fig. 4h) showed modest vulnerability to both large flow increases or decreases and a minimal loss of taxa with temperature increases >2 °C, where most of the GCM projections lie in our conservative CO_2 emission storylines.

The use of both CMIP3 and CMIP5 climate data revealed some small differences in projected extinctions. The CMIP5 climate scenarios encompass a greater range of temperature and streamflow changes than the CMIP3 scenarios, with greater possible temperature increases, particularly in the Great Plains, Northern Temperate Mountains, and Northwestern Wet Forests ecoregions. The CMIP5 scenario models also project slightly wetter conditions for the Desert and potentially lower flow conditions for the Klamath ecoregions. Hotter and wetter conditions in the western USA projected from the CMIP5 database are consistent with other studies comparing the two modeling scenarios (Brekke *et al.*, 2013). Based on our sensitivity analysis above, the range climate scenario models in Fig. 4 should encompass the uncertainty associated with our extirpation predictions.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(h)
(i)
(j)
Δ in mean July air temperature (°C)
0
1
2
3
4
5
1.0
0.8
0.6
0.4
0.2
0.0
−0.5
0
0.5
1
Prop. Δ in mean annual runoff

Fig. 3 Vulnerability heat maps of 10 representative taxa to climate change to simulated changes in temperature and streamflow. The colors represent the expected proportion of sites where a taxon was defined as vulnerable to extirpation under incremental temperature increases and streamflow changes (increase or decrease). All 88 taxa in the dataset can be associated qualitatively with one of these 10 climate response heat maps. Taxon vulnerability to warming is represented by a strong vertical gradient, and vulnerability to streamflow change is represented by a strong horizontal gradient. A diagonal gradient indicates sensitivity to the interaction between temperature and streamflow, and a parabolic response reflects sensitivity to a quadratic temperature or streamflow change. Taxonomic membership for each of the 10 qualitative groups is given in Table 1. Representative taxa plotted here are (a) *Baetis*, (b) *Prosimulium*, (c) *Ecclisomyia*, (d) Taeniopterygidae, (e) *Tipula*, (f) *Neothremma*, (g) *Centroptilum*, (h) *Tricorythodes*, (i) *Limnophila*, and (j) *Gumaga*. The 78 remaining taxa can be affiliated with one of these 10 groups as indicated in Table 1 (see text for further explanation).

Taxon buffering to thermal warming and stream drying

We calculated the site-specific warming tolerance and drying tolerance of all taxa whose distribution ranges across the 253 sites were shown by individual GLMs to be limited by Temp increases or Flow reductions. Of the 88 taxa, 42 were identified as sensitive to temperature (i.e., not occurring at sites exceeding a maximum thermal threshold) and 55 were identified as sensitive to flow decreases (i.e., not occurring at sites below a minimum streamflow threshold). These taxa are indicated in Table S5. Taxa sensitive to warming and streamflow reductions in the Great Plains (Fig. 5a), Southern Dry Highlands (Fig. 5b), and Desert (Fig. 5c) ecoregions are moderately buffered against thermal increases, but poorly buffered against streamflow reductions. The Mediterranean (Fig. 5c) and Klamath (Fig. 5e) ecoregions are poorly buffered against temperature increases. The Mediterranean ecoregion is moderately to poorly buffered against streamflow reductions, while the Klamath ecoregion is well buffered against streamflow decreases. Taxa in the Northern Temperate Mountains, Middle Temperate Mountains, and Northwest Wet Forests ecoregions (Fig. 5f–h) are well buffered against both temperature increases and streamflow decreases.

Potential vulnerability of ecosystem function

Functional traits of climate-vulnerable taxa were not uniformly distributed geographically (Fig. S1). Shredder taxa comprise 1–4 taxa per site per ecoregion (ca. 2.5–12.5% of all taxa), but these few taxa perform a critical function. Grazer taxa comprise 1–7 taxa per site (5–17.5% of all taxa) per ecoregion. In six of the eight ecoregions, we found the shredder foraging guild was highly vulnerable, with an average of >40% of shredder taxa projected to be extirpated in the Great Plains, Southern Dry Highlands, Desert, and Klamath ecoregions (Fig. 6). Algal grazers were also relatively vulnerable in the Desert and Mediterranean ecoregions, with projected >30% loss of grazer taxa. The Desert ecoregion also had a >40% extirpation rate for predator taxa (Fig. 6). Sensitivity analysis by reducing the threshold by 10% did not change the pattern of functional group sensitivity but did reduce the proportion loss by 5–10% of that shown in Fig. 6 for vulnerable shredders and grazers.

Discussion

Stream insect taxa and ecosystem function show significant and variable ecoregion-scale vulnerability to projected global warming and hydrologic change in the western USA. Site-specific taxon vulnerability depends on how much change in temperature and streamflow is projected and whether that increment of change creates conditions that exceed the taxon's tolerance limits. Taxa vary in their sensitivity to small changes in temperature and streamflow, which when coupled with site-to-site variation in projected exposure leads to regional variation in taxon and community vulnerability (Figs 3 and 4). Our use of genus-level taxa identifications for this analysis suggests that our estimates of taxon sensitivity are probably conservative. Species within a genus characteristically have a smaller range size (and hence more narrow thermal and streamflow niche) than the genus as a whole, and thus, we are averaging over species and losing fine-grain (small scale) resolution of potential species loss. Our use of modest CO_2 emissions scenarios also suggests conservative estimation of extirpation risk for many taxa.

Vulnerability of aquatic invertebrates to thermal warming has been well documented (e.g., Chessman, 2009; Stewart *et al*., 2013; Verberk & Bilton, 2013). Species in habitats near the limits of their thermal tolerance are particularly vulnerable, not only to mean temperature increases but also to occasional extreme warming events (e.g., Durance & Ormerod, 2010). Our finding that species distributions can also be described in terms of their 'drying tolerance' strongly suggests an additional source of vulnerability to climate change stemming from projected precipitation change across many western US ecoregions. The interaction of warming and drying landscapes portends potential extensive change in stream ecosystem structure and function at local to regional scales.

Table 1 The projected percent of sites considered extirpated for each taxon given the 5 CMIP5 climate models and each taxon's general vulnerability response class (as illustrated in Fig. 3)

Taxa	FFG	Warm-wet	Warm-dry	Mean	Hot-wet	Hot-dry	Sensitivity of mean model
Class A							
Baetis (E)	CG	1.8	1.8	1.8	1.8	2.8	0 to +0.9
Chironominae (D)	CG	0.4	0.4	0	0	0	0
Orthocladiinae (D)	CG	0	0	0	0	0	0
Tanypodinae (D)	Pr	3.8	4.4	0.5	0	0	0 to +2.2
Class B							
Chelifera (D)	Pr	48.5	42.4	63.6	72.7	66.7	−10.6 to +4.5
Dicosmoecus (T)	Hb	10	10	35	40	45	0
Ephemerella (E)	CG	46.7	43.3	63.3	71.7	66.7	−15 to +8.3
Narpus (C)	CG	29.2	20.8	37.5	45.8	37.5	0
Prosimulium (D)	CF	31	27.6	65.5	79.3	69	−6.9 to +3.4
Class C							
Apatania (T)	Hb	12.2	14.6	14.6	14.6	22	0
Ecclisomyia (T)	CG	14.3	28.6	23.8	14.3	28.6	0 to +4.8
Glossosoma (T)	Hb	7.9	10.5	13.2	6.6	18.4	−3.9 to 0
Serratella (E)	CG	25.7	23	23	24.3	29.7	−4.1 to +10.8
Class D							
Ameletus (E)	CG	20.5	21.3	28.3	29.9	37	−3.1 to +5.5
Antocha (D)	CG	19.5	20.8	18.2	23.4	31.2	−3.9 to +11.7
Capniidae (P)	Sh	23.1	23.1	25.6	30.8	43.6	−2.6 to +15.4
Caudatella (E)	CG	15.7	15.7	23.5	25.5	29.4	0
Cinygmula (E)	Hb	20.2	21	28.6	30.3	36.1	−0.8 to +4.2
Clinocera (D)	Pr	29.8	29.8	46.8	51.1	61.7	−10.6 to +2.1
Dicranota (D)	Pr	29.1	34.2	35.4	41.8	43	−6.3 to +10.1
Drunella (E)	Hb	9.9	10.5	13.8	11.8	19.7	−1.3 to +2.6
Heterlimnius (C)	CG	19	20.3	34.2	31.6	38	−7.6 to +3.8
Leuctridae (P)	Sh	11.3	16.1	24.2	17.7	37.1	−6.5 to +3.2
Neophylax (T)	Hb	15.6	15.6	31.3	37.5	40.6	0 to +3.1
Oligophlebodes (T)	Hb	22.7	18.2	40.9	63.6	72.7	−4.5 to +9.1
Rhyacophila (T)	Pr	9.3	10.5	13	10.5	19.1	0 to +2.5
Skwala (P)	Pr	20	20	28	32	40	−8 to +12
Sweltsa (P)	Pr	20.8	20.8	30	31.5	34.6	−7.7 to +5.4
Taeniopterygidae (P)	Sh	13.6	9.1	50	81.8	81.8	−9.1 to +4.5
Yoraperla (P)	Sh	22.8	26.3	29.8	31.6	36.8	−1.8 to +1.8
Zapada (P)	Sh	25.9	24.4	34.1	35.6	40	−3.7 to +3.7
Class E							
Acentrella (E)	CG	26.7	16.7	16.7	40	16.7	−6.7 to +16.7
Brachycentrus (T)	CF	40.5	33.3	54.8	71.4	59.5	−7.1 to +2.4
Tipula (D)	Sh	33.3	16.7	50	83.3	50	−8.3 to +4.2
Class F							
Arctopsyche (T)	CF	13.9	11.1	11.1	11.1	13.9	−2.8 to 0
Cleptelmis (C)	CG	21.6	10.8	32.4	29.7	37.8	−8.1 to +5.4
Diamesinae (D)	CG	31.7	26	43.9	51.2	49.6	−7.3 to +4.9
Dolophilodes (T)	CF	20.8	20.8	20.8	37.5	41.7	0 to +8.3
Doroneuria (P)	Pr	19.2	19.2	28.8	40.4	36.5	−1.9 to +1.9
Epeorus (E)	CG	14.5	12.5	15.1	19.1	20.4	−1.3 to +9.9
Hesperoperla (P)	Pr	37	28.3	41.3	37	41.3	−17.4 to +13
Hexatoma (D)	Pr	26.7	26.7	31.4	36	38.4	−3.5 to +5.8
Megarcys (P)	Pr	17.9	12.5	32.1	41.1	48.2	−1.8 to +3.6
Neothremma (T)	Hb	28.6	20	48.6	57.1	77.1	−8.6 to +5.7
Oreogeton (D)	Pr	23.5	20.6	32.4	47.1	52.9	−5.9 to +11.8
Parapsyche (T)	CF	17.7	17.7	24.2	25.8	32.3	−1.6 to +1.6

Table 1 (continued)

Taxa	FFG	Warm-wet	Warm-dry	Mean	Hot-wet	Hot-dry	Sensitivity of mean model
Pericoma (D)	CG	27	24.3	27	27	21.6	−16.2 to +2.7
Pteronarcys (P)	Sh	22.7	22.7	31.8	45.5	50	−4.5 to 0
Rhithrogena (E)	CG	14.8	13	19.1	21.7	27	−3.5 to +6.1
Suwallia (P)	Pr	13	13	34.8	52.2	43.5	−4.3 to 0
Visoka (P)	Sh	13.3	13.3	26.7	28.9	31.1	−2.2 to 0
Wiedemannia (D)	Pr	25	17.9	25	28.6	35.7	−7.1 to +10.7
Class G							
Agapetus (T)	Hb	7.7	11.5	15.4	15.4	19.2	−3.8 to 0
Calineuria (P)	Pr	9.8	15.7	3.9	2	5.9	0
Centroptilum (E)	CG	14.3	23.8	4.8	2.4	7.1	0 to +2.4
Eubrianax (C)	Hb	3.2	3.2	3.2	0	3.2	0
Hydropsyche (T)	CF	14.6	14.6	8.7	6.8	7.8	−1 to +2.9
Ironodes (E)	Hb	18.8	18.8	21.9	18.8	28.1	−3.1 to 0
Lepidostoma (T)	Sh	17.8	21.2	17.8	10.2	18.6	−9.3 to +1.7
Malenka (P)	Sh	13.8	12.3	20	12.3	21.5	−6.2 to 0
Micrasema (T)	Hb	17.3	22.1	12.5	8.7	21.2	−6.7 to +10.6
Neoplasta (D)	Pr	16.1	19.4	16.1	12.9	19.4	0 to +9.7
Ordobrevia (C)	CG	14.3	14.3	10.7	3.6	10.7	0
Paraleptophlebia (E)	CG	17.7	22.1	19.5	9.7	21.2	−10.6 to +8
Polycentropus (T)	Pr	16.1	16.1	3.2	0	3.2	0 to +3.2
Wormaldia (T)	CF	7.7	11.5	7.7	3.8	3.8	0
Zaitzevia (C)	CG	11	11	9.9	9.9	13.2	0
Class H							
Argia (O)	Pr	10	6.7	6.7	3.3	6.7	0
Cheumatopsyche (T)	CF	20.8	12.5	8.3	4.2	4.2	0
Hemerodromia (D)	Pr	14.3	14.3	14.3	9.5	9.5	0
Simulium (D)	CF	8.7	9.3	5.6	6.8	4.3	−2.5 to +3.7
Tricorythodes (E)	CG	4.9	4.9	2.4	0	0	0 to +2.4
Class I							
Bezzia (D)	Pr	21.1	24.2	12.5	7	7.8	−5.5 to +6.3
Fallceon (E)	CG	4	0	0	0	0	0
Glutops (D)	Pr	9.1	9.1	6.1	6.1	12.1	0 to +3
Helicopsyche (T)	Hb	14.8	11.1	7.4	7.4	3.7	0 to +3.7
Limnophila (D)	Pr	18.5	29.6	11.1	7.4	7.4	−3.7 to +3.7
Microcylloepus (C)	CG	9.4	3.1	3.1	3.1	3.1	0
Ochrotrichia (T)	CG	15.4	10.3	7.7	10.3	7.7	0
Class J							
Caenis (E)	CG	8.1	8.1	8.1	13.5	5.4	0
Diphetor (E)	CG	23.2	23.2	25.6	24.4	30.5	−6.1 to +8.5
Dixa (D)	CG	22.9	22.9	17.1	11.4	14.3	−2.9 to +8.6
Gumaga (T)	Sh	0	0	0	8	0	0
Hydroptila (T)	Hb	10.4	10.4	10.4	12.5	12.5	−6.3 to +6.3
Maruina (D)	Hb	3.8	0	3.8	11.5	7.7	0 to +3.8
Optioservus (C)	CG	20.9	20	13	12.2	14.8	−3.5 to +2.6
Oreodytes (C)	Pr	14.3	17.1	25.7	20	37.1	−5.7 to +2.9
Sialis (M)	Pr	5.1	2.6	5.1	5.1	15.4	0

Taxa are grouped according to response class with taxon order in parentheses. The insect orders are Coleoptera (C), Diptera (D), Ephemeroptera (E), Megaloptera (M), Odonata (O), Plecoptera (P), Trichoptera (T). Foraging guild (also known as Functional Feeding Group; FFG) for each taxon are also listed, labeled as collector-gatherer (CG), collector-filterer (CF), herbivore (Hb), predator (Pr), and shredder (Sh). Sensitivity of the mean model is the change in percent of sites extirpated using the mean climate model predictions, but changing each taxon's threshold by ±10% of the threshold. Greater positive and negative values indicate that the taxon's climate change predictions are more sensitive to changes in the extirpation threshold.

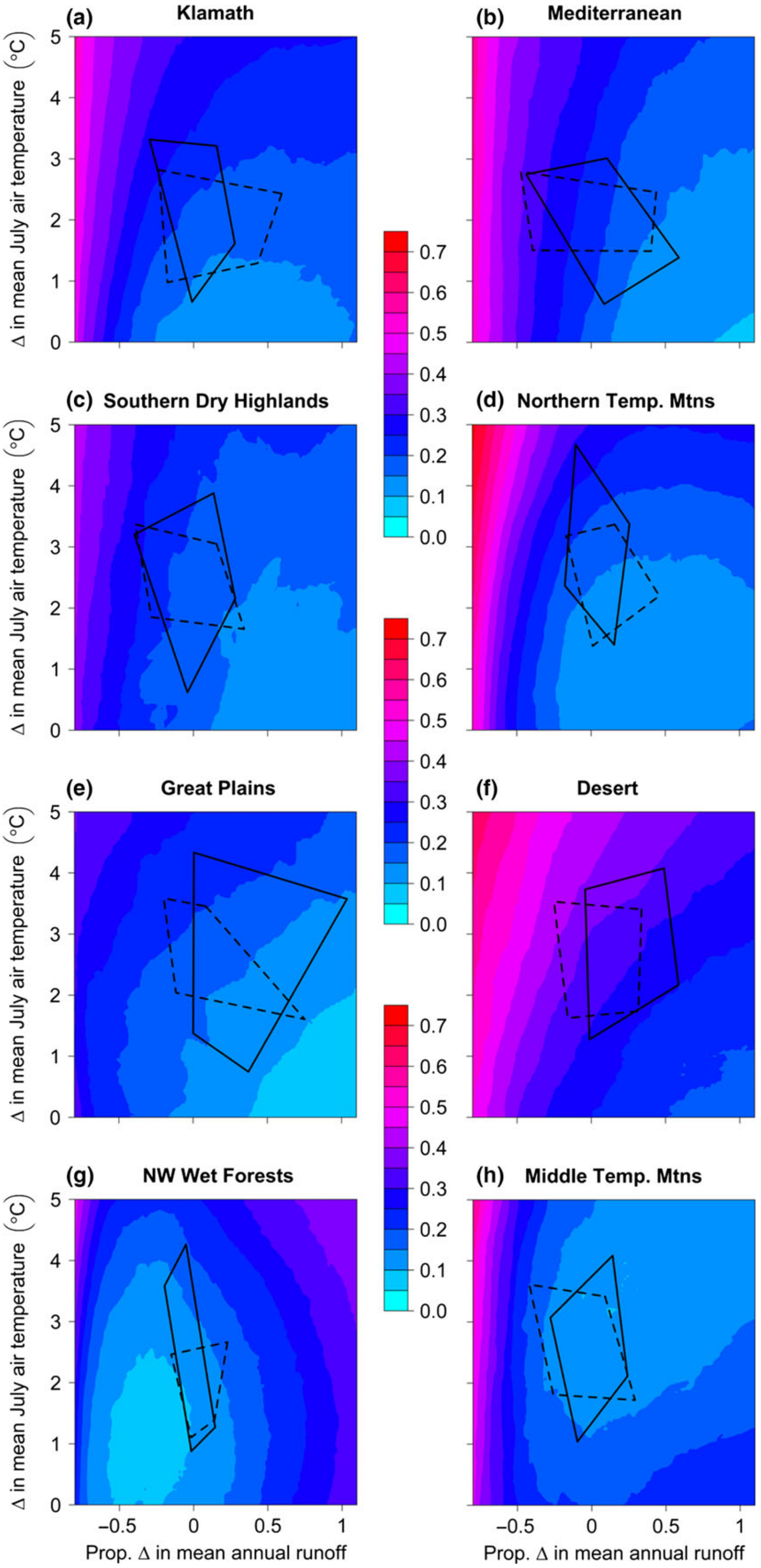
(a) Klamath
(b) Mediterranean
(c) Southern Dry Highlands
(d) Northern Temp. Mtns
(e) Great Plains
(f) Desert
(g) NW Wet Forests
(h) Middle Temp. Mtns
Δ in mean July air temperature (°C)
0
1
2
3
4
5
Prop. Δ in mean annual runoff
−0.5
0
0.5
1
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7

Fig. 4 The projected average proportion of taxa per site within each of eight ecoregions (a–h) defined as vulnerable to extirpation with increasing temperature and directional changes in streamflow. Polygons represent envelopes of general circulation model (GCM) projections of warming and change in streamflow, with vertices defining four extreme models (warm-dry, warm-wet, hot-dry, hot-wet) selected as most appropriate for each ecoregion, selected from the CMIP3 (dashed line, Table S3) and CMIP5 (solid line, Table S4) databases.

The strong sensitivity of many taxa to streamflow depletion in describing range limitation is consistent with ecological theory and empirical observations (Poff *et al*., 1997; McHugh *et al*., 2015). Arid ecoregions are particularly vulnerable to combined temperature and streamflow reductions (Figs 4 and 5). Similar vulnerability is likely in arid lands globally, as they are projected to increase in extent and harshness under climate change (Kundzewicz *et al*., 2008). Arid regions are also expected to experience greater precipitation variability in the future, leading to 'supraseasonal' droughts (*sensu* Lake, 2011) that superimpose severe hydrologic stress beyond that expected from average climate change. Indeed, ongoing extreme droughts in the southwestern USA may be imposing an ecological bottleneck by causing some perennial streams to dry and permanently lose sensitive taxa (e.g., see Bogan *et al*., 2014; Williams *et al*., 2015). Similar vulnerabilities of native fishes in the desert southwest to stream drying under large, anomalous droughts expected under climate change have recently been reported (Ruhí *et al*., 2015).

Drying from climate change and from increased human demand for water abstraction with increasing regional population growth poses serious threats to freshwater biodiversity in small streams for ecoregions across the southwestern USA (Sabo *et al*., 2010b). Particularly in snowmelt-driven streams throughout the western USA, warming alone will reduce annual snow pack, leading to earlier snow melt and diminished and potentially warmer late summer flows (Barnett *et al*., 2008; Wu *et al*., 2012; Seager *et al*., 2013; Reynolds *et al*., 2015; Service, 2015). Thus, in these streams, warming and drying may combine to further cause taxa loss and ecosystem change. Our use of heat maps allowed us to visualize a wide range of plausible, incremental changes in temperature and streamflow into a space where taxon vulnerability can be continuously plotted against many possible climate futures (Poff *et al*., 2015). This approach is more robust and adaptable compared to using only single-value climate (GCM) predictions, allowing us to incorporate additional anthropogenic activities, such as abstraction.

Our findings reveal interesting implications for the effects of climate change in less vulnerable ecoregions. Previous studies have posited that communities in regions with colder temperatures or higher streamflows are more likely to experience taxa range reductions and loss of taxa with warming or drying (Buisson & Grenouillet, 2009; Fenoglio *et al*., 2010; Poff *et al*., 2010). Those investigations, however, did not consider geographically variable taxon sensitivity to warming or hydrologic change exposure. We found that minimal vulnerability in colder and wetter ecoregions (Middle Temperate Mountains, Northwest Wet Forests and Northern Temperate Mountains) where many taxa (defined at the genus level) reside well within their thermal and streamflow limits and are therefore relatively well buffered against projected warming and drying. Similar results have recently been reported for coldwater vertebrate species in the northern and western USA (Isaak *et al*., 2016).

A continuing challenge for climate change science is to better predict how species may expand ranges under warming and altered precipitation. Our models project extirpation risk, but not possible compensatory responses, such as taxa range expansions, which have been recorded for some aquatic insects during periods of general temperature increases (Chessman, 2012). Organism dispersal is an important mechanism to adjust to climate change (Urban, 2015); however, knowledge of stream insect dispersal is incomplete (Poff *et al*., 2006) and thus infeasible to model rigorously. Under the assumption of no dispersal limitation, some studies (Domisch *et al*., 2013; Shah *et al*., 2014) have projected an increased richness of aquatic insects in mountain regions as low-elevation, warm-adapted species move to cooler, higher elevation habitats as climate warms.

Our results, however, suggest the possibility that range expansions might be limited by both environmental and biotic processes. For example, range expansion by lowland taxa into montane streams would be challenged by environmental barriers, such as major differences in habitat structure, including stream velocities and streambed particle sizes (see Poff *et al*., 2010). Further, communities comprised of taxa having strong buffering against projected thermal warming and streamflow reductions (e.g., Middle Temperate Mountains) may present some biotic resistance to colonization by vulnerable taxa from adjacent ecoregions from warmer, lower altitude streams (e.g., Great Plains or Desert ecoregions). Knowledge of species interactions would improve these kinds of range expansion considerations (Buisson & Grenouillet, 2009; Woodward *et al*., 2010; Wenger *et al*., 2011), but such information is generally lacking for stream insects.

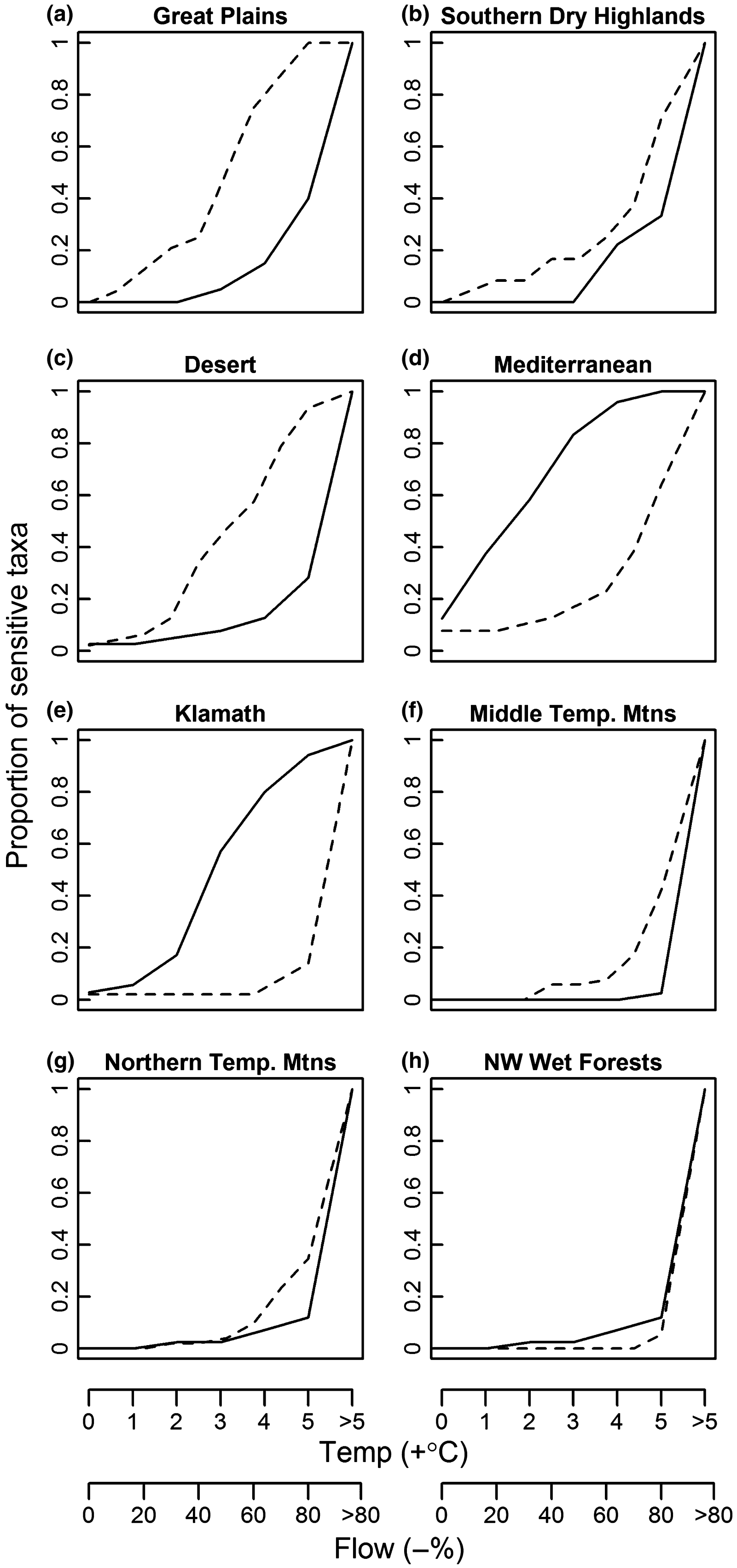
(a) Great Plains
(b) Southern Dry Highlands
(c) Desert
(d) Mediterranean
(e) Klamath
(f) Middle Temp. Mtns
(g) Northern Temp. Mtns
(h) NW Wet Forests
Proportion of sensitive taxa
0
0.2
0.4
0.6
0.8
1
0
1
2
3
4
5
>5
Temp (+°C)
0
20
40
60
80
>80
Flow (−%)

Fig. 5 The percent of taxa predicted to be lost based on crossing a taxon-specific tolerance threshold for increased mean temperature (solid line) and streamflow reductions (dashed line) relative to current conditions for each of eight ecoregions (a–h). Interactions between Temp and Flow are not shown in this graph, although they are revealed in the general circulation model (GLM) modeling in Table S2. The range of GCM-projected temperature increases, and streamflow changes for each ecoregion are shown by the polygons in Fig. 4.

One of the key findings of this analysis is the potential for climate change to modify aspects of stream ecosystem function through the linkage of functional traits with climate-sensitive traits (see Suding *et al*., 2008; Díaz *et al*., 2013). Our analysis suggests that detrital shredders and algal grazers are disproportionately vulnerable to projected thermal warming and streamflow reductions, indicating that food web structure and energy flow through stream ecosystems are vulnerable to climate change, particularly in warming and drying ecoregions. Shredders are especially vulnerable, as has been previously suggested (Boyero *et al*., 2012). These taxa play a critical role in stream ecosystem function by consuming carbon-rich, terrestrially derived detritus (e.g., leaf fall from deciduous trees) and producing finer particles that fuel growth in diverse, smaller bodied insect detritivores that constitute prey for aquatic predators (Covich *et al*., 1999). Deletion of shredder species from local communities could induce a strong effect on whole ecosystem energy flow through stream detritus-based food webs.

Our measure of vulnerability is based on the presumption that increased taxa richness within a foraging guild contributes to greater effect on ecosystem process and that the deletion of a taxon will therefore translate into reduced ecosystem function. This premise is supported by various research that has shown that detritivore species richness increases detritus processing rate (Dangles & Malmqvist, 2004) and that individual taxa can vary in their effects on a given ecosystem process (Boyero *et al*., 2007). Some species are capable of dominating ecosystem processing rates, including certain detritivores (Creed *et al*., 2009) and grazers (Kohler & Wiley, 1997). Potentially, the deletion of a species from a functional guild could be partially or fully compensated by increased abundance of remaining species, but we cannot evaluate this possibility in our analysis. Nonetheless, species identity is often an important determinant of ecosystem function, and therefore, our finding that shredder and grazer taxa show particular vulnerability to climate change in warm, dry ecoregions raises important concerns about the resilience of stream ecosystem function under projected climate change.

A persistent challenge of modeling climate change risks will be distinguishing the climate signal from the variety of other anthropogenic stressors currently degrading most stream ecosystems (Meyer *et al*., 1999; Palmer *et al*., 2009; Woodward *et al*., 2010). Appropriately modeling the climate signal itself remains a challenge due to spatial variation in local-scale controls on thermal and hydrologic buffering, such as riparian shading, groundwater inputs, and topographic shading (Clews *et al*., 2010; Isaak *et al*., 2016). Use of air temperature as a surrogate for water temperature introduces a source of sensitivity in thermal projections that may substantially modify projected thermal vulnerabilities for some taxa (Domisch *et al*., 2013). Unfortunately, availability of water temperature is generally limited (see Maheu *et al*., 2015), but efforts to extend a monitoring network to record actual are critical to refining projected vulnerabilities of riverine taxa to thermal warming (see Isaak *et al*., 2016). Other factors that complicate the modeling of climate responses of aquatic taxa include changing land use (Kuemmerlen *et al*., 2015), and more modeling effort is needed to account for the variety of interactions that occur between temperature, streamflow, and land cover alteration.

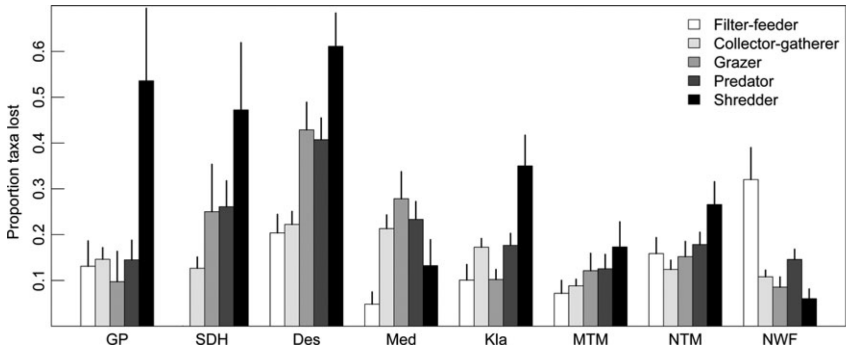

Fig. 6 Proportion of stream insect taxa lost from each of five trophic guilds (foraging modes) for ecoregion-averaged communities based on predicted loss of taxa due to climate change (using mean CMIP5 projection for each of eight ecoregions). Ecoregion abbreviations are defined in Fig. 2. See Methods for definitions of feeding groups. Standard error bars are shown.

Despite these potential limitations, our results show that taxa and ecoregions can differ substantially in their vulnerability to projected thermal warming and stream drying. Using well-monitored 'reference' streams in the USA and other countries provides an important opportunity to inform basic research into the direct thermal and precipitation-driven hydrologic effects of climate change. Combining this understanding with models that incorporate other anthropogenic stressors will lead to better regional-scale projection of species vulnerability and potential alterations in ecosystem function. Such information is needed to support identification of management intervention strategies or 'adaptation' (see Lawrence *et al.*, 2014; Poff, 2014; Thomas *et al.*, 2016) necessary to help sustain biodiversity and key ecological functions of vulnerable stream ecosystems at local to regional scales.

Acknowledgements

This work was funded by Colorado State University Department of Biology's Edward and Phyllis Reed Fellowship to M.I.P. and by EPA STAR grant R833833 and NSF DEB-104640, to N.L.P. Insect data were provided by A. T. Herlihy; C. Cuhaciyan and D. Baker developed temperature variable for each site catchment and D. Carlisle developed the hydrology variable used in this analysis. The Program for Climate Model Diagnosis and Intercomparison (PCMDI), and WCRP's Working Group on Coupled Modelling (WGCM) developed, archived, and organized the climate models. C. T. Webb, J. Hoeting, and B. Bledsoe provided helpful insight and suggestions into the analytical methods, and C. T. Webb, M. D. Smith, and C. L. Atkinson provided constructive comments on an early draft. S. J. Ormerod and two anonymous reviewers provided valuable comments on the submitted manuscript. M.I.P. and N.L.P conceived of the study; M.I.P. developed and analyzed the models; M.I.P. and N.L.P. wrote the manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. AUC weights of 12 GLM analysis for each taxon.
Table S2. Coefficients and AUC scores from the composite GLM analysis for each taxon.
Table S3. CMIP3 models used to estimate changes in temperature and precipitation.
Table S4. CMIP5 models used to estimate changes in temperature and precipitation.
Table S5. Taxon temperature and streamflow tolerance classifications for the buffering analysis.
Figure S1. Number and proportion of taxa in each foraging guild.