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Drought attenuates the impact of fish on aquatic macroinvertebrate richness and community composition

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Abstract

1. Identifying ecological niche filters that shape species community composition is a critical first step in understanding the relative contributions of deterministic and stochastic processes in structuring communities. Systems with harsh ecological filters often have a more deterministic basis to community structure. Although these filters are often treated as static, investigations into their stability through time are rare, particularly in combination with extreme forms of environmental change such as drought.
2. We examined the richness and composition of aquatic macroinvertebrate communities from 36 ponds over 4 years during the onset of a megadrought to answer the following questions: (a) what are the relative influences of non-native fish presence and pond permanence in structuring communities? And (b) how do the magnitudes of such filters vary through time?
3. As predicted, fish presence had a strong, negative effect on both alpha and gamma diversity, lowering average invertebrate richness in pond communities by 23%. However, fish presence and sample year interacted to determine both richness and taxa composition: as drought conditions intensified, the effects of fish weakened such that there were no differences in the richness or composition between fish and fishless ponds by the later sampling years. Moreover, large-bodied invertebrate groups—often considered highly vulnerable to fish predation—were detected within fish-occupied sites by the final year of the study.
4. This pattern was associated with progressive decreases in precipitation due to a severe drought in California, emphasising the importance of exogenous, regional factors in moderating the strength of biotic niche filters on local community structure over time. Given that all detected fish species were non-native, these results also have application to understanding and forecasting changes in the diversity of aquatic invertebrates in response to biological invasions.

KEYWORDS
community composition, drought, fish, macroinvertebrate, niche filter

1 | INTRODUCTION

While there has been considerable debate on the relative importance of niche and neutral factors in shaping ecological communities, emerging evidence illustrates that both processes often play significant roles in community structure (Cadotte, 2007; Kalyuzhny, Serum, Chocron, Kadmon, & Shnerb, 2014; Stegen, Lin, Konopka, & Fredrickson, 2012; Vergnon, Dulvy, & Freckleton, 2009). Thus, rather than constituting alternative frameworks, niche and neutral forces likely represent ends of a continuum, with most ecological communities falling somewhere in between (e.g., Chase & Myers, 2011; Vellend et al., 2014). A key first step in understanding the factors contributing to community composition and diversity is therefore to test the influence of hypothesised niche filters (Chase & Myers, 2011). Using experimental mesocosms, for example, Chase (2010) illustrated the importance of net primary productivity as a niche filter in aquatic systems. While both low and high productivity treatments had similar levels of local (alpha) richness over 4 years, mesocosms in the low productivity treatment had 33% fewer species at the regional level (gamma diversity) and thus much lower variation in species composition among replicates (lower beta diversity). These observations suggest that low productivity functioned as a strong niche filter, leading to more consistent and predictable community structures relative to high productivity sites in which neutral forces manifested more prominently. Less clear, however, is the degree to which these defined niche filters shift in strength over time and in response to environmental change.

In small aquatic ecosystems, one of the most well-supported paradigms classifies wetlands according to two major niche filters represented by hydroperiod (e.g., temporary versus permanent) and the top predator type (e.g., fishes versus invertebrates) (Crowder & Cooper, 1982; Shurin, Cottenie, & Hillebrand, 2009; Wellborn, Skelly, & Werner, 1996). The effect of fish presence on invertebrate community structure has been extensively studied (Chase, Biro, Ryberg, & Smith, 2009; Knorp & Dorn,2014; McCauley et al., 2008; McPeek, 1990), often leading to lower diversity, smaller average body size and a shift in composition towards more cryptic species that are less vulnerable to fish predators (Batzer, Pusateri, & Vetter, 2000; Dixon & Baker, 1988; Pierce, 1988). As a result, the introduction and transport of non-native fishes among ecosystems can result in substantial changes in freshwater biodiversity, with consequences for both the local community and aquatic–terrestrial linkages (Amundsen, Siwertsson, Primicerio, & Bøhn, 2009; Baxter, Fausch, Murakami, & Chapman, 2004; Cox & Lima, 2006). Ponds that are more temporary in hydroperiod, which rarely sustain fishes, tend to support higher invertebrate diversity and a greater fraction of large-bodied, active invertebrate predators (Wellborn et al., 1996). In these systems, the timing of colonisation (i.e., "priority effects") can play an important role in determining the outcome of species interactions, such as competition and predation. This often results in active and strongly dispersing taxa being over-represented in temporary ponds (Boix, Sala, Quintana, & Moreno-Amich, 2004; Padeffke & Suhling, 2003). Despite the strength of this framework for understanding wetland communities (Batzer, 2013; Ellis et al., 2011), comparatively little research has explored how major niche filters interact or change in magnitude over time.

In accordance with the "consumer stress model," different taxa often showed varied responses to temporal changes in environmental quality (Menge & Sutherland, 1987); thus, the stability and intensity of a biological niche filter (e.g., fishes) likely depend on its response to changing environments relative to the taxa it regulates. For example, the effects of fish presence on the invertebrate community can be significantly reduced with the addition of nutrients, resulting in the formation of large algal mats that function as invertebrate predation refuges; conversely, the loss of macrophytic vegetation in ponds can increase the strength of fish effects on local invertebrate communities by enhancing visibility of potential prey (Diehl & Kornijów, 1998). These observations suggest that temporal variation in exogenous factors, such as climate or nutrients, has the potential to regulate the intensity of fish-mediated controls of invertebrate community composition and diversity. Fish predation rates are additionally affected by factors such as ambient light and relative light contrasts, pH and turbidity (Atchison, Henry, & Sandheinrich, 1987; Howick & O'Brien, 1983; Lazzaro, 1987). Shifts in water levels also have the potential to alter both the standing biomass of fish and their top-down control of macroinvertebrates in ponds and streams, in some cases causing local extirpations of fish species and a resulting trophic cascade (Dorn, 2008; Power, Parker, & Dietrich, 2008). The relaxation of the fish niche filter would allow for the colonisation or increased in abundance of sensitive macroinvertebrate taxa (Dorn, 2008). The importance of fluctuating environmental conditions generally in maintaining biological diversity is often associated with "storage effects," in which temporal variation in niche filters prevent competitive exclusion or dampen top-down regulation (Chesson, 1985; Descamps-Julien & Gonzalez, 2005; Vasseur & Fox, 2007). While the storage effect has been well developed conceptually and in experimental settings, evidence in the field outside of plant communities remains rare (Facelli, Chesson, & Barns, 2005; Napier, Mordecai, & Heckman, 2016; Vasseur & Fox, 2007). Here, we explore how the capacity of a predator-based niche filter to regulate macroinvertebrate communities shifted through time with rapidly changing environmental conditions (i.e., severe drought).

We intensively sampled the aquatic macroinvertebrate communities of 36 natural and artificial ponds in California between 2011 and 2014 to evaluate the influence of fishes on invertebrate richness and taxonomic composition. Because this period corresponded with the onset of a megadrought (Griffin & Anchukaitis, 2014), it afforded a timely opportunity to evaluate shifts in the strength of presumptive niche filters in response to a regional environmental change. Using a mixed-modelling approach, we examined the effects of fish occurrence and pond permanence on site-level taxonomic richness and community composition, both among ponds and across the 4-year study period. We expected that fish presence would act as a strong niche filter, decreasing richness and excluding large-bodied, active predators, but that the magnitude of such effects would be mitigated by the annual effect of drought severity. Forecasted increases in climate variation, including the frequency of both droughts and floods, emphasise the importance of understanding how environmental fluctuations moderate classical niche filters.

2 | METHODS

2.1 | Field surveys

Each year between 2011 and 2014, we sampled 36 ponds distributed across Alameda and Santa Clara counties in the East Bay

Region of California. These ponds, many of which were built to support livestock grazing, are now managed as part of regional or county parks and can range in depth from less than 1 m to over 5 m deep and vary in perimeter from 50 m to over 400 m (Bobzien & DiDonato, 2007; Garone, 2011). Shoreline vegetation was dominated by three major plant genera, *Juncus* sp., *Typha* sp. and *Scirpus* sp. Ponds permanence ranged from "permanent," which we defined as continually holding water over the course of the study, to "temporary," which included ponds that went dry at least once during the study. Pond permanence was determined based on a combination of direct observation (visits to the ponds through late August) and the use of the time slider function in Google Earth. Although it is possible that some ponds classified as permanent actually went dry during the months of September through December, we consider this unlikely based on measurements of depth and presence of taxa that depend on water year round, that is fish and developing bullfrog tadpoles. Each pond was sampled once per season during the window between late spring and early summer (mid-May and early-July) to assess their biotic and abiotic characteristics. Sampling was targeted to begin at the end of the wet season after the majority of taxa had established and prior to emergence events in late summer. To account for any effect of the timing of the sampling event on patterns of macroinvertebrate taxonomic richness, we included the sampling event's Julian date as a covariate in our models. Using a YSI MDS 550 probe held 10 cm below the surface, we measured pH, salinity and total dissolved solids. We collected a water sample from each site to measure turbidity using a LaMotte 2020i turbidity meter and to assess nutrient concentrations (dissolved organic carbon, total dissolved nitrogen and total dissolved phosphorus, using standard methods: http://snobear.colorado.edu/Kiowa/Kiowaref/procedure.html). As pond area was not available for all years, pond perimeter (in metres) was used to quantify pond size. Based on sites with both metrics, $\log_{10}$-transformed pond perimeter and pond surface area were strongly correlated (Pearson's $r = 0.95$, $p < 0.001$). Pond perimeter was calculated using the tracking function on a hand-held GPS unit (Garmin GPSMAP 60) as the researcher walked the shoreline of the pond. During the course of our study, California experienced a megadrought, with precipitation falling to the lowest observed since 1974 and the second lowest 3-year average since 1895 (Seager et al., 2014). Drought intensity was determined based on mean annual Palmer's drought severity index (PDSI) (Palmer, 1965), which uses temperature and precipitation to calculate soil moisture supply and demand. Negative values represent a deficit of soil moisture relative to the demand, for which a value of −3 or below indicates a severe drought while positive values indicate a surplus of moisture relative to the soil demand (Mishra & Singh, 2011). PDSI data were obtained from the National Oceanic and Atmosphere Administration (NOAA) for the California central coast drainage division (http://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp#).

To assess the biological community, we conducted 1-m-long dipnet sweeps every 10 m or a max of 20 sweeps along the pond perimeter using a D-frame dipnet (30.5 cm by 35.5 cm, 900 μm mesh size). We identified all organisms larger than a copepod or cladocerans (i.e., macroinvertebrates) to family or lowest taxonomic level possible and collected a representative sample of each family for further identification. We ignored zooplankton taxa from our surveys since our standard sampling protocol is not sufficient for accurately capturing these communities due to both the net mesh size used and the focus along the shoreline. Collected macroinvertebrate samples were identified to the lowest taxonomic level using an Olympus SZX10 dissecting microscope and taxonomic guides for aquatic invertebrates (Merritt, Cummins, & Berg, 1996; Thorp & Covich, 2009). The majority of the taxa were identified to the genus level with aquatic mites, leeches, three families of Diptera and the Hemiptera, Corixidae, only identified to the family level. Due to only obtaining a subsample of the taxa encountered during dipnet sampling, we focused on the occurrence (presence/absence) rather than relative abundance of encountered macroinvertebrate taxa. To assess the occurrence of fish, we relied on multiple methods of detection including the capture of fishes obtained during the dipnet sweeps, any visual observations during a walk of the pond perimeter and past records of fish detections from scientists and land managers. We also conducted 3–5 habitat-stratified seine hauls across the open water (net size: 0.9 m × 1.8 m or 1.8 m × 4.2 m). The combination of these methods helps instil confidence in the classification of sites by fish presence, even for cases in which fish abundances are low. While these methods were reliable in detecting the occurrence of different families of fishes, all of which are non-native in these ponds, they were insufficient to provide detailed data on the fish abundance or the full suite of species present. We therefore focused our analyses on the presence/absence of fish family.

2.2 | Statistical analysis

To investigate the processes shaping macroinvertebrate communities and how they varied over time, we performed analyses both among ponds and among years. Our analyses assessed shifts in either total invertebrate taxonomic richness, which was estimated as the number of macroinvertebrate taxa for each site-by-year combination (i.e., taxa richness) or taxonomic composition within a site using a presence/absence table with each row representing a site and each column a taxon. Within each year, we also calculated total (gamma) diversity of macroinvertebrates among ponds that either supported fish or were fishless. We used rarefaction curves to assess the validity of our sampling protocol on regional gamma diversity using the vegan package (Oksanen et al., 2007) in R (R Development Core Team, 2017).

To model macroinvertebrate taxonomic richness, we used a generalised linear mixed effects model (GLMM) with a Poisson distribution and a log-link using the glmer function in the lme4 package (Bates, Maechler, Bolker, & Walker, 2014) in R. As explanatory variables, we used detection of fish (yes or no), pond perimeter ($\log_{10}$-transformed), permanence (temporary or permanent), the first two PCA axes of water quality data (pH, conductivity, turbidity, dissolved organic carbon, total nitrogen and total phosphorus, see

Appendix S1 in Supporting Information) and the Julian date of the sampling event. We include Julian date to account for the variation in sampling period where ponds sampled later in the summer may vary in their richness due to either a longer colonisation window before sampling or the possibility of a loss of taxa from mass emergence events. For the among-pond analysis, we included sample year and site identity as random intercept terms, thereby recognising that samples collected from the same site or in the same year are not independent. This allowed us to explore factors that influenced the overall pattern of macroinvertebrate taxa richness across the spatial extent of our study while accounting for site identity and any temporal patterns across years (both as factors). For the among-year analysis, we made year a fixed factor and included its interactions with permanence and fish presence, thereby explicitly testing the role of sample year and how it affected hypothesised niche filters. Site identity was kept as a random intercept to account for repeated samples across years. Subsequently, we also replaced the year factor with annual PDSI to determine whether drought-related data offered comparable explanatory power. For both the among-pond and among-year analyses, we initially constructed a model that included all main effects and targeted interactions between fish status and pond perimeter based on prior research (Ryberg & Chase, 2007; Wellborn et al., 1996). We subsequently dropped nonsignificant explanatory terms one at a time and reran the model (Bolker et al., 2009). We compared among models using likelihood-ratio tests and selected the best supported model(s) when the result of dropping an explanatory variable resulted in a significantly less informative model based on the weighted Akaike information criterion (AICc). We considered any models with ΔAICc ≤ 2 to be comparable.

To assess the drivers of macroinvertebrate community composition, we used the mvabund package in R (Wang, Naumann, Wright, & Warton, 2012). The mvabund package fits generalised linear models to each taxon in a taxa-by-site incidence matrix, including as output both an overall effect of each explanatory variable and taxon-specific responses. To help predict the occurrence of each invertebrate taxon (a binomial response), we included the same explanatory variables from the mixed model fit for taxa richness. For the among-pond analysis, we also included a fixed effect of year and its two-way interactions with both pond permanence and predator type, as described above. However, because mvabund does not allow inclusion of random effects, we did not include an effect for site. We chose to use mvabund to analyse beta diversity over approaches involving beta null deviances (Chase, Kraft, Smith, Vellend, & Inouye, 2011) because the beta null deviance method does a poor job of capturing community composition patterns in the presence/absence data (Tucker, Shoemaker, Davies, Nemergut, & Melbourne, 2015). Finally, to test for spatial autocorrelation in community composition, we performed a Mantel test that examined whether the similarity in taxa composition between any two sites was related to their geographic distance. Specifically, we compared the Euclidean distance between each site pair with their Jaccard's dissimilarity index using the vegan package in R (Oksanen et al., 2007).

3 | RESULTS

Of the 36 sites sampled, 12 had fishes and 24 were fishless. All sites maintained a consistent fish status throughout the course of the study (i.e., no sites lost or gained fishes). Observed fish species—all of which were non-native warm-water game fish or an introduced species for insect control (Moyle, 1976)—included the following: three in the family Centrarchidae, *Lepomis macrochirus* (bluegill), *Lepomis cyanellus* (green sunfish) and *Micropterus salmoides* (largemouth bass), and one in the family Poeciliidae, *Gambusia affinis* (mosquitofish). The majority of fish sites contained both *G. affinis* and a member of the Centrarchidae family with only 4 of 12 fish sites alone having *G. affinis*. Statistical analysis showed that sites with both Centrarchidae and *G. affinis* and sites with just *G. affinis* were associated with similar patterns in macroinvertebrate communities, and thus, we aggregated all sites with any fish species as fish positive sites (see Appendix S2). Nineteen sites were permanent, and 17 sites dried at least once during our sampling period (temporary). In 2014, which was the third consecutive year of drought in California (Seager et al., 2014), five sites failed to hold water at all. We excluded these sites from the 2014 data set, but kept them for years in which they held water. Of the fishless sites, seven were permanent and 17 were temporary. Water chemistry data and nutrient data were combined in a principal components analysis (PCA) to reduce their dimensionality, for which we retained axes with eigenvalues above 1 (Abdi & Williams, 2010). The first axis of the PCA for water chemistry data accounted for 49% of the variation with positive loading from all variables. The second axis of the PCA accounted for 19% with pH, turbidity, TDS and salinity had positive loadings and dissolved organic carbon, total phosphorus and total nitrogen had negative loadings (Appendix S1, Supporting Information).

We identified 44 macroinvertebrate taxa spanning four phyla, 10 orders and 17 families. Total site-level taxa richness varied from 4 to 24 taxa (mean taxa richness 12.35 ± 0.44) within a given year. Overall richness was dominated by coleopterans with 18 unique taxa representing three families, followed by odonates with 15 unique taxa from four families (Appendix S3, Supporting Information). It should be noted that these estimates of macroinvertebrate taxa richness are surely an underestimate due to the lack of taxonomic resolution on diverse taxa such as members of the family Chironomidae. Based on the model selection procedure, there were three comparable models for the among-pond analysis of taxonomic richness. The best-fit model according to the likelihood-ratio test retained the following predictors: water chemistry PCA axis 2, fish status, $\log_{10}$-transformed pond perimeter and the fish status-by-perimeter interaction; the model with the lowest AICc value additionally retained Julian date and water chemistry PCA axis 1 (see Tables 1 and 2). Local richness was negatively affected by fish occurrence (Poisson GLMM; fish presence coefficient = 1.04 ± 0.32; $z = 3.28$, $p = 0.001$). On average, sites with fish supported 23% fewer invertebrate taxa relative to sites without fish (Figure 1a). We also found an interaction between pond size (perimeter) and fish occurrence, such that increases in a pond size had a much stronger positive effect on richness at fishless sites than at sites with fish across all years (fishless-by-pond perimeter interaction

TABLE 1 Results of generalised linear mixed effects model with a Poisson distribution to model site-level macroinvertebrate taxa richness. For the among-pond analysis, both site and year surveyed were assigned as random effects, and for across-year analysis, only site was assigned as a random effect.

Analysis	Variables	Number of covariates	Log likelihood	AICc	ΔAICc
Among Ponds	**Fish + Perimeter + Julian Date + Water Chem PCA 1 + Water Chem PCA 2 + Fish:Perimeter**	**6**	**−363.7**	**746.8**	**0**
Among Ponds	**Fish + Perimeter + Water Chem PCA 2 + Fish:Perimeter**	**4**	**−366.6**	**748.0**	**1.2**
Among Ponds	**Fish + Perimeter + Julian Date + Water Chem PCA 2 + Fish:Perimeter**	**5**	**−365.5**	**748.1**	**1.3**
Among Ponds	Permanence + Fish + Perimeter + Julian Date + Water Chem PCA 1 + Water Chem PCA 2 + Fish:Perimeter	7	−363.7	749.2	2.4
Among Ponds	Fish + Perimeter + Fish:Perimeter	3	−371.9	756.4	9.6
Across Year	**Fish + Perimeter + Water Chem PCA 1 + Year + Fish:Perimeter + Fish:Year**	**6**	**−355.7**	**738.0**	**0**
Across Year	**Fish + Water Chem PCA 1 + Year + Fish:Year**	**4**	**−358.3**	**738.3**	**0.3**
Across Year	Permanence + Fish + Perimeter + Water Chem PCA 1 + Year + Fish: Perimeter + Fish:Year	7	−355.6	740.3	2.3
Across Year	Fish + Perimeter + Water Chem PCA 1 + Year + Fish:Year	5	−355.7	740.6	2.6
Across Year	Permanence + Fish + Perimeter + Water Chem PCA 1 + Water Chem PCA 2 + Year + Fish:Perimeter + Fish:Year	8	−355.4	742.4	4.4
Across Year	Permanence + Fish + Perimeter + Water Chem PCA 1 + Water Chem PCA 2 + Julian Date +Year + Fish:Perimeter + Fish:Year	9	−355.4	744.8	6.8
Across Year	Fish + Water Chem PCA 1 + Year	3	−365.1	745.1	7.1
Across Year	Permanence + Fish + Perimeter + Water Chem PCA 1 + Water Chem PCA 2 + Julian Date + Year + Fish:Perimeter + Fish:Year + Permanence:Year	10	−353.2	748.3	10.3
Across Year	Fish + Perimeter + Water Chem PCA 1 + PDSI + Fish:Perimeter + Fish:PDSI	4	−363.7	744.6	6.6

Bold text represents the best fitted model for both analysis types.

TABLE 2 Estimated parameter coefficients from the best fitting models of both the among-pond and across-year analyses

	Estimated coefficient ± *SE*	*Z* value	*p* Value
Among-pond model variables			
Fish Status	1.04 ± 0.32	3.28	0.001
Log$_{10}$ (Pond Perimeter)	−0.55 ± 0.26	−2.13	0.03
Water Chemistry PCA Axis 1	−0.07 ± 0.04	−1.83	0.07
Water Chemistry PCA Axis 2	0.12 ± 0.03	−3.37	0.001
Scaled Julian Date	0.10 ± 0.04	2.50	0.01
Fish : Log$_{10}$ (Pond Perimeter) Interaction	0.36 ± 0.13	2.28	0.02
Across-year model variables			
Fish Status	−1.16 ± 0.75	−1.54	0.12
Log$_{10}$ (Pond Perimeter)	−0.44 ± 0.26	−1.67	0.09
Water Chemistry PCA Axis 1	−0.14 ± 0.05	−3.13	0.001
Year 2012	0.16 ± 0.14	1.14	0.26
Year 2013	0.41 ± 0.14	3.02	0.002
Year 2014	0.75 ± 0.15	4.91	0.001
Fish:Log$_{10}$ (Pond Perimeter) Interaction	0.78 ± 0.33	2.33	0.02
Fish:Year 2012 Interaction	0.00 ± 0.16	0.03	0.97
Fish:Year 2013 Interaction	−0.41 ± 0.15	−2.55	0.008
Fish:Year 2014 Interaction	−0.31 ± 0.16	−1.97	0.08

coefficient = 0.36 ± 0.13; $z = 2.28$, $p = 0.02$) (see Appendix S4, Supporting Information). The second axis of the water chemistry PCA had a positive effect on alpha richness (coefficient = 0.12 ± 0.03; $z = -3.37$, $p < 0.001$). Julian date of sampling had a positive effect on taxonomic richness (coefficient = 0.10 ± 0.04; $z = 2.50$, $p = 0.01$), although this term was not retained based on the likelihood-ratio test. Site permanence did not have a significant effect on invertebrate diversity (Figure 2a).

Similarly, invertebrate community composition among ponds was best explained by fish presence, pond permanence and their interaction (overall model results from mvabund: predator deviance = 266.50, $p = 0.001$, permanence deviance = 190.48, $p = 0.001$, predator by perimeter interaction deviance = 64.17, $p = 0.008$). The presence of fish was negatively associated with large-bodied and active invertebrates across multiple orders, including the hemipterans (e.g., *Lethocerus* sp.: deviance = 29.03, $p = 0.001$, *Notonecta* sp.: deviance = 25.30, $p = 0.001$ and Corixidae; deviance = 21.76, $p = 0.001$) as well as the larger Coleoptera (e.g., *Cybister* sp.: deviance = 19.53, $p = 0.001$). Increase in pond permanence correlated positively with large-bodied dragonfly nymphs in the family Libellulidae (e.g., *Erythemis* sp.: deviance = 23.65, $p = 0.001$) as well as the potentially dispersal-limited taxa such as the hemipteran (*Ranatra* sp.: deviance = 26.24, $p = 0.001$).

The among-year analysis revealed two comparable models (ΔAICc < 2, see Table 1) with both models retaining fish status,

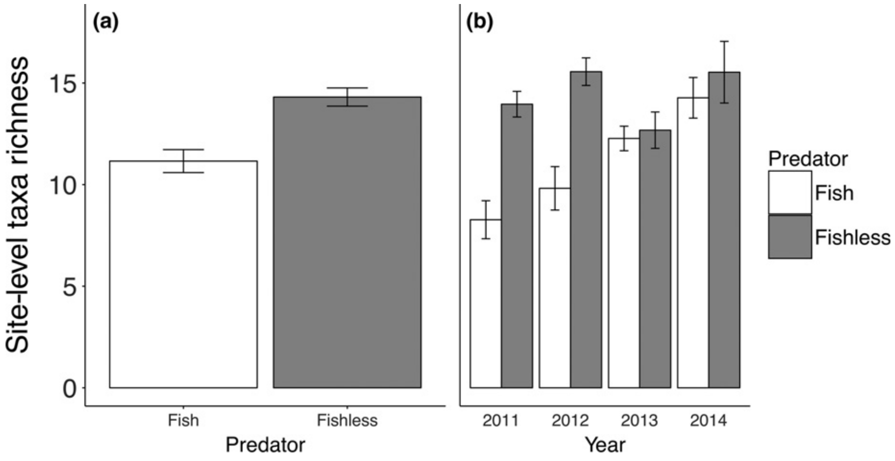

FIGURE 1 Variation in site-level taxa richness between sites with fish present and sites without fish. (a) Total effect of fish presence on taxa richness during the duration of the study. Presented is the mean richness ± 1 standard error, estimated fish present coefficient = −1.29 ± 0.71, *p* = 0.04. (b) The effect of fish presence on taxa richness across the 4 years of the study, mean ± standard error. Predator type and year 2013 interaction: −0.41 ± 0.15, *p* = 0.007, predator type and year 2014 interaction: −0.31 ± 0.16, *p* = 0.08

water chemistry PCA axis 1, year and the fish and year interaction, and the model with the lower AICc value retaining the $\log_{10}$-transformed perimeter and its interaction with fish status. Among years, the presence of fishes interacted with year to determine alpha richness (Poisson GLMM; year 2013 by predator interaction coefficient = −0.41 ± 0.15; *z* = −2.55, *p* = 0.007, year 2014 by predator interaction coefficient = −0.31 ± 0.16; *z* = −1.97, *p* = 0.08) (Figure 1b). Thus, while fish presence negatively affected macroinvertebrate taxa richness in 2011 and 2012, it had no effect in 2013 and marginal effect in 2014 (Figure 1b). This weakening of the fish niche filter was congruent with a progressive decline in PDSI, which decreased from 2.8 in 2011 to −6.23 PDSI in 2014. Incorporation of

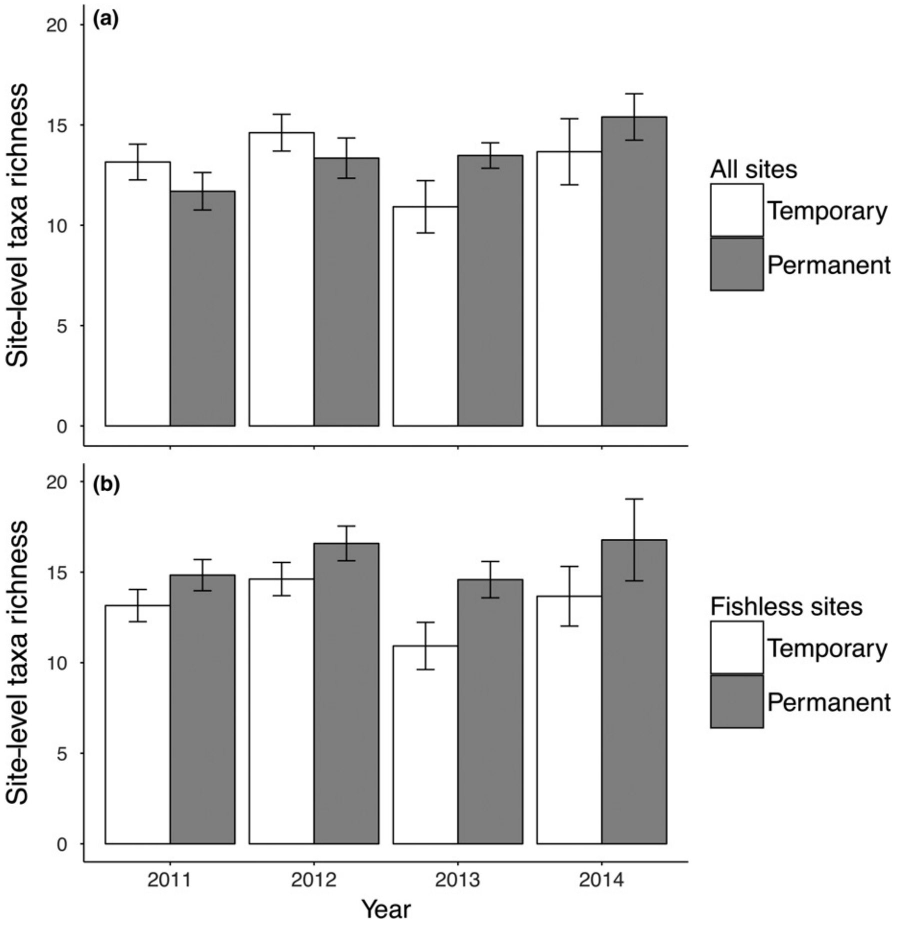

FIGURE 2 Change in mean site-level taxa diversity across years between temporary and permanent sites. (a) includes all sites, and there was no significant interaction between pond permanence and year. (b) includes only fishless sites. The lack of a significant interaction between pond permanence and time provides further evidence that the change in the fish niche filter strength is not a result of change in the strength of the hydroperiod niche filter

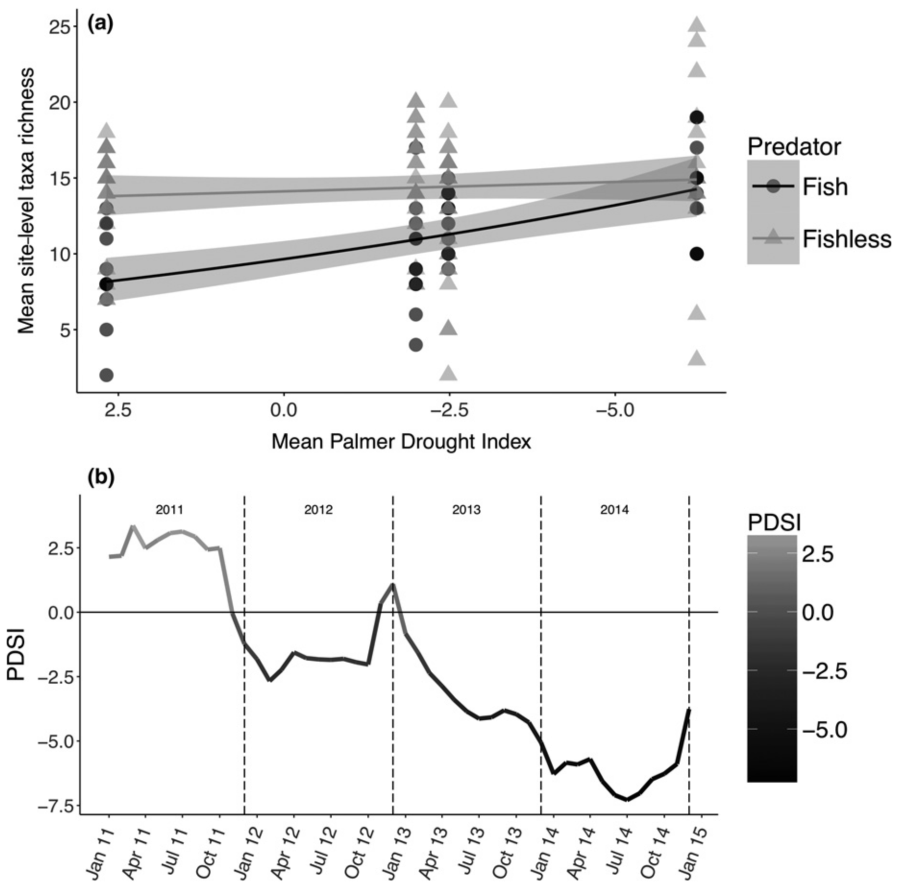

FIGURE 3 (a) The effect of mean annual Palmer's drought severity index (PDSI) on site-level taxa richness between fish and fishless sites. Predator type and PDSI interaction estimated coefficient = 0.042 ± 0.018. (b) Monthly changes in PDSI values for central coast valley region ranging from January 2011 to December 2014

mean annual PDSI into the models of local taxa richness provided a poorer fit than the best fitting model although it contained a significant interaction between fish and PDSI (predator type by PDSI interaction coefficient = 0.042 ± 0.018; $z = 2.38$ $p = 0.01$, conditional $R^2 = 0.45$) (Figure 3a, b). Correspondingly, in the analysis of invertebrate community composition among years, the interaction term between year and fishes was significant (fish-by-year interaction: deviance = 78.52, $p = 0.004$). This corresponded with the detection of previously absent taxa at fish sites in the final 2 years of the survey, including *Notonecta* sp., *Cybister* sp. and *Lethocerus* sp., resulting in an increase in fish site gamma diversity (Figure 4).

We found no evidence for spatial autocorrelation when using all years and sites (Mantel $r = 0.1093$, $p = 0.128$), looking at each year independently (Mantel r range = –0.04 to 0.10, p range: 0.11–0.64).

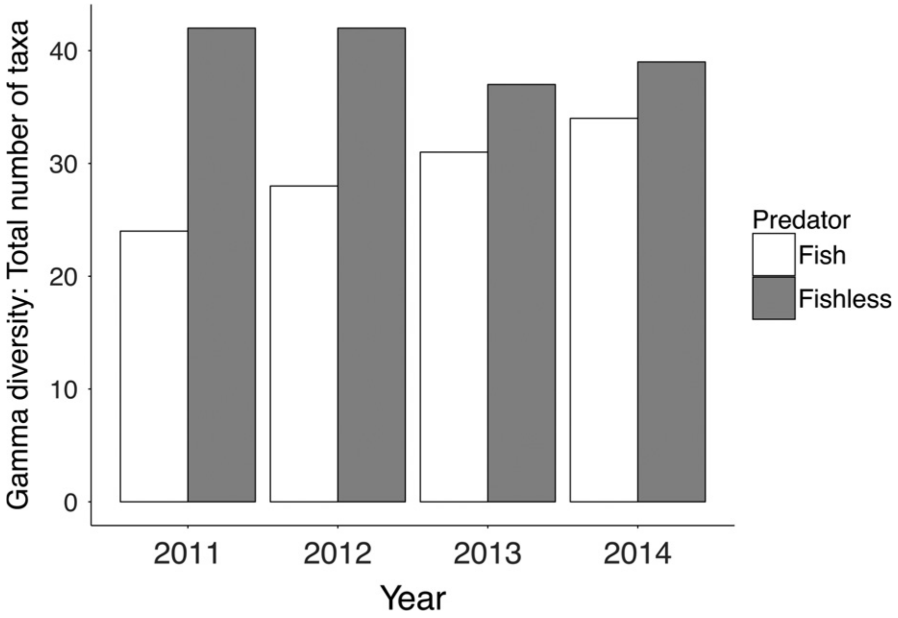

FIGURE 4 Change in the cumulative taxa presence (gamma diversity) between fish and fishless sites through time

After invertebrate groups were broken into passive- and active-dispersing taxa based on published sources (Merritt et al., 1996; Thorp & Covich, 2009), we observed no significant effect of spatial autocorrelation (passive dispersers: Mantel $r = 0.063$, $p = 0.07$; active dispersers: Mantel $r = 0.05$, $p = 0.10$).

4 | DISCUSSION

In this study, we show how a major niche filter of macroinvertebrate communities within pond ecosystems shifts in strength over the course of a prolonged drought. In particular, our analysis revealed that the effects of fish presence on aquatic invertebrate richness and composition weakened as the drought progressed. While the occurrence of fishes was the primary determinant of macroinvertebrate richness and taxa composition early in the study, these effects became nondetectable in the third and fourth year of sampling. Correspondingly, invertebrate richness in ponds with fishes increased over the study period, including the addition of taxa often thought to be sensitive to fish predation such as predacious beetles in the family Dytiscidae (Wellborn et al., 1996). These macroinvertebrates could have been released from the top-down pressure of fish predators due to the increased sensitivity of drought effect on taxa in the higher trophic levels (Ledger, Brown, Edwards, Milner, & Woodward, 2013; McHugh, Thompson, Greig, Warburton, & McIntosh, 2015). Such findings suggest that even well-established ecological niche filters can interact with climate to create temporal variation in their influence on observed communities. Given that all of the detected fish species in this study are non-native, these results have relevance for understanding and forecasting changes in the diversity of native insects and other aquatic invertebrates.

Consistent with previous literature and established theory, the presence of fishes had a strong, negative effect on invertebrate richness and was an important determinant of the invertebrate community composition (Chase, 2007; Chase et al., 2009; Diehl, 1992; Holomuzki, Feminella, & Power, 2010; Hoverman et al., 2011; McPeek, 1998; Williams, 1997). Within our study region, sites with fish supported, on average, 23% fewer taxa. These observations parallel those from previous studies highlighting the inhibitory effects of fishes on invertebrate abundance and overall richness (Batzer et al., 2000), which is often attributed to reduced colonisation and intense predation pressure (McPeek, 1997). In the first 2 years of the study, active, large-bodied invertebrate taxa such as several hemipterans (*Notonecta* sp. and *Lethocerus* sp.) and adult dytiscid beetles were conspicuously absent in ponds with fish. However, as the severity of the California megadrought intensified, these previously “filtered” taxa colonised sites with fish. With the addition of these taxa, the differences between fish and fishless sites became less pronounced. By the end of the study, both the macroinvertebrate richness and taxa composition of ponds with and without fishes became largely indistinguishable. Although the megadrought caused ponds to shrink concentrating the macroinvertebrates and resulting in an increased chance of encountering rare taxa, it is worth noting that ponds with fish showed little evidence of a persistent shift in perimeter or area across the study period (Appendix S5). Thus, it is unlikely that changes in detection alone can explain the observed increase in macroinvertebrate taxonomic richness over time.

Alternatively, this pattern could be associated with an increase in harshness of the hydroperiod niche filter, which is a major driver of the community richness and composition in small pond ecosystems (Wellborn et al., 1996). Although many of these ponds rely on winter rain events to recharge, we found limited evidence of a strong hydroperiod niche filter in this system. Pond permanence status (temporary and permanent) was not significantly correlated with macroinvertebrate richness across all ponds, and we found no temporal change in this pattern with the worsening drought even when permanent fish positive sites were removed (Figure 2a,b). The lack of a hydroperiod niche filter could stem from human modification of these ponds for cattle grazing, which largely resulted in deeper more permanent ponds (Garone, 2011). These increases in both depth and hydroperiod may have allowed temporary ponds to hold water long enough to allow the majority of macroinvertebrates to complete their life cycles, thus effectively removing the niche filtering mechanism. However, it is worth noting that during the year where the drought effect was at its highest (2014), 10 temporary ponds remained dry and were thus unavailable to support invertebrate populations. A prolonged dry phase of a temporary pond may lead to a lagged and larger hydroperiod effect on both the community composition and pond taxa richness.

The specific mechanisms through which drought altered the effects of fishes on invertebrate communities could involve several direct and indirect pathways. Although the locations and identities of fish species observed over the sampling period remained consistent (i.e., there was no evidence of local extirpations or colonisations of fish), it is possible that drought-driven decreases in fish abundance or size distribution could have dampened the intensity of predation risk on sensitive macroinvertebrate taxa (Dorn & Cook, 2015). Alternatively, evaporation and reduction in pond size are associated with numerous physiochemical changes that can have significant effects on fish behaviour and microhabitat use, such as warmer temperatures, higher salinity and reduced areas of vegetated shoreline (Crowder & Cooper, 1982; Magoulick & Kobza, 2003; Webster, Atton, Ward, & Hart, 2007). For instance, studies have demonstrated that predacious fish may disproportionately use the nearshore littoral habitat for foraging and nutrient acquisition (Dolson, McCann, Rooney, & Ridgway, 2009; Hampton, Fradkin, Leavitt, & Rosenberger, 2011), yet the relative importance of this habitat has shown to decrease with increased water temperatures (Tunney, McCann, Lester, & Shuter, 2014). Thus, increases in littoral zone temperature may cause fish to forage and take refuge in deeper microhabitats (Grossman & Ratajczak, 1998; Lake, 2003), thereby providing a refuge for formerly “filtered” taxa along the shoreline. It is worth noting that the majority of the sampled fish species were non-native, warm-water game fish, which may respond differently to the effects of drought compared with native species (Kiernan & Moyle, 2012). In

California, a recent trait-based vulnerability assessment identified native fish species as being more vulnerable to climate change compared to non-native species (Moyle, Kiernan, Crain, & Quinones, 2013). Thus, aquatic habitats with native fish species could experience an even greater relaxation of the predatory niche filter than what we observed with non-native fishes, although this hypothesis awaits direct empirical testing.

A final possibility involves a progressive loss of the number of fishless sites over time. By 2014, five sites failed to hold water for the first time and 10 ponds held water for <1 month. This change in the spatial arrangement and number of available ponds on the landscape could have caused dispersing invertebrates to colonise suboptimal habitats, such as those with fishes (Steiner, Siegert, Schulz, & Suhling, 2000). Whether these invertebrates were successful in their development and able to further colonise additional sites was not measured, such that future work is needed to shed light on temporal variation in the identity of potential niche filters and their intensity.

Alternatively, the onset of a severe drought may have intensified effects of the hydroperiod niche filter resulting in more taxa selecting permanent waterbodies, which also have a higher chance of being stocked with fish. Changing hydroperiods in freshwater environments have frequently been identified as important factors in driving changes in species composition and species interactions (Bogan & Lytle, 2011; Chase, 2007; Knorp & Dorn, 2014). In this scenario, we would expect to see an increase in the number of macroinvertebrate taxa present in permanent waterbodies, including those that support fishes, as the drought worsened. Instead, however, we detected no temporal changes in invertebrate richness within permanent ponds that lacked fish (see Figure 2). This suggests that the increase in invertebrate occurrence was specific to fish habitats and was not associated with overall changes in the hydroperiod niche filter strength. Similar patterns have been observed in lotic habitats where drought conditions altered feeding behaviour of insect feeding fish resulting in a release of the benthic insect grazers from the top-down control of fish predation (Power et al., 2008). Our results thus provide further evidence of the role of changing environments in the outcome of species interactions, particularly with respect to changes in the interaction strength between predators and prey.

These findings suggest that, in response to a rapidly changing environment, biotic niche filters can relax to the point of allowing previously excluded species to recolonise, consistent with ecological theory (e.g., storage effect: Chesson, 1985; consumer resource model: Menge & Sutherland, 1987), and emphasising the importance of fluctuating environments in allowing for coexistence and maintaining species richness. While the storage effect has frequently been demonstrated in systems involving competing species, it can also be extended to cases in which the interaction strength between predators (in this case fishes) and the prey (macroinvertebrates) shifts in response to the environment fluctuations (Angert, Huxman, Chesson, & Venable, 2009; Power, 1990). Such investigations require multiyear studies to understand how variation in factors such as climate and disturbance interacts to determine the intensity of established niche filters. While prolonged drought is likely to adversely affect many aquatic taxa, if the effects are disproportionately harsh on predators or, in this case, non-native taxa such as fishes, shifts in water availability could have extensive indirect effects on invertebrate community composition and abundance. Further insight can be gained by applying species-trait-by-environment matching to illustrate the expanse or constriction of a species' niche over time and in response to environmental changes (Lavorel & Garnier, 2002).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

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

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