A freshwater conservation blueprint for California: prioritizing watersheds for freshwater biodiversity

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Abstract: Conservation scientists have adapted conservation planning principles designed for protection of habitats ranging from terrestrial to freshwater ecosystems. We applied current approaches in conservation planning to prioritize California watersheds for management of biodiversity. For all watersheds, we compiled data on the presence/absence of herpetofauna and fishes; observations of freshwater-dependent mammals, selected invertebrates, and plants; maps of freshwater habitat types; measures of habitat condition and vulnerability; and current management status. We analyzed species-distribution data to identify areas of high freshwater conservation value that optimized representation of target taxa on the landscape and leveraged existing protected areas. The resulting priority network encompasses 34% of the area of California and includes ≥10% of the geographic range for all target taxa. High-value watersheds supported nontarget freshwater taxa and habitats, and focusing on target taxa may provide broad conservation value. Most of the priority conservation network occurs on public lands (69% by area), and 46% overlaps with protected areas already managed for biodiversity. A significant proportion of the network area is on private land and underscores the value of programs that incentivize landowners to manage freshwater species and habitats. The priority conservation areas encompass more freshwater habitats/ha than existing protected areas. Land use (agriculture and urbanization), altered fire regimes, nonnative fish communities, and flow impairment are the most important threats to freshwater habitat in the priority network, whereas factors associated with changing climate are the key drivers of habitat vulnerability. Our study is a guide to a comprehensive approach to freshwater conservation currently lacking in California. Conservation resources are often limited, so prioritization tools are valuable assets to land and water managers.

Key words: conservation planning, freshwater biodiversity, protected areas, Zonation software, California

Freshwater ecosystems are in peril globally. Threats to freshwater biodiversity are numerous and include habitat degradation, pollution, overexploitation, dam construction, species invasion, and hydroclimatic change (Dudgeon et al. 2006, Strayer and Dudgeon 2010, Vörösmarty et al. 2010, Arthington et al. 2016, He et al. 2017). Over the past de-

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cade, conservation scientists have focused on adapting conservation planning principles designed for protection of terrestrial habitats and species (sensu Margules and Pressey 2000) to the particularities of freshwater ecosystems (Abell et al. 2007, Moilanen et al. 2008, Turak and Linke 2011). Early approaches to freshwater conservation planning, such as those outlined by Abell (2002), were designed to identify conservation networks by prioritizing areas based on the representation of species (Higgins et al. 2005, Abell et al. 2007, Thieme et al. 2007). Nel et al. (2009a) expanded this approach by considering threats to potential conservation areas, recognizing that existing and future human pressures on freshwater resources will have an overriding influence on conservation outcomes. Despite these advances in conservation planning approaches, implementation of conservation recommendations remains a challenge, especially in highly modified landscapes where potential conflicts exist between habitat and species protection and human activities (Hermoso et al. 2016).

Linke et al. (2011) reviewed various analytical approaches and concluded that the most effective conservation planning for freshwater systems incorporates the CARE principles: comprehensive, adequate, representative, and efficient (CARE). Comprehensiveness refers to inclusion of the full range of species, processes, and ecosystems in a target area. Adequacy ensures that conservation area networks are designed to promote persistence of biodiversity attributes. Representativeness acknowledges that the full range of biodiversity should be represented. Efficiency recognizes that conservation resources are limited, and an efficient plan should minimize conservation costs and negative effects on stakeholders. We used CARE principles to identify priority freshwater conservation areas in the state of California. Our goal was to support biodiversity in the context of other human uses and demands on land and water resources by identifying and building on existing protected areas and places where conservation and restoration actions can be focused to maintain the inherent value of connected watersheds.

California is recognized simultaneously as a global biodiversity hotspot (Myers et al. 2000, Calsbeek et al. 2003) harboring high levels of richness and endemism in its biota and as a highly altered landscape (Hanak et al. 2011). For the past 150 y, growing human population and economic development throughout California have transformed natural ecosystems into one of the most productive agricultural and urbanized landscapes in the world. This landscape modification has resulted in reduction of aquatic and wetland habitats to a small fraction of their historic extent (<95%) (Warner and Hendrix 1984, Moyle and Williams 1990, Moyle and Leidy 1992, Seavy et al. 2009). Subsequently—and in combination with massive hydrologic alteration caused by dam building and water diversions—dramatic population declines of aquatic species have been observed. For example, >60% of all native freshwater reptile and amphibian taxa found in California are vulnerable to extinction (Howard et al. 2015), and >80% of California's native fishes are likely to be lost in the next 100 y if changes in management are not made and negative effects of climate change are not averted or reversed (Moyle et al. 2011).

In response to declining freshwater resources and lack of advanced, systematic conservation planning, we developed a freshwater conservation blueprint designed to incorporate California's freshwater biodiversity in a statewide network of priority freshwater conservation areas. Our objectives were to identify watersheds critical to long-term preservation of all target species in distinct freshwater taxonomic groups, assess the representation of other nontarget freshwater taxa and habitats in high-priority watersheds, and characterize the condition of and threats to those watersheds to inform conservation management strategies based on a systematic conservation planning framework (e.g., defining planning units, mapping biodiversity features, identifying targets, and using a complementarity-based algorithm to arrive at a solution). Following best practices for systematic freshwater conservation planning (Margules and Pressey 2000, Nel et al. 2009b), we: 1) identified freshwater species as conservation targets and mapped their patterns of distribution within California watersheds; 2) represented freshwater targets in an efficiently configured network of watersheds with the aid of conservation planning software, while accounting for contributions from existing protected areas; 3) identified a network of priority watersheds for conservation based on the representation of the state's freshwater biodiversity, and evaluated that network relative to existing protected areas, observations of freshwater biodiversity lacking comprehensive distribution information, and freshwater habitats; and 4) used outcomes of prioritization to characterize the condition and threats to priority watersheds to inform and enhance conservation strategies.

METHODS

Freshwater conservation targets

To select the target taxa for identifying priority freshwater conservation areas in California, we evaluated a list of 3906 freshwater-dependent taxa historically found in the state, including mammals ($n = 6$), fish ($n = 130$), birds ($n = 105$), herpetofauna ($n = 62$), invertebrates ($n = 2777$), and vascular plants ($n = 826$) (Howard et al. 2015). We considered the final taxa for inclusion based on: 1) availability of quality, contemporary range data for characterizing distribution, 2) complementarity of habitat requirements among groups, and 3) lack of existing group/taxon-specific conservation planning efforts.

Our final focal taxon list included 3 taxonomic groups: fishes, amphibians, and reptiles (Table S1). We selected fish because of the availability of well-reviewed, recent range data (Santos et al. 2014), their reliance on riverine and lacustrine habitat, and lack of an existing statewide conserva-

tion plan. Of the 130 freshwater fish species and subspecies found in the state, we identified 122 extant taxa as targets. We selected freshwater-dependent reptile and amphibian taxa based on the availability of an expert-reviewed observational data set (Thomson et al. 2016) supplemented with generalized range data (CDFW 2014). Of 62 reptile and amphibian species and subspecies historically found in the state, we identified 33 extant amphibian species and 9 extant reptile species as targets. We excluded mammals, invertebrates, and vascular plants as targets because of the lack of comprehensive distributional data sets, but reserved observational data sets for post hoc evaluation of our priority areas (described below). We also excluded birds as a focal group because of existing conservation planning efforts (RHJV 2004).

Watershed prioritization

We identified an efficiently configured network of priority conservation areas that represented all target native fish, amphibian, and reptile taxa with the aid of the conservation planning software Zonation (version 3.1.11; Conservation Biology Informatics Group 2014), a publicly available decision-support system designed for use in systematic conservation planning. Zonation applies a complementarity-based optimization algorithm to distribution data to produce a priority ranking of watersheds based on the representation of target taxa. The priority ranking is implemented by iteratively removing map units associated with the smallest marginal loss of conservation value, which is calculated from the total and remaining species representation within a study area.

We conducted the Zonation optimization based on 12-digit hydrologic unit code (HUC12) subwatersheds in California ($n = 4465$, mean area = 9000 ha) as the basic planning unit of analysis. Each subwatershed was attributed with presence or absence for each target taxon based on whether it overlapped with range maps (fish, herpetofauna) or contained a recent locality record (herpetofauna) in recently assembled spatial data related to California's freshwater biodiversity (e.g., CDFW 2014, Santos et al. 2014, Thomson et al. 2016).

We ran a single Zonation analysis for the combined target taxonomic groups with Zonation's additive benefit function algorithm, which calculates the marginal value of each map unit as the sum of the proportion of range remaining for each target taxa at each iteration of the cell removal process. The algorithm starts with the full landscape and incrementally removes the least valuable cell, resulting in a hierarchy or ranking of cell importance for biodiversity (Moilanen 2007). The algorithm emphasizes richness while accounting for rarity. Thus, it is well suited for analyses where taxa serve as surrogates for a larger pool of conservation targets (Moilanen 2007, Lehtomäki and Moilanen 2013). For fish, we also used Zonation's directed connectivity feature to account for up- and downstream connectivity of planning units and species-specific connectivity requirements in the solution (Moilanen et al. 2008, Grantham et al. 2016). This optional setting applies a penalty for removing interconnected catchments and favors solutions that preserve contiguous watersheds. Many of California's freshwater fish require interconnected habitats from estuaries to headwaters across their life history (e.g., anadromous salmonids). For herpetofauna, we used Zonation's distributional uncertainty feature to assign greater weight ($3\times$) to those planning units within each species' range that contain recent observational data (Moilanen et al. 2006). Our use of this option reflects our greater confidence in optimization outputs based on generalized range data confirmed by recent, expert-reviewed observational information.

For the target taxonomic groups, we sought to identify priority areas that build upon existing protected areas that emphasize biodiversity as a management objective, such as National Wildlife Refuges and National Parks. We used those lands as a foundation for our conservation area network in an attempt to leverage prior conservation investments and existing management objectives. We structured the Zonation analysis to account for existing protected areas through the optional mask feature (Lehtomäki et al. 2009, Grantham et al. 2016). Planning units were forced into the top-ranked Zonation outcomes if ≥75% of their total area or perennial stream network fell within an area managed specifically for conservation (GAP Status Codes 1 and 2), as identified in Protected Areas Database of the USA (PAD-US, version 1.4; Gergely and McKerrow 2013), a product of the US Gap Analysis Program (GAP). PAD-US is the official inventory of protected open space in the USA, and the database provides conservation rankings using GAP Status Codes that describe the degree to which land is managed for conservation. Land in Codes 1 and 2 have the highest degree of management for conservation, whereas status-3 lands support multiple uses, including resource extraction (e.g., forestry, mining). Status 4 lands are either unprotected or of unknown management intent. Hereafter, we refer to protected areas as those categorized as GAP Status 1 and 2, and public lands as areas with GAP Status 1–4.

We selected the final network of proposed conservation areas based on a trade-off between the overall amount of landscape included and the representation of target taxa within the Zonation results. We sought to include some portion of the distribution of all targets within a priority network ≤50% of the total area of California.

Other freshwater taxa

To evaluate the overlap of our proposed network with other (nontarget) freshwater taxa, we compared the proportion of recent, taxon-specific observations of mammals, selected invertebrates, and vascular plants in California (Table S2) at 3 taxonomic levels (family, genus, and species)

within the final network and within existing protected areas. For both analyses, we used modern (post-1979) observational data aggregated by Howard et al. (2015) across 408 sources, including museum records, bioassessment monitoring and rare-species sampling data sets, citizen-science data sets, and agency collections, and coarsened observations spatially to the nearest 100 m to minimize the duplicate counting of observations that occur in multiple source data sets. For freshwater invertebrates, we identified a subset of 81 invertebrate families for evaluation after excluding ubiquitous families (e.g., mosquitoes [Culicidae]), families typically absent from bioassessment data sets (e.g., shore flies [Ephydridae]), and rare families, those with <40 observations in California (e.g., water mites [Aturidae]), except when the family includes endangered species (e.g., family Astacidae, which is represented by a single endangered crayfish species), to reduce noise in the spatial patterns. For all taxa, we calculated the proportion of observations in California that occur in the proposed conservation network and existing protected areas. We considered taxa to be adequately represented by the priority network if the proportion of their observed occupied range in the network was greater than the proportion of the study area in the network. For example, if 40% of the statewide distribution of a taxonomic group occurs in the priority conservation network, it would be considered adequately represented in a conservation network that encompassed 30% of the area of California. Alternatively, if 20% of the statewide distribution is in a priority network that encompasses 30% of the area of the state, it would be considered underrepresented.

Freshwater habitats

To evaluate the effectiveness of the proposed network in protecting freshwater habitats, we calculated the proportion of multiple distinct freshwater habitats in California occurring within our priority conservation areas and compared it to the proportion of the study area occupied by the final conservation network. Habitat data include a variety of natural stream types ($n = 11$), water bodies ($n = 2$), wetland and riparian vegetation communities ($n = 2$), and habitats of conservation interest, such as springs and seeps, high-elevation meadows, and groundwater-dependent systems (Table 1). We evaluated representation of freshwater systems based on the methods outlined for the nontarget freshwater taxa.

Threats assessment and conservation strategies

We developed composite habitat-condition and vulnerability indices for each HUC12 planning unit to assess habitat integrity and future threats within the conservation network. We summarized 8 habitat-condition metrics related to water quality and habitat fragmentation from California's Integrated Assessment of Watershed Health (CIAWH) data set (USEPA 2013) and created 4 additional condition metrics: groundwater well count, proportion of the fish community composed of nonnative fish (Santos et al. 2014), flow impairment from local and upstream dams (Grantham et al. 2014) and surface water diversions (Grantham and Viers 2014) as the ratio of diverted or stored water to mean annual flow volume. Nine vulnerability metrics from the CIAWH related to climate change, land conversion, and wildfire risk factors were considered. A complete list of habitat-condition and vulnerability metrics and sources is provided in Table S3. The CIAWH metrics are provided as rank-normalized scores ranging from 0 to 1 (reflecting low-to-high impairment or vulnerability) at the National Hydrography Dataset plus catchment scale. We used spatial averaging to rescale these data to the HUC12 planning unit. We then sorted these data and our 4 additional habitat metrics by impairment or vulnerability and applied rank-normalization and ordering to match the scaling of the original data set as follows:

$$\text{Rank Normalized Score} = \frac{\text{Planning Unit Rank} - 1}{\text{Maximum Planning Unit Rank} - 1}. \quad \text{(Eq. 1)}$$

We evaluated correlations and patterns among metrics within the conservation areas with principal component analysis (PCA) to identify primary stressor and vulnerability gradients in priority freshwater conservation areas. PCA evaluates and minimizes the pattern of covariance in complex data sets and has been broadly applied in freshwater assessment as a tool for data reduction (Bailey et al. 2007, Linke et al. 2007, Hermoso et al. 2011). We ran PCA on rank-normalized habitat condition ($n = 12$) and vulnerability metrics ($n = 9$) in R (version 3.1.2; R Project for Statistical Computing, Vienna, Austria) to identify the uncorrelated and nonredundant metrics associated with the primary disturbance and threat gradients. We used the highest positive or negative PCA component loading values for each axis to identify the metrics associated with each gradient that should be retained for inclusion in a final composite index. We created composite condition and vulnerability indices by summing the original rank-normalized scores for each of the selected metrics.

Combining factors into composite indices of habitat condition and vulnerability allows assignment of generalized status and conservation strategies to each HUC12 planning unit in a condition and vulnerability matrix (as in Margules and Pressey 2000, Linke et al. 2007; Table 2). The condition axis reflects restoration need and complexity in terms of the number of stressors and threats. For example, for low-condition planning units, more sources of impairment are present that will require more effort and expense to reach a restored state compared to planning units with high condition scores. The vulnerability axis re-

Table 1. Summary of freshwater habitats within the study area and priority freshwater conservation areas. Bold = habitats that are adequately represented within the priority conservation areas. These habitats have ≥34% of their distribution within the priority areas. Thirty-one percent is the % of the study area identified as a priority conservation area. CA = California, USGS = US Geological Survey, NHD = National Hydrography data set, NLCD = National Land Cover Dataset, NWI = National Wetlands Inventory, USFWS = US Fish and Wildlife Service, cfs = cubic feet per second, T = temperature.

			% in		
Data type	Habitat	Total in CA	Existing protected areas	Priority conservation areas	Source
Points (count)	Springs/seeps	23,123	15.8	**37.8**	USGS NHD - high resolution
Lines (km)	Perennial streams	77,199	24.6	**48.1**	USGS NHD - Plus
	Intermittent streams	203,419	22.8	27.3	USGS NHD - Plus
	Cool-water streams (cumulative annual mean T < 16°C)	176,261	20.3	**36.0**	USGS NHD - Plus
	Warm-water streams (cumulative annual mean T ≥ 16°C)	69,315	28.9	27.0	USGS NHD - Plus
	Headwater streams (mean annual flow: 0–1 cfs)	157,317	23.2	28.3	USGS NHD - Plus
	Small rivers/creeks (mean annual flow: 1–100 cfs)	76,803	21.9	**42.3**	USGS NHD - Plus
	Large rivers (mean annual flow ≥ 100 cfs)	11,456	22.5	**46.4**	USGS NHD - Plus
	Pool/riffle systems (gradient 0–4%)	118,179	17.0	30.3	USGS NHD - Plus
	Step-pool systems (gradient 4–8%)	51,625	25.5	32.6	USGS NHD - Plus
	Cascade–colluvial systems (gradient ≥ 8%)	75,772	29.8	**39.2**	USGS NHD - Plus
Polygons (ha)	Intermittent natural waterbodies	195,267	34.5	32.8	USFWS NWI
	Perennial natural waterbodies	232,745	27.7	**47.6**	USFWS NWI
	Herbaceous wetlands	85,372	15.9	29.8	USGS NLCD 2006
	Woody wetlands	206,922	29.5	24.6	USGS NLCD 2006
	Sierra meadows	77,301	46.7	**60.6**	Fryjoff-Hung and Viers 2012
	Groundwater-dependent ecosystems	2,395,369	26.5	**41.3**	https://www.scienceforconservation.org/products/groundwater-dependent-ecosystems-data

flects uncertainty in conservation status—greater vulnerability indicates less certainty about permanence of current habitat condition and long-term biological value independent of monitoring and climate-related mitigation actions. We assigned composite scores to each HUC12 planning unit identified as a priority conservation area and conservation strategies based on median index values.

RESULTS

Watershed prioritization

We identified a freshwater conservation network that optimized the representation of target taxa ranges while minimizing the overall size of the network (Fig. 1). The final network corresponded to a representation threshold of 10%, meaning that the priority watersheds overlapped with ≥10% of the distribution of all target taxa. The final network of priority watersheds encompasses nearly 140,000 km^2, representing 34% of California. The minimum % of taxon ranges represented by the network was 10% for amphibians, 17% for reptiles, and 14% for fish. However, the median % of range representation was 78% for all target taxa: 51% for amphibians, 29% for reptiles, and 92% for fishes (Fig. 2, Table S1). Such representation is a substantial increase in % fish and herpetofauna target ranges encompassed by existing protected areas. Existing protected areas encompass 23% of the state (94,800 km^2), do not overlap the ranges of 4 fish targets, and have a median range representation of

Table 2. Condition and vulnerability matrix representing the composite habitat condition and threats indices. The condition categories reflects restoration need and complexity. The vulnerability categories reflects conservation uncertainty. Greater vulnerability indicates less certainty about permanence of current habitat condition and long-term biological value independent of monitoring and mitigation action (modified from Linke et al. 2007).

		Condition	
		High	Low
Threat and vulnerability	High	*Status:* High condition and high vulnerability–single acute or multiple low-level stressors and multiple acute threats	*Status:* Low condition and high vulnerability–multiple acute stressors and threats
		Conservation strategy: Protection from new stressor development, limited restoration to address existing stressors, and conservation actions to minimize future threats (e.g., conservation easements, habitat conservation plans on working forest lands with large riparian buffers to maintain riparian and floodplain function and ensure ample stream shading)	*Conservation strategy:* Restoration actions to address existing stressors and conservation action to minimize future threats (e.g., diversion consolidation or removal, altered crop selection, buffer strips, and water-efficiency measures on agricultural lands to decrease surface water use and agricultural runoff in all years, especially during drought)
	Low	*Status:* High condition and low vulnerability–single acute stressors and threats or multiple low-level individual stressors and threats possible.	*Status:* Low condition and low vulnerability–multiple acute stressors and single acute or multiple low-level threats.
		Conservation strategy: Protect from new stressor development, secure by monitoring and addressing the few existing stressors and threats (e.g., road obliteration or levee removal to restore natural floodplain function)	*Conservation strategy:* Restoration actions to address existing stressors, monitoring, and evaluation (e.g., stormwater management practices and artificial wetland construction with streamflow monitoring to increase infiltration and decrease runoff in urbanized watersheds)

14% for all taxa (12% for fish, 17% for amphibians, and 12% for reptiles; Fig. 2, Table S1).

The priority freshwater conservation network includes large portions of the Sierra Nevada Mountains, Mojave Desert, and northwestern California (Fig. 1), which include several large protected areas (e.g., Yosemite, Sequoia, Joshua Tree National Parks; Anza Borrego Desert State Park; Siskiyou, Marble Mountain, and Trinity Wilderness Areas). Notable features within the priority network that fall outside of existing protected areas include hotspots of fish diversity and endemism, including Pit River, Klamath River, Goose Lake, Russian River, Santa Clara River, Clear Lake, and Sacramento/San Joaquin Delta and hotspots of herpetofauna diversity and endemism, including the Owens and Colorado Rivers and coastal northwest California (Fig. 1).

Over 46% (64,700 km^2) of the final priority freshwater conservation network occurs in protected areas managed for biodiversity and 69% (97,000 km^2) occurs on public lands managed for all uses, including biodiversity, mining, and timber harvest. The priority conservation network occupies 68% of protected areas and 43% of public lands. Thirty-one percent (42,900 km^2) of the priority freshwater conservation areas are outside of existing public lands. Land cover in these areas held by private land owners includes agriculture (21%), timberlands that may be managed for forestry (31%), and low-to-high density urban lands (14%). Nearly 44% of target taxa have most of their distribution in the priority conservation areas on these private lands, whereas only 3 targets have the entirety of their distribution on public lands.

Other freshwater taxa

We evaluated the overlap of the priority conservation areas and existing protected areas with >324,000 total observations for our final list of other freshwater taxa representing 4 families, 5 genera, and 5 species of mammals; 81 families, 354 genera, and 914 species of sensitive invertebrate families; and 83 families, 228 genera, and 676 species of plants (Table S2). All taxonomic levels of mammals have been observed in existing protected areas and priority conservation areas, as have all plants and sensitive invertebrates at the family level (Fig. 3A–C). Overall, taxa were better represented by the priority conservation network than existing protected areas across all taxonomic levels (Fig. 3A–C). The % of observations of each taxon within the priority network were generally higher than the network's land-area representation (34%).

Freshwater habitats

The priority freshwater conservation network well represents the diversity of freshwater habitats in the state (Table 1). Sierra meadows are the best-represented habitat in the priority network with ~61% of the total area occurring in the priority conservation network, whereas woody

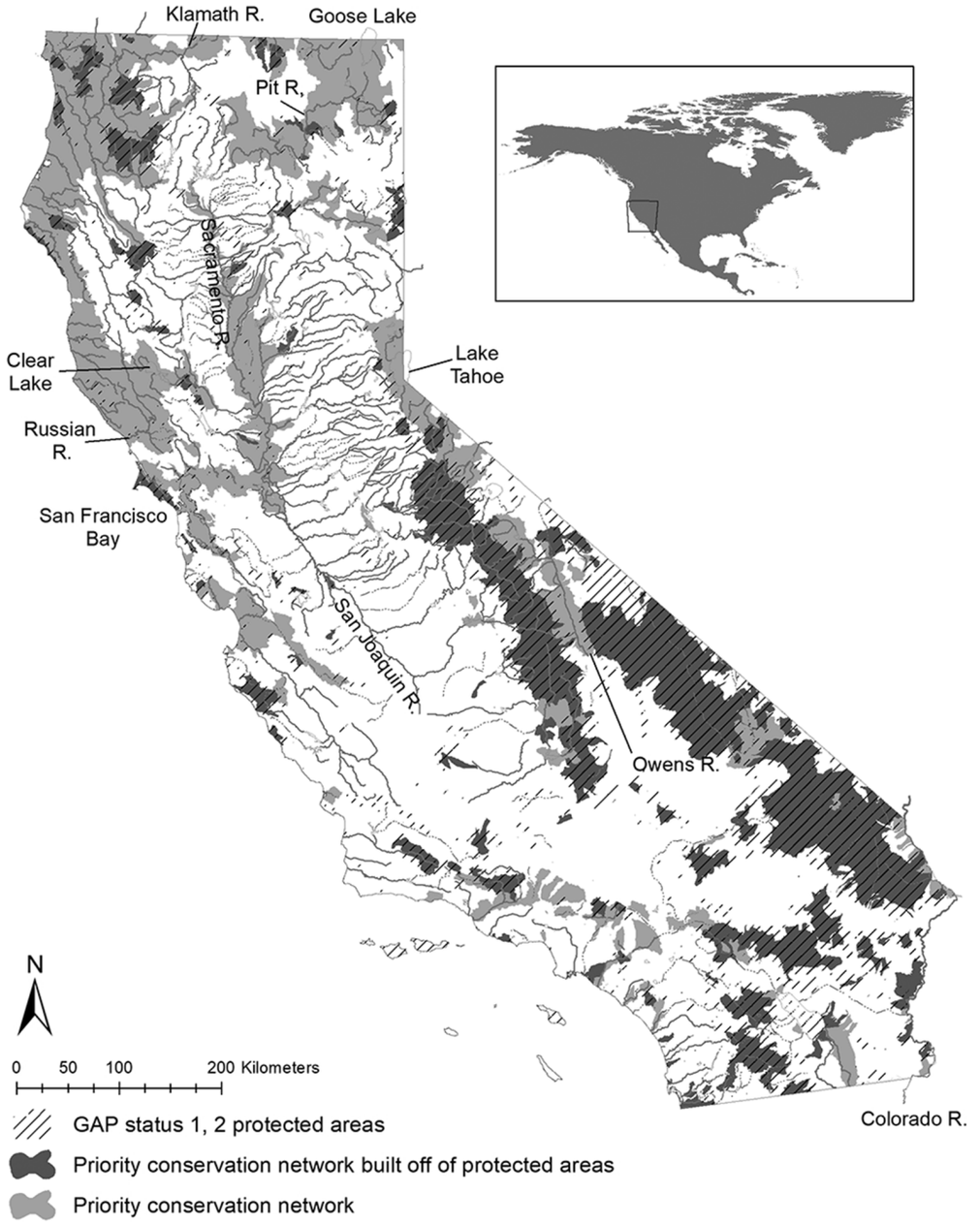


Figure 1. Priority conservation areas and locations of existing protected areas (Gap Analysis Program [GAP] status 1, 2).

wetlands are the least represented with ~25% included (Table 1). The priority conservation network adequately represents freshwater habitats for springs/seeps, perennial streams, cool-water streams, small rivers/creeks, large rivers, cascade–colluvial systems, perennial natural waterbodies, and groundwater-dependent ecosystems. Underrepresented habitat types in the priority conservation areas are intermittent and warm-water streams, headwaters, pool-riffle systems, and herbaceous and woody wetlands. These systems are all adequately represented in existing protected areas. Both existing protected areas and the proposed priority conservation areas inadequately represent pool/riffle systems and herbaceous wetlands.

Threats assessment and conservation strategies

Sixty-five percent of the variation in the habitat-condition metrics in priority conservation value areas was accounted for by 3 principal components (PCs; Fig. 4A–C). PC1 explained 42.6% of the variation and corresponded to an anthropogenic landuse gradient, with urbanization and agricultural landuse stressors. PC2 explained 13.7% of the

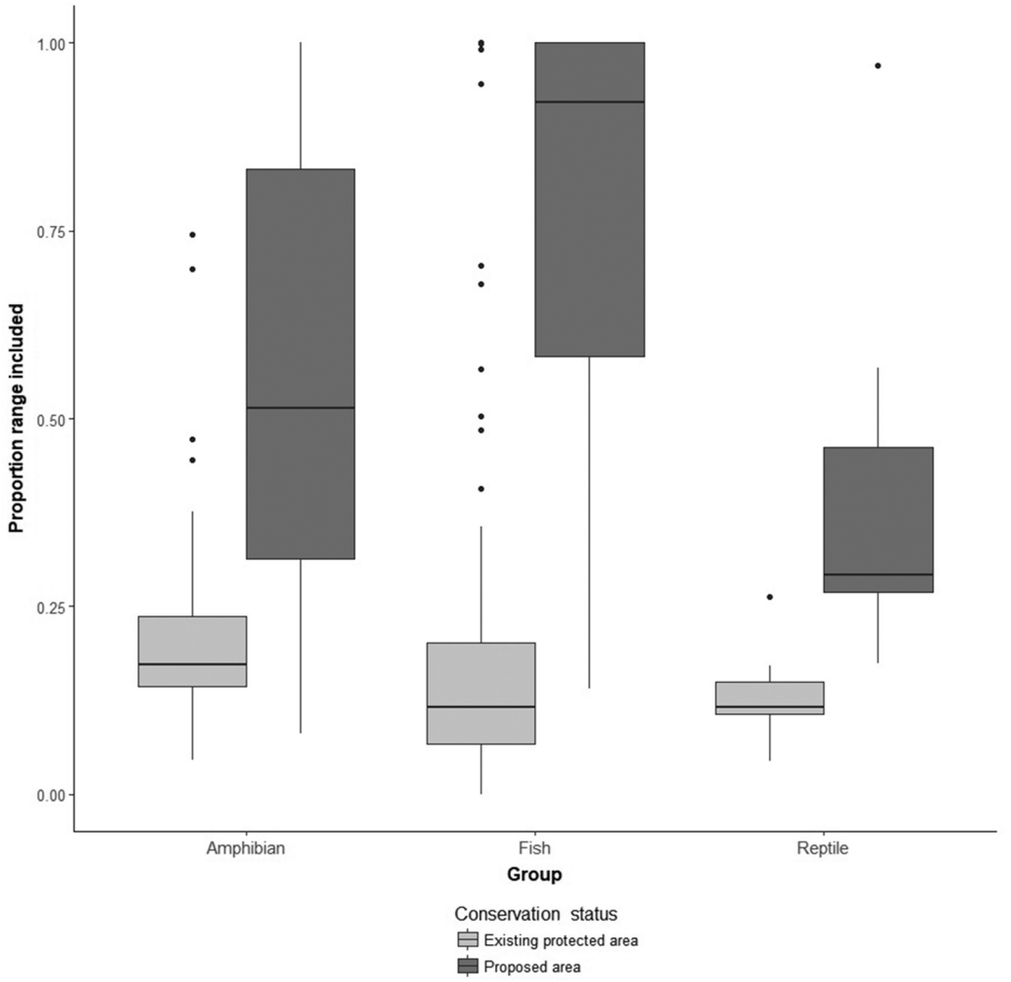


Figure 2. Box-and-whisker plots of the proportion of freshwater fish, amphibian, and reptile taxa range included in existing Gap Analysis Program (GAP) status 1, 2 protected areas and priority conservation areas. Lines in boxes are sample medians, box-ends are upper or lower quartiles, whiskers are minimum and maximum, and points represent outliers (defined as values greater than 1.5 times upper or lower quartile).

variation and corresponded to a gradient associated with proportion of the fish community composed of nonnative taxa and fire-regime condition class (departure of vegetation type and structure from historical conditions because of wildfire suppression). PC3 explained 8.7% of the variation and corresponded to a gradient associated with water use related to dams and diversions.

Over 73% of the variation in the vulnerability metrics within conservation value areas was described by 3 PCs (Fig. 5A–C). PC1 explained 44.4% of the variation and corresponded to a gradient associated with changing temperature, including change in wildfire risk and base flow, and land conversion risk. PC2 explained 16.2% of the variation and corresponded to a gradient associated with factors related to changes in precipitation, including runoff volume and total precipitation. PC3 explained 12.6% of the variation and corresponded to a gradient associated with changes in water storage indicated by change in base flow and snowpack water storage risk. Except for landuse conversion risk, the vulnerability metrics reflected predicted climate-change effects.

We created composite condition and vulnerability indices based on these PCs by using the sum of the indices with the highest axis-loading values for each gradient. The composite habitat condition index comprised metrics related to the extent of floodplain development, fire-regime condition class, proportion of fish community consisting of nonnatives, dam-related flow impairment, and artificial drainage of wetlands and hydric soils. The composite vulnerability index comprised average temperature change, land-conversion risk, runoff change, baseflow change, and snow water-equivalent change. Conservation strategies associated with the unique threat and vulnerability profile assigned to each conservation area are shown in Fig. 6A–D.

Areas of highest habitat condition in the priority network occur in portions of the North Coast region, high-elevation

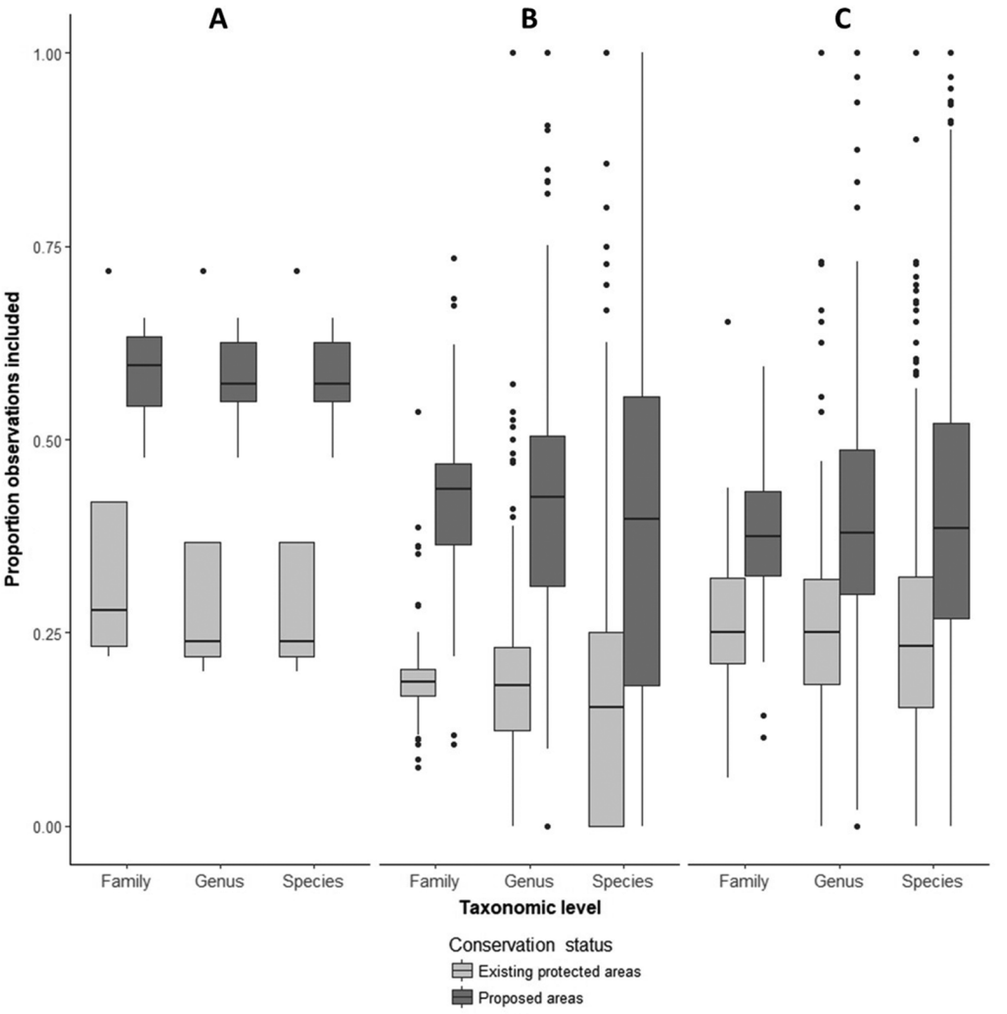
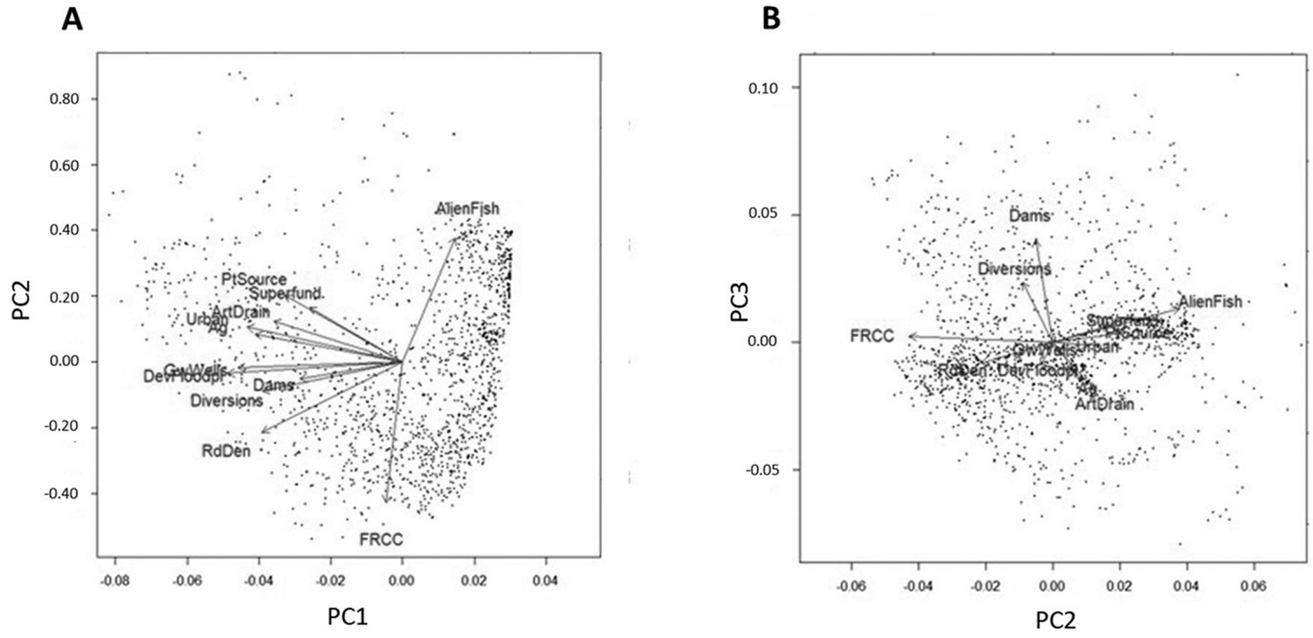


Figure 3. Box-and-whisker plots of the proportion of observations of mammal (A), sensitive invertebrate (B), and vascular plant (C) taxa that overlap with existing Gap Analysis Program (GAP) status 1, 2 protected areas and priority conservation network. Lines in boxes are sample medians, box-ends are upper or lower quartiles, whiskers are minimum and maximum, and points represent outliers (defined as values greater than 1.5 times upper or lower quartile).

portions of the southern Sierra Nevada Mountains, and undeveloped portions of the Mojave Desert. Lowest condition areas correspond to urban areas surrounding San Francisco and Los Angeles and along mainstem rivers, such as the Sacramento and Klamath Rivers (Fig. 6A). Areas of lowest vulnerability are along the north coast and Mojave Desert, whereas highest vulnerability areas correspond to interior and high-elevation portions of northern California (Fig. 6B). When evaluated in a conservation strategy framework (Fig. 6C), areas with the least-impaired habitat conditions and least vulnerability should be secured and monitored and are scattered throughout the North Coast, southern Sierra Nevada Mountains, and Mojave Desert. Areas with more impaired conditions, but least vulnerability, should be targeted for restoration and are concentrated in high-elevation portions of coastal central and southern California. Conservation priority areas with relatively least-impaired condition but also greatest vulnerability should be secured, but mitigation actions probably will be required. These areas are primarily in northwestern California. Areas with degraded conditions and greatest vulnerability have restoration and mitigation needs and are scattered across the state in low- and moderate-elevation portions of northern California and along major river systems, such as the Sacramento, Pit, Klamath, and Russian Rivers.

DISCUSSION

We identified a network of conservation areas that include a range of freshwater species and habitats to encourage their persistence. The priority conservation network captures ≥10% of the range of all target freshwater taxa. However, for most taxa, the priority conservation network includes a much larger proportion of their range (Fig. 2).



C

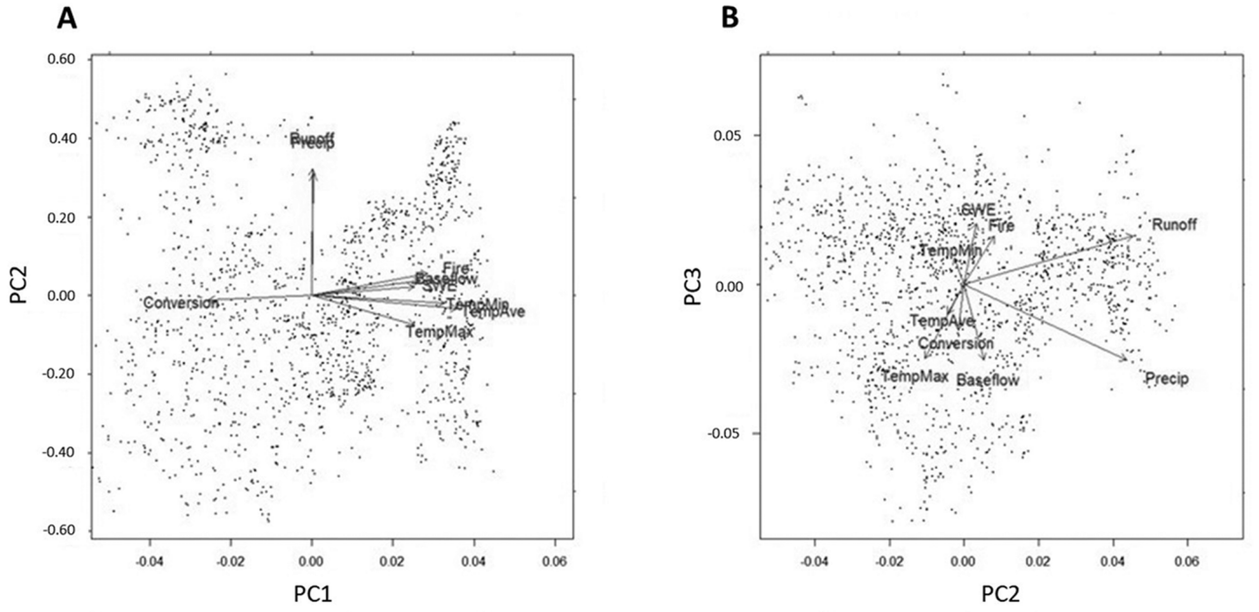
PC 1: Land conversion (42.6% explained)	PC2: Alien fish & fire regime (13.7% explained)	PC3: Water use (8.7% explained)
*Dev. floodpl. (-0.4)	*Fire reg. cond. class (-0.61)	*Dams (0.72)
Groundwater wells (-0.37)	* Alien fish (0.54)	Diversions (0.42)
Urban land use (-0.35)		* Artificial drainage (-0.34)

Figure 4. Principal components (PCs) 1 vs 2 (A) and 2 vs 3 (B) and axis-loading values for condition metrics (C). * = used in the final composite habitat condition index. AlienFish = proportion of fish community composed of nonnatives, PtSource = point source discharge density, Superfund = superfund site density, ArtDrain = percent artificial drainage area, Urban = % urban land use, Ag = % agricultural land use, GwWells = groundwater well count, DevFloodpl = % developed active river area; Dams = ratio of dam capacity to annual runoff; Diversions = ratio of volume of surface water diverted to annual runoff; RdDen = road density; FRCC = fire-regime condition class.

For all taxa, the priority network includes a much higher % of taxon distributions than the existing protected area network managed primarily for conservation purposes.

Approximately 70% of the priority conservation network occurs on public lands and 46% within existing protected areas, suggesting that deliberate management of public lands with multiple use mandates (i.e., US Forest Service and Bureau of Land Management lands) could provide substantial conservation benefits to freshwater biodiversity in California. However, the remaining 30% of priority conservation areas occur outside of the protected area network, so thoughtful management of private lands also will be critical for preserving freshwater diversity in the state. More than 40% of target taxa have ≥½ of their distribution in the priority conservation areas on private lands. For some targets, particularly for regional endemic taxa of the Sacramento and San Joaquin river drainages and the North Coast, such as the Delta Smelt (*Hypomesus pacificus*) and Gualala Roach (*Lavinia parvipinnis*), the percentage is >75%.

The identified priority conservation network, in general, adequately represents nontarget freshwater biodiversity at multiple taxonomic levels and existing freshwater habitats in the state. This finding provides evidence that a multitaxonomic conservation planning approach also is effective at representing diverse freshwater habitats and elements of biodiversity for which distributional data sets are not available. The observational data sets we evaluated may not comprehensively represent the distribution of other freshwater taxa in California, but the priority conservation areas do largely capture diversity at the family and genus level across taxonomic groups. The priority conservation areas do miss some elements of biodiversity at the species level. A close look at which species are missing can reveal specific shortcomings of our network; e.g., the priority areas include no observations of several habitat-specialist inverte-



C

PC 1: Temp. change & conversion risk (44.4% explained)	PC2: Runoff change (16.2% explained)	PC3: Baseflow & snow water change (12.6% explained)
*Ave. temp. change (0.47)	*Runoff change (0.7)	*Baseflow change (-0.44)
Min. temp. change (0.43)	Precipitation change (0.67)	Precipitation change (-0.44)
Fire risk (0.37)		Max. temp. change (-0.43)
Baseflow change (0.35)		*SWE change (0.36)
*Conversion risk (-0.34)		

Figure 5. Principal components (PCs) 1 vs 2 (A) and 2 vs 3 (B) and axis-loading values for vulnerability metrics (C). * = used in the final composite vulnerability index. Conversion = predicted risk of urban land conversion, Runoff = projected change in surface runoff (2010–2050), Precip = projected change in precipitation (2010–2050), Fire = predicted change in wildfire severity, Baseflow = projected change in baseflow (2010–2050), SWE = projected change in snow water equivalent (2010–2050), TempMin = projected change in minimum temperature (2010–2050), TempAve = projected change in mean temperature (2010–2050), TempMax = projected change in maximum temperature (2010–2050).

brate species (e.g., *Branchinecta longiantenna*, a federally endangered fairy shrimp found in vernal pools).

The condition and vulnerability assessment shows that impairment and threats are ubiquitous. However, this assessment provides a landscape-scale filter for evaluating where conservation investments will be most effective. For example, where habitat condition is least impaired and vulnerability is low, acquisition of private lands or a change in protection status of existing public lands may have immediate benefit to aquatic taxa while requiring minimal additional investment for restoration and mitigation of future threats. This assessment suggests that most watersheds in the state are affected by multiple stressors, including land use (agriculture and urbanization), invasions by nonnative fish, and flow impairment. In such cases, we recommend that the recovery of stream flow be a prioritized strategy because improved flow management is likely to have both direct (e.g., improved habitat) and indirect (e.g., depression of nonnative species populations and maintenance of fluvial processes) benefits for native freshwater taxa, as documented in previous studies (Kiernan et al. 2012, Poff and Schmidt 2016). Improvements to river flow regimes in California can be achieved through modification of dam operations (Grantham et al. 2014, Yarnell et al. 2015) or changes in the timing (Ta et al. 2016) or rate of diversions. In California, forecasted reductions in mountain snowpack and earlier snowmelt timing will affect both ecosystems and water-management systems that rely on the predictable, natural release of snowmelt water in the early summer (Stewart 2009). A projected increase in the frequency of severe droughts (Diffenbaugh et al. 2015) will stress both human and natural systems. Conservation actions that increase resiliency of species and habitats to climate-change

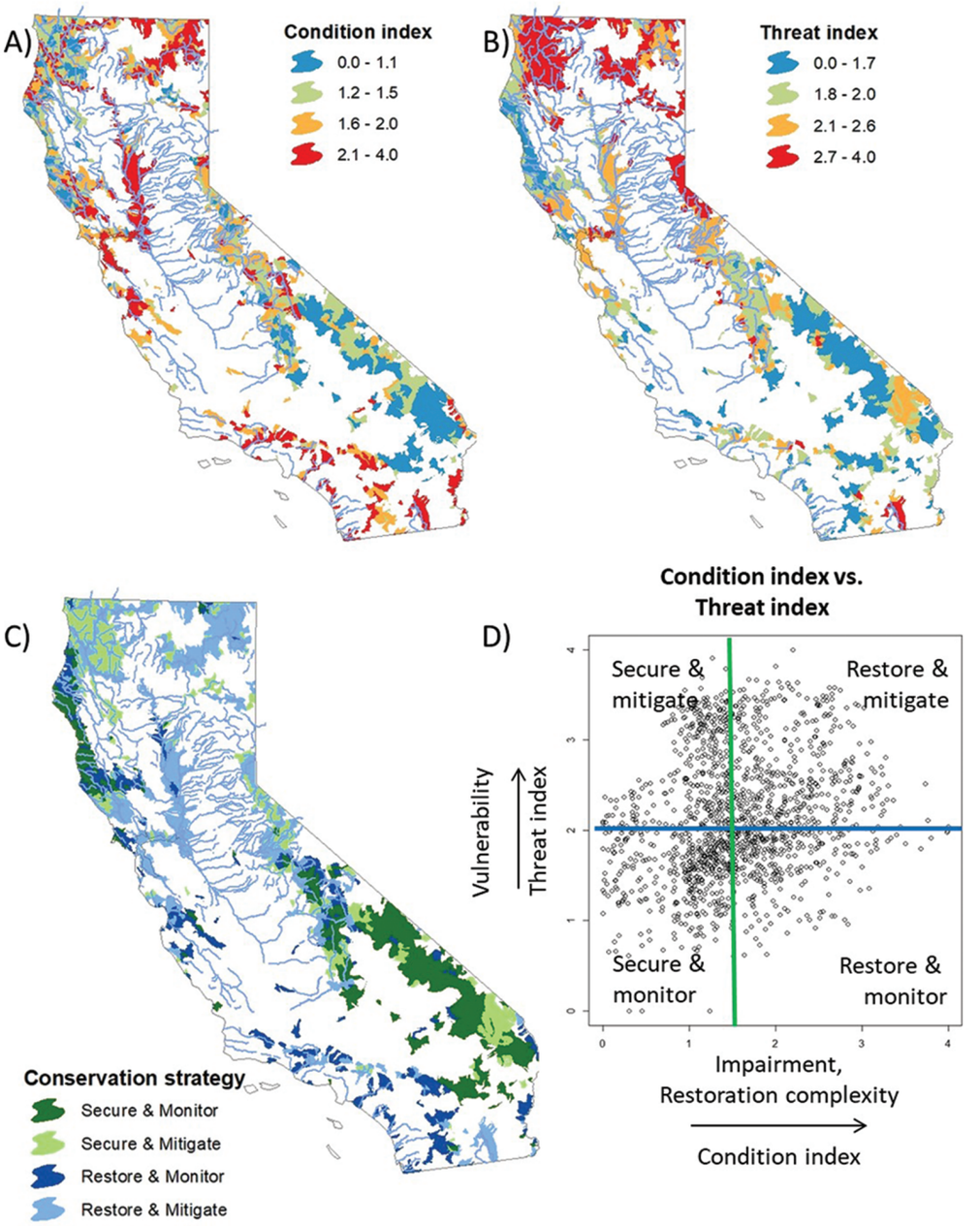


Figure 6. A.—Map of habitat condition index (lower number = better condition). B.—Map of threat index (higher number = higher threat). C.—Composite index of condition and threats and associated conservation strategy. D.—Scatterplot of individual subwatersheds and condition and threat indices.

effects (Seavy et al. 2009) are particularly important in California, especially in areas vulnerable to climate change. Such strategies include floodplain reconnection and other habitat-connectivity enhancements, meadow and wetland restoration (Viers and Rheinheimer 2011), and revegetating riparian zones to improve stream shading (Williams et al. 2015).

PCA of condition and vulnerability metrics is a useful approach for analyzing multidimensional data but can be difficult to interpret. In other approaches to delineating priority conservation areas, measures of condition and threat have been integrated directly into the Zonation optimization algorithm (as in Moilanen et al. 2011). However, we chose not to use such an approach because of the wide diversity of habitat requirements and tolerances of freshwater taxa that were included in our analysis and the added complexity of interpreting results. We present generalized conservation strategies here, but recognize that conservation is most likely to be successful when condition and vul-

nerability metrics, in addition to other social, economic, and environmental factors, are directly evaluated and used to inform context-specific management strategies. Nevertheless, we think that protection and management of priority areas with low impairment and vulnerability is a logical first step in conserving California's freshwater diversity. Subsequent steps will require more detailed evaluation of condition, vulnerability, and habitat requirements of species found in priority areas affected by multiple stressors.

The priority conservation network identifies watersheds where conservation management actions could be implemented to conserve native freshwater biodiversity. We acknowledge that richness and rarity of freshwater taxa targets is not the only way to design conservation networks. Physical-habitat diversity and connectivity are increasingly the focus of conservation planning efforts (Comer et al. 2015, Lawler et al. 2015), but given the degree to which our priority network is effective at capturing both taxonomic richness and habitats, we think it provides a foundation for future planning efforts. Future directions for conservation planning in California could include integration of terrestrial and freshwater realms in a single effort (Amis et al. 2009, Leonard et al. 2017), and consideration of restoration potential for portions of the state that historically supported greater target freshwater taxon richness.

Our analysis incorporates the CARE principles identified by Linke et al. (2011) by providing a comprehensive, adequate, representative, and efficient freshwater conservation network. In lieu of the formal establishment of a new protected area network based on freshwater species or specific management designations (e.g., aquatic diversity management areas; Moyle and Yoshiyama 1994) or native fish conservation areas (Williams et al. 2011), our objective was to create a more comprehensive approach to freshwater conservation that is currently lacking in California. Conservation resources are limited and many conservation areas occur on private lands, so land and water managers may want to consider actions that can accommodate freshwater species within existing management regimes. In many places, this strategy will mean reconciling ecosystem conservation with existing human activities and competing management objectives (Rosenzweig 2003, Moyle 2014). Evidence that managing for freshwater biodiversity and ecosystems can be compatible with human uses is growing. For example, efforts to restore environmental flows to places such as Putah Creek via dam releases (Marchetti and Moyle 2001) and the Shasta River through changes in agricultural irrigation practices (Willis et al. 2015) have resulted in improved conditions for native fishes without adversely affecting primary human uses. Restoring floodplain connectivity in human-dominated landscapes through managed floodways (Sommer et al. 2001, Opperman et al. 2009), offseason flooding of fields (Reiter et al. 2015), or active levee breaching (Florsheim and Mount 2002, Ahearn et al. 2006, Jeffres et al. 2008), can provide multiple ecosystem benefits, help reduce flood risk, and be compatible with floodplain agriculture. These and other efforts in the state show how species can be restored within existing management regimes and in highly modified environments.

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