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ARTICLE
Freshwater Ecology

Crossing boundaries: Introduced trout alter the bird community in a naturally fishless headwaters ecosystem

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Abstract

Alpine areas such as the headwaters of California's Sierra Nevada are increasingly imperiled by climate change and other human-induced stressors. For one, the introduction of non-native fishes into over 60% of its historically fishless watersheds has profoundly restructured the aquatic food web, depressed the abundance, biomass, and diversity of native invertebrates, and endangered endemic vertebrate taxa. Lakes and their surrounding land are reciprocally connected through flows of organic matter, such as emerging aquatic insects; however, the extent to which trout introductions disrupt such flows to the terrestrial environment is poorly understood. Emerging aquatic insects are a potentially important prey source for birds; thus, we hypothesized that the community composition, diversity, and abundance of birds differ between fishless lakes and those stocked with trout due to reduced emerging aquatic insect biomass and diversity. We conducted lakeside bird surveys in headwater lake basins in Sequoia and Kings Canyon National Parks for three summers (2014–2015, 2020) at a total of 39 lakes and quantified the emergence of mayflies between lake types using sticky traps. In addition to major reductions in mayfly densities, we documented lower overall bird abundance at stocked lakes, as well as turnover in avian community composition between stocked and fishless lakes. A fish eradication project at one lake between 2016 and 2019 allowed us to conduct a multiple-control before-after-control-impact (M-BACI) case study to assess changes in the avian community following fish removal. After fish were removed, bird abundance was two times higher than at the control lake. Given the global decline of insect populations and their importance in bird diets, this study reinforces the importance of studying aquatic and terrestrial habitats as interdependent systems and motivates the restoration of naturally fishless habitats impacted by introduced fishes.

KEYWORDS
alpine ecology, aquatic-terrestrial linkages, avian ecology, introduced species, Sierra Nevada

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INTRODUCTION

One of the most significant threats to global biodiversity and ecosystem function is the spread of introduced species (Blackburn et al., 2019; Mack & D'Antonio, 1998; Pimentel et al., 2005). Postindustrial colonial human settlement across the globe has been characterized by the incidental and intentional spread of organisms to places outside their native and historical ranges, producing socioecological impacts at scales far exceeding such activities by most precolonial human societies and by natural disturbances (Reo & Parker, 2013; Ricciardi, 2007). **Of all species introductions, relatively few result in an invasive or ecosystem-changing outcome; however, those that do can radically alter biodiversity and habitat structure, drive native species extinctions, and create "no-analogue" ecological states (Strayer, 2010; Vitousek et al., 1996). Studies of species introductions serve as powerful natural experiments that test fundamental evolutionary and ecological theories, deepening the understanding of the natural world (Sax et al., 2007). Additionally, understanding the effects of introduced species is essential for developing effective conservation strategies, including efforts to mitigate their impacts and assess when removal is feasible (Ceballos et al., 2015).

Freshwater systems worldwide are particularly vulnerable to species invasions compared to terrestrial or marine systems (Cox & Lima, 2006). One type of species introduction common in freshwater systems is the creation and maintenance of new fisheries through fish stocking, the intentional movement of commercially and recreationally valuable fishes into water bodies outside their natural range (Cowx, 1994). There is ample evidence that these introduced fish radically alter aquatic ecosystems at multiple levels of organization (Korsu et al., 2010; Simon & Townsend, 2003). Fish introductions, especially into historically fishless water systems, can result in alternative stable states (Holling, 1973) with different (often simplified) food webs (Strayer, 2010), alterations to nutrient cycling (Schindler et al., 2001), decreased emerging aquatic insect biomass (Pope et al., 2009), altered predator–prey dynamics (Wainright et al., 2021), and in some cases, extirpation of native biota (Eby et al., 2006). Introduced fish are notably a major contributor to amphibian declines and extirpations worldwide (Kats & Ferrer, 2003).

The headwaters of the Sierra Nevada of California provide an example of the reverberating effects of non-native fish introduction in a freshwater ecosystem. Through both direct predation and indirectly through competition for insect food, trout have driven local extirpations of the mountain yellow-legged frog (*Rana sierrae/muscosa*) (Finlay & Vredenburg, 2007), listed as federally endangered in 2002 (US Fish and Wildlife Service, 2002). The presence of trout also decreases the likelihood of occurrence of other native herptiles such as the Pacific treefrog (*Pseudacris regilla*) (via direct predation) and the mountain garter snake (*Thamnophis elegans elegans*) (via the depletion of their amphibian prey) (Knapp, 2005; Matthews et al., 2002). Trout also reduce the abundance, biomass, and diversity of large-bodied aquatic invertebrates, such as mayflies (Order: Ephemeroptera) and caddisflies (Order: Trichoptera). These insects, when present, emerge as winged adults and comprise a voluminous transfer of energy from the aquatic to the terrestrial environment, sufficiently extensive to impact their consumers in water and on land (Piovia-Scott et al., 2016).

Via the suppression of a substantial aquatic subsidy to the terrestrial environment—emerging aquatic insects—the influence of introduced trout may extend beyond the lakeshore to the terrestrial food web. Gray-crowned Rosy-finches (*Leucosticte tephrocotis*), alpine endemic songbirds, are more abundant at fishless lakes during the summer, as they aggregate to forage on brief but intense emergences of mayflies, which comprise 22%–38% of their summer diet (Epanchin et al., 2010). Aside from rosy-finches, little is known about introduced trout's indirect impacts on the bird community in this system, despite growing recognition that cross-system resource subsidies are widespread in nature and play an integral role in the structure and function of ecosystems (Polis & Strong, 1996; Soininen et al., 2015). Overlooking these landscape-scale interactions may lead to an underestimation of the ecological and conservation impacts of trout introductions. Birds that depend on alpine habitats, such as Clark's Nutcracker (*Nucifraga columbiana*), are already highly vulnerable to climate change (Siegel et al., 2014), and disruptions to aquatic-derived subsidies may compound these existing stressors.

Aquatically derived resource subsidies represent "vital flows" of energy into terrestrial environments (Schindler & Smits, 2017). Across biomes, these subsidies have been found to enhance diet quality (Nakano & Murakami, 2001; Twining et al., 2016), growth rates (Wright et al., 2013), reproductive success (Twining et al., 2018), and abundance (Iwata et al., 2003) of terrestrial consumers, with cascading stabilizing effects on recipient food webs by increasing nutrient flow and supporting functional redundancy (Collins & Baxter, 2020; Recalde et al., 2020; Takimoto et al., 2002). Conversely, disruptions to these flows—such as those caused by non-native fish—can restructure terrestrial food webs (Benjamin et al., 2013; Collins et al., 2020) and impact consumers at higher trophic levels such as bears, birds of prey, and bats (Gruenstein et al., 2021; Koel et al., 2019). *Allochthonous*

(Greek: "from another place") subsidies can support more consumers in the recipient system than would normally be sustainable on *autochthonous*, or in situ only, resources, when certain conditions are met, each described below.

Allochthonous subsidies are likely to be important to consumers when the (1) energy available in the donor subsidy is substantial relative to the total energy available in the recipient habitat, (2) the density and concentration (both quantity and quality) of the subsidy in time and/or space are sufficiently high, and (3) consumers are behaviorally able to exploit the subsidy (Polis et al., 1997; Yang et al., 2010). Alpine headwater systems, such as the lake basins of the Sierra Nevada, meet all three criteria. Terrestrial productivity is extremely low (Rundel & Millar, 2016), and aquatic insect pulses are voluminous and highly temporally pulsed, making them conspicuous and valuable for terrestrial consumers limited by autochthonous prey (Piovia-Scott et al., 2016). In general, insects are rich in macro- (e.g., fat, protein) and micronutrients (e.g., calcium, carotenoids) essential for growth and development, and are thus preferred prey for many bird species during the breeding season, especially for provisioning nestlings (Eeva et al., 2010; Razeng & Watson, 2015). Aquatically derived insects in particular can be more nutritious than terrestrial insects due to the abundance of algal-derived highly unsaturated fatty acids in their tissues (Schindler & Smits, 2017; Twining et al., 2019). Finally, birds are likely able to exploit ephemeral subsidies by responding numerically, reproducing in higher numbers where the subsidy is more pronounced (e.g., Polis & Hurd, 1996), and/or aggregatively, whereby they travel to exploit the subsidy (e.g., Gray, 1993). Species-level differences in home range size, dietary flexibility, and nesting behavior are all likely to influence subsidy use. Some foraging guilds are expected to more readily exploit aquatic insect emergences over others, for example, insectivores (Schilke et al., 2020), but many generalist species are also known to diet switch to insects over the breeding season. For example, both Gray-crowned Rosy-finches and Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) exhibit seasonal increases in bill length as they switch from granivory to insectivory during the summer months (Johnson, 1977; Morton & Morton, 1987). Thus, Sierra headwaters are a prime model system in which to study the effects of cross-system resource subsidies from the aquatic ecosystem on the terrestrial consumer community.

In this study, we tested the hypothesis that the resource subsidy of emerging aquatic insects at fishless lakes increases alpine lakeside habitat use by birds. We used mayfly emergence as indicative of large-bodied aquatic insect prey availability and predicted that emerging mayfly density would exhibit large pulses in fishless lakes and be near-absent in stocked lakes, concordant with a robust literature on insect community differences between lake types. Following this increase in high-value prey availability, we predicted that overall avian abundance and alpha diversity (species richness) would both be higher at fishless lakes during the breeding season. We further predicted that the presence of fish in lakes impacts individual bird species differently, resulting in a shift in avian beta diversity (species composition) between stocked and fishless lakes.

METHODS

Study location

The Sierra Nevada's high-elevation headwaters and their montane tributaries were historically devoid of all fishes above ~1800 m in elevation (Knapp, 1996). As the most recent Ice Age ended roughly 12,000 years ago, glaciers carved deep valleys as they receded, resulting in steep gradients between headwater lake basins and the lowland valleys that prevented low-elevation fishes from populating the headwaters (Rundel & Millar, 2016). In the mid-1800s, Euro-American settlers began stocking high-elevation areas with trout collected from lower elevation habitats to which they were native (i.e., Kern River golden trout [*Oncorhynchus aguabonita*]), motivated by a desire to increase the recreational value of the mountainous areas they colonized (Pister, 2001). Adopted by the California Department of Fish and Wildlife (then the California Fish and Game Commission) in the 1920s, stocking expanded into the mid-20th century and began to include hatchery-raised trout, including rainbow (*Oncorhynchus mykiss*), eastern brook (*Salvelinus fontinalis*) and brown (*Salmo trutta*) trout (Pister, 2001). Despite a complete halt to stocking in the range's National Parks by 1991 and reductions in stocking elsewhere throughout the range, over half of the Sierra Nevada's many thousand lakes and thousands of kilometers of stream now contain self-sustaining populations of non-native trout (Armstrong & Knapp, 2004; Knapp, 1996).

Sequoia and Kings Canyon National Parks (SEKI) are two contiguous National Parks on the southern end of the Sierra Nevada of California. Ninety-six percent of the Parks' 141,819 ha is federally designated wilderness, accessible only by foot. The focus of this study was the high-elevation headwaters of the Parks. These lake basins are comprised primarily of perennial graminoid vegetation (wet grasses and forbs), sparse evergreen woodland (foxtail and whitebark pine/*Pinus balfouriana* and *P. albicaulis*), riparian scrub (primarily willow/*Salix* sp.), and talus or boulderfield (Figure 1). Alpine headwaters are highly seasonal, covered in deep snowpack for roughly half the year. The breeding bird community is comprised of a few alpine-adapted residents, plus several short- and long-range migratory species that winter elsewhere (Siegel et al., 2011; Siegel & Wilkerson, 2005).

Study design

We identified study lakes with and without trout in headwater basins throughout SEKI using a spatial database containing eco-geomorphological information about the Park's >3000 water bodies, including the presence of fish (Knapp et al., 2020). We restricted our selection to permanent lakes higher than 3000 m in elevation, greater than 7000 m^2 in area, and deeper than 2.5 m in order to confine variation among fishless lakes to those which could possibly host trout populations if they were introduced (Armstrong & Knapp, 2004). For initial surveys in 2014–2015, we located six pairs of stocked and fishless lakes, each within distinct lake basins (12 lakes total). In 2020, we expanded the study design to include multiple lakes per basin and added 4 new basins for a total of 39 lakes within 10 basins.

To the extent possible, we balanced our design by minimizing differences in the overall distributions of environmental characteristics of stocked and fishless lakes to minimize confounding effects with fish (Appendix S1, Figure S1). Site selection was nonrandom with respect to accessibility: basins are clustered spatially in north and south-central regions of the Parks to facilitate data collection at multiple basins within single multiday backpacking trips. All lakes are located >16 km by foot from the closest trailhead and >3 km from maintained trails. April 1 Snow Water Equivalent for the southern Sierra Nevada was below average in all sample years (2014: 31%, 2015: 5%, and 2020: 45%) (California Department of Water Resources, 2020).

Birds

To survey for birds, we established survey points every 200 m along the shoreline of each of the 39 study lakes as point count locations. Because lakes vary in size, the number of points at each lake also varies, with the

FIGURE 1 A typical alpine lake basin at ~3400 m elevation in Sequoia National Park, surrounded by a mix of talus, bare rock, and sparse graminoid, willow, and stunted conifer vegetation. Photo credit: M. Clapp.

smallest lakes containing one survey point and the largest containing five (Appendix S1: Figure S1). The number of surveys per season and basins visited per year varied due to the challenges of backcountry travel and the distances between the study sites (Appendix S1: Table S1). During the avian breeding season (June–July) and within the hours of 0530–1000, the first author performed 10-min unlimited-count-radius point counts at each point along the lakesides following standard methods (Matsuoka et al., 2014; Ralph et al., 1995). At each point, every bird detected by sight or sound was recorded, as well as the estimated distance of the bird from the point and whether the bird had been detected at a previous point during the day's survey (subsequent detections of previously counted birds were filtered from the data for analysis).

One study lake (hereafter the "fish removal lake") was a stocked lake at the start of the study but underwent trout removal by Park personnel beginning in September 2016. By 2020, the trout population of the fish removal lake was estimated to be substantially reduced from its pre-removal numbers (NPS, unpublished data) and was exhibiting signs of nearing a "functionally fishless" state, characterized by a robust mayfly emergence and colonization by adult mountain yellow-legged frogs (*Rana muscosa*) (NPS, unpublished data; MKC, personal observation). This lake's restoration allowed an initial experimental test of the hypothesis that introduced trout suppress bird abundance. Bird survey data from the fish removal lake in 2020 were not included in any analyses besides the before-after-control-impact analysis (described in *Statistical analyses* below).

Insects

We sampled for emerging aquatic insects using sticky traps at 10 study lakes during the summer of 2015. Unlike emergence traps, sticky traps are smaller, less conspicuous, and can collect insects unmonitored, allowing us to survey multiple locations at once and increasing the likelihood of sampling at peak emergence (Collier & Smith, 1995). We painted the insides of 150-mm plastic Petri dishes with colorless TangleTrap adhesive and mounted four halves to a 1-m length of PVC pipe anchored into the shore at two locations around the shore of each lake, following published methods (Smith et al., 2014). We swapped the traps monthly as travel to each site allowed, resulting in three temporally coarse samples (roughly 1 month in duration each) of the flying insect community at each lake.

Benthic insect communities differ markedly between fishless and stocked lakes (Knapp et al., 2005). Mayflies are among the most abundant large-bodied macroinvertebrates in fishless lakes in this system and are representative of a suite of large-bodied aquatic insects that are more abundant in fishless lakes (Knapp et al., 2001) and are a known prey item for at least one bird species (Epanchin et al., 2010). We used the count of mayflies (Order: Ephemeroptera) on sticky traps as an indicator of large-bodied aquatic prey availability for birds.

While introduced trout depress the emergence flux of large-bodied aquatic insects, other taxa—notably, mosquitos (Family: Culicidae)—are more abundant at stocked lakes (Knapp et al., 2001), and may also represent potential prey for birds (Jedlicka et al., 2017). To quantify total emerging insect flux more generally, we processed a random subset of plates from each lake (two plates per sampling round from the first two sampling rounds) using image processing software ImageJ (Schneider et al., 2012). Briefly, we set the scale of the image using the diameter of the dish (150 mm) and used the Analyze Particles tool to obtain the number of particles (representing distinct insect bodies) > 0.1 mm long, and total trap area covered by insects (in square millimeters).

Sticky traps can saturate over time, leading to lower capture rates and underestimates of insect populations (Kuenen & Siegel, 2016). We thus interpret our insect data as relative indices of emerging aquatic insect volume, and not direct estimates of population size.

Statistical analyses

All final analyses were conducted in R version 4.4.1, in RStudio version 024.04.2 + 764.

Birds

We used the avian point count data to test for the effect of fish presence on four response variables: (1) total abundance; (2) alpha diversity (species richness), (3) beta diversity (pairwise dissimilarity), and (4) the abundance of the nine most common species in the regional species pool. Due to the limitation to sample size imposed by the logistical challenges of wilderness travel, we could not account for imperfect detectability of birds in our analyses. As such, we do not interpret our results as estimates of true abundance/density or richness, but as relative indices thereof. We included elevation as a predictor in our bird models because we expected a priori that bird abundance and richness would have a strong negative relationship with increasing elevation (Siegel et al., 2011).

Bird abundance

Total count of birds detected per point was analyzed using generalized linear mixed models (GLMM) with a Poisson distribution and log link, which are suitable for count data, using the glmer() function in the R package "lme4" (Bolker et al., 2009). We specified *fish* (categorical with two levels; stocked and fishless) and *elevation* (continuous, scaled and centered) as fixed effects, a random effect for *year* (a factor with three levels), and a nested random effect structure of *point* within *lake* within *basin* to account for spatial nonindependence. Model evaluation for GLMMs followed the recommendations in Zuur and Ieno (2016): to validate model assumptions, we inspected the residuals for homogeneity by plotting them against fitted values and against all model covariates. We checked for overdispersion in the model by comparing the sum of squared Pearson residuals with the residual degrees of freedom using a χ^2 test (Bolker et al., 2009).

Bird diversity: Species richness

We modeled species richness using the same modeling procedure, structure, and evaluation as the abundance models above, but with species count (number of species detected) per point as the response variable.

Bird diversity: Community composition

We used data from 2020, our most spatially extensive survey year, to quantify dissimilarity in bird community composition between lakes. We pooled point-level counts of species by lake, correcting for variable sampling effort (different numbers of points per lake) by dividing lake-level counts by the number of survey points. We quantified pairwise dissimilarity using the Bray-Curtis index, a distance metric weighted by species' relative abundances (Anderson et al., 2011).

We used nonmetric multidimensional scaling (NMDS; package "vegan") to visualize pairwise dissimilarity (Bray-Curtis distances) with respect to lake type (Oksanen et al., 2024). Stress was high using only two dimensions, so we set the number of dimensions (k) to 3, but for visual simplicity, we plotted the results using only the first two ordination axes. To describe quantitatively how our two key environmental variables, *fish* and *elevation*, are associated with lake-level community dissimilarity, we performed linear regressions of both covariates onto lake-level NMDS scores from each of the three axes.

Dissimilarity between two samples can be due to nestedness (when individuals of a species are added or lost without replacement), turnover (when species are lost and replaced by other species), or both (Baselga, 2010). Calculating total dissimilarity without investigating the contributions of each can obscure the effects of either process (Soininen et al., 2018). In addition to calculating total dissimilarity, we decomposed the Bray-Curtis index into its nestedness and turnover components using the beta.pair.abund() function in the R package "betapart" (Baselga et al., 2012). To determine whether fish presence influences these components of avian beta diversity, we conducted a permutational multivariate analysis of variance (PERMANOVA; adonis2() function in R package "vegan") on total dissimilarity as well as on nestedness and turnover (Anderson, 2017; Oksanen et al., 2024), using *fish* and *elevation* as independent variables and using 999 permutations. We originally set basin as a blocking factor in the permutations to account for spatial nonindependence, but results were similar whether it was included or not.

Species-level abundance

Bird species within a community vary in their niche space and resource use (MacArthur & MacArthur, 1961), potentially driving differential responses to an environmental perturbation such as fish introduction. To investigate these responses, we built a multispecies, zero-inflated mixture model for the nine most common species in the dataset (comprising ~88% of all detections and 8 out of 14 detected bird families; bolded in Table 1). Zero-inflated data contain more zeros than expected from the SE distributions specified by the assumed distribution (in this case, the Poisson). The zero-inflated model has a hierarchical structure: a Bernoulli process is used to model the probability of getting a 0 on the count, and abundance is modeled using a Poisson distribution and log link. We used the function glmmTMB() in R package glmmTMB (Brooks et al., 2017) to model individual species counts as a function of *fish, species*, and their interaction as fixed effects, plus nested random effects of *point* within *lake* within *basin*. We explored different structures for the zero-inflated component of the model by holding the count portion of the model constant. We then modeled the probability of 0 as a function of elevation, Julian day, time of morning, and as Intercept-only, and then compared the four models' Akaike information criterion (AIC) and their deviance. The Intercept-only model had both the lowest AIC and deviance, and none of the estimates for the candidate explanatory variables was a significant predictor of variation in extra-zero probability, so we chose the Intercept-only model for the zero-inflated component.

Insects

Counts of mayflies on sticky traps were zero-inflated and overdispersed due to the highly pulsed, localized nature of their emergences. We obtained mayfly counts for each plate and used a zero-inflated model with a Poisson

TABLE 1 List of all species detected during point count surveys, ordered by the proportion of points ($n = 80$) at which they were ever detected throughout 2014–2020.

Abbreviation	Common name	Scientific name	Total no. detections	Proportion of points detected	No. lakes detected	
					Stocked	Fishless
ROWR	**Rock Wren**	***Salpinctes obsoletus***	**121**	**0.82**	**14**	**18**
GCRF	**Gray-crowned Rosy-finch**	***Leucosticte tephrocotis***	**161**	**0.79**	**12**	**19**
WCSP	**White-crowned Sparrow**	***Zonotrichia leucophrys oriantha***	**140**	**0.79**	**15**	**16**
DEJU	**Dark-eyed Junco**	***Junco hyemalis***	**131**	**0.74**	**12**	**17**
HETH	**Hermit Thrush**	***Catharus guttatus***	**40**	**0.51**	**10**	**10**
AMPI	**American Pipit**	***Anthus rubescens***	**73**	**0.49**	**8**	**11**
YRWA	**Yellow-rumped Warbler**	***Setophaga coronata***	**32**	**0.49**	**8**	**11**
CLNU	**Clark's Nutcracker**	***Nucifraga columbiana***	**69**	**0.46**	**6**	**12**
DUFL	**Dusky Flycatcher**	***Empidonax oberholseri***	**45**	**0.44**	**8**	**9**
MOCH	Mountain Chickadee	*Poecile gambeli*	21	0.28	4	7
AMRO	American Robin	*Turdus migratorius*	17	0.21	3	5
WIWA	Wilson's Warbler	*Cardellina pusilla*	12	0.21	5	3
CAFI	Cassin's Finch	*Haemorhous cassinii*	7	0.18	4	3
SPSA	Spotted Sandpiper	*Actitis macularius*	10	0.13	3	2
AMDI	American Dipper	*Cinclus mexicanus*	4	0.10	3	1
FOSP	Fox Sparrow	*Passerella iliaca*	11	0.08	0	3
MOBL	Mountain Bluebird	*Sialia currucoides*	4	0.08	2	1
RBNU	Red-breasted Nuthatch	*Sitta canadensis*	3	0.08	2	1
NOFL	Northern Flicker	*Colaptes auratus*	3	0.05	1	1
WTPT	White-tailed Ptarmigan	*Lagopus leucura*	2	0.05	1	1
BRBL	Brewer's Blackbird	*Euphagus cyanocephalus*	1	0.03	0	1
BRSP	Brewer's Sparrow	*Spizella breweri*	1	0.03	1	0
EAGR	Eared Grebe	*Podiceps nigricollis*	1	0.03	0	1
OSFL	Olive-sided Flycatcher	*Contopus cooperi*	1	0.03	0	1
TOSO	Townsend's Solitaire	*Myadestes townsendi*	1	0.03	0	1

Note: Bolded species signify those for which species-level abundance was modeled.

distribution to model them using *fish* and *sampling round* as fixed effects and a nested random effects structure of *lake* within *basin* to account for spatial autocorrelation. We used *fish* as a predictor for the zero-inflated component of the model. The number of days in each sampling round varied slightly, so we included an offset in the model for the number of days in each round.

Fish removal case study

We used a multiple-control before-after-control-impact (M-BACI) design to assess whether bird abundance or richness changed at the "fish removal lake" after trout removal occurred while controlling for variation in count data both across the study period and other lakes (McDonald et al., 2000). As a contrast to the fish removal lake, three lakes (one fishless lake within the same "impact" basin and a pair of fishless and stocked lakes from another basin; the "control" basin) served as control lakes, as we collected bird count data at these locations at least once per year in all three sampling years. We used GLMMs with a Poisson distribution and log link to model the response variables of point-level avian abundance and richness, with a fixed-effects structure that included the factors "before–after" (whether the survey was pre- or post-trout removal at the fish removal lake) and "control–impact" (a three-level factor designating whether the survey was at the fish removal lake, the control lake within the impact basin, or at the control basin), and an interaction term between the two, where a significant interaction term indicates a significant effect of the "impact" (fish removal) taking into account variation in time. We specified a nested random effects structure of *point* within *lake* to account for spatial nonindependence.

RESULTS

Birds

Bird abundance

Fewer individual birds were counted at stocked compared to fishless lakes (fish, β (log-scale) = −0.24 ± 0.11 SE; Wald's *z*, $p = 0.037$; Appendix S1: Table S2a). Model estimates on the response scale (per-point count of birds), adjusted for mean elevation (3390 m), were 5.15 birds per stocked point and 6.48 birds per fishless point, a difference of roughly 1 bird detection per 300-m radius count (Figure 2a). As expected, the abundance GLMM also indicates a strong negative relationship between abundance and elevation (elevation, β = −0.20 ± 0.07; $p = 0.006$; Appendix S1: Table S2a).

Bird diversity: Species richness

Adjusting for the effects of elevation, our model results indicated a marginal but weak difference in species richness between lake types (fish, β = −0.20 ± 0.11; Wald's *z*, $p = 0.07$; Figure 2b; Appendix S1: Table S2b). As with abundance, avian species richness declined significantly with elevation (elevation, β = −0.20 ± 0.07; $p = 0.004$).

Bird diversity: Community composition

Total beta diversity of bird communities between stocked and fishless lakes was explained by both elevation (PERMANOVA, $R^2 = 0.161$, $F = 14.30$, $p = 0.001$; Table 2) and fish presence ($R^2 = 0.043$, $F = 3.80$, $p = 0.004$). Both differences can be attributed to turnover (the even replacement of individuals from one species by individuals from another species), not to nestedness (the loss of species without replacement) (Figure 3a, Table 2). NMDS axes 1 and 2 were strongly correlated with elevation and fish, respectively (Figure 3; Appendix S1: Table S3).

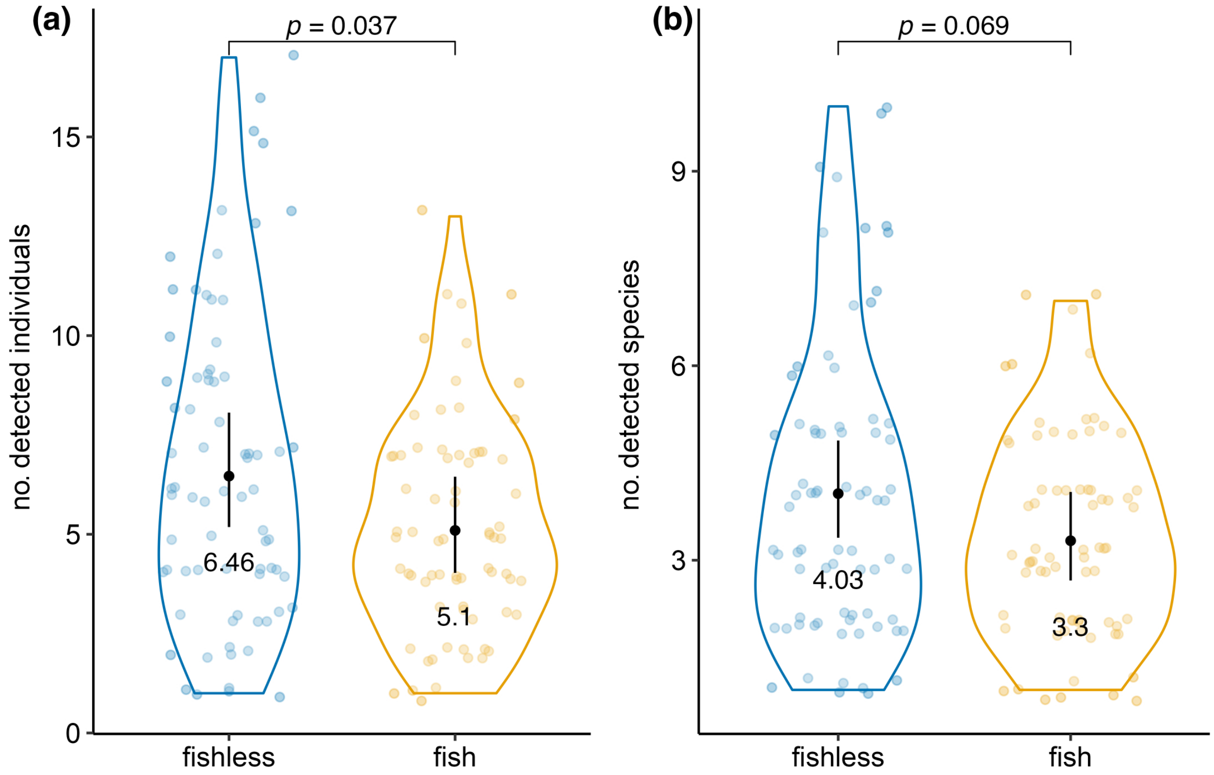

FIGURE 2 Marginal means estimates and 95% population-level CIs of point-level (a) avian abundance and (b) avian species richness at fishless and stocked lakes, transformed to the response scale. Colored points and violin plots represent the values and distributions of the raw count data, jittered for legibility.

TABLE 2 Permutational analysis of variance (PERMANOVA) of pairwise Bray-Curtis dissimilarity and its nestedness and turnover components suggests that beta diversity is mostly driven by turnover (i.e., the balanced replacement of individuals).

	Effect of fish				Effect of elevation					
Model	**SS**	R^2	F	p	**SS**	R^2	F	p	**Residual SS**	**Residual** R^2
Total	**0.553**	**0.066**	**3.533**	**0.008**	**2.341**	**0.279**	**14.96**	**0.001**	5.479	0.654
Nested-ness	−0.042	−0.049	−1.310	0.921	−0.236	−0.278	−7.332	0.999	1.124	1.328
Turn-over	**0.478**	**0.085**	**5.988**	**0.008**	**2.333**	**0.416**	**29.19**	**0.001**	2.797	0.499

Note: Of the two variables modeled, turnover is explained primarily by elevation ($R^2 = 0.416$) and to a lesser degree by fish presence ($R^2 = 0.085$). Bolded species signify those for which species-level abundance was modeled.

Species-level abundance

The nine most common species in the regional species pool exhibited various responses to elevation and fish presence (Figure 4; Appendix S1: Table S4). Gray-crowned Rosy-finch (fish × species, $\beta = -0.71 \pm 0.35$; Wald's *z*, $p = 0.041$) and Clark's Nutcracker (fish × species, $\beta = -0.97 \pm 0.41$; $p = 0.019$) were counted in fewer numbers at stocked lakes. In contrast, Mountain White-crowned Sparrow was counted in greater numbers at stocked lakes (fish × species, $\beta = 0.61 \pm 0.34$; $p = 0.072$). The remaining six species modeled did not exhibit discernible differences in abundance between lake types (Figure 4).

Insects

The probability of getting a count of 0 on a mayfly count was strongly explained by fish presence (GLMM, fish, $\beta = 4.73 \pm 1.08$, Wald's *z*, $p < 0.0001$; Appendix S1: Table S5). When mayflies were present, they were counted in greater numbers at fishless lakes (fish, $\beta = -1.14 \pm 0.32$, Wald's *z*, $p < 0.001$). Mayfly emergence was highly temporally pulsed over the course of the season, peaking in late June at most lakes (Figure 5). The mean number of particles (insects) per trap, mean trap area covered by insects, and the mean particle size were similar between lake types, but variation in each measure was much greater at fishless lakes compared to stocked lakes (Table 3, Figure 5).

Fish removal case study

In 2020, the number of birds counted per point at the fish-removal lake increased beyond the range of its historic (2014–2015) variation (5.9 ± 1.2 individuals) and into the range of variation (10.8 ± 0.98) of the fishless reference lake within the basin (Figure 6a). This positive effect of trout removal on abundance was supported in the M-BACI GLMM after accounting for spatiotemporal variation in counts (BA×CI, β (log-scale) = 0.71 ± 0.24, Wald's *z*, $p = 0.004$; Appendix S1: Table S6a). Avian species richness at both the fish removal lake and the control lake within the treatment basin displayed a trend toward higher richness after trout removal (Figure 6b), but the interaction term in the richness M-BACI GLMM was not significant, indicating no effect of trout removal specifically on avian species richness (BA×CI [Removal Lake], β (log scale) = 0.49 ± 0.35, $p = 0.15$; Appendix S1: Table S6b). Both lakes within the control basin had significantly lower abundance and richness than did the lakes in the impact basin and did not exhibit significant changes in abundance or species richness in 2020 (Figure 6; Table S6b).

At the fish removal lake, 8 out of 16 (50%) of all detected species increased in abundance beyond 1 SE of the mean from previous surveys (Figure 6c). Two species were detected in 2020 that had never previously been detected in any survey of the fish removal lake prior to trout removal: American Dipper (*Cinclus mexicanus*) and Mountain Bluebird (*Sialia currucoides*) (Figure 6c). In contrast, we detected two species in 2014–2015 that were not detected in the 2020 survey: Wilson's Warbler (*Cardellina pusilla*) and Yellow-rumped Warbler (*Setophaga coronata auduboni*).

DISCUSSION

The fishless lakes in this study supported more birds compared to lakes with fish—a difference of roughly one bird per 300 m radius area around the shoreline, or a 20% increase in total abundance—and hosted a different distribution of individuals among species, after controlling for elevation-driven differences in community composition. There were few, if any, mayflies emerging from stocked lakes, which corroborates well-documented patterns of this large-bodied insect in lakes with and without trout across the Sierra Nevada as a whole. Finally, we demonstrated experimentally via whole-lake trout

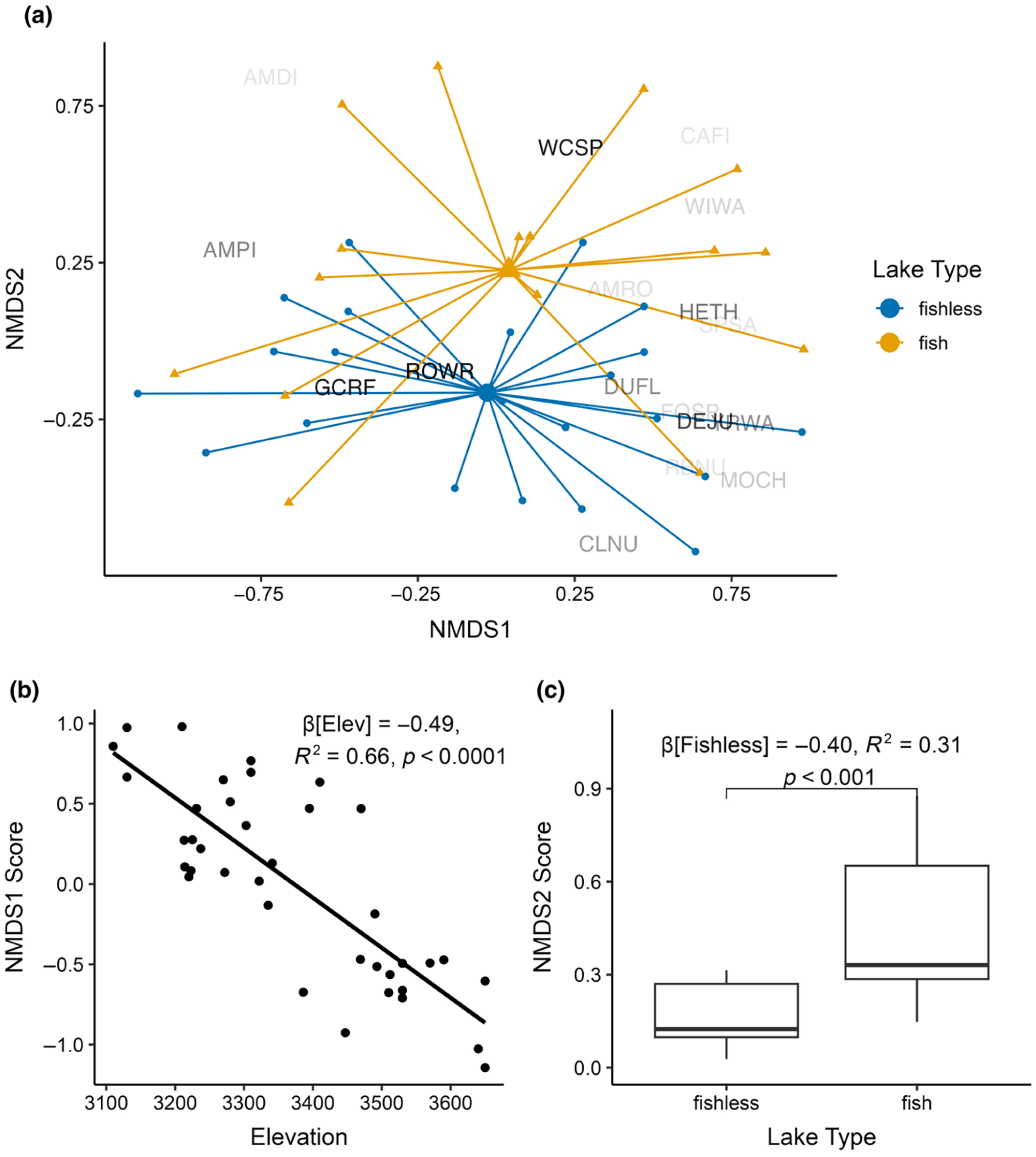

FIGURE 3 (a) Nonmetric multidimensional scaling (NMDS) ordination (stress = 0.12, $k = 3$; first and second NMDS axes shown) illustrates differences in lake-level avian community composition with respect to fish. Centroids represent mean ordination space for all fishless (blue circle) and stocked (gold triangle) lakes, and connected nodes represent avian community composition of lakes. The position of individual bird species in two-dimensional ordination space is represented by their four-letter abbreviations, with increasing opacity corresponding to their relative abundance. (See Table 1 for explanations of species abbreviations.) (b) Regressions of elevation on all lakes' NMDS1 scores, and (c) fish presence on all lakes' NMDS2 scores demonstrate strong associations between those environmental variables and lake-level avian community composition as quantified by NMDS. Boxplots in (c) depict the median (central bar), 25%–75% quartile (box limits), and 1.56× the interquartile range divided by the square root of the sample size (whiskers) for NMDS2 scores as grouped by lake type. Beta values represent marginal mean estimates for the displayed parameter, but models for both axes contained both environmental covariates. R^2 values refer to the fit of the full model to the data. See full model table in Appendix S1: Table S3.

removal that bird abundance doubled after fish were removed, indicating release from competition with trout for aquatic insect prey. Taken together, these results provide support for the hypothesis that trout introductions have had cascading impacts into the terrestrial ecosystem and influence avian abundance and community structure. These results are consistent with both a comprehensive body of literature about the prevalence of aquatic subsidies to terrestrial consumers in nature (Bartels et al., 2012; Piovia-Scott et al., 2016; Polis et al., 1997) and with a growing literature about the potential for perturbations to aquatic systems to cause trophic cascades that extend to terrestrial consumers (Epanchin et al., 2010; Koel et al., 2019; Lawler &

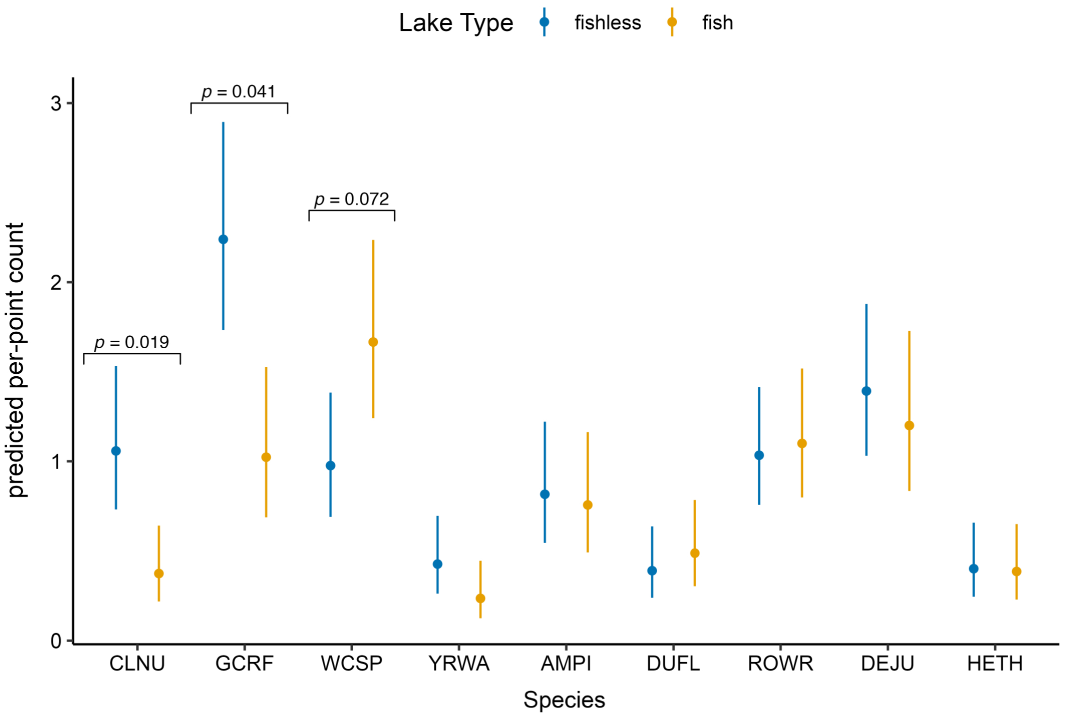

FIGURE 4 Marginal means estimates of the effect of fish on individual species' counts at lakesides indicate that three of nine species modeled are counted in different numbers at fishless versus stocked lakes. Error bars represent 95% CIs for fixed effects. See Appendix S1: Table S4 for full model summary table and Table 1 for an explanation of species abbreviations.

Pope, 2006; Matthews et al., 2002; Rudman et al., 2016). Beyond the study of a single terrestrial species, this study documents the effects of an aquatic trophic cascade on an entire community of terrestrial consumers: birds.

Our hypothesis that species richness is higher at fish-containing lakes was not strongly supported by our results. However, the turnover in community composition that we observed between lake types—driven in part by an increase in two alpine specialists (Gray-crowned Rosy-finch and Clark's Nutcracker) at fishless lakes and an increase in a generalist species (White-crowned Sparrow) at stocked lakes—reflects that beta diversity, a crucial component of functional diversity (Socolar et al., 2016), is impacted by fish introductions. The strong positive association between Gray-crowned Rosy-finch abundance and fishless lakes that we documented corroborates previous research on this species (Epanchin et al., 2010), but the negative and positive effects of fish on the abundance of Clark's Nutcracker and White-crowned Sparrow, respectively, are novel findings.

Birds can respond to resource subsidies numerically (by increasing number of breeding pairs around the subsidy), aggregatively (opportunistically recruiting to the ephemeral resource), or both. Both rosy-finches and nutcrackers have unique adaptations and life histories that may enable an aggregative response: Gray-crowned Rosy-finches possess buccal pouches, or extendable "cheek" pouches that can be filled with prey; this adaptation likely facilitates a much wider home range because they can collect more prey per foraging bout than typical songbird species (Miller, 1941; Twining, 1940). Similarly, Clark's Nutcrackers have evolved a sublingual pouch for carrying large amounts of food, typically whitebark pine seeds, but sometimes insects (Bock et al., 1973). Their home ranges also span several kilometers (Lorenz et al., 2011) and would enable them to prospect for resource pulses across large areas. It is possible that these species also exhibit a numerical response to resource subsidies from fishless lakes, but given their large home ranges and nesting associations, any difference in breeding pairs associated with fishless habitat may occur at the basin level, not at the lake level.

We did not expect Clark's Nutcracker to be so strongly associated with fishless lakes. Clark's Nutcrackers are known to be specialists on, and mutualists with, whitebark pine (*Pinus albicaulis*), caching and relying on their fatty seeds for food throughout the year (Barringer et al., 2012; Hutchins & Lanner, 1982; Tomback, 1982). However, they have also been documented eating insects, mammals, amphibians, and birds during summer months prior to the ripening of whitebark pine cones (Mulder et al., 1978), including species known to be associated with fishless lake food webs, such as Black Rosy-finch (*Leucosticte atrata*) eggs in

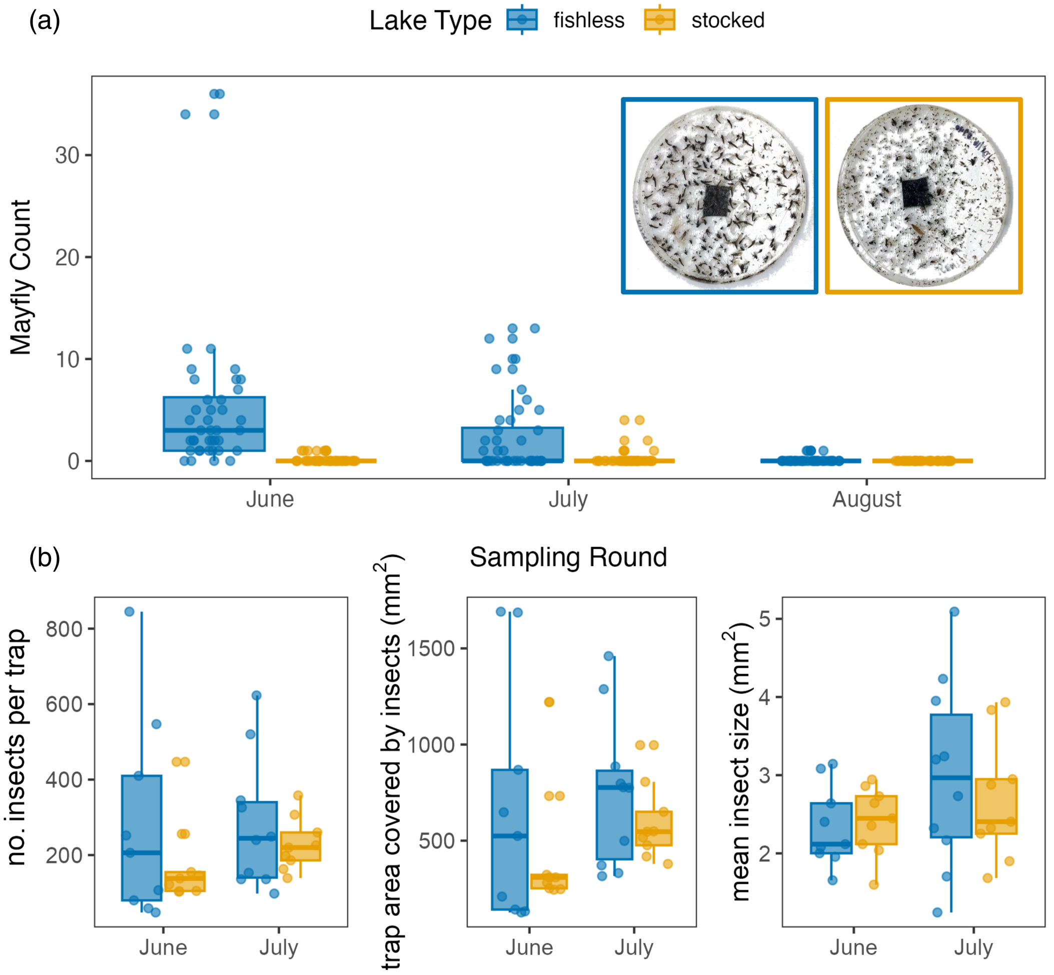

FIGURE 5 (a) Counts of mayflies on sticky traps differ significantly between stocked and fishless lakes and by sampling round. (b) Image analysis of sticky traps ($n = 37$ traps) reveals wide variation in the number of insects per trap, trap area covered by insects, and mean insect size between lake types and sampling rounds. All boxplots depict the median (central bar), 25%–75% quartile, and 1.56× the interquartile range divided by the square root of the sample size. Photographs of sticky traps (M. Clapp) demonstrate the body size of mayflies relative to the insects typically found on sticky traps next to fishless versus stocked lakes.

TABLE 3 Summary statistics for image analysis of sticky traps at fishless and stocked lakes.

			No. insects		Area covered (mm^2)		Insect size (mm^2)	
Lake type	**Sampling round**	**No. traps**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Fishless	June	9	283.78	90.23	669.83	211.23	2.36	1.39
Stocked	June	9	175.11	37.47	435.63	110.48	2.49	1.40
Fishless	July	10	282.60	55.26	750.22	124.08	2.65	2.18
Stocked	July	9	228.56	23.29	593.22	65.82	2.60	1.34

Wyoming (French, 1955) and mountain yellow-legged frog tadpoles in the Sierra Nevada (Schaming et al., 2024). It is thus plausible that nutcrackers benefit from fishless lake habitat through more predation opportunities on animals at higher trophic levels associated with fishless lake food webs. Given the nutcracker's keystone ecological role as the primary disperser of the federally endangered whitebark pine, further investigation of how fishless habitat may mediate habitat selection and/or meta-population dynamics of Clark's Nutcracker is especially warranted.

The remaining bird species in this system appeared not to differ significantly in observed abundance between lake types, suggesting that they either do not exhibit a

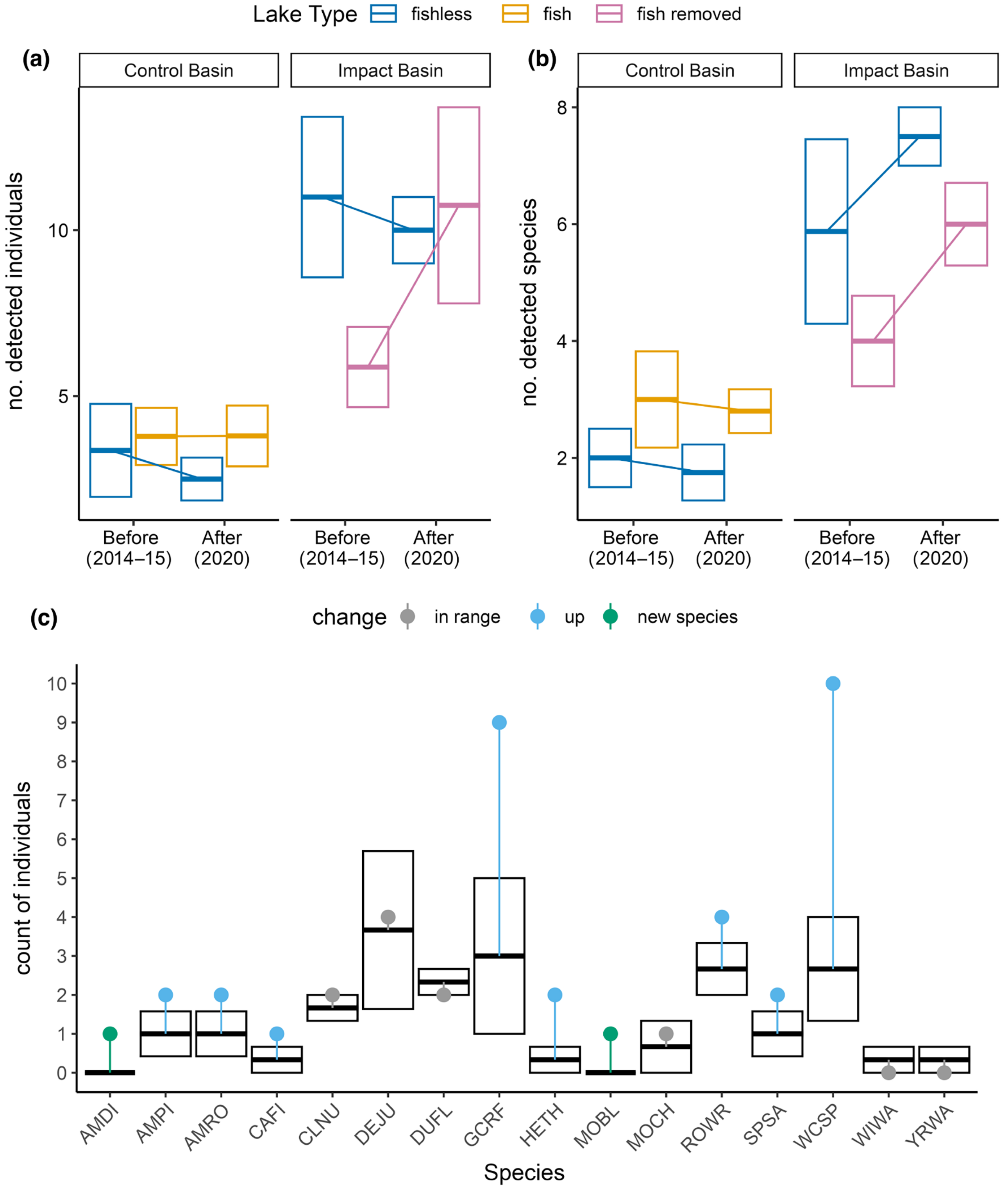

FIGURE 6 A multiple before-after-control-impact (M-BACI) study of the effects of single-lake fish removal on (a) per-point bird abundance, (b) per-point species richness, and (c) counts of individual species at the fish removal lake. Boxplots in (a) and (b) represent per-point means (midlines) ± 1 SE (box limits) of bird abundance and richness, respectively. Boxplots in (c) represent lake-level (points pooled) means (midlines) ± 1 SE (box limits) of bird counts across 2014–2015 surveys ($n = 3$), and dots represent lake-level counts (points pooled) from 2020. Blue dots represent species whose 2020 counts exceeded the pre-removal mean + 1 SE, gray points represent species whose 2020 counts were within the pre-removal mean ± 1 SE, and green points represent species never recorded on pre-removal counts. No species were counted in fewer numbers than their pre-removal means (±1 SE) in 2020.

preference for, or an ability to distinguish between, lakes with and without trout. Aquatic subsidies associated with fishless lakes may be less important for upland-adapted bird species, which are able to biochemically synthesize polyunsaturated long-chain fatty acids from shorter chain fatty acids found in terrestrial prey items (C. W. Twining et al., 2019, 2021). This may be the case with Rock Wren (*Salpinctes obsoletus*), a bird adapted to arid environments known to specialize in terrestrial insects such as grasshoppers (Family: Orthoptera) (Benedict et al., 2021).

However, given the high nutritional value of aquatically derived prey (e.g., calcium, polyunsaturated fatty acids), it is plausible that a diet enriched in aquatic insects would affect bird consumers not by altering their occupancy across the landscape, but by altering their reproductive success within it. Specifically, disruptions to aquatic resource pulses have negative effects on clutch sizes and nestling growth rates of breeding birds (Grames et al., 2023; Schindler & Smits, 2017; St. Louis & Barlow, 1993; Twining et al., 2016). Decreases in local availability of mayflies, specifically, resulted in significantly slower growth rates of Prothonotary Warbler nestlings compared to those nesting in areas with higher mayfly densities, because parents provisioned their nestlings' prey in relation to its local availability (Dodson et al., 2016). Central-place foragers (such as breeding birds with an active nest within a socially enforced territory) could be particularly vulnerable to losses of aquatic subsidies because the distance they can forage is ultimately restricted by the need to regularly feed nestlings or to avoid territorial conflict (Andersson, 1978). Further, if birds cannot distinguish between fishless and stocked lakes upon settlement (which is likely, given that lakes are often covered in ice and snow when they arrive), they may nest in similar numbers around each but experience different nutritional environments around fishless and stocked lakes, with consequences to reproductive output.

It is also possible that birds that were equally or more common at stocked lakes may meet their nutritional needs from aquatic invertebrates associated with fish-containing lakes, such as mosquitos (Trevelline et al., 2018). While we observed drastic differences in mayfly abundance between lake types, fish-containing lakes still exhibited pulses of emerging aquatic insects of smaller size, most commonly of midges, flies, and mosquitos (Figure 5, Table 3). Mountain White-crowned Sparrows have been documented eating mosquitos in the Sierra Nevada (Morton, 2002), which are one of the few aquatic species relatively more abundant at fish-containing lakes (Knapp et al., 2001). Within the existing mosaic across the landscape, they (and individuals of other species still present at fish-containing lakes) may be able to utilize the available prey there and avoid competition for space or food at fishless ones. However, the fact that White-crowned Sparrows are rarely absent from fishless lakes and nearly doubled in number after fish removal suggests that they, too, may benefit from fishless habitat. A comparative study investigating the effects of diet on clutch size and nestling condition of different bird species at stocked versus fishless lakes would illuminate the mechanisms by which avian communities and population dynamics are mediated by fish presence.

The extent to which the unique nutritional contents of aquatic insects are limiting for terrestrial consumers is an important mechanistic link in understanding the landscape-level dynamics of aquatic–terrestrial resource subsidies in this and other systems (Schindler & Smits, 2017). Birds in lower elevation riparian areas of the Sierra Nevada can have summer diets of up to 50% aquatic origin, and of similar isotopic composition to predatory fish (B. K. Jackson et al., 2020). In the alpine ecosystem, where terrestrial productivity is much lower than in mid-elevation riparian corridors, we might expect the contributions of aquatic insects to bird diets to be at least as high when they are available. Non-native fish in the southern Sierra Nevada have suppressed large-bodied aquatic insect populations at the landscape scale, since well over half of their watersheds are impacted by trout (Knapp & Matthews, 2000). At this scale, losses of such a subsidy could result in source-sink dynamics or pose an ecological trap to birds, especially if they are naïve to the lower nutritional quality of lakeside habitat at stocked lakes.

Aside from directly reducing an important food source for birds (e.g., mayflies), introduced trout could impact bird consumers indirectly by influencing complex interactions throughout the food web (Ostfeld & Keesing, 2000) that we did not directly consider. For example, introduced fish could be reducing profitable terrestrial prey for birds, such as spiders, by outcompeting spiders for aquatic insect prey, as has been described in stream systems in the Rocky Mountains and in South Africa (Benjamin et al., 2011; Jackson et al., 2016). Fish presence could also indirectly influence densities of avian predators, such as garter snakes or Clark's Nutcrackers, both of which are more common at fishless lakes and known predators on the eggs and nestlings of ground-nesting birds such as White-crowned Sparrows (James et al., 1983; Morton et al., 1993). Increased nest predation pressure may offset the nutritional benefits of fishless habitat and dampen birds' numerical responses to the aquatic prey subsidy there. Such complex food web dynamics were not examined in this study but may drive some of the interspecific variation we observed in birds' relative abundances at fishless versus stocked lakeside habitat.

This study may have underestimated the effect of fish on birds, specifically the opportunistic response of birds to insect emergences, due to its design. The likelihood of conducting a bird survey during an insect emergence was low, either within the span of a morning or on the day(s) within the season. Insect emergences typically occur later in the morning, after avian surveys conclude and once water temperature has increased (Harper & Peckarsky, 2006). Over the course of our study, we incidentally observed groups of many species (including Yellow-rumped Warbler, American Pipit [*Anthus rubescens*], White-crowned Sparrow, Dark-eyed Junco [*Junco hypemalis*], and Mountain Bluebird) feeding on mayfly emergences outside of survey windows, both late in the morning and with fledglings late in the season after nesting had ended. Such visits suggest how important the timing of a subsidy is to consumers' ability to exploit it (Leroux & Loreau, 2012; Sato et al., 2016). It is possible that our avian sampling protocol, while congruent with well-established standards for avian survey and reliable in measuring patterns of avian breeding residency at lakesides, did not fully capture the pulse in activity exhibited by songbirds exploiting the subsidy, especially if the mechanism behind the difference in bird abundance was aggregative. The magnitude of birds' opportunistic response to these resource pulses might be better measured with more targeted sampling of lakes at the time of aquatic insect emergence (Adams et al., 2023).

In ecological study design, a challenging tradeoff exists between extensive spatial replication and intensive temporal resurvey, both important to establishing sufficient statistical power to detect ecological patterns in data of species that are mobile or cryptic, and/or where detection-given-presence is not a guarantee. Our sample size and complex spatial structure likely resulted in incomplete sampling (i.e., not detecting every individual present), and precluded the use of hierarchical modeling approaches that explicitly account for such imperfect detection (Kéry & Royle, 2015; MacKenzie et al., 2003). Not accounting for imperfect detection may result in an underestimation of abundance or diversity (MacKenzie et al., 2003). To reduce uncertainty around the estimated trends we report here, and to further investigate the mechanisms behind them, we encourage two directions of further study. The first would be to maximize spatial and/or temporal replication, utilizing tools such as passive acoustic recording (PAM) to augment traditional surveys (Clapp et al., 2023). PAM approaches require sophisticated machine-learning-based methods that efficiently and reliably label acoustic signals to species or finer classifications (Huus et al., 2025; Kahl et al., 2021), along with statistical methods that accommodate such outputs (Doser et al., 2021; Fiss et al., 2024), which have only recently been developed for widespread use. The other would focus on mechanism, employing field and lab techniques such as nest-monitoring and stable isotope and/or eDNA diet analysis (Hoenig et al., 2022), to better understand the importance of aquatic subsidies to avian diet, productivity, and survivorship.

Our study suggests that preserving and restoring fishless habitat in the alpine is important for the larger community beyond the aquatic ecosystem. Current trout removal projects in California's designated wilderness areas are primarily motivated by the need to restore suitable habitat for the endangered mountain yellow-legged frog. Mountain yellow-legged frog populations recover successfully at restored fishless lakes; however, they are doubly threatened by the spread of *Batrachochytrium dendrobatidis*, or Bd, a fungal pathogen that has resulted in extensive die-offs of frogs across the Sierra Nevada and worldwide (Scheele et al., 2019; Vredenburg et al., 2010). Fifteen years of intensive conservation measures, including introductions of Bd-resistant frogs to previously extirpated locations, have demonstrably improved the outlook of *Rana sierrae* populations in the Sierra Nevada (Knapp et al., 2024), an extraordinary achievement of single-species conservation. At the same time, conservation and management practitioners are increasingly called to move toward a holistic conservation paradigm that prioritizes ecological stability, biodiversity, and ecosystem services (Kremen & Ostfeld, 2010; Wenny et al., 2011; White et al., 2013). The present study reinforces the ecological importance of fishless habitat that was first established by studies of mountain yellow-legged frogs and lends legitimacy to ongoing and future trout removal projects that restore habitat for native alpine biodiversity across ecosystem boundaries.

Conclusions

Mountaintops and alpine areas are one of the most quickly changing biomes in the world. They are already critically important areas for many bird species throughout their annual cycle, as many birds migrate upslope after breeding to track resource availability (Boyle & Martin, 2015). Adding to the ample standing evidence that fishless alpine waters host greater aquatic biodiversity than their stocked counterparts, we have demonstrated that fishless areas support greater numbers of breeding birds, many of whom have been categorized as "moderately vulnerable" to the effects of climate change (Siegel et al., 2014). As the pace of climate change quickens, alpine areas may become even more important habitat for birds, acting as refugia for both endemic specialists and for biodiversity at large, "sheltering" lowland species into the future as they track their niches upslope (Loarie et al., 2009; Morelli et al., 2020). High-elevation fishless waters may thus serve as particularly important buffers against climate change impacts for taxa across systems and trophic levels amid the shrinking alpine zone. Advancing our knowledge of how alpine communities function now will aid in our ability to mitigate biodiversity loss and steward our ecosystems forward through the Anthropocene.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Clapp & Patricelli, 2025) are available from Zenodo: https://doi.org/10.5281/zenodo.16622129.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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