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ARTICLE

Freshwater Ecology

Effects of drying and orientation to perennial refuges on aquatic biodiversity across two basins differing in aridity

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Abstract

Intermittent streams are globally distributed, comprise over half the length of the global river network, and are expected to become more prevalent. However, most studies of intermittent streams are conducted at extremes of scale, are limited in taxonomic and temporal scope, and focus exclusively on drying patterns. Here, we assessed how both flow intermittency and orientation to perennial refuges affect aquatic invertebrates and aquatic and semiaquatic vertebrates across 2 years within two intermittent river basins differing in their aridity. We used loggers to characterize flow intermittency and wet–dry mapping to determine orientation to perennial refuges of reaches. In winter and summer 2015 and 2016, we collected and identified invertebrates and visually surveyed vertebrates. Using permutational multivariate analyses of variance with distance matrices, we found distinct invertebrate communities by basin, flow class (perennial or intermittent), and season, and distinct vertebrate communities by basin, and between flow classes and seasons in the more arid basin. Invertebrate communities had higher beta diversity in the more arid than mesic basin, whereas the opposite was true for vertebrates. We identified indicator species for all combinations of basin and flow class, perennial reaches combined from both basins, each basin, and some combinations of flow class and season within basins. Flow intermittency and orientation to perennial refuge predictors correlated well with both invertebrate and vertebrate communities. However, we did not find nestedness of communities that differed significantly from that expected by chance in response to increasing flow intermittency or distance to refuges. Lastly, basin, flow intermittency, and orientation to perennial refuge predictors were generally important for modeling taxon richness and densities, and richness and densities decreased with increasing flow intermittency and distance to perennial refuges. Collectively, our data suggest that intermittent streams harbor unique biodiversity, but also that some taxa have context-dependent responses to intermittency and orientation to perennial refuges. These findings also suggest that future increases in stream drying are likely to lead to changes to stream communities with high potential for the loss of aquatic biodiversity.

KEYWORDS
drying, macroinvertebrates, refuges, temporary streams, vertebrates

INTRODUCTION

Intermittent stream ecosystems are globally distributed and found in vastly different biogeographic regions, ranging from the Dry Valleys of Antarctica to the wet tropics (Datry et al., 2017). Numerically, they are estimated to comprise greater than 50% of the length of the global river network and thus contribute substantial numbers of stream segments and discharge (Datry, Larned, & Tockner, 2014; Messager et al., 2021). In the future, the prevalence of intermittent streams is expected to increase as a result of water use and climate change, particularly in arid and semiarid regions (Larkin et al., 2020; Seager et al., 2013).

Flow intermittency is a major driver of aquatic biodiversity via its effects on habitat availability, connectivity, and quality in streams (Leigh & Datry, 2017; Soria et al., 2017). As flow is reduced during drying, aquatic habitat is progressively lost, reaches become disconnected, and conditions such as temperature, oxygen, and resource availability within remnant pools change (Lake, 2003; Stanley et al., 1997). In response to drying, aquatic species may be lost, enter dormancy (Williams, 1998), transition to terrestrial life stages (Velasco & Millan, 1998), or move to remnant pools (Bogan et al., 2017), the hyporheic zone (Vander Vorste et al., 2016), or perennial water in other parts of the river network (Boulton, 2003). Reshuffling of species associated with drying causes aquatic communities to temporarily shift toward species capable of surviving in pools (Hill & Milner, 2018), and different pools may have species compositions that diverge at varying rates (Drummond et al., 2015; Larned et al., 2010). As aquatic habitat shrinks during drying, terrestrial habitat abundance and connectivity increases, providing new habitat for semiaquatic and terrestrial species (Sánchez-Montoya et al., 2018; Steward et al., 2017).

Besides flow intermittency and its direct effects, the availability of colonist species is also a major determinant of intermittent stream biodiversity. In response to flow resumption, aquatic species that entered dormancy to withstand drying can reactivate (Williams, 1998). From surrounding riparian areas, aquatic species with terrestrial adult life stages timed to coincide with drying can deposit eggs in streams to initiate recruitment (Bogan & Boersma, 2012). Other aquatic species that moved into the hyporheic zone (Kawanishi et al., 2013; Rodríguez-Lozano et al., 2019; Stubbington, 2012) or remnant pools (Bogan et al., 2019; Marshall et al., 2016) during dry periods can recolonize newly flowing reaches nearby. From outside of the immediate area, drift and swimming can bring colonists from upstream refuges (Brittain & Eikeland, 1988), species can swim or crawl upstream from downstream refuges (Davey & Kelly, 2007; Mackay, 1992), or terrestrial adult forms can immigrate from other parts of the river network (Bilton et al., 2001; Sánchez-Montoya et al., 2017). While some of these modes of recolonization involve sources of colonists close to newly flowing streams and thus occur more quickly, others are dependent on colonists from distant sources and require more time (Resh, 1992; Robson et al., 2011). The distance and direction of refuges within landscapes (Datry, Larned, Fritz, et al., 2014) and the dispersal ability of colonist species (Robson et al., 2011) are thus also likely to affect intermittent stream biodiversity.

Traditionally, the aquatic communities of intermittent streams were described as species-poor with low densities of individuals, because periodic drying can be a harsh environmental filter (Poff & Ward, 1989). With increasing interest in these habitats, this viewpoint has been challenged by integrating community data from lentic, lotic, and terrestrial phases of intermittent streams (Datry, Larned, & Tockner, 2014). Nevertheless, the lotic aquatic fauna of intermittent streams is often described as a nested subset of nearby perennial communities with few species specialized for intermittent habitats (Datry, 2012; Datry, Larned, Fritz, et al., 2014). Over time, analyses of the relationship between flow intermittency and biodiversity have also become more sophisticated by characterizing flow intermittency using continuous metrics (Leigh & Datry, 2017). The recognition that intermittent streams are metacommunities has also led to increased recognition of the spatial orientation of drying and refuges as important for recolonization dynamics (Crabot et al., 2020; Sarremejane et al., 2020; Stubbington et al., 2017). Indeed, the existence of multiple community recovery states and trajectories has been proposed as an explanation for high beta diversity at the network scale in intermittent stream systems (Larned et al., 2010).

Despite this progress, many studies of the biodiversity of intermittent streams are often conducted at extremes of scale such as focused studies of single areas or meta-analyses of global datasets and consequently are either lacking generality or potentially missing informative variation apparent only at intermediate scales. However, two notable exceptions are recent works by Crabot et al. (2020) and Gauthier et al. (2020) who studied the temporal dynamics and dispersal of stream invertebrates across many stream networks in France, respectively. Additionally, to characterize communities, sampling a locality once is often considered sufficient despite expected temporal and interannual variation. The biodiversity of intermittent streams is also often studied with focus on particular taxonomic groups (e.g., invertebrates only), limiting our ability to detect effects of drying that might resonate across levels of biological organization in these ecosystems. Finally, biodiversity data are often related to either flow intermittency or orientation to perennial refuge variables but not both in the same study, precluding our ability to understand the impacts of intermittency and availability of colonists in combination.

Here, we examined relationships between flow intermittency, orientation to perennial refuges, and stream communities in Chalone Creek basin at Pinnacles National Park and Pine Gulch basin at Point Reyes National Seashore, CA, USA. These two basins share a regional species pool, but vary in environmental harshness, with Chalone Creek being drier than Pine Gulch. In each area, we selected study reaches from across a continuum of intermittency intensity and quantified several biologically important metrics of flow over 2 years. We also found the nearest perennial refuge to each study reach and determined its direction and distance by wet–dry mapping. Lastly, in both wet winter and dry summer months, we surveyed both invertebrate and vertebrate communities. Using these data, we asked (1) how basin, flow class, and season affect invertebrate and vertebrate community composition and variability (spatial beta diversity); (2) which invertebrate or vertebrate species could be used as an indicators for different basins, flow classes, seasons, or combinations of these groupings; (3) if and how flow intermittency and orientation to perennial refuge predictors relate to community composition and nestedness; and (4) if differences in richness (alpha diversity) and density could be predicted based on flow intermittency and orientation to perennial refuge and whether those effects varied by basin? We hypothesized (1) that different basins, flow classes, and seasons would have different community compositions and that intermittent stream communities and samples collected in the summer would be more variable than perennial stream communities and samples collected in the winter; (2) that unique indicator taxa would be identified for different basins, flow classes, and seasons; (3) that flow intermittency and distance to perennial refuge predictors would correlate strongly with community composition and drive gradients of nestedness; (4) that richness and density would be positively related to flow permanence and access to perennial refuges; and (5) that more diverse invertebrate communities would support more diverse vertebrate communities and thus that trends for invertebrates and vertebrates would mirror each other.

METHODS

Study areas

Pinnacles National Park and Point Reyes National Seashore are in north-central California (Figure 1a). Although they are separated by ~190 km, both areas are in the same floristic and faunistic province and share a Mediterranean climate characterized by cool, wet winters (December–April) and warm, dry summers (May–September). In this region, intermittent reaches often flow from December to April in response to rainfall, but may be dry the rest of the year (Bogan et al., 2017, 2019). Generally, the environment at Pinnacles is drier than that of Point Reyes, and so we anticipated that contrasts between locations could provide insight into responses of biotic communities under these different conditions.

Chalone Creek basin in Pinnacles National Park drains approximately 100 km^2 and has an annual average rainfall of 420 mm. Due to its inland location, air temperatures vary greatly through the year, with highs that exceed 40°C in summer and lows below 0°C in winter (Bogan & Carlson, 2018). Upland vegetation is primarily oak–pine woodland on north-facing slopes and chaparral on drier south-facing slopes. When present, riparian vegetation consists of western sycamore (*Platanus racemosa*), willow (*Salix* spp.), and Fremont cottonwood (*Populus fremontii fremontii*).

By contrast, the Pine Gulch basin of Point Reyes National Seashore drains approximately 30 km^2 and has an annual average rainfall of 900 mm. Due to its coastal location, air temperatures are buffered through the year, with highs that rarely exceed 25°C in summer and lows of 5–10°C in winter. Fog is also a frequent component of the climate during the summer dry season, moderating the air temperatures and solar radiation that dry streambeds experience (Bogan et al., 2017). Upland vegetation is mixed-conifer forest on north-facing slopes and oak woodland with chaparral on south-facing slopes. Riparian vegetation includes coast redwood (*Sequoia sempervirens*), red alder (*Alnus rubra*), and willow (*Salix* spp.).

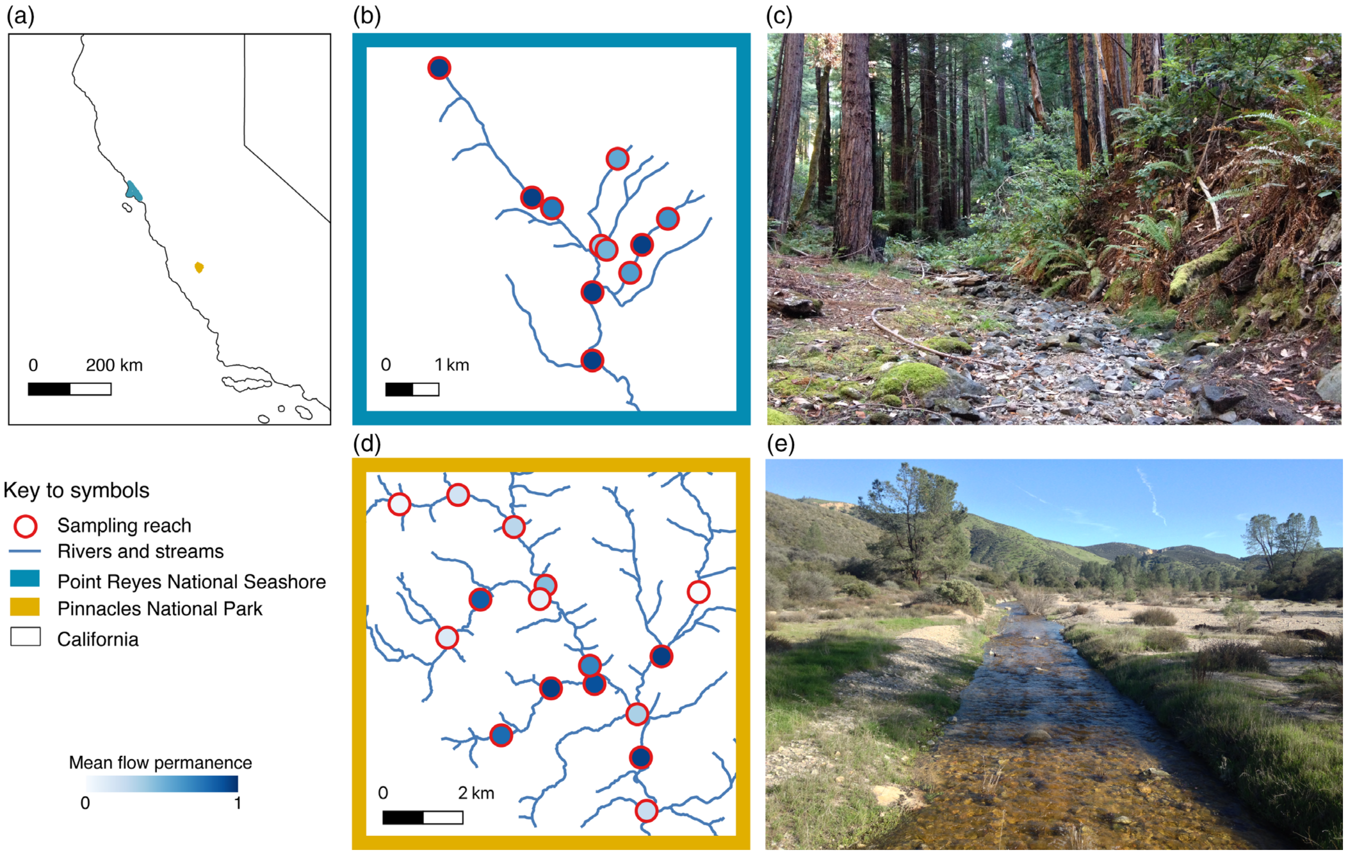

FIGURE 1 Locations of (a) Pinnacles National Park (Chalone Creek) and Point Reyes National Seashore (Pine Gulch) in California, USA; (b) reaches sampled within Chalone Creek basin; (c) an example photo of a Chalone Creek intermittent reach; (d) reaches sampled within Pine Gulch basin; and (e) an example photo of a Pine Gulch intermittent reach. On reach maps (b and d), mean flow permanence for all available sampling × reach events is indicated by the degree of blue shading within red circles

We established 16 reaches in the Chalone Creek basin of Pinnacles National Park and 11 reaches in the Pine Gulch basin of Point Reyes National Seashore (Figure 1b,d). We selected locations separated by a minimum distance of ~1 km. Following established protocols for sampling streams in California, at each site we delimited a 30-m reach for study (Ode et al., 2016).

Characterization of flow intermittency

To characterize drying patterns at each reach, we deployed Hobo Pendant temperature data loggers (Model UA-002-64, Onset Computer Corp, Bourne, MA, USA) that had been modified to record conductivity, and hence the presence or absence of water (Bogan & Carlson, 2018; Chapin et al., 2014). Although these loggers cannot distinguish between still and flowing water, they allowed us to calculate flow regime metrics, including (1) the number of days a reach had water prior to biological sampling (days flowing), (2) the number of times per water year a reach had dried (drying frequency), and (3) the proportion of days a reach had water per water year prior to biological sampling (flow permanence) (Jaeger & Olden, 2012). We defined a water year as the period from 1 October to 30 September. Loggers were deployed from May 2014 through June 2016 in the deepest portions of each reach to detect when the entire reach had dried. We also deployed loggers at perennial study reaches to confirm they were indeed perennial. For perennial reaches, days flowing was reported as 365 (a full year), drying frequency was 0, and flow permanence was 1.

Determination of orientation to perennial refuge

In each study basin, we walked the entire stream network and conducted wet–dry mapping at the beginning and end of the dry season in May and September 2014 (Turner & Richter, 2011). This second mapping period happened to coincide with the height of the Great California Drought, a 4-year drought event with a 0.005% chance of being exceeded in any one year (Kwon &

Lall, 2016; Robeson, 2015). Given these record drought conditions, we assumed that any reaches with flowing water in September 2014 were perennial and highly reliable across years. We then measured Euclidean channel distances (on US Geological Survey digital topographic maps) between each intermittent study reach and its nearest perennial refuge (absolute values) as identified during wet–dry mapping. We determined the direction of the nearest perennial refuge for intermittent reaches as either upstream or downstream.

Biological sampling

Benthic macroinvertebrates

We collected invertebrate samples at Chalone Creek and Pine Gulch during winter wet (February–March) and summer dry (May–June) seasons in 2015 and 2016 (108 potential sampling × reach events total). For each reach and collection date, we sampled invertebrates following a reach-wide benthic sampling protocol with a 500-μm mesh D-net (Ode et al., 2016). In this approach, we collected 1 "kick" (0.09 m^2 each) every 3 m at a reach, alternating between left, right, and center parts of the channel. The 11 "kicks" collected across the 30-m reach then were combined into a single composite sample that represents benthic communities found in various habitat units (e.g., riffles, pools, runs) across the reach (total sampled area = 0.99 m^2). All reach-wide benthic samples were processed in the field to remove large organic matter and mineral substrate, and then were preserved in 95% ethanol. In the laboratory, samples were enumerated and individuals were identified to genus for insects and family or order for noninsects, primarily using Merritt et al. (2019) and Thorp and Covich (2001).

Aquatic and semiaquatic vertebrates

We also conducted 30-min visual encounter surveys for vertebrate species at each reach during each sampling visit (Bogan et al., 2014). Briefly, during warm daylight hours, one observer (Michael T. Bogan) walked along the margins of each 30-m reach slowly, using binoculars to look ahead for amphibians and aquatic or semiaquatic reptiles (e.g., turtles, garter snakes) along the margins of the reach. Complex habitat structure (e.g., fallen logs, flood debris) was examined closely as well. In a subsequent pass through the reach while walking in the water, fish and larval amphibians were sought visually and, when necessary, individuals were captured with a D-net or seine net to confirm identification. Water clarity was generally high and depths shallow, facilitating sight identifications from the surface, but snorkel surveys also were conducted to maximize detection of cryptic fishes and larval amphibians. Notes on the relative abundances of vertebrates were taken, but only presence or absence data were used in analyses.

Data analysis

Study reach characteristics

To test for differences between basins in days flowing, drying frequency, flow permanence, and distance to perennial refuge, we determined whether data were normally distributed using Shapiro–Wilk normality tests and had equal variances using *F* tests in R version 3.6.3 (R Core Team, 2020). For *F* tests and all other statistical tests hereafter, we considered p values less than 0.05 to be significant and less than 0.10 to be marginally significant. For flow metrics (days flowing, drying frequency, and flow permanence), we tested for differences in intermittent reaches only, because they did not vary in perennial reaches. In all cases, values were not normally distributed. Consequently, we compared values among basins using nonparametric Wilcoxon rank-sum tests.

Community composition

To test for differences in the composition of communities between groups, we analyzed community data using permutational multivariate analyses of variance (PERMANOVA) using distance matrices in the R package vegan (Oksanen et al., 2020) using the function adonis. For this and all other analyses, we analyzed community data for invertebrate and vertebrates separately to identify possible differences in trends between taxonomic groups. Calculating community dissimilarities based on the Bray–Curtis index (Bray & Curtis, 1957), we ran PERMANOVA for our entire dataset with basin, flow class, and season as predictors. For each basin separately, we tested for differences in community composition based on flow class, season, and the interaction of flow class and season. In cases of significant interactions between flow class and season, we further examined differences by testing for seasonal effects within flow classes.

Beta diversity

To test for differences in the variability of communities among groups (beta diversity), we analyzed community data using analyses of multivariate homogeneity of group dispersions in vegan using the function betadisper. These tests compare beta diversity among groups by analyzing distributions of community dissimilarity values relative to group centroids in multidimensional space (Anderson et al., 2006). Because analyses of multivariate homogeneity of group dispersions are limited to single predictor variables, we evaluated differences in beta diversity for our entire dataset using the Bray–Curtis index based on basin alone, flow class alone, and season alone. We also coded all combinations of basin and flow class as distinct factor levels for our entire dataset and all combinations of flow class and season for each basin. We used Tukey's honestly significant differences (HSD) for pairwise comparisons of factor levels and to adjust p values for multiple testing.

Indicator species

We used the R package indicspecies (De Cáceres & Legendre, 2009) to determine which taxa were significantly associated with different basins, flow classes, and seasons. Because of the large number of potential combinations of these groupings, we conducted our analysis by first looking at associations by basin and flow class for our entire dataset and then for different flow classes and seasons within each basin. For both analyses, we corrected for differences in group sample sizes using func = "r.g" (Tichý & Chytrý, 2006) and for multiple testing using the false discovery rate method (Benjamini & Hochberg, 1995).

Relationships between environmental predictors and communities

Environmental vectors

For our entire dataset, we ordinated community data by nonmetric multidimensional scaling using vegan. To visualize relationships between environmental predictors and communities, we fit vectors of continuous predictors (days flowing, drying frequency, flow permanence, and distance to perennial refuge) to ordinations. We tested for significant correlations with ordination configurations by permutation in vegan.

Nestedness along environmental gradients

To test whether communities with intermittent flows and further from perennial refuges are nested subsets of perennial communities, we combined nestedness and gradient analyses (Leibold & Mikkelson, 2002; Ulrich, 2009) using vegan. We tested for nestedness for each basin alone because of differences between basins in faunas and to detect any differences in nestedness among basins. For each basin, we ordered samples in our community data matrix according to levels of intermittency (perennial to progressively intermittent using data on days flowing, drying frequency, and flow permanence) and distances to perennial refuge (perennial to further from perennial refuges using data on distances). We then calculated the "nestedness metric based on overlap and decreasing fill" (NODF) (Almeida-Neto et al., 2008) for each ordering. The NODF increases with nestedness and ranges from 0 to 100. We chose the NODF nestedness metric because it consistently controls Type 1 error better than other common nestedness metrics (Almeida-Neto et al., 2008). As recommended by Ulrich et al. (2009), we tested the significance of observed NODF values with a fixed-fixed null model used to generate 1000 random matrices.

Modeling of richness (alpha diversity) and density

To test for differences in richness and density, we fit ANOVA models with basin, flow class, and the interaction between basin and flow class for our entire dataset. We checked the residuals of models for normality by visually inspecting Q–Q plots and for homogeneity of variances by visually inspecting plots of residual versus fitted values. We conducted pairwise comparisons of groups and adjusted p values for multiple comparisons using Tukey's HSD. Because we quantified vertebrate presence or absence rather than densities, we examined differences in density for invertebrates only. Invertebrate density and vertebrate richness data were skewed and consequently log and square-root transformed, respectively.

We also evaluated relationships between flow intermittency, orientation to perennial refuge, and richness and density using a linear modeling approach. Prior to modeling, we assessed collinearity of variables by calculating all possible pairwise correlations of predictors (Appendix S1: Table S1). We found that the days flowing and flow permanence predictors were strongly correlated (r = 0.93) and consequently excluded flow permanence as a predictor from models. To facilitate interpretation of model coefficients, we scaled continuous predictors to have a mean of zero and standard deviation of 0.5 using the R package *arm* (Gelman & Su, 2020). We then constructed global models for richness and density with the following predictors: days flowing, drying frequency, distance to perennial refuge, direction to perennial refuge (perennial, upstream, or downstream), and basin. We also included interactions between all predictors (besides basin) and basin in the global model to test for the dependency of predictor effects based on basin. Using the global models, we generated all possible models containing subsets of global model terms using the R package glmulti (Calcagno & de Mazancourt, 2010) and enforced marginality (requiring both fixed effects in an interaction to include an interaction term). We ranked models by the information criterion AIC_c (Hurvich & Tsai, 1989) and dropped any models from the model set that fit less well than the intercept only model. For all sets of models, the weights of the best models were less than 0.9, and so we took all models within 2 AIC_c as a top model set for model averaging (Grueber et al., 2011). Using model averaging, we estimated model parameters, unconditional variances, confidence intervals, and the importance of predictors. Invertebrate densities and vertebrate richness data were skewed and consequently log and square-root transformed, respectively, prior to analyses. Because vertebrate abundances were qualitative, we did not construct quantitative abundance models for vertebrates.

RESULTS

Study reach characteristics

Of the 16 reaches established at Chalone Creek basin, we classified three as perennial and 12 as intermittent. For intermittent reaches at Chalone Creek, mean days flowing, drying frequency, flow permanence, and distance to perennial refuges were 80 days (SD = 53), 2 drying events (SD = 1), 0.48 (SD = 0.22), and 1250 m (SD = 1351), respectively. One reach was dry for the entire 2-year study period and was consequently excluded from analyses. Of the 11 reaches established at Pine Gulch basin, we classified 5 as perennial and 6 as intermittent. For intermittent reaches at Pine Gulch, mean days flowing, drying frequency, flow permanence, and distance to perennial refuges were 96 days (SD = 64), 4 drying events (SD = 3), 0.51 (SD = 0.14), and 189 m (SD = 96), respectively.

For intermittent reaches, days flowing and flow permanence were not different in Chalone Creek versus Pine Gulch (Appendix S1: Figures S1 and S2). However, drying frequency was lower (Appendix S1: Figure S3) and distance to perennial refuge was higher (Appendix S1: Figure S4) at Chalone Creek than Pine Gulch.

Benthic macroinvertebrates

Community composition

In total, we collected 82 samples containing 109,664 specimens that we classified as 299 invertebrate taxa, with 194 found at Chalone Creek and 187 at Pine Gulch (Appendix S1: Figure S5a). The orders with the highest number of taxa included true flies (Diptera: 109 taxa), beetles (Coleoptera: 42 taxa), caddisflies (Trichoptera: 41 taxa), and stoneflies (Plecoptera: 29 taxa). Other invertebrate taxa with a few representatives each included aquatic mites (Arachnida), worms (Annelida), freshwater crustaceans (Branchiopoda, Hexanauplia, Malacostraca, and Ostracoda), mollusks (Mollusca), and springtails (Collembola).

We found significant differences in the composition of invertebrate communities in different basins, flow classes, and seasons (basin: $F_{1,78} = 12.312$, $R^2 = 0.12$, $p < 0.001$; flow class: $F_{1,78} = 3.778$, $R^2 = 0.04$, $p < 0.001$; season: $F_{1,78} = 5.207$, $R^2 = 0.05$, $p < 0.001$; Figure 2a,c). For Chalone Creek, we found significant effects of flow class, season, and the interaction of flow class and season (flow class: $F_{1,40} = 3.153$, $R^2 = 0.06$, $p < 0.001$; season: $F_{1,40} = 4.920$, $R^2 = 0.10$, $p < 0.001$; interaction: $F_{1,40} = 1.927$, $R^2 = 0.04$, $p = 0.015$). Community composition at Chalone Creek differed by season for intermittent (season: $F_{1,30} = 5.332$, $R^2 = 0.15$, $p < 0.001$) but not perennial reaches (season: $F_{1,10} = 1.546$, $R^2 = 0.13$, $p = 0.075$). For Pine Gulch, we also found significant effects of flow class, season, and the interaction of flow class and season (flow class: $F_{1,34} = 4.990$, $R^2 = 0.10$, $p < 0.001$; season: $F_{1,34} = 5.357$, $R^2 = 0.11$, $p < 0.001$; interaction: $F_{1,34} = 3.503$, $R^2 = 0.07$, $p < 0.001$). Community composition varied by season for both intermittent (season: $F_{1,16} = 3.456$, $R^2 = 0.18$, $p < 0.001$) and perennial reaches (season: $F_{1,18} = 5.600$, $R^2 = 0.24$, $p < 0.001$).

Beta diversity

Mean distances to group centroids were 0.607 and 0.531 for Chalone Creek and Pine Gulch, 0.606 and 0.582 for intermittent and perennial flow classes, and 0.595 for both summer and winter, respectively. Invertebrate communities had higher beta diversity at Chalone Creek than Pine Gulch ($F_{1,80} = 23.721$, $p < 0.001$), but there was no difference in beta diversity based on flow class ($F_{1,80} = 1.910$, $p = 0.163$; Figure 2a) or season ($F_{1,80} = 0$, $p = 0.998$; Figure 2c). All comparisons of beta diversity between Chalone Creek and Pine Gulch were significantly different regardless of flow class (Tukey's HSD, all adjusted $p < 0.05$). Within both Chalone Creek and Pine Gulch, we also found no differences in beta diversity by flow class or season (Tukey's HSD, all adjusted $p > 0.05$).

Indicator species

Ninety-eight taxa were associated with a basin, flow class, or a combination of basin and flow class (Figure 3). Across

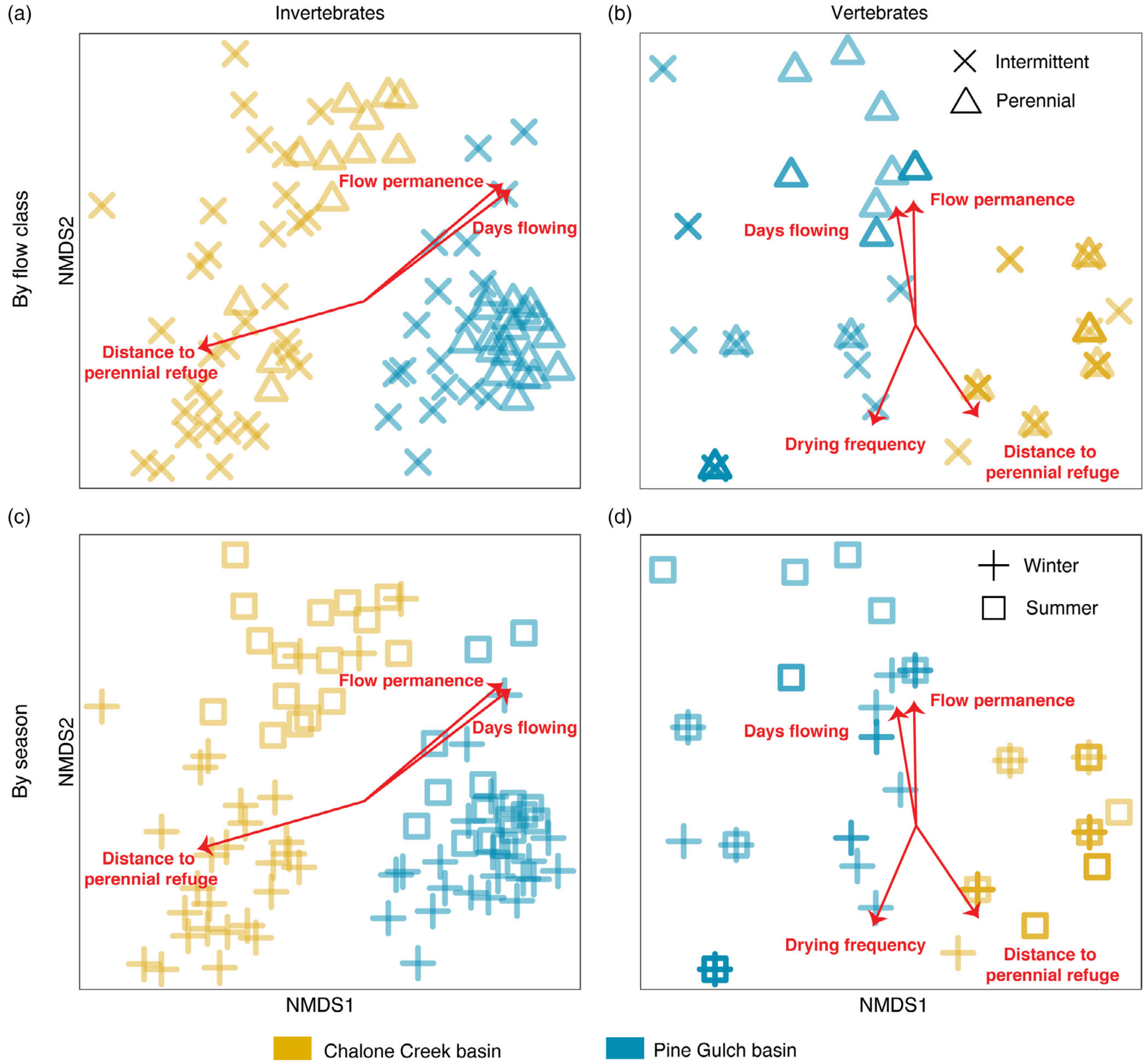

FIGURE 2 Nonmetric multidimensional scaling ordination of invertebrate and vertebrate communities with symbols representing flow classes (a and b) and seasons (c and d). Red arrows are vectors of environmental data with significant correlations with the ordination configuration with lengths scaled based on correlation strength. Plots (a) and (c) are the same ordination (weighted using counts; stress: 0.188), whereas plots (b) and (d) are the same ordination (weighted using presence/absence; stress: 0.058). Scale differs between plots (a)/(c) and (b)/(d). Symbol opacity has been modified such that overlapping symbols result in darker colors

basins, the taxa *Lebertia* (Trombidiformes: Lebertiidae) and *Apsectrotanypus* (Diptera: Chironomidae) were associated with perennial reaches; however, no taxon was associated with intermittent reaches across basins. For Chalone Creek alone, five taxa were associated with perennial reaches sampled in the summer. For Pine Gulch alone, *Parthina* (Trichoptera: Odontoceridae) was associated with perennial reaches generally. Also at Pine Gulch, a total of 18 other taxa were associated with combinations of flow class and season, including seven taxa from intermittent summer samples, *Ameletus* (Ephemeroptera: Ameletidae) from intermittent winter samples, five taxa from perennial summer samples, and five taxa from perennial winter samples.

Relationships between environmental predictors and communities

Environmental vectors

Days flowing ($R^2 = 0.40$, $p = 0.001$), flow permanence ($R^2 = 0.39$, $p = 0.001$), and distance to perennial refuge ($R^2 = 0.38$, $p = 0.001$) were correlated with ordination

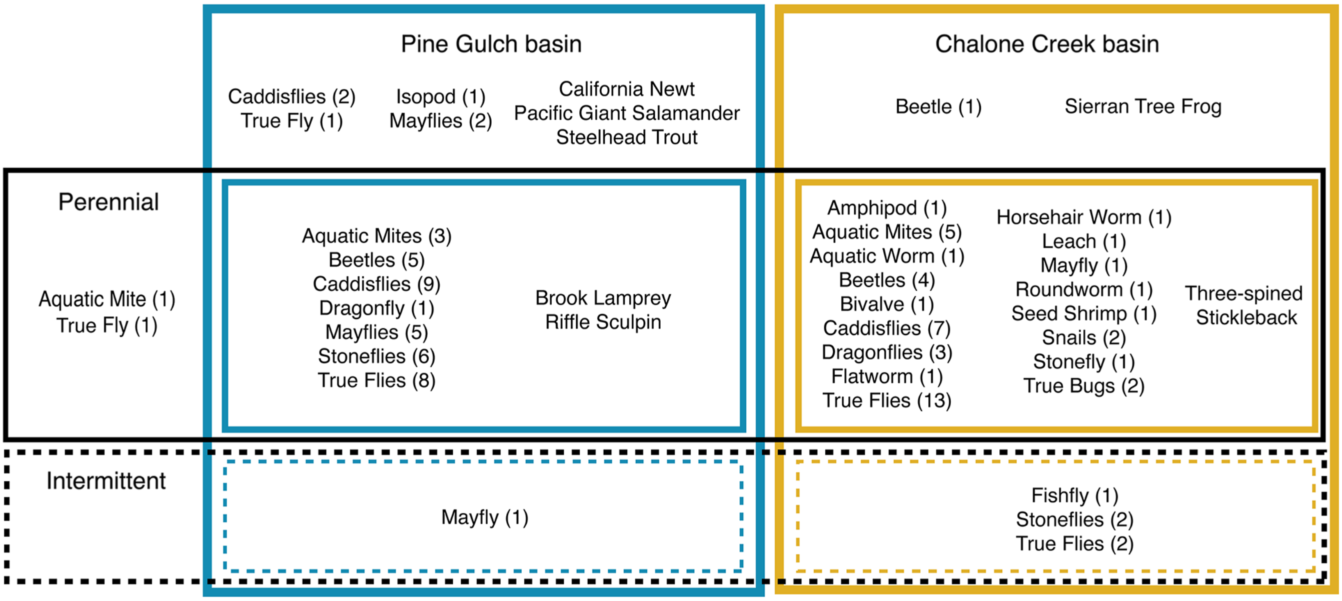

FIGURE 3 Invertebrate and vertebrate indicator species associated with Chalone Creek basin (Pinnacles National Park), Pine Gulch basin (Point Reyes National Seashore), intermittent reaches, perennial reaches, and intermittent and perennial flow classes within basins. Numbers inside of parentheses indicate the number of indicators identified within higher-level taxa (e.g., orders, families)

axes, but not drying frequency ($R^2 = 0.00$, $p = 0.833$; Figure 2a,c).

Nestedness along environmental gradients

The mean NODF values for matrices ordered by days flowing, drying frequency, flow permanence, and distance to perennial refuge were 16.927 (SD = 0.068) for Chalone Creek and 23.023 (SD = 0.022) for Pine Gulch. However, for both Chalone Creek and Pine Gulch, we did not detect significant nestedness of reaches with fewer days flowing, higher drying frequency, lower flow permanence, or higher distance to perennial refuge (all $p > 0.05$).

Modeling of richness (alpha diversity) and density

We found significant effects of basin and flow class on invertebrate richness, and a marginally significant interaction for these predictors (basin: $F_{1,78} = 64.838$, $p < 0.001$; flow class: $F_{1,78} = 61.469$, $p < 0.001$; interaction: $F_{1,78} = 3.957$, $p = 0.0502$; Figure 4a). All combinations of basin and flow class except for Chalone Creek perennial versus Pine Gulch intermittent were significantly different (Tukey's HSD, adjusted $p < 0.05$). For log invertebrate density, we found significant effects of basin, flow class, and their interaction (basin: $F_{1,78} = 12.829$, $p < 0.001$; flow class: $F_{1,78} = 30.367$, $p < 0.001$; interaction: $F_{1,78} = 6.369$, $p = 0.014$; Figure 4c). Log invertebrate densities at Chalone Creek perennial reaches were significantly different from all other combinations of basin and flow class (Tukey's HSD, adjusted $p < 0.05$).

We analyzed 97 models for invertebrate richness as a response to flow intermittency and orientation to perennial refuge predictors. The best model explained considerable variation in invertebrate richness (adjusted $R^2 = 0.69$), but the model weight was low (0.083) and 12 other models were within 2 AIC_c of the best model (Appendix S1: Figure S6). We consequently averaged the top 13 models to estimate parameters and their importance (Appendix S1: Table S2). Basin and distance to perennial refuge had importance values of 1, indicating that they were present in all models within 2 AIC_c of the best model. Drying frequency also appeared in many top models (importance = 0.77; Figure 4b). Model-averaged parameter estimates indicated that being in Chalone Creek basin or increasing distance to perennial refuge or drying frequency would decrease invertebrate taxon richness on average by 6, 10, and 1 taxon, respectively.

We analyzed 96 models for log invertebrate density as a response to flow intermittency and orientation to perennial refuge predictors. The best model explained moderate variation in log invertebrate density (adjusted $R^2 = 0.38$), but the model weight was low (weight = 0.186) and five other models were within 2 AIC_c of the best model (Appendix S1: Figure S7). We consequently averaged the top six models to estimate parameters and their importance (Appendix S1: Table S3). Only basin had an importance value of 1, but drying frequency also appeared in many of the top models (importance = 0.77; Figure 4d). Model-averaged parameter estimates indicated that being in Point Reyes basin or increasing drying frequency would decrease invertebrate density on average by 40% and 36%, respectively.

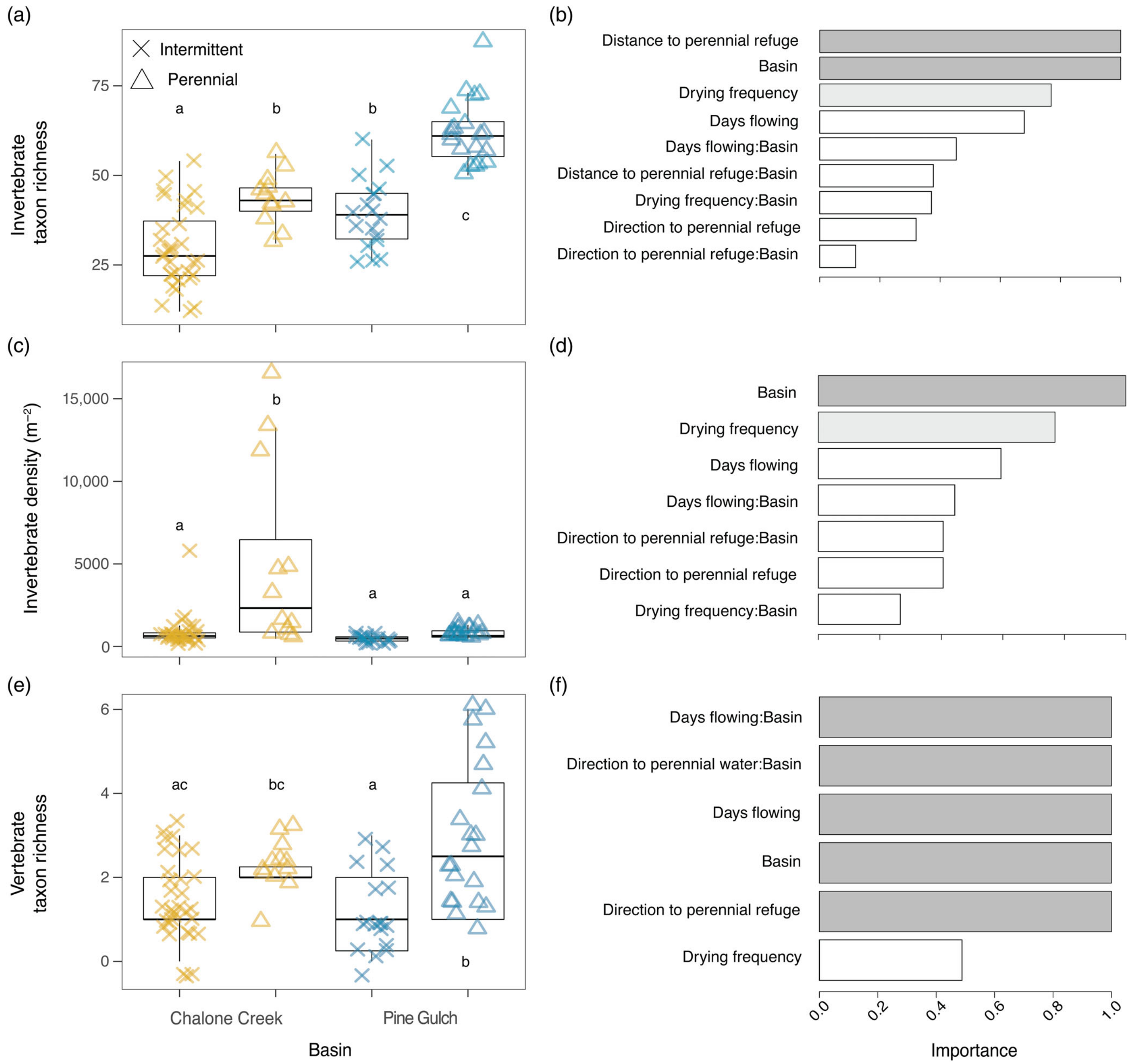

FIGURE 4 Boxplots of (a) invertebrate richness, (c) invertebrate density, and (e) vertebrate richness by basin and flow class. For boxplots, the lower, middle, and upper hinges represent the 25%, 50%, and 75% quantiles, respectively. The lower whisker extends to the smallest observation greater than or equal to lower hinge − 1.5 × interquartile range, whereas the upper whisker extends to the largest observation less than or equal to upper hinge + 1.5 × interquartile range. Bar plots in rows corresponding to box plots are predictors included in the model set within 2 AIC_c of the best model for (b) invertebrate richness, (d) invertebrate density, and (f) vertebrate richness. Important parameters are filled gray (dark gray: predictor importance = 1; lighter gray: predictor importance ~0.8)

Aquatic and semiaquatic vertebrates

Community composition

The 10 vertebrate species observed included amphibians, reptiles, and fishes. A total of five species were observed at Chalone Creek, whereas seven were observed at Pine Gulch. At Chalone Creek, four species were observed in perennial reaches and five in intermittent reaches (Appendix S1: Figure S5b). At Pine Gulch, seven species were observed in perennial reaches, and four in intermittent reaches.

We found significant differences in the composition of vertebrate communities in different basins, flow classes, and seasons (basin: $F_{1,70} = 62.431$, $R^2 = 0.44$, $p < 0.001$; flow class: $F_{1,70} = 3.549$, $R^2 = 0.03$, $p = 0.020$;

season: $F_{1,70} = 5.163$, $R^2 = 0.04$, $p = 0.006$; Figure 2b,d). For Chalone Creek, we found significant effects of flow class and season, but the effect of flow class did not depend on season (flow class: $F_{1,37} = 7.035$, $R^2 = 0.12$, $p = 0.002$; season: $F_{1,37} = 13.142$, $R^2 = 0.22$, $p < 0.001$; interaction: $F_{1,37} = 1.645$, $R^2 = 0.03$, $p = 0.232$). For Pine Gulch, flow class, season, and the interaction of flow class and season did not affect community composition (all $p > 0.05$).

Beta diversity

Mean distances to group centroids were 0.232 and 0.457 for Chalone Creek and Pine Gulch, 0.385 and 0.510 for intermittent and perennial flow classes, and 0.535 for summer and 0.3832 for winter, respectively. Vertebrate communities had higher beta diversity at Pine Gulch than Chalone Creek ($F_{1,72} = 28.18$, $p < 0.001$; Figure 2) and in summer than winter ($F_{1,72} = 4.637$, $p < 0.043$; Figure 2d). There was no difference in beta diversity based on flow class ($F_{1,72} = 3.059$, $p = 0.090$; Figure 2b). All comparisons of beta diversity between Chalone Creek and Pine Gulch were different regardless of flow class (Tukey's HSD, all adjusted $p < 0.05$). For each basin individually, there were no differences in beta diversity depending on flow class and season (Tukey's HSD, all adjusted $p > 0.05$).

Indicator species

Seven vertebrate taxa were associated with either basin, flow class, or a combination of basin and flow class (Figure 3). Across basins, no vertebrate taxon was associated with intermittent or perennial reaches in general. For Chalone Creek alone, we found that aquatic garter snakes (*Thamnophis atratus*) were associated with summer sampling regardless of flow class and three-spined stickleback (*Gasterosteus aculeatus*) were associated with all combinations of flow class and season except intermittent winter. For Point Reyes alone, riffle sculpin (*Cottus gulosus*) were associated with perennial reaches regardless of season.

Relationships between environmental predictors and communities

Environmental vectors

For our entire vertebrate dataset, we found significant correlations between vectors for days flowing ($R^2 = 0.13$, $p = 0.008$), drying frequency ($R^2 = 0.11$, $p = 0.019$), flow permanence ($R^2 = 0.14$, $p = 0.006$), distance to perennial refuge ($R^2 = 0.11$, $p = 0.020$; Figure 2b,d), and ordination axes.

Nestedness along environmental gradients

The mean NODF values for matrices ordered by days flowing, drying frequency, flow permanence, and distance to perennial refuge were 41.187 (SD = 2.092) for Chalone Creek and 18.977 (SD = 0.788) for Pine Gulch. For Chalone Creek, we did not detect nestedness of vertebrate communities along any gradients of increasing flow intermittency or distance to perennial refuge (all $p > 0.05$). At Pine Gulch, we detected anti-nestedness along gradients of fewer days flowing (NODF = 18.476, 95% confidence interval [CI] = 23.246–26.098, $p < 0.001$), higher drying frequency (NODF = 20.133, 95% CI = 24.099–27.077, $p < 0.001$), lower flow permanence (NODF = 18.821, 95% CI = 23.467–26.330, $p < 0.001$), and higher distance to perennial refuge (NODF = 18.476, 95% CI = 23.428–26.224, $p < 0.001$).

Modeling of richness (alpha diversity)

We found significant effects of flow class, but not basin or the interaction between basin and flow class on square-root-transformed vertebrate richness (basin: $F_{1,78} = 0.179$, $p = 0.673$; flow class: $F_{1,78} = 20.192$, $p < 0.001$; interaction: $F_{1,78} = 3.029$, $p = 0.086$; Figure 4e). We fit 95 models for square-root-transformed vertebrate richness. The best model explained moderate variation in square-root-transformed vertebrate richness (adjusted $R^2 = 0.31$). However, the model weight was low (0.246) and 1 other model was within 2 AIC_c of the best model (Appendix S1: Figure S8). We consequently averaged the top two models to estimate parameters and their importance (Appendix S1: Table S4). Basin, days flowing, direction to perennial refuge, and interactions between basin and days flowing and direction to perennial refuge had importance values of 1 (Figure 4f). Model-averaged parameter estimates indicated that being in Chalone Creek or increasing days flowing would increase square-root-transformed vertebrate richness on average by 1.370 and 1.634, respectively. Relative to reaches with downstream perennial refuges, reaches being perennial themselves, or having upstream perennial refuges decreased square-root-transformed vertebrate richness on average by 1.469 and 0.183, respectively. The effects of days flowing and direction to perennial refuges on vertebrate richness were dependent on basin.

DISCUSSION

Many dimensions of aquatic biodiversity at Chalone Creek and Pine Gulch responded to variation in flow intermittency and orientation to perennial refuge. Specifically, we found different invertebrate communities in different basins, flow classes, and seasons, whereas vertebrate communities only varied by basin, and flow classes and seasons at Chalone Creek. Invertebrate communities had higher beta diversity at Chalone Creek than Pine Gulch, whereas the opposite was true for vertebrates. Both flow intermittency and distance to perennial refuge were correlated with overall community composition across basins, and communities did not form nested subsets by either increasing flow intermittency or distance to perennial refuge. Lastly, results of modeling indicated that basin, flow intermittency, and orientation to perennial refuge were generally important for predicting invertebrate richness and densities and vertebrate richness.

Seasonal changes in community composition detected for both invertebrates and vertebrates highlight the importance of sampling multiple times per year to better approximate the total diversity of reaches. If we were to sample in just the winter or summer, our view of these communities would be quite different and potentially limited in the way we understand relationships between community composition, flow intermittency, and orientation to perennial refuge. While it is known that stream communities change through time and in response to drying (Vander Vorste et al., 2021), our study provides a unique systematic contrast between the extent of that change in intermittent and perennial reaches, which depends on the taxon and basin examined.

Based on high levels of community variability reported in the literature, we predicted that beta diversity should be higher in intermittent than perennial reaches (Bogan & Lytle, 2007; Larned et al., 2010; Schriever & Lytle, 2016). We also predicted that community variability associated with progressive drying during summer sampling should result in higher beta diversity of communities sampled in the summer than winter. However, for invertebrates, we found no difference in beta diversity based on flow class or season, and for vertebrates, an apparent seasonal difference present for the entire dataset disappeared when tested at the basin level. The lack of differences in beta diversity based on flow class in our study may be a product of sampling across seasons and years, which could capture changes in communities typically missed by sampling during only one season or year. Alternatively, sampling of intermittent reaches at similar stages of recolonization (no difference in days flowing between basins) could have minimized their apparent variability relative to sampling across wider ranges of recolonization or drying stages (Drummond et al., 2015; Larned et al., 2010).

Differences in beta diversity for invertebrates and vertebrates in different basins may also be the result of the abiotic characteristics and relative sizes of the basins, or interactions between trophic levels. We found that beta diversity of invertebrates was higher at Chalone Creek than Pine Gulch, whereas the opposite was true for vertebrates. As beta diversity tends to increase with area, the larger study area and higher distances to perennial refuge at Chalone Creek compared with Pine Gulch may explain higher beta diversity of invertebrate communities observed there (Barton et al., 2013). On the other hand, a less-harsh, more-hospitable environment (lower temperature range and more moisture) at Pine Gulch may lead to the potential for widespread aquatic vertebrate presence, increased importance of biotic factors such as competition, and explain higher variability of vertebrate communities at Pine Gulch (Segre et al., 2014). Alternatively, predictable top-down pressure by homogenous vertebrate communities at Chalone Creek or unpredictable top-down pressure by heterogeneous vertebrate communities at Pine Gulch could release or homogenize invertebrate communities, respectively (Power, 1992). Manipulative experiments would be needed to further examine the potential effects of different trophic levels on each other (e.g., Flecker, 1992).

In contrast to our predictions, we did not detect significant nestedness of communities along flow intermittence or distance to perennial refuge gradients. The idea that intermittent streams are nested subsets of perennial communities was proposed by Arscott et al. (2010) and later Datry (2012) both of whom found that community nestedness increased with stream flow intermittency using community nestedness analyses (Atmar & Patterson, 1993, 1995). At a near-global scale, Datry, Larned, Fritz, et al. (2014) later found nestedness of 10 of 14 intermittent stream systems (71%) using the highest taxonomic resolution available. Yet, many studies of nestedness to date have relied on nestedness metrics and null models known to have high Type 1 error (Ulrich et al., 2009; Ulrich & Gotelli, 2007), utilized samples collected in longitudinal patterns from the same river main stem (e.g., Arscott et al., 2010; Datry, 2012), and often had coarse taxonomic identifications for challenging taxa (e.g., Chironomidae: Datry, Larned, Fritz, et al., 2014). Each of these factors could obscure the detection of shifts in community composition rather than nestedness. Here, we used a nestedness metric (NODF) known to have appropriate Type 1 error, utilized samples largely collected from across basins and not limited to the river main stem, and identified taxa to the lowest level practical. While nestedness may be characteristic of intermittent stream systems generally (Arscott et al., 2010; Datry, 2012; Datry, Larned, Fritz, et al., 2014), it seems that in the cases of Chalone Creek and Pine Gulch basins there is also support for substantial shifts in communities between flow classes (turnover).

Our results also provide insight into different mechanisms underlying invertebrate and vertebrate community structure. For invertebrates, increasing drying frequency reduced richness and densities, and larger distances to perennial refuges decreased richness. Invertebrates responded uniformly to predictors regardless of basin (low support for importance of interactions) and direction to perennial refuge was not important. This lack of importance of direction to refuge may be the result of many invertebrates having aerial adult stages, meaning their recolonization potential may not be constrained by the geometry of the stream network (Bogan et al., 2017). On the other hand, for vertebrates, our analysis indicated that days flowing, direction to perennial refuge, and interactions between these predictors and basin were all important. These results are consistent with the fact that many aquatic vertebrates can only move through the stream channel (Jaeger et al., 2014), potentially limiting their avenues for dispersal and amplifying the importance of the location of perennial refuges within stream networks (Kerezsy et al., 2017; Sánchez-Montoya et al., 2017).

Collectively, our study of the effects of variation in flow intermittency and orientation to perennial refuge on aquatic biodiversity across a variety of flow and climate settings provides a glimpse of potential climate change impacts in our study region. Our findings indicate that we can expect changes in both invertebrate and vertebrate community composition, and reductions in the richness and density of invertebrates, as streams experience increased intermittency. At the same time, shifts toward intermittency may provide opportunities for some species that are adapted or endemic to intermittent streams (Bogan & Carlson, 2018). Additional research is needed to better understand effects of different trophic levels on each other in these systems and conditions that modify the relative importance of flow intermittency versus orientation to perennial refuge in determining observed levels of aquatic biodiversity.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Gill et al., 2022a), R code (Gill et al., 2022b), and supplemental results (Gill et al., 2022c), respectively, are available from the University of Arizona's Research Data Repository: https://doi.org/10.25422/azu.data.16606736, https://doi.org/10.25422/azu.data.16606745, and https://doi.org/10.25422/azu.data.16606754.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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