Communities at the extreme: Aquatic food webs in desert landscapes

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Abstract
Studying food webs across contrasting abiotic conditions is an important tool in understanding how environmental variability impacts community structure and ecosystem dynamics. The study of extreme environments provides insight into community-wide level responses to environmental pressures with relevance to the future management of aquatic ecosystems. In the western Lake Eyre Basin of arid Australia, there are two characteristic and contrasting aquatic habitats: springs and rivers. Permanent isolated Great Artesian Basin springs represent hydrologically persistent environments in an arid desert landscape. In contrast, hydrologically variable river waterholes are ephemeral in space and time. We comprehensively sampled aquatic assemblages in contrasting ecosystem types to assess patterns in community composition and to quantify food web attributes with stable isotopes. Springs and rivers were found to have markedly different invertebrate communities, with rivers dominated by more dispersive species and springs associated with species that show high local endemism. Qualitative assessment of basal resources shows autochthonous carbon appears to be a key basal resource in both types of habitat, although the particular sources differed between habitats. Food-web variables such as trophic length, trophic breadth, and community isotopic niche size were relatively similar in the two habitat types. The basis for the similarity in food-web structure despite differences in community composition appears to be broader isotopic niches for predatory invertebrates and fish in springs as compared with rivers. In contrast to published theory, our findings suggest that the food webs of the hydrologically variable river sites may show less dietary generalization and more compact food-web modules than in springs.

KEYWORDS
community, food webs, ground water, stable isotopes, temporary pools
1 | INTRODUCTION

Studying ecological communities across environmental gradients is a key step toward predicting how complex communities respond to their abiotic environment, providing insight into how they persist over time (Dunne, Saleska, Fischer, & Harte, 2004; Thompson, Dunne, & Woodward, 2012). Changes along environmental gradients can alter which taxa are present and their abundance (community composition) and the trophic interactions between taxa (food-web structure). Food-web analysis includes all species in the system and the movement of energy between those species (Cole et al., 2006; Thompson, Brose, et al., 2012). By including all species present and their interactions, we can understand how whole ecosystems respond to stressors such as invasive species (Ho, Bond, & Lake, 2011), drought (Ledger, Brown, Edwards, Milner, & Woodward, 2013), or climate change (Binzer, Guil, Brose, & Rall, 2012). Instead of focusing on effects on individual species, food-web approaches can account for emergent and interactive effects of stressors on whole communities (Layer et al., 2011).

Analysis of carbon and nitrogen isotopes quantifies the relative trophic positions of species, which allows the structure of the food web to be characterized and emergent food-web variables to be quantified (Post, 2002). For example, food-chain length (i.e., the number of trophic transfers from basal resources to top predators) is a commonly studied response metric that can assess the factors that support high trophic-level species, overall community complexity, and biodiversity (McHugh, McIntosh, & Jellyman, 2010). Similarly, the ecological niche occupied by functional groups and species can be quantified using the "isotopic niche" concept, where the isotopic composition of an organism’s tissue reflects what it consumes (Jackson, Inger, Parnell, & Bearhop, 2011; Newsome, Martinez del Rio, Bearhop, & Phillips, 2007). The size and shape of the niche occupied by taxa or functional groups can be a sensitive measure of community trophic characteristics under varying levels of abiotic stress (McGill, Enquist, Weiher, & Westoby, 2006).

In aquatic ecosystems, hydrology is a key ecological driver which can influence community composition both directly through disturbance effects (Bunn & Arthington, 2002; Lake, 2003) and indirectly through impacts on basal resource availability (Takimoto & Post, 2013; Townsend et al., 1998). Natural disturbance, such as the extreme high flow events and droughts experienced by desert rivers, has been hypothesized as a key driver of patterns of diversity generally, although empirical evidence remains weak for classical ecological hypotheses such as the "intermediate disturbance hypothesis" (Connell, 1978; Fox, 2013). More disturbed habitats may be more likely to contain species with broad diets, including omnivores (e.g., Menge & Sutherland, 1987). This hypothesis is supported by empirical studies of early successional communities, where trophic generalists are more common (e.g., Brown & Southwood, 1983; Kullberg & Scheibe, 1989). Applying stable isotope analysis to communities’ subject to differences in flow permanence allows us to assess how disturbance may influence total niche width and isotopic niche size (Jackson et al., 2011).

The effects of disturbance on food-web characteristics have long been of interest to ecologists, particularly from a perspective of understanding food-web attributes that may promote resilience and resistance (e.g., Kondoh, 2003; Krause, Frank, Mason, Ulanowicz, & Taylor, 2003; Wootton, Parker, & Power, 1996). It has been hypothesized that more variable habitats will have shorter food chains, due to stochastic loss of numerically rare top predators (McHugh et al., 2010; Pimm & Lawton, 1977). Experimental support for this found negative effects of hydrologic variability on food-chain length in North American rivers (Sabo, Finlay, Kennedy, & Post, 2010). However, Walters and Post (2008) found that a low-flow disturbance altered the body size characteristics of communities but not the length of the food chain. A recent meta-analysis also found little evidence of an effect of disturbance on food-chain length (Takimoto & Post, 2013).

Indirect effects of disturbance on diversity through impacts on the basal resource supply have received relatively less attention (Wootton, 1994a, 1994b; but see Townsend et al., 1998). Across aquatic ecosystems, and particularly in river systems, basal carbon from in-stream autochthonous (e.g., algal and macrophyte) and allochthonous (e.g., riparian and floodplain) sources are fundamental processes underpinning food webs (Bunn, Davies, & Winning, 2003; Cole et al., 2006). Carbon isotope analysis allows for tracking basal resources such as algal or terrestrial carbon through food webs (Post, 2002). Isotope studies of primary productivity have provided unique insights into the relative influence of carbon sources, where flow variability can play an important role in facilitating inputs of terrestrial riparian and floodplain carbon (Bunn et al., 2003; Hadwen, Fellows, et al., 2010; Robertson, Bunn, Boon, & Walker, 1999).

Two aquatic ecosystems in arid Australia provide an opportunity to analyze whether differences in flow permanence and abiotic variability influence community composition and food-web structure. In northern South Australia, the Great Artesian Basin (GAB) forms a series of highly stable and extremely isolated groundwater springs (Mudd, 2000; Murphy, Breed, Guzik, Cooper, & Austin, 2012), while the Lake Eyre Basin (LEB) is a largely ephemeral surface water basin that includes some of the most hydrologically variable rivers in the world (Kotwicki & Allan, 1998; McNiel, Schmarr, & Rosenberger, 2011). Western LEB waterholes range from semi-permanent to highly ephemeral, and the flow variation is coupled with variation in physiochemical properties; for example, salinity can range from near fresh during high flows to hypersaline in recession phases (Costelloe, Grayson, McMahon, & Argent, 2005; Costelloe & Russell, 2014). Biodiversity studies have shown that assemblages have been highly conserved in arid Australian waterholes over time, with more persistent waterholes being key ecological refugia (Davis, Pavlova, Thompson, & Sunnucks, 2013). Furthermore, studies have shown that some taxa are reliant on GAB waterbodies and show high spring- and catchment-specific endemism (Murphy, Adams, & Austin, 2009; Murphy et al., 2012), and permanent springs across arid Australia broadly tend to be characterized by endemic species in contrast to the riverine communities (Davis et al., 2018). This suggests that present-day assemblages are likely to be the product of long-term
physical differences between waterbodies and their connectivity within the landscape, and the contrasting abiotic regimes provide an opportunity to study their influence on community characteristics.

We integrated community composition analysis with stable isotope approaches (Layman et al., 2012) and contemporary methods to quantify isotopic niche size (Jackson et al., 2011). This approach was used to explore how physical variability influences aquatic food-web characteristics (Thompson, Brose, et al., 2012). Specifically, we sought to determine whether the differences in the abiotic characteristics of river and spring habitats influence:

1. Community composition, where we predicted that river environments would be characterized by broadly dispersed, highly mobile species, whereas spring habitats would contain taxa with poorer dispersal abilities and have higher local endemism.
2. Basal resource base, where we predicted that river environments may have a broader resource base due to lateral connectivity with riparian and floodplain energy sources.
3. Isotopic niche size of the community, which we predicted would be larger in more disturbed sites due to selection for generalist taxa.

### TABLE 1

| Site name         | Latitude/longitude | Habitat | Conductivity mean/range (μS/cm²) | Temperature mean/range (°C) | Turbidity mean/range (NTU) |
|-------------------|--------------------|---------|----------------------------------|-----------------------------|----------------------------|
| Blanche Cup       | −29.452850/136.858733° | Spring  | 7,100 (6,809–7,270)              | 20.9 (20.2–21.7)            | 17.3 (10.9–25.9)           |
| The Bubbler       | −29.446483°/136.857849° | Spring  | 5,746 (5,490–6,127)              | 29.7 (29.1–30.5)            | 7.22 (7.11–7.36)           |
| Coward Springs    | −29.400388°/136.794193° | Spring  | 6,769 (6,550–6,980)              | 24.3 (22.2–26.9)            | 6.44 (4.72–9.00)           |
| The Fountain      | −28.348694°/136.283585° | Spring  | 6,318 (6,233–6,390)              | 21.4 (18.5–23.7)            | 9.54 (8.09–11.9)           |
| Freeling Springs  | −28.071861°/135.903622° | Spring  | 8,433 (8,180–8,598)              | 22.3 (19.6–24.5)            | 4.76 (1.98–3.70)           |
| Finniss Creek     | −29.610250°/137.458289° | River   | 12,900 (12,690–13,030)           | 23.0 (18.6–26.9)            | 6.23 (3.50–8.06)           |
| Algebuckina       | −27.899995°/135.814456° | River   | 8,200 (2,900–12,150)             | 23.9 (12.9–32.3)            | 35.1 (8.68–59.8)           |
| Screechowl Creek  | −29.627539°/137.336036° | River   | 143,800 (73,700–231,000)         | 21.9 (15.4–28.3)            | 94.8 (19.3–224)            |
| Margaret Creek    | −29.490222°/137.039383° | River   | 118,330 (26,100–227,300)         | 23.1 (17.7–29.5)            | 76.3 (9.97–172)            |
| Warriner Creek    | −29.137986°/136.568422° | River   | 57,268 (35,400–78,704)           | 20.7 (19.2–22.1)            | 6.31 (4.28–9.04)           |
| Levi Creek        | −28.317600°/136.270933° | River   | 182,980 (100,600–265,360)        | 25.7 (17.6–33.7)            | 14.3 (11.9–16.6)           |

### FIGURE 1

Map of the 11 study sites in northern South Australia, within the western Lake Eyre Basin. Both spring (sites 1–5) and river (sites 6–11) sites span multiple river systems that feed into Lake Eyre, with the northern sites (4, 5, 7, 11) within the Neales River Catchment, and the remaining sites in smaller creek catchments that flow into the lake’s southern lagoon. 2013–2014 rainfall records at towns/stations shown are available in Appendix S1 (Figures A1–A3)
4. Food-chain length, where we predicted that food chains would be shorter in the more physical-disturbance prone river food webs compared to the more stable spring food webs.

2 | METHODS

2.1 | Study location

Sites were selected to represent permanent groundwater springs (n = 5) and intermittent river waterholes spanning multiple catchments in the western Lake Eyre Basin (n = 6; Table 1, Figure 1). Spring sites chosen were the largest accessible springs in the area, while waterholes chosen were the largest known accessible pools to maximize the chance that sites were not dry during sampling. Both aquatic habitat types span a range of sizes and to ensure consistent areas were sampled, entire pools/spring outlets were sampled where they were >50 m length and a maximum 50 m reach was sampled for larger sites (e.g., Algebuckina, The Bubbler). In April 2014, invertebrate and fish communities were sampled as well as basal resources, including plant material from riparian and aquatic vegetation, phytoplankton, and algae. At sampling, all river sites were nonflowing pools, with physicochemical properties showing high among- and within-site variation relative to springs during the study period and measured parameters (e.g., temperature, conductivity, salinity) ranging from below that of spring sites to significantly higher (Table 1). A rainfall event in February 2014 impacting the entire region (although potentially more strongly in southern sites; see Appendix S1 for 2013–2014 rainfall data, Figures A1–A3) may have temporarily provided increased longitudinal connectivity in river sites, despite most ephemeral sites (i.e., Screechowl, Margaret, and Levi Creeks) likely being almost entirely dry prior to that rainfall.

2.2 | Stable isotope sampling and processing

For basal resources, three replicate samples (predominantly leaves) were collected from all plant species observed at sites and frozen. After transport to Monash University, samples were rinsed with reverse osmosis (RO) water and oven-dried for 1 week at 60°C. Samples were then ground to a fine powder using a mortar and pestle (HCl 1 N acid-washed) or a mill grinder. Phytoplankton/FPOM samples (100 ml) were collected using a 40-µm mesh plankton sampling net (25 cm opening, 5 m sweeps). Samples were frozen for storage and transport before being prefiltered through a 125-µm sieve and vacuum-filtered onto a GF-75 filter (0.7 µm mesh size; Advantec MFS Inc.). Filters were rinsed with 1 N HCl to remove carbonates and rinsed well with RO water, before drying for 1 week at 60°C. Algal resources, particularly filamentous or benthic mats, could be sampled by hand. Replicate samples were rinsed with RO water, and all invertebrates and other organic matter were removed under a dissecting microscope before the algae was dried and ground.

Invertebrate composite samples were collected by scooping a dip net through benthic sediment and the water column (two sweep and one kick sample per site), excluding Blanche Cup where three sweeps were collected as the delicate banks did not allow kick samples. Composite samples were rinsed with RO water and held for 24 hr before freezing to allow invertebrate gut contents to be voided, to avoid biasing isotope values with undigested gut material that may not ultimately be assimilated into tissue. Invertebrates were identified to the finest possible taxonomic level, generally family or species, and their presence/absence in each sample was recorded. Gastropods, which were common, had their shells removed before processing, as carbon-based precipitates reflect the isotopic ratios of the inorganic environment, whereas their soft tissue reflects their diet (Post, 2002). Where enough biomass was available, three independent (distinct individuals/groups of individuals) replicates were analyzed. If insufficient biomass was sampled, samples were pooled to give a mean value per species/site. Replicates were dried and ground before analysis. For fish and crayfish sampling, differences in the depth between sites did not allow a standardized approach to be used. In springs, unbaited box traps (45 cm × 25 cm × 25 cm, 5 cm aperture, 1 mm mesh) and hand dip nets (20 cm × 25 cm, 1 mm mesh) were used. At river sites, three fyke nets (single 5 m wing, 60 cm drop, 19 mm mesh, deployed overnight) and a seine net (7 m × 2 m, 6 mm mesh) were also used, water depth permitting. Individuals were removed and euthanized by immersion in a solution of clove oil and water sourced from the site, before freezing. Where enough individuals were collected, three independent samples of muscle tissue were rinsed, dried, and ground before analysis. If there were insufficient individuals/biomass to provide three independent samples, three samples were analyzed wherever possible and a mean isotope value reported.

2.3 | Stable isotope analysis

Samples were analyzed for carbon (carbon-12–carbon-13; hereafter δ13C) and nitrogen (nitrogen-14–nitrogen-15; hereafter δ15N) isotope ratios at the Water Studies Centre (Monash University) on an ANCA GSL2 elemental analyzer interfaced to a Hydra 20–22 continuous-flow isotope ratio mass-spectrometer (Sercon Ltd.). The precision of the stable isotope analysis was ±0.1‰ for δ13C and ±0.2‰ for δ15N. Stable isotope data are expressed in the delta notation (δ13C and δ15N), relative to the stable isotope ratio of Vienna Pee Dee Belemnite standard (RVPDB = 0.0111779) for carbon and atmospheric N2 (RAIR = 0.0036765) for nitrogen.

2.4 | Statistical analysis

All statistical analyses were conducted using R Statistical Package 3.5.1 (R Core Team, 2018). To analyze community composition, we used invertebrate taxa presence/absence data by site in multidimensional scaling (MDS) analysis. Invertebrate data (cf. fish) were used as we were able to apply a more strictly standardized sampling methodology across sites and because the desert goby (Chlamydogobius eremius) is known to be the only species present in any spring site. Only taxa caught using kick/sweep sampling were used in this analysis, while all taxa (including those captured using other methods, e.g.,
Cherax destructor) are used in isotope analysis. PERANOVA hypothesis tests (adonis function, vegan package; Oksanen et al., 2007) tested for differences in composition associated with habitat type. We also tested for an effect of region as genetic isolation between northern (e.g., Algebuckina) and southern (e.g., Warriner Creek) catchments has been detected in previous studies (see Mossop et al., 2015). As compositional differences were found between springs and rivers, the contribution of each taxa to the effect of habitat type was estimated using Bray–Curtis dissimilarity (SIMPER function). We considered taxa with a percentage contribution greater than its standard deviation to be substantially contributing to the habitat differences in composition, and their taxa-specific NMDS scores were calculated.

In addition to the descriptive analysis of stable isotope plots, the sample size-corrected standard ellipse area (SEAc; Jackson et al., 2011) was calculated at each site for all animal taxa collectively as well as separately by functional feeding groups. Coarse functional groupings for aquatic invertebrate were made at the finest taxonomic level available by (a) nonpredatory invertebrates (including scrapers, gathering and filtering collectors, and shredders) and (b) predatory invertebrates and fish (via the MDFRC Bug Guide; Hawking, Smith, LeBusque, & Davey, 2013). Predatory invertebrates and fish were grouped out of necessity as most sites lacked sufficient taxa to calculate SEAc for each group separately, and this grouping gives a measure of the trophic niche occupied by species that we are assuming to be feeding at higher (>2) trophic levels. SEAc represents size of the 40% prediction interval of the posterior distribution derived from an input set of isotope values, to give an estimate of isotopic niche size, whereas convex hull area measures the area of a polygon encompassing all input isotope values (Jackson et al., 2011). Additional food-web attributes were calculated for animal communities, such as the δ15N range (community trophic range taken as the difference from the maximum to mean basal δ15N, a nontransferable but similar measure to food-chain length), δ13C range (community trophic breadth), mean δ15N (corrected for basal δ15N, to estimate mean trophic position of taxa, Vander Zanden, Cabana, & Rasmussen, 1997), mean δ13C, and total number of taxa. One-way ANOVAs compared each measure between spring and river sites.

3 | RESULTS

We found a significant effect of habitat type on invertebrate community composition (F1,8 = 12.1370, p = .001, Figure 2) and no effect of region. Eleven invertebrate taxa were found to be substantially contributing to the habitat effect via SIMPER analysis, and their NMDS scores were calculated (Table 2). Rivers were primarily associated with Coleoptera taxa, whereas springs were associated with several groupings, including arachnids, gastropods, and isopods (Figure 2).

Isotope plots across spring sites (Figure 3a–e) show apparent differences in basal resources, such as filamentous algae at The Bubbler (δ15N = −13.20‰ [SD 0.64], δ13C = −31.54‰ [SD 0.31]) and phytoplankton at Blanche Cup (δ15N = −1.35‰, δ13C = −23.79‰). Standard ellipse plots (Figure 4a) and the high among-site variation in δ15N and δ13C values relative to river sites (Table 3) indicate variability in carbon sources and isotopic niches between springs.

Isotope plots of river sites (Figure 3f–k) and mean δ13C values (Table 3) show animal communities clustered around −20‰, and standard ellipse plots (Figure 4b) showed that there was a high degree of isotopic niche overlap centered in around this value. This appears to be associated with riverine algae (mostly filamentous algae and benthic mats), which commonly had δ13C values from −15 to −20‰ (median = −16.38‰, mean = −14.99 [SD 4.46]). At several
TABLE 2 Key invertebrate groups, SIMPER and NMDS analysis

| Group                              | SIMPER % contribution to the habitat type effect | NMDS1 score | NMDS2 score | Functional feeding group                  |
|------------------------------------|-------------------------------------------------|-------------|-------------|-------------------------------------------|
| Isopoda, Amphisopidae Phreatolus latipes | 0.0532 (SD 0.0125)                              | 0.6512      | -0.0601     | Shredders, gathering collectors            |
| Gastropoda, Hydrobiidae Fonscochlea spp | 0.0532 (SD 0.0125)                              | 0.6512      | -0.0601     | Scrapers                                  |
| Gastropoda, Hydrobiidae Trochidria spp | 0.0532 (SD 0.0125)                              | 0.6512      | -0.0601     | Scrapers                                  |
| Diptera, Ceratopogonidae           | 0.0532 (SD 0.0125)                              | 0.6512      | -0.0601     | Predators, gathering collectors, scrapers  |
| Coleoptera, Hydrophilidae Berosus spp (larv.) | 0.0532 (SD 0.0125)                              | -0.5613     | 0.0056      | Predators                                  |
| Araneae, Lycosidae (Arachnida)     | 0.0390 (SD 0.0282)                              | 0.4438      | 0.1279      | Predators                                  |
| Coleoptera, Dytiscidae Eretes australis | 0.0345 (SD 0.0268)                              | -0.5827     | -0.0513     | Predators                                  |
| Coleoptera, Dytiscidae Necterosoma spp | 0.0334 (SD 0.0299)                              | -0.2694     | -0.0216     | Predators                                  |
| Coleoptera, Dytiscidae Limobedus spp | 0.0312 (SD 0.0274)                              | -0.3265     | 0.2921      | Predators                                  |
| Coleoptera, Hydrophilidae Unknown spp | 0.0290 (SD 0.0290)                              | -0.1632     | -0.1964     | Shredder                                   |

river sites, δ13C was below −25‰, likely reflecting inputs of terrestrial vegetation, which commonly had δ13C values from −25 to −30‰ (median = −26.35‰; mean = −24.01‰ [SD 5.40]).

For the animal communities at springs and river sites, there were no overall differences in SEAc, δ15N mean/range, δ13C mean/range, or total taxa richness based on habitat type (Table 3). Among spring sites, the largest SEAc and δ15N ranges were recorded at The Bubbler, suggesting high diet generalization and longer food chains, followed by Blanche Cup and Coward Springs. Among river sites, the largest and most persistent site, Algebuckina Waterhole, had the highest range of δ15N (indicating longer food chains) and the largest number of taxa, whereas the more ephemeral Warriner Creek exhibited the largest SEAc niches (indicating higher diet generalization).

The SEAc of functional groupings (Table 3) showed that the isotopic niche space occupied by predatory invertebrates and fish was larger in springs than river sites ($F_{1,7} = 18.09, p = .0038$), despite spring sites tending to have fewer predatory invertebrate taxa and fish. Although this should be interpreted cautiously as two spring sites did not have sufficient taxa to calculate SEAc for this group. There was no significant habitat difference for nonpredatory invertebrates.

**4 | DISCUSSION**

Invertebrate assemblages across a wide geographical range in the western LEB were strongly associated with their local habitat type. Springs were linked with taxa that have low active dispersal capability and are less likely to be adept at coping with physically variable environments (i.e., isopods and gastropods), whereas rivers were linked to Coleoptera taxa with the capacity for active flight and dispersal (Boda & Csabai, 2013). Temporal patterns in hydrology and connectivity have been shown to be an important driver of invertebrate assemblages and diversity in the arid Cooper Creek (Marshall, Sheldon, Thoms, & Choy, 2006), so the possible flow event within 2 months of sampling may have been a factor driving the observed similarity between river waterholes. Directly following a flow disturbance and the re-wetting of dry or drying waterholes, species succession can favor dispersive invertebrates, and in this case, Coleopterans may represent early colonizers (Sousa, 1979; Ward, Tockner, Arscott, & Clare, 2002).

While dispersal strategies appear to allow certain taxa to persist across more physically variable LEB rivers, in temperate streams and isolated pools on the Iberian Peninsula, the opposite pattern was observed, with lentic waterbodies linked to dispersive Coleopteran species (Ribera & Vogler, 2000). Nonetheless, the mechanism underlying this is consistent with what we observed, as Ribera and Vogler's isolated pools were also more ephemeral and required frequent migration for aquatic species, so may be considered more like LEB waterholes. Consistent findings from the Pilbara region in northwest Australia show that the local physical conditions and connectivity drive invertebrate assemblages in arid waterholes (Moran-Ordonez et al., 2015). These results reinforce the ecological importance of
FIGURE 3  Stable isotope plots across sites (a–k), as of April 2014. Error bars represent one standard deviation in the mean score for that taxa. Error bars were omitted where insufficient individuals/biomass was available for three independent measures.
The broad interconnected network of ephemeral river channels to the persistence of certain aquatic taxa in arid landscapes (Mossop et al., 2015).

Our results support previous studies showing permanent groundwater is vital to the persistence and evolution of certain endemic aquatic taxa in this and landscape (Brim-Box et al., 2014, 2008; Davis et al., 2013; Murphy, Guzik, Cooper, & Austin, 2015), including isopods and gastropods that show catchment- or spring-specific endemism (Guzik, Adams, Murphy, Cooper, & Austin, 2012).

### FIGURE 4

Standard ellipse areas based on 95% prediction intervals across (a) spring habitats and (b) river habitats. Spring site ellipses are differentiated according to shade and number in order from 1. Blanche Cup, 2. The Bubbler, 3. Coward Springs, 4. The Fountain, to 5. Freeling Springs (light gray). River site ellipses are similarly differentiated according to shade. In order from 1. Finniss Creek (dark black), 2. Algebuckina, 3. Screechowl Creek, 4. Margaret Creek, 5. Warriner Creek, to 6. Levi Creek (light gray).

### TABLE 3

Analysis of animal food-web characteristics by site, April 2014

| Site               | Total number of taxa | Corrected ellipse area (SEAc) | Predatory invertebrates and fish | All animals | \(\delta^{15}N\) Adjusted mean and range (‰) | \(\delta^{13}C\) Mean and range (‰) |
|--------------------|----------------------|-------------------------------|---------------------------------|-------------|---------------------------------------------|-----------------------------------|
| Blanche Cup        | 13                   | 28.9196                       | 29.5561                         | 34.2473     | -0.6319 (range = 7.4871)                    | -21.5157 (range = 15.0809)       |
| The Bubbler        | 12                   | 58.8392                       | 42.5405                         | 52.5168     | 4.1906 (range = 10.7520)                    | -22.0875 (range = 14.3445)       |
| Coward Springs     | 6                    | 2.0853                        | a                               | 56.3905     | 5.2625 (range = 9.0569)                     | -19.0385 (range = 9.1887)        |
| The Fountain       | 9                    | 5.3309                        | a                               | 7.1458      | 2.1159 (range = 5.8225)                     | -22.7351 (range = 3.7478)        |
| Freeling Springs   | 15                   | 4.9830                        | 22.7581                         | 15.3107     | 3.2957 (range = 6.8801)                     | -29.4565 (range = 10.9020)       |
| Finniss Creek      | 12                   | 1.2662                        | 13.3044                         | 12.0191     | 5.3571 (range = 4.4746)                     | -22.6357 (range = 10.1431)       |
| Algebuckina        | 20                   | 55.7328                       | 18.2851                         | 27.9873     | 3.7092 (range = 9.0442)                     | -21.6240 (range = 15.1613)       |
| Screechowl Creek   | 7                    | 6.2202                        | 1.2875                          | 11.4238     | 4.6727 (range = 3.4637)                     | -19.4025 (range = 8.4726)        |
| Margaret Creek     | 15                   | 15.3502                       | 7.6874                          | 9.0739      | 4.1933 (range = 4.8095)                     | -19.1181 (range = 11.1474)       |
| Warriner Creek     | 10                   | 59.1374                       | 3.2488                          | 38.096      | 2.7114 (range = 7.3205)                     | -19.4187 (range = 11.8375)       |
| Levi Creek*        | 7                    | a                             | 9.3009                          | 12.8956     | 2.3955 (range = 4.5242)                     | -17.7366 (range = 7.7868)        |

*Insufficient data points to calculate SEAc.

*A single Hemiptera individual was excluded, as isotope values suggest it is a recent immigrant and unrelated to local food-web conditions.
Murphy et al., 2012). This is also true of terrestrial wolf spiders (Araneae, Lycosidae), which are dominant invertebrate predators in GAB springs and were commonly detected in aquatic invertebrate samples (Gotch, Adams, Murphy, & Austin, 2008).

Patterns in fish distributions similarly support the dual ecological significance of permanent and ephemeral habitats, where mound springs are key refuges for the poor swimming desert goby, which shows genetic structuring separated according to the north and south springs are key refuges for the poor swimming desert goby, which shows genetic structuring separated according to the north and south springs are key refuges for the poor swimming desert goby, which shows genetic structuring separated according to the north and south...
AUTHOR CONTRIBUTIONS

NPM wrote the main manuscript and prepared all figures and tables. All authors contributed to the formulation and execution of the experiments described therein, and all authors reviewed the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the Dryad Digital Repository (Moran, Wong, & Thompson, 2019, https://doi.org/10.5061/dryad.j18jt4n).

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

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