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Drying modulates cross-habitat subsidies and meta-ecosystem food webs in temporary saline inland waters

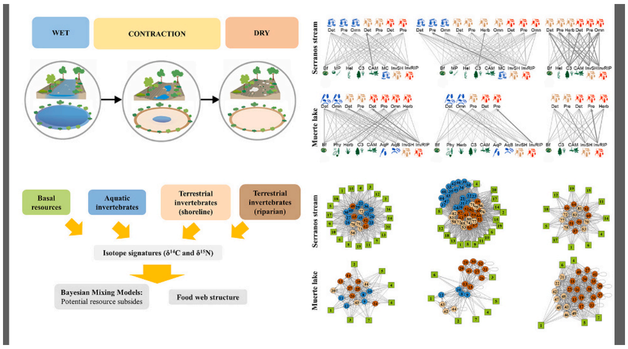
Zeus Freixinos [a,*], Paloma Alcorlo [b,c], Rosa Gómez [a], Jesús Miñano [a], Judit Boadella [d], María Mar Sánchez-Montoya [a,e]

[a] *Department of Ecology and Hydrology, Faculty of Biology, University of Murcia, Campus de Espinardo, 30100 Murcia, Spain*
[b] *Department of Ecology, Universidad Autónoma de Madrid, Campus de Cantoblanco, 28049 Madrid, Spain*
[c] *Centro de Investigación en Biodiversidad y Cambio Global (CIBC), C/Darwin 2, Universidad Autónoma de Madrid, Campus de Cantoblanco, 28049 Madrid, Spain*
[d] *Institute of Aquatic Ecology, University of Girona, Campus de Montilivi, 17003 Girona, Spain*
[e] *Department of Biodiversity, Ecology and Evolution, Faculty of Biological Sciences, Complutense University of Madrid, 28040 Madrid, Spain*

HIGHLIGHTS

- Drying drives changes in cross-habitat subsidies and meta-ecosystems food webs.
- Aquatic subsidies' role for terrestrial communities declines with habitat distance.
- Biofilm can be an important subsidy to terrestrial invertebrates at the dry phase.
- Drying increases meta-ecosystem food web complexity by raising nodes and links.

GRAPHICAL ABSTRACT



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ABSTRACT

The connections between aquatic and adjacent terrestrial ecosystem in inland water through cross-habitat subsidies are increasingly recognized. However, we still have a limited understanding on how temporal variations of environmental factors (e.g., hydrological conditions) affect these flows. To address this gap, we investigated the effects drying has on cross-habitat subsidy flows and meta-ecosystem food webs by integrating both aquatic and terrestrial communities across the different hydrological phases (wet, contraction, and dry) in temporary saline lotic and lentic ecosystems. We analyzed the $\delta^{15}N$ and $\delta^{13}C$ signatures of aquatic and terrestrial basal subsidies, aquatic and terrestrial invertebrates, distinguishing between aquatic, riparian, shoreline and dry bed habitats. In the two temporary inland waters studied, drying of aquatic habitat and the subsequent expansion of the terrestrial habitat, significantly influenced cross-habitat subsidies and the meta-ecosystem food webs. In the wet and contraction phases, we found that the importance of aquatic subsidies in terrestrial food webs was constrained to terrestrial invertebrates near the aquatic habitat. Also, the contraction phase led to higher consumption of aquatic subsidies by aquatic and shoreline invertebrates, through a higher predation between aquatic invertebrates, and an enhanced accessibility of terrestrial invertebrates to aquatic subsidies. Whereas,

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* Corresponding author.
E-mail address: zeus.freixinos@um.es (Z. Freixinos).

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riparian invertebrates showed prevalence for terrestrial subsidies throughout drying. Biofilm emerged as an important subsidy for both riparian and shoreline terrestrial invertebrates in the dry phase. In addition, the complexity of meta-ecosystem food web increased during drying, led by invertebrate diversity, omnivory and the type of temporary inland water. Our findings emphasize the significant impact drying has on cross-habitat subsidies and meta-ecosystem food webs, and the importance of integrating both aquatic and terrestrial communities in food web studies in temporary inland waters. This calls for further research to better understand the dynamics of temporary water ecosystems in the face of global change.

1. Introduction

In inland waters, aquatic and adjacent terrestrial ecosystems are linked by a reciprocal flow of energy and matter produced by organisms and other energy subsidies that coexist and move between both realms (Nakano and Murakami, 2001). As aquatic communities and adjacent terrestrial habitats are supported by these reciprocal flow subsidies, it is key to study these flows to preserve biodiversity and ecosystem functions (Power and Rainey, 2000; Sabo and Power, 2002). Despite the growing understanding of how cross-habitat subsidies determine food webs (e.g., Baxter et al., 2005; Dahlin et al., 2021), their temporal dynamics due to environmental factors such as hydrological conditions remain poorly understood (Moran et al., 2019). In the context of global change, climatic and anthropogenic factors such as low precipitation, high evaporation, water deviation and aquatic overexploitation are expected to impact cross-habitat subsidies in inland ecosystems throughout many regions (Döll and Schmied, 2012; Larsen et al., 2016; Woolway et al., 2022).

In inland waters, ecologists have long recognized the critical role of reciprocal subsidies flows in sustaining biological communities across both aquatic and adjacent terrestrial ecosystems (e.g., Baxter et al., 2005; Paetzold et al., 2008; Dahlin et al., 2021). These subsidies are essential for driving productivity, growth rates, consumer abundance, and niche diversity within the meta-ecosystem (sensu Allen et al., 2024). These reciprocal exchanges are usually highly asymmetric and dynamics (Rundio and Lindley, 2012). While aquatic ecosystems receive large quantities of lower-quality terrestrial resource subsidies, terrestrial ecosystems receive smaller quantities of higher-quality aquatic subsidies (Muehlbauer et al., 2014). Despite this disparity, experimental quantification has shown that in both ecosystems consumers are linked to allochthonous subsidies to a similar extent ($\geq$40 %) (Dahlin et al., 2021). For instance, in streams and lakes, the allochthonous inputs of terrestrial organic matter, such as leaves and woody debris, contributes in some cases over 50 % to the diet of aquatic shredders (Cole et al., 2006; Collins et al., 2016). Also, the inputs of terrestrial seeds and fruits to streams are an important subsidy for stream fishes (Chick et al., 2003) and the accidental fallen terrestrial invertebrates often account for up to 50 % of at fish's diet (Nakano and Murakami, 2001). Inputs of terrestrial invertebrates (Baxter et al., 2005) could also benefit aquatic invertebrates, but this fact is still poorly known. In terrestrial ecosystems the emergence of adult aquatic insects represents between 25 and 100 % of the diet for a wide variety of terrestrial consumers such as birds (Uesugi and Murakami, 2007), bats (Fukui et al., 2006), lizards (Sabo and Power, 2002), and terrestrial invertebrates (Sanzone et al., 2003). Terrestrial consumers also obtain aquatic resource subsidies along the exposed sediments located nearest to the aquatic ecosystems (i.e., shoreline habitat) (Steward et al., 2022). In this type of habitat, aquatic subsidies such as aquatic insects, stranded organic matter, algal mats, and vegetation constitute a major part of terrestrial invertebrate predators and scavengers' diet (e.g., spiders, ants and beetles) (Sanzone et al., 2003; Paetzold et al., 2005). In addition, the influence of aquatic subsidies on terrestrial consumers varies significantly depending on both the distance from the aquatic ecosystem and the dispersion capacity of each subsidy (Muehlbauer et al., 2014).

These cross-habitats subsidies are subject to asymmetrical pulses because of variability in environmental factors, thus resulting in weaker or noisier aquatic-terrestrial connections (Sroczyńska et al., 2020; Dahlin et al., 2021; Allen et al., 2024). This is particularly expected in temporary inland waters, where drying promotes a changing mosaic of aquatic (lotic and lentic) and terrestrial habitats (dry beds and shoreline) over space and time throughout the three hydrological phases (wet, contraction and dry), leading to significant environmental variations (Datry et al., 2016). Indeed, drying of the aquatic habitat is a natural disturbance that modifies the physical and chemical conditions of water, which in turn drives harsher conditions for aquatic communities as temperature, turbidity, and pH increases (Gómez et al., 2017). This flow cessation, aquatic habitat contraction and the consequent expansion of terrestrial habitats, strongly affect aquatic and terrestrial communities (Sánchez-Montoya et al., 2016, 2018; Freixinos et al., 2024) and these effects extend to trophic interactions and food webs dynamics (McIntosh et al., 2017).

With drying structural changes in aquatic invertebrate communities are expected, such as diversity decline and increases in biotic interactions like competition and predation (Stubbington et al., 2017; de Necker et al., 2020). As a result, aquatic food webs become less complex and reduce both their spatial dimensions and length (McIntosh et al., 2017; Mdidimba et al., 2021). But drying also indirectly impacts aquatic communities by altering the availability and quality of both aquatic and terrestrial resource subsidies, which in turn affects food webs (Larsen et al., 2016). Drying reduces the quantity and quality of aquatic basal resource subsidies by reducing primary production and affecting the C-N-P balance (higher C:P and C:N ratios) (Timoner et al., 2012; Sabater et al., 2016; Nelson et al., 2023). At the same time, the inputs of terrestrial resources (e.g., leaves and invertebrates) may decline during the contraction phase as aquatic habitats shrink and become more isolated from the terrestrial habitats (McIntosh et al., 2017; Dolabela et al., 2022). In summary, it is expected that the negative effects of drying in the quantity and quality of both aquatic and terrestrial subsidies may directly affect the aquatic food web configuration (Wallace et al., 1997; Courtwright and May, 2013).

While drying may have a negative impact on the aquatic food web, the expansion of the terrestrial habitat in temporary inland waters may benefit the terrestrial food web (McIntosh et al., 2017). Indeed, in the contraction phase (the onset of drying), when shoreline habitats extend, the terrestrial invertebrate predators and scavengers inhabiting these habitats may obtain greater quantities of aquatic subsidies compared to the wet phase (Steward et al., 2022). Later, in the dry phase, the absence of aquatic habitats allows terrestrial invertebrates from both shoreline and riparian zones to colonize the dry stream and lakebed (Freixinos et al., 2024). At this stage, stranded aquatic resources may become a crucial temporary food source for terrestrial invertebrates, being this terrestrial community key for recycling the accumulated aquatic organic matter (Boulton and Suter, 1986; Lake, 2003). Although the drying phase serves as a key mechanism for transferring aquatic subsidies to terrestrial food webs in temporary inland waters, this process remains poorly explored (Steward et al., 2022).

Despite the mentioned potential effects of drying on communities and food webs in inland water ecosystems, our knowledge about its effect on cross-habitat subsidies and therefore the meta-ecosystem food web (integrating both aquatic and terrestrial communities) remains unknown. This is especially true in saline temporary aquatic ecosystems, even though they represent 25 % of lotic ecosystems worldwide

(Meybeck, 1995), a percentage which is expected to increase due to climate and global change (Woolway et al., 2022). In general, salinity has profound impacts on community composition, biomass, and diversity, limiting aquatic communities to poor abundance and diversity due to osmotic pressure effects (Hart et al., 1991; Carter et al., 2020). Consequently, saline ecosystems typically exhibit lower diversity and a scarcity of predators, with primary consumers occupying the highest trophic positions in the food webs (Cooper and Wissel, 2012). Therefore, compared to freshwater systems, saline ecosystems are generally characterized by lower productivity, simpler food webs, and shorter food web lengths (Dahlin et al., 2021; Vidal et al., 2021).

Here, we investigated the effect of drying on reciprocal flow subsidies between aquatic and terrestrial habitats (cross-habitat subsidies) in temporary saline inland ecosystems and its impact on aquatic and terrestrial food webs (meta-ecosystem food web). To this end we analyzed changes in: i) δ^{15}N and δ^{13}C signatures and C:N ratio of basal resources and consumers, ii) diet contributions, and iii) food webs metrics describing its structure and complexity by integrating both aquatic and adjacent terrestrial habitats (shoreline and riparian). We described these changes over the three hydrological phases (wet, contraction and dry) occurring in a lotic (stream) and lentic (shallow lake) temporary and saline aquatic ecosystem. We studied both types of inland waters (lotic and lentic) in order to describe if the observed responses to drying were influenced by the contrasting spatial drying pattern characteristic of these two ecosystems (i.e., aquatic habitat loss and terrestrial habitat expansion) and the resulting variation in environmental conditions, despite they underwent similar hydrological phases (wet, contraction and dry). Comparing how both ecosystems responded to drying allowed us to increase our knowledge about the effect hydrological variations have on cross-habitat subsidies in inland aquatic ecosystems. Similarly, focusing on temporary saline ecosystems provides novel ecological information about this poorly studied temporary aquatic ecosystems. In both studied ecosystems, we hypothesized that drying would alter reciprocal subsidies flow among aquatic, terrestrial shoreline and riparian habitats, and meta-ecosystem food web metrics (Fig. 1). Regarding flow subsidies, we predicted that: i) in the contraction phase, bed to shoreline subsidies would increase as exposed bed areas increased, thus resulting in greater accessibility of terrestrial invertebrates (mainly predators and scavengers) to aquatic subsidies (Fig. 1). On the contrary, subsidies from the shoreline and riparian to bed areas would decrease when compared to the wet phase as aquatic ecosystems are further isolated from adjacent terrestrial habitats. ii) In the dry phase, reciprocal subsidies between dry bed and riparian would increase compared to the previous two phases. As to the meta-ecosystem food web, we predicted that: iii) in the contraction phase, food web complexity would increase given the higher number of nodes, links, connectance, food web length, and prey:predator ratio when compared to the wet phase (Fig. 1), because of an increase in terrestrial invertebrates (mainly predators and scavengers) in the shoreline. Finally, iv) in the dry phase, food web complexity would decrease with respect to the two previous phases (Fig. 1), due to the absence of aquatic communities and decrease in terrestrial invertebrates.

2. Methods

2.1. Study area and sites

This study was carried out in a temporary saline stream (Serranos stream, in the Segura River Basin Murcia, SE Spain) and a temporary saline shallow lake (Muerte lake, in the Monegros district, Zaragoza, NE Spain). Both study areas have a warm semi-arid Mediterranean climate, according to Kopen - Geiger climate classification (Rubel and Kottek, 2010), with similar average annual temperatures and precipitation (15–19 °C and 250–300 mm, respectively). Both study sites are in calcareous sedimentary basins, which explain the origin of their water salinity. In Serranos stream, the riparian zone is characterized by the presence of halophyle shrubs, and in Muerte lake exclusively by saline marsh plants (xerophytes and halophiles). Macrophytes and benthic

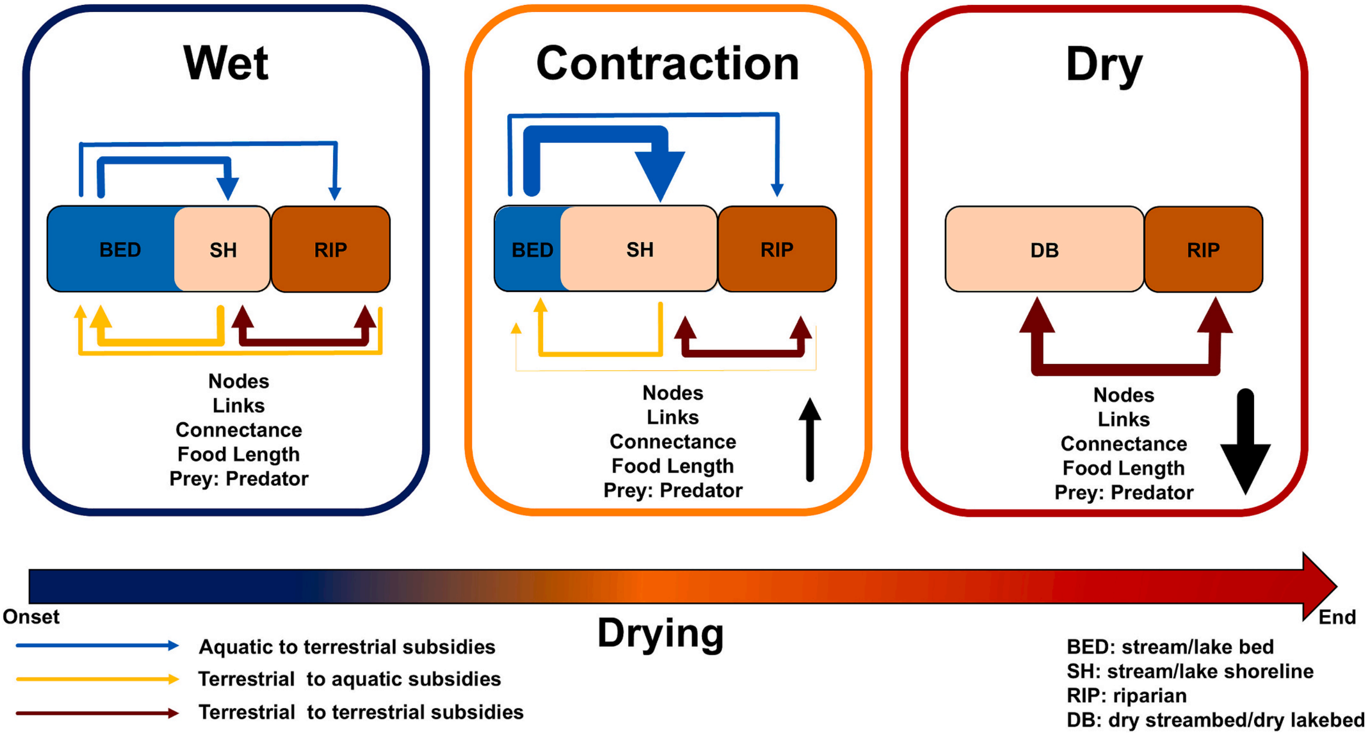


Fig. 1. Conceptual diagram of expected changes in cross-habitat subsidies flows among aquatic and terrestrial habitats and meta-ecosystem food web among the three study habitats (BED: aquatic habitat; SH: shoreline; DB: dry bed, and RIP: riparian) across three contrasting phases (wet, contraction and dry) in both lotic and lentic ecosystems. Habitats were represented by boxes (BED as blue; SH at the wet and contraction phases, and DB at the dry phase, as light brown; and RIP as dark brown). Subsidies flows were represented by lines (BED → SH/DB and RIP as blue; SH/DB and RIP → BED as yellow; and SH/DB ↔ RIP as red).

biofilm are present in Serranos stream, whereas a benthic microbial mat domain in Muerte lake. In both sites, we sampled in the three hydrological phases (wet, contraction, dry) which may characterize temporary systems. Assuming high interannual variation among hydrological cycles, the wet phase corresponded with the period of base flow. We considered the contraction phase to be when the aquatic habitat drastically reduced its size (at least 50 %); this meant the stream and lake had to be monitored until a significant decrease (at least 50 %) in discharge (Serranos stream) was observed, as well as a reduction in water surface area and depth (Muerte lake) when compared to the previous wet phase. Finally, we considered the dry phase to be when surface water was totally absent in both ecosystem types. According to this, we sampled the wet phase of Serranos stream in February in 2020, the contraction phase in June, and the dry phase in July (Fig. S1). In 2021 we sampled the wet phase of Muerte lake in early March, the contraction phase at the end of March, and the dry phase in July (Fig. S1).

2.2. Environmental characterisation

In Serranos stream, in the wet and contraction phases, water column depth and water velocity (current meter; MiniAir2; Schiltknecht Co., Zurich, Switzerland) were recorded along a longitudinal aquatic transect of 100-m reach to estimate flow discharge. In Muerte lake, in the wet and contraction phases, we recorded water column depth by walking along a radial aquatic transect of 50-m with a water depth gauge, and water sheet surface by using aerial images of each sampling date with EO Browser (Sinergise Ltd). Water physico-chemical conditions such as temperature, electrical conductivity (mS/cm) and salinity (g/L) were measured using handheld probes (Intellical HQ40D, Hach Lange, USA) in both water bodies in the wet and contraction phases.

2.3. Sampling design collection and processing

We collected aquatic communities in the wet and contraction phases from aquatic habitat, and terrestrial communities from shoreline and riparian habitats in the wet, contraction, and dry phases (Fig. S2) to study trophic structure, isotope signatures (δ^{13}C and δ^{15}N), and changes in taxonomic and functional structure in both ecosystems. We defined the shoreline in the wet and contraction phases to be the exposed sediments closest to both the stream and lake bed's water edge; whereas in the dry phase, the shoreline was the middle of the dry stream and lakebed. The riparian habitat was defined as the area extending from the edge of the high-water channel and bankfull to the edge of the upland, which is distinguished by unique riparian vegetation and substrate type (see Sánchez-Montoya et al., 2016).

For aquatic invertebrates in Serranos stream, we collected ten samples along a longitudinal aquatic transect of 100-m reach, using a hand net in pools and a surber sampler in riffles (both 20 cm × 20 cm, mesh size 250 μm). We distributed samples along this transect according to the relative proportion of the pools and riffles. In Muerte lake, we collected five samples distributed regularly along a radial aquatic transect of 50-m, using a hand net (25 cm diameter, mesh size 53 μm). These samplings were carried out in two occasions (wet and contraction phases).

For terrestrial invertebrates, in both Serranos stream and Muerte lake, we collected ten samples along a 100-m terrestrial transects in the riparian habitat (wet, contraction and dry phases), in the shoreline (wet and contraction phases), and in the dry stream and lakebed (dry phase). Invertebrate samples were obtained by ten pitfall traps installed 10 m apart along the terrestrial transects. Pitfall traps consisted of plastic containers filled with water (13 cm × 19.5 cm × 7 cm) inserted into the sediment for 24 h (e.g., Steward et al., 2011; Sánchez-Montoya et al., 2016; Freixinos et al., 2024).

Aquatic and terrestrial invertebrates were identified by a binocular microscope with the assistance of taxonomic experts. The aquatic invertebrates of Serranos stream were identified at the genus level, except for Diptera, which were identified at the family level. The aquatic invertebrates of Muerte lake were identified at the species level, except for Nematoda, which were identified at the order level. All terrestrial invertebrates from Araneae, Formicidae and Coleoptera were identified at the species level, and at morphospecies for other taxa. Flying taxa (Diptera, Lepidoptera, and Hymenoptera) were not included in the analysis because pitfall traps are unsuitable for sampling these taxa (as per Corti and Datry, 2016; Sánchez-Montoya et al., 2016, 2020; Freixinos et al., 2024). We classified all invertebrates in functional feeding groups of aquatic and terrestrial invertebrates using previous literature (Alcorlo, 1999; Tachet et al., 2010; Bonada and Dolédec, 2011; Cardoso et al., 2011; Arnan et al., 2014; Parr et al., 2017) and the assistance of taxonomic experts.

In addition, we collected aquatic and terrestrial basal subsidies (along the previously defined transects) in both Serranos stream and Muerte lake to describe their isotopes signatures (δ^{13}C and δ^{15}N). We collected three samples of biofilm (adhered to the superficial sediments) in each of the three sampling phases along the aquatic transect. Biofilm was collected in the three phases: completely submerged (wet phase), newly exposed (contraction phase), and totally dried (dry phase). In Serranos stream, three samples of each macrophyte and helophyte were also handpicked and collected in the three phases along the aquatic transect. In Muerte lake, five samples of water were taken with a of 0.25 L syringe and filtered through pre-combusted GF/C glass-fibre filters to collect phytoplankton (approx. 1.25 L total). Along the terrestrial riparian transect of both studied ecosystems, three samples of each terrestrial plant (distinguishing between C3 and CAM) were collected in the three studied phases. For all plants, healthy green leaves and stems were handpicked from various stands. Finally, biofilm and phytoplankton were identified at the morphospecies level due to their taxonomic complexity, while terrestrial plants and helophytes were identified at species level with the assistance of taxonomic experts.

On the other hand, given the significant role of biofilm in aquatic food webs and its potential connections with terrestrial food webs, we measured the biofilm quantity in both lotic and lentic ecosystems. To do this, we collected along the aquatic transect five sediment cores (10 cm in diameter, and 15 cm deep) spaced 20 m apart in each studied phase. To assess the total organic matter content, the dried samples (previously weighed and dried at 70 °C, until constant weight) were burned for 4.5 h at 450 °C (MF12-124, Hobersal, Barcelona, Spain) and weighed again. The biofilm content was expressed in grams of ash-free dry mass (gAFDM/cm^2).

2.4. Stable isotope analysis (SIA)

Study of stable isotopes (SIA) was used to differentiate the contributions of δ^{13}C and δ^{15}N of basal resources, trace the contributions between aquatic and terrestrial ecosystems and the subsidy strength of both aquatic-terrestrial interactions across space (bed, shoreline and riparian habitats) and time (wet, contraction and dry phases). The enrichment in δ^{13}C, which varies with the photosynthetic pathways of primary resources, helps to identify the carbon source in the diet of consumers (Layman et al., 2012; Abrantes et al., 2014; Cashman et al., 2016). Meanwhile, δ^{15}N enrichment, which increases stepwise by 3–4 ‰ from the base to the top of the food web, reveals the trophic levels (Potapov et al., 2019). We measured the δ^{13}C and δ^{15}N content for each taxa, after identification, sampled at both sites during each hydrological phase. Firstly, we thawed all samples of basal resources, and aquatic and terrestrial invertebrate consumers. Biofilm and microcrustaceans from the aquatic invertebrates of Muerte lake were additionally suspended in a solution of 0.2 N HCL for 24 h at room temperature to remove non-dietary carbonates (Gearing et al., 1984). Then, basal resources and aquatic and terrestrial invertebrates from both sites were dried at 60 °C until no further water loss occurred. Later, basal resources, aquatic and terrestrial invertebrates were milled using mortar and pestle (biofilm and invertebrates) and an analytical mill (model IKA-A10) for plants.

Phytoplankton samples were stored dry in vials until analyzed (Gearing et al., 1984). As a result, each basal resource, as well as each aquatic and terrestrial invertebrate, were stored dried and milled in 15 mL vials until analyzed. Finally, $\delta^{15}N$ and $\delta^{13}C$ stable isotopes analysis were performed on 1 mg subsamples of homogenised materials placed in tin cups and measured through Isotope Ratio Mass Spectrometry (IRMS) using Delta V Advantage isotope ratio mass spectrometer (Thermo Finnigan) at the *Servicio Interdepartamental de Investigación* (*SIdI*) lab of the *Universidad Autónoma de Madrid*.

Stable isotope abundances were expressed in δ notation as the deviation from standards in parts per thousand (‰) according to the following equation:

$$\delta X = \left[\left(R_{sample} / R_{\mathrm{standard}} \right) - 1 \right] \times 1000$$

where *X* is the isotope ^{15}N or ^{13}C, and *R* is the corresponding ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$. The R_{standard} for ^{15}N is that for atmospheric N_2 (air) and for ^{13}C it is that for Pee Bee Belemmnite (PDB) limestone formation. Based on numerous measurements of organic and inorganic standards done by the lab performing the analysis, the precision of these measurements is estimated to be ±01 and ±0.2 ‰ for carbon and nitrogen respectively.

Finally, considering the values of isotopes signatures ($\delta^{13}C$ and $\delta^{15}N$) and C:N ratio of each basal resource and each site separately, we tested significant differences between the wet, contraction and dry phases through Kruskal-Wallis test. We also used Dunn test to identify pair-wise significant differences among phases for each resource and functional group.

All analysis were performed in *R* software (R Core Team, 2020) using the R basic packages. SigmaPlot v12 (Systat Software, San Jose, CA) was used to create a biplot with mean values of $\delta^{15}N$ and $\delta\ ^{13}C$.

2.5. *Food web isotopic model construction*

To quantify the energy subsidies among the components of the food web of each sampling phase, we used Bayesian Stable Isotope Mixing Models (Parnell et al., 2013) to analyse both $\delta^{15}N$ and $\delta^{13}C$ content of each functional feeding group. This approach allowed us to identify the proportional diet contributions of resource pools for each functional feeding group in terms of probability distributions (Layman et al., 2012). To also identify predation, the resources set included not only aquatic and terrestrial basal resources but also a set that distinguished aquatic invertebrates, terrestrial invertebrates from shoreline, and terrestrial invertebrates from riparian Finally, including the trophic enrichment factor values (for aquatic invertebrates 2.2 ± 0.3 ‰ for $\delta\ ^{15}N$ and 0.5 ±0.19 ‰ for $\delta\ ^{13}C$ (McCutchan et al., 2003); and for terrestrial invertebrates 2.5 ± 0.3 ‰ for $\delta\ ^{15}N$ and 0.4±0.19 ‰ for $\delta\ ^{13}C$ (Wolters et al., 2018)), the models were run with 10.000 iterations obtaining the distribution of plausible values of the dietary composition. Resources with values with lower limit of the 50 % confidence intervals (LIC50) $\geq$ 5 % were considered as reliable resources and the rest as nonpotential resources (Careddu et al., 2015). All analysis were done in *R* software (R Core Team, 2020) using simmr package (Parnell, 2021).

2.6. *Food web topological metric calculations*

Finally, according to Bayesian Stable Isotope Mixing Models results, we established feeding links to construct one matrix of predation for each study site and hydrological phase. Feeding links were established in accordance with (LIC50) $\geq$ 5 % aforementioned. Then, we used the predatory matrices to calculate fundamental food webs topological metrics through the R-foodweb package (Perdomo et al., 2012): number of nodes or richness (S) which is the number of trophic groups in the food web; number of links (L) as the number of feeding relationships between trophic groups; connectance (C) which is the fraction of undertaken interactions from the pool of all probable interactions between nodes; links per specie or density (L/S), food web length and prey: predator ratio. The resulting food webs were represented with R-igraph package (Csardi and Nepusz, 2006). Additionally, we calculated the percentage of basal taxa (Bas) referred to taxa which only acts as a resource, intermediate taxa (Int) referred to taxa which acts as a consumer and resource and, top taxa (Top) referred as taxa which only acts as consumer (Dunne, 2009).

3. Results

3.1. *Environmental conditions*

In Serranos stream, mean discharge, channel width and water depth decreased approximately 50 % from the wet to the contraction phase (Table 1). As a result, the stream exhibited a decrease of riffles and an increase of connected pools compared to the wet phase. In Muerte lake, we observed a reduction of 50 % in the surface area and 60 % in the water column depth from the wet to the contraction phase (Table 1). Water surface was fragmented into disconnected aquatic patches. A slight increase in water conductivity and salinity was found in both systems from the wet to the contraction phase. On the other hand, biofilm quantity was lower in Serranos stream than in Muerte lake for the three studied phases; in the latter biofilm quantity increased along drying.

Table 1
Main environmental characteristics of Serranos stream and Muerte lake. Hydrological and salinity parameters were measured at the wet (W), contraction (C), and dry phases (D).

		Serranos stream		Muerte lake	
UTM		3756254N, 14149W		412452N, 01541W	
Altitude (m.a.s.l.)		113.0		332.1	
Dominant lithology		Calcareous (marls and limestone)		Calcareous (marls and limestone)	
Dominant riparian vegetation		*Pinus* spp. and Halophytes shrubs		Salt marsh plants (Xerophytes and halophiles)	
Dominant benthic vegetation		Biofilm, Chara sp. and Chlorophyceae		Biofilm (microbial mat)	
Hydrological phases		W	C	W	C
Sampling month, year		02, 2020	07, 2020	03, 2021	03, 2021
Mean width of the channel (m)		1.90 ± 0.14	0.92 ± 0.02		
Water surface area (m^2)				59,577	31,003
Mean water depth (cm)		14.3 ± 5.7	11.3 ± 3.0	2.8 ± 0.5	1.7 ± 0.2
Mean discharge (l/s)		0.3 ± 0.1	0.1 ± 0.0		
Riffles/pools		6/4	4/6		
Water conductivity (mS/cm)		11.41	13.40	180.30	185.80
Water salinity (g/L)		7.26	8.58	132.71	137.12
Biofilm (gAFDM/cm^2)	W	0.03 ± 0.00		0.16 ± 0.01	
	C	0.02 ± 0.01		0.51 ± 0.06	
	D	0.02 ± 0.00		0.53 ± 0.14	

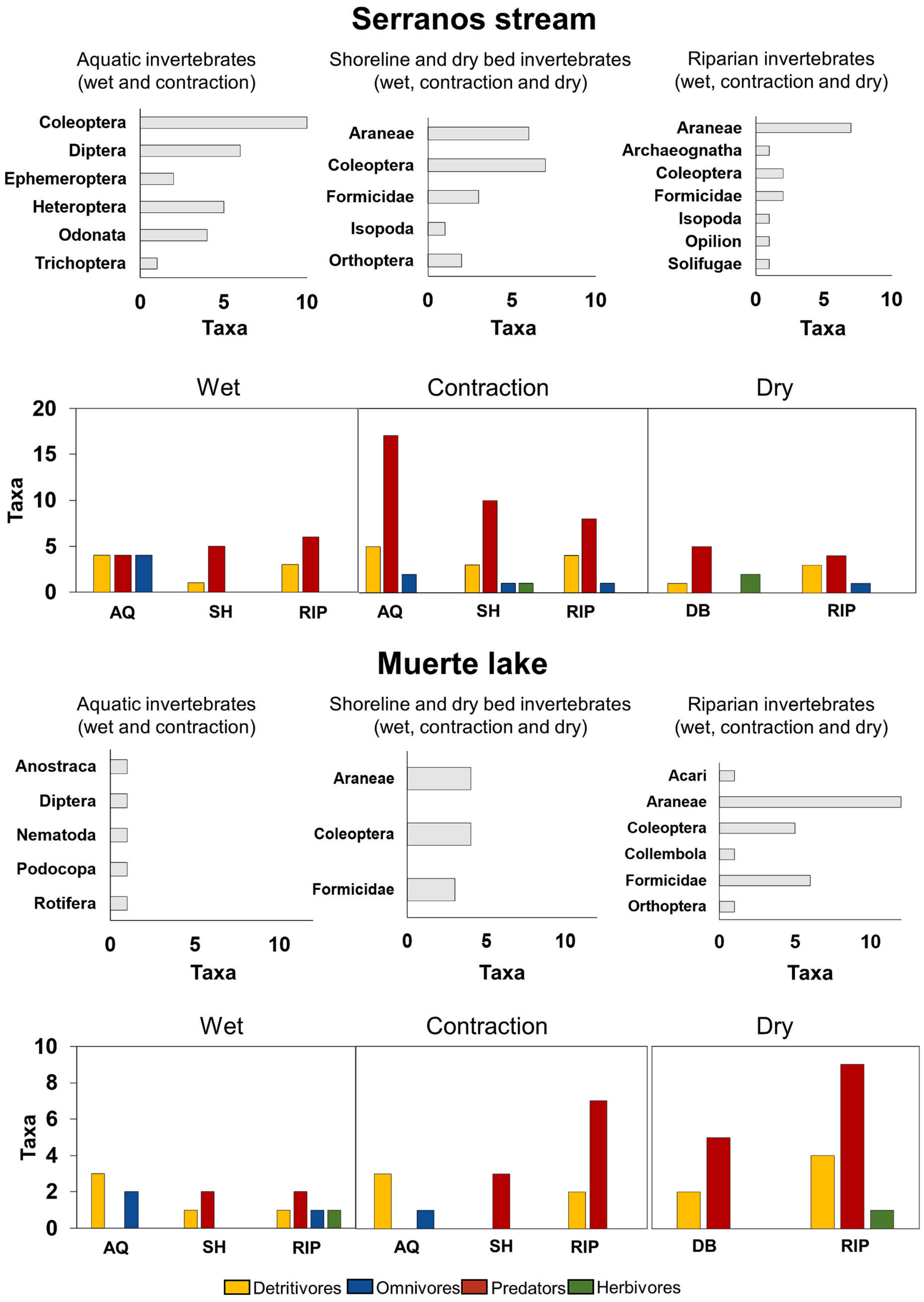


Fig. 2. Taxonomic composition of the aquatic (AQ) and terrestrial communities (SH: shoreline and DB: dry riverbed/lakebed invertebrates and, RIP: riparian invertebrates) sampled (up) and their distribution in functional groups (yellow for detritivores, blue for omnivores, red for predators, and green to herbivores) through the three hydrological phases (wet, contraction and dry) (down) in both Serranos stream and Muerte lake.

3.2. Taxonomic and functional structure of aquatic and terrestrial communities

In Serranos stream, an increase in aquatic taxonomic richness was observed from the wet to the contraction phase. This increase was driven by a rise in the diversity of predators and detritivores, particularly from Coleoptera, Heteroptera and Odonata (Fig. 2, Table S1). Regarding terrestrial invertebrates, in both shoreline and riparian habitats taxonomic richness showed similar patterns along drying. Firstly, from the wet to the contraction phase, taxonomic richness increased, mainly driven by a higher diversity of predators (Araneae, Coleoptera and Formicidae) and detritivores (Formicidae and Coleoptera). Later, from the contraction to the dry phase, taxonomic richness decreased, promoted by a lower diversity of all functional groups in the shoreline, and by the lower diversity of predators in the riparian habitats.

In Muerte lake, contrary to Serranos stream, aquatic communities experienced a decrease in taxonomic richness from the wet to the contraction phase, mainly due to lower diversity of omnivores such as Anostracea (Fig. 2, Table S1). Regarding terrestrial invertebrates, contrary patterns were observed between shoreline and riparian habitats. Firstly, from the wet to the contraction phase, in riparian habitat taxonomic richness, driven by a higher diversity of predators (Araneae, Formicidae, and Coleoptera) and detritivores (Formicidae, and Coleoptera), increased; whereas taxonomic richness remained similar in shoreline. From the contraction to the dry phase, in both shoreline and riparian habitats taxonomic richness increased with a rise in the diversity of predators (Araneae and Coleoptera), detritivores (Formicidae) and herbivores (Orthoptera).

3.3. Isotopic composition of basal subsidies

In Serranos stream, the δ^{13}C and δ^{15}N signatures and the C:N ratio of aquatic and terrestrial basal resources, in general, remained stable along drying (Fig. 3, Tables S2, S3 and S4). However, exceptionally the C:N ratio of biofilm decreased significantly. In the wet phase, the δ^{13}C signature of basal resources covered from −27.0 ‰ (terrestrial plants C3) to −18.7 ‰ (biofilm), and the δ^{15}N covered the range from 0.3 ‰ (helophytes) to 12.8 ‰ (biofilm). The C:N ratio covered from 18.8 (macrophytes) to 46.9 (terrestrial plants CAM). In the contraction phase, the δ^{13}C signature covered from −29.0 ‰ (terrestrial plants C3) to −17.5 % (macrophytes), and the δ^{15}N covered the range from −0.3 ‰ (terrestrial plants CAM) to 12.5 ‰ (biofilm). The C:N ratio covered from 19.0 (biofilm) to 70.6 (terrestrial plants CAM). Finally, in the dry phase, the δ^{13}C signature covered from −27.8 ‰ (terrestrial plants C3) to −19.7 % (biofilm), and the δ^{15}N covered the range from 0.7 ‰ (terrestrial plants C3) to 11.8 ‰ (biofilm). The C:N ratio covered from 11.3 (biofilm) to 62.4 (terrestrial plants CAM). Overall, aquatic basal resources were more enriched in both δ^{13}C and δ^{15}N than terrestrial basal resources along drying; while terrestrial basal resources showed higher C:N ratio than aquatic basal resources.

In Muerte lake, similarly to Serranos stream, the δ^{13}C and δ^{15}N signatures and the C:N ratio of aquatic and terrestrial basal resources, in general, remained stable along drying (Fig. 3, Tables S2, S3 and S4). Whereas the biofilm was impoverished in δ^{13}C along drying. In the wet phase, the δ^{13}C signature of basal resources covered from −28.5 ‰ (herbaceous) to −11.5 ‰ (biofilm), and the δ^{15}N covered the range from 1.5 ‰ (terrestrial plants C3) to 5.4 ‰ (terrestrial plants CAM). The C:N ratio covered from 8.9 (terrestrial plants CAM) to 15.5 (biofilm). In the contraction phase, the δ^{13}C signature covered from −28.4 ‰ (herbaceous) to −13.3 % (biofilm), and the δ^{15}N covered the range from 2.4 ‰ (terrestrial plants C3) to 4.9 ‰ (terrestrial plants CAM). The C:N ratio covered from 9.3 (terrestrial plants CAM) to 26.0 (terrestrial plants C3) Finally, in the dry phase, the δ^{13}C signature covered from −25.2 ‰ (terrestrial plants CAM) to −13.1 % (biofilm), and the δ^{15}N covered the range from 2.6 ‰ (terrestrial plants C3) to 5.6 ‰ (terrestrial plants CAM). The C:N ratio covered from 11.1 (terrestrial plants CAM) to 49.7 (terrestrial plants C3). Accordingly, along drying, in general aquatic basal resources were more enriched in δ^{13}C, but lower in δ^{15}N than terrestrial basal resources. Also, terrestrial basal resources showed higher C:N ratio than aquatic basal resources.

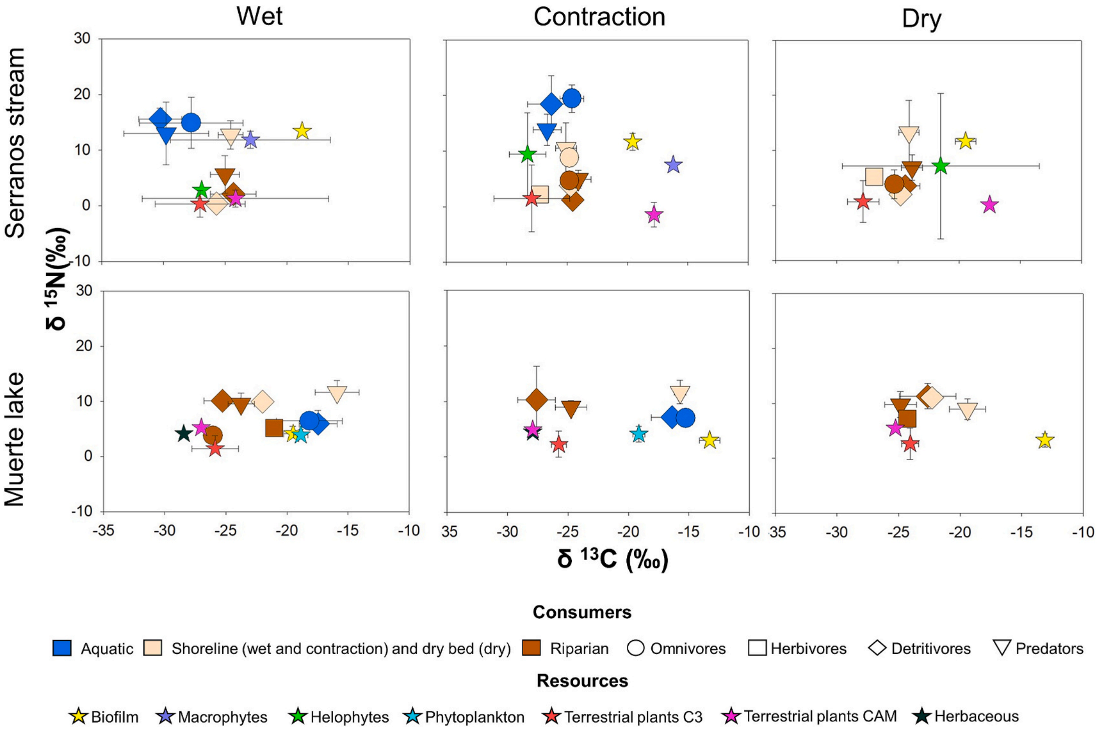


Fig. 3. Biplots of the means (±SE) δ^{13}C and δ^{15}N values for resources and consumers in each studied phase (wet, contraction and dry) and study site Serranos stream (up) and Muerte lake (down). See Table S2 for more detailed values.

3.4. Isotopic composition of consumers

In Serranos stream, the $\delta^{13}C$ and $\delta^{15}N$ signatures and the C:N ratio of aquatic and terrestrial consumers, remained stable along the drying process (Fig. 3, Tables S2, S3, and S4). In the wet phase, $\delta^{13}C$ signatures ranged from −31.0 ‰ (aquatic detritivores) to −24.3 ‰ (terrestrial detritivores from riparian), while $\delta^{15}N$ ranged from 15.6 ‰ (aquatic detritivores) to 0.4 ‰ (terrestrial detritivores from both riparian and shoreline). C:N ratios varied from 4.3 (terrestrial detritivores from riparian) to 6.1 (terrestrial detritivores from shoreline). In the contraction phase, $\delta^{13}C$ signatures ranged from −27.9 ‰ (terrestrial herbivores from shoreline) to −24.2 ‰ (terrestrial predators from riparian), and $\delta^{15}N$ ranged from 19.4 ‰ (aquatic omnivores) to 2.2 ‰ (terrestrial herbivores from shoreline). C:N ratios varied from 3.8 (terrestrial omnivores from shoreline) to 4.9 (terrestrial detritivores from riparian). Finally, in the dry phase, $\delta^{13}C$ signatures ranged from −26.9 ‰ (terrestrial herbivores from riparian) to −23.8 ‰ (terrestrial predators from riparian), and $\delta^{15}N$ ranged from 11.3 ‰ (terrestrial predators from shoreline) to 2.0 ‰ (terrestrial detritivores from shoreline). C:N ratios varied from 3.9 (terrestrial predators from riparian) to 4.6 (terrestrial detritivores from riparian). Overall, contrary to basal resources, aquatic consumers were more enriched in $\delta^{15}N$ and more depleted in $\delta^{13}C$ compared to terrestrial consumers. Additionally, terrestrial consumers from the shoreline were generally more enriched in $\delta^{15}N$ than riparian consumers. Along drying, aquatic consumers and terrestrial invertebrates from the shoreline, particularly predators, occupied similar isotopic niches and held top positions in the stream's food web.

In Muerte lake, the $\delta^{13}C$ and $\delta^{15}N$ signatures, as well as the C:N ratio of aquatic and terrestrial consumers, generally remained stable throughout drying, except for terrestrial detritivores from riparian and terrestrial predators from the shoreline, which showed changes in $\delta^{13}C$ (Fig. 3, Tables S2, S3, and S4). In the wet phase, $\delta^{13}C$ signatures ranged from −26.3 ‰ (terrestrial detritivores from riparian) to −15.6 ‰ (terrestrial predators from shoreline), while $\delta^{15}N$ ranged from 10.1 ‰ (terrestrial detritivores from riparian) to 1.9 ‰ (terrestrial predators from riparian). C:N ratios varied from 3.75 (terrestrial omnivores from riparian) to 5.5 (aquatic detritivores). In the contraction phase, $\delta^{13}C$ signatures ranged from −25.6 ‰ (terrestrial herbivores from shoreline) to −15.7 ‰ (terrestrial predators from shoreline), and $\delta^{15}N$ ranged from 6.9 ‰ (aquatic omnivores) to 11.7 ‰ (terrestrial predators from shoreline). C:N ratios varied from 3.8 (terrestrial predators from riparian) to 6.9 (aquatic omnivores). Finally, in the dry phase, $\delta^{13}C$ signatures ranged from −24.9 ‰ (terrestrial predators from riparian) to −19.4 ‰ (terrestrial predators from shoreline), and $\delta^{15}N$ ranged from 7.2 ‰

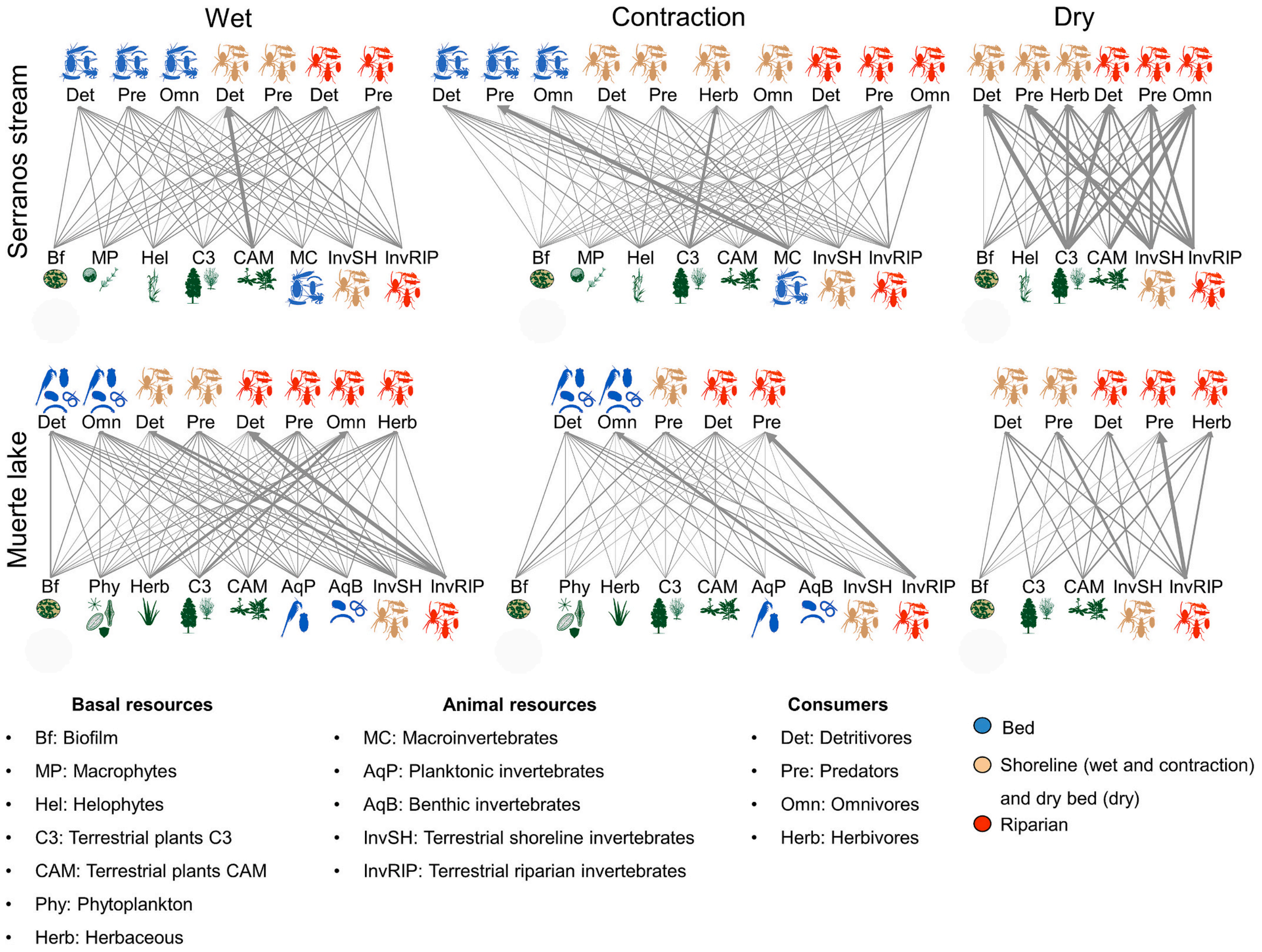


Fig. 4. Dietary contributions in Serranos stream (up) and Muerte lake (down) revealed by Bayesian Mixing Model of primary basal resources (Bf: Biofilm; MP: Macrophytes; Hel: Helophytes; C3: Terrestrial plants C3; CAM: Terrestrial plants CAM; Phy: Phytoplankton; Herb: Herbaceous) and animal resources (MC: Macroinvertebrates; AqP: Planktonic invertebrates; AqB: Benthic invertebrates; InvSH: Terrestrial shoreline invertebrates; InvRIP: terrestrial riparian invertebrates) in consumers (Det: Detritivores; Pre: Predators; Omn: Omnivores; Herb: Herbivores) Color distinguish consumers from aquatic (blue), shoreline (brown) and riparian (orange) habitats. The thickness of the lines indicates the percentage of contribution (% see Tables S5 and S6) and the narrow indicates the feeding direction.

(terrestrial herbivores from riparian) to 11.3 ‰ (terrestrial detritivores from riparian). C:N ratios varied from 3.7 (terrestrial herbivores from riparian) to 4.7 (terrestrial predators from shoreline). Unlike the pattern observed in Serranos stream, aquatic consumers were more enriched in δ^{13}C and depleted in δ^{15}N compared to terrestrial consumers during drying. Additionally, terrestrial shoreline consumers were generally more enriched in δ^{13}C than terrestrial riparian consumers. Overall, terrestrial consumers occupied similar isotopic niches and held top positions in the lake food web.

3.5. *Diet contributions (subsidies)*

The aquatic and terrestrial consumers' dietary compositions indicated shifts in the importance of the resource subsidies analyzed (aquatic invertebrates, biofilm, macrophytes, helophytes, terrestrial invertebrates, and terrestrial plants) across the three phases.

In Serranos stream (Fig. 4, Table S5), for aquatic consumers (predators, detritivores, and omnivores), all the potential aquatic subsidies analyzed contributed equally in the wet phase. However, in the contraction phase, macroinvertebrates became the most important subsidy. Meanwhile the importance of terrestrial subsidies remained similar, except for the lower importance of riparian invertebrates in the contraction phase when compared to the wet phase. For terrestrial consumers, changes in the contribution of potential subsidies throughout drying differ depending on the terrestrial habitat (shoreline and riparian). For terrestrial shoreline consumers, all potential subsidies contributed equally to predators, while riparian invertebrates and CAM plants were key to detritivores in the wet phase. However, in the contraction phase, macroinvertebrates, biofilm and shoreline invertebrates gained importance for both shoreline predators and detritivores. Finally, in the dry phase, terrestrial subsidies (terrestrial plants C3 and invertebrates) were the most important subsides for the shoreline community. On the contrary, for terrestrial riparian consumers, all potential subsidies contributed equally to all functional groups in the wet phase. The potential contribution of aquatic subsidies decreased (macroinvertebrates, macrophytes and biofilm) in the contraction phase, and the contribution of riparian invertebrates increased. Finally, in the dry phase, terrestrial subsidies were the most important to the riparian community, similarly to the shoreline community.

In Muerte lake (Fig. 4, Table S6), for aquatic consumers, all potential aquatic subsidies contributed similarly in the wet phase, except for a significant contribution of biofilm to detritivores. In the contraction phase, for both detritivores and omnivores, aquatic invertebrates became predominant in their diets, while contributions from the rest of potential basal subsidies, notably phytoplankton, decreased. As an exception, biofilm contribution increased to omnivores. For terrestrial consumers, similarly to Serranos stream, the contribution of potential subsidies along drying varied based on the terrestrial habitat type (shoreline and riparian). For terrestrial shoreline consumers in the wet phase, all potential subsidies contributed equally to predators, while terrestrial invertebrates from both shoreline and riparian areas were crucial to detritivores. However, in the contraction phase, terrestrial invertebrates from shoreline habitat were predominant in predators' diets, along with an increasing trend of the importance of biofilm and aquatic invertebrates. In the dry phase, terrestrial invertebrates (shoreline and riparian) dominated the diet of all the shoreline functional groups. For terrestrial riparian consumers, in the wet phase all potential subsidies contributed equally to predators; while terrestrial invertebrates (from riparian and shoreline) were essential for detritivores, and herbaceous and terrestrial plants C3 for omnivores. In the contraction phase, terrestrial invertebrates from both riparian and shoreline were crucial to predators, while detritivores relied equally on all aquatic and terrestrial potential subsidies. Finally, in the dry phase, there was an overall increase in contributions from biofilm and all potential terrestrial subsidies across all functional groups.

3.6. *Food web metrics*

In Serranos stream (Fig. 5), peak values for nodes, links, link density, and connectance were observed in the contraction phase, while the lowest values across all food web metrics occurred in the dry phase. The exception was in the wet phase which had the lowest value of connectance. The longest food web chain was observed in the wet phase, followed by the contraction and dry phases with similar values (Fig. 5). Additionally, the highest prey-to-predator ratio was observed in the wet phase, contrasting with the lowest ratio observed in the dry phase. Basal taxa were most abundant in the wet phase, followed by the dry and contraction phases, while intermediate taxa peaked in the contraction phase and were lowest in the dry phase. Finally, top taxa exhibited their highest abundance in the dry phase and their lowest in the wet phase.

In Muerte lake (Fig. 5), unlike Serranos, the dry phase displayed peak values for nodes, links, link density, and connectance. The wet phase recorded the lowest node values, while the contraction phase had the lowest values for links, link density, and connectance. The longest food web chain occurred in the contraction phase and the shortest in the dry phase (Fig. 5). The highest prey-to-predator ratio was observed in the wet phase while the lowest was in the contraction phase. Regarding taxa percentages, the contraction phase had the highest value for basal taxa, while the wet phase had the highest for intermediate taxa. Conversely, the dry phase exhibited the lowest values for both basal and intermediate taxa; however, the dry phase recorded the highest value for top taxa, followed by the contraction and wet phases.

4. Discussion

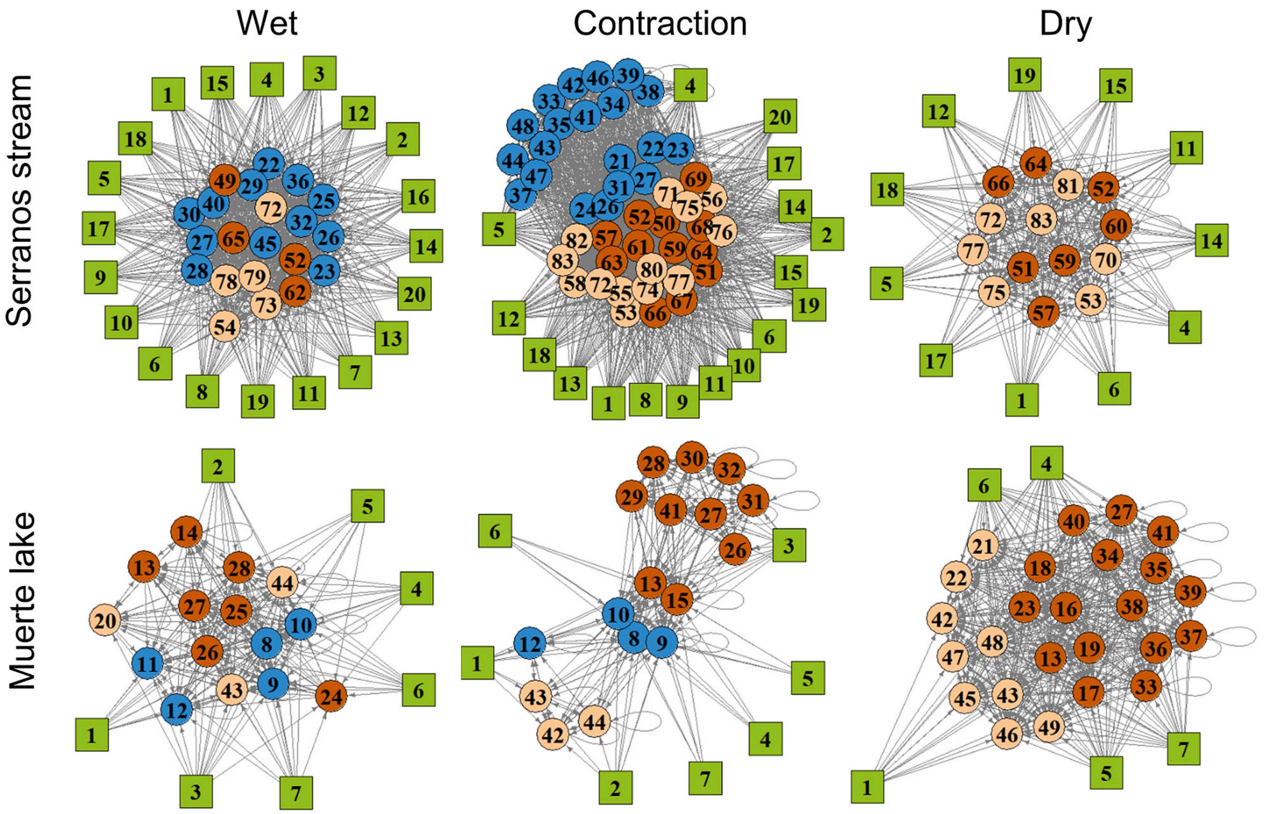
In this study, we analyzed the effect of drying on cross-habitat subsidies and the meta-ecosystem food web in temporary saline inland waters. Through the meta-ecosystem food web approach (sensu Allen et al., 2024), which included aquatic (bed) and terrestrial habitats (shoreline, dry beds, and riparian), we revealed that drying significantly impacts the cross-habitat subsidies and food webs of a temporary, saline lotic (stream) and lentic (shallow lake) aquatic ecosystems. In both cases, drying increased the flow of aquatic subsidies to shoreline habitats, but not to riparian. Notably, in the lentic ecosystem, terrestrial invertebrates fed on exposed biofilm in the dry phase, more than in the lotic ecosystem. Similarly in both studied ecosystems, drying increased food web complexity by amplifying the role of terrestrial communities. However, food web length dynamics varied between ecosystems, potentially due to differences in spatial drying patterns between the study inland waters. Therefore, this study highlights the importance of including terrestrial communities and the hydrologic variability when studying temporary inland waters.

4.1. *δ^{13}C and δ^{15}N abundance in the basal resources along drying*

Traditionally, food webs have been described by stable isotope analysis (SIA) of δ ^{15}N and δ ^{13}C of the animal tissues (Hopkins and Ferguson, 2012). However, food webs in temporary inland waters and their changes due to flow intermittence are less known (Siebers et al., 2019). In our study, isotopes signatures and C:N changed slightly along drying for basal resources and consumers in both studied temporary and saline ecosystems. C:N ratio of biofilm was the exception as it decreased along drying, probably because biofilm is particularly sensitive to environmental changes such as hydrological conditions, temperature and light (Battin et al., 2006; Sabater et al., 2016).

4.2. *Effect of drying on cross-habitat subsidies*

As we hypothesized (Fig. 1), in the contraction phase in both study sites, the flow of aquatic resource subsidies (macroinvertebrates and biofilm) to adjacent terrestrial habitats (shoreline) increased significantly. On the contrary, in the riparian habitat, consumers continued to



🟩 Primary resources

● Aquatic invertebrates

○ Terrestrial invertebrates (shoreline and dry bed)

● Terrestrial invertebrates (riparian)

	Serranos			Muerte		
Food web metrics	**Wet**	**Contraction**	**Dry**	**Wet**	**Contraction**	**Dry**
Nodes	41	62	25	22	24	30
Links	846	2260	350	291	244	736
Links/specie	20.63	36.41	14	13.22	10.16	24.53
Connectance	0.51	0.58	0.56	0.62	0.42	0.81
Food web length	1.23	1.18	1.18	1.21	1.44	1.05
Prey:Predator	1.38	0.82	0.78	1.31	0.11	0.21
Basal taxa (%)	49	27	44	27	30	16
Intermediate taxa (%)	22	32	0	68	50	0
Top taxa (%)	29	41	56	5	20	84

(caption on next page)

Fig. 5. Resulting meta-ecosystems food webs of Serranos stream (up) and Muerte lake (down) among the three hydrological phases (wet, contraction and dry). Food webs metrics for both Serranos stream and Muerte lake are also included. A positive interaction is shown with a gray arrow. Nodes are distinguished by resources which are indicated as green square, aquatic groups which are indicated as blue circle, terrestrial shoreline/dry beb groups which are indicated as light brown circle and terrestrial riparian groups as orange circle. The nodes (taxa) of the food web resulting in Serranos stream are (1) Biofilm, (2) Chara sp., (3) Chlorophyceae, (4) *Scirpus holoschoenus*, (5) *Phragmites Australys*, (6) *Artemisia campestris*, (7) *Asphodelus fistolosus*, (8) *Diplotaxis euricoides*, (9) *Ephedra fragilis*, (10) *Foeniculum vulgare*, (11) *Globularia alypum*, (12) *Limonium cossonianum*, (13) *Lotus corniculatus*, (14) *Pinus halepensis*, (15) *Rosmarinus officinalis*, (16) *Sarcocornia fruticosa*, (17) *Stipa canensis*, (18) *Thymus vulgaris*, (19) *Sedum vulgaris*, (20) *Zigophyllum fabago*, (21) Baetis, (22) Chironomidae, (23) Cloeon, (24) Hydrocara, (25) Sericostoma, (26) Simuliidae, (27) Ceratopogonidae, (28) Culicidae, (29) Ephydridae, (30) Limoniidae, (31) Sigara, (32) Agabus, (33) Agrion, (34) Berosus, (35) Cordulia, (36) Deronectes, (37) Enochrus, (38) Gerris, (39) Girinus, (40) Hydaticus, (41) Hydrometra, (42) Lacobius, (43) Nebrioporus, (44) Nepa, (45) Notonecta, (46) Ortethrum, (47) Somatochlora, (48) Stictonectes, (49) Archaeognatha from riparian, (50) *Pimelia baetica* from riparian, (51) *Cataglyphis iberica* from riparian, (52) Isopoda from riparian, (53) *Cataglyphis iberica* from shoreline/dry bed, (54) Galeruca from shoreline/dry bed, (55) Isopoda from shoreline/dry bed, (56) *Pimelia baetica* from shoreline/dry bed, (57) *Aphaenogaster iberica* from riparian, (58) *Aphaenogaster iberica* from shoreline/dry bed, (59) *Aelurillus blandus* from riparian, (60) *Argiope trifasciata* from riparian, (61) *Camponatus sylvaticus* from riparian, (62) *Dysdera ortunoi* from riparian, (63) *Gluvia dorsalis* from riparian, (64) *Hersiliola macullata* from riparian, (65) *Licinus granulatus* from riparian, (66) *Nemesia dorthesi* from riparian, (67) Opilion from riparian, (68) *Oxyopes mediterraneus* from riparian, (69) *Talavera aequines* from riparian, (70) *Aelurillus blandus* from shoreline/dry bed, (71) *Agraecina lineata* from shoreline/dry bed, (72) *Arctosa perita* from shoreline/dry bed, (73) *Arctosa variana* from shoreline/dry bed, (74) *Camponatus sylvaticus* from shoreline/dry bed, (75) *Cassolaia maura* from shoreline/dry bed, (76) *Chlaenius vestitus* from shoreline/dry bed, (77) Hogna from shoreline/dry bed, (78) *Licinus granulatus* from shoreline/dry bed, (79) *Paranchus albipes* from shoreline/dry bed, (80) Pardosa from shoreline/dry bed, (81) *Scaurus rugosus* from shoreline/dry bed and (82) Caelifera from shoreline/dry bed and (83) Grilloidea from shoreline/dry bed. The nodes (taxa) of the food web resulting in Muerte lake were (1) Biofilm, (2) Phytoplankton, (3) Herbaceous, (4) *Stipa canensis*, (5) *Sarcocornia fruticosa*, (6) *Artemisia campestris*, (7) *Suaeda vera*, (8) Ephidridae, (9) *Candelacypris aragonica*, (10) Nematoda, (11) *Brachinectella media*, (12) *Hexarthra fennica*, (13) *Tentyria pieloreli* from riparian, (14) Collembola from riparian,(15) *Pimelia baetica* from riparian, (16) *Liparoderus venator* from riparian, (17) *Cataglyphis iberica* from riparian, (18) *Camponatus sylvaticus* from riparian, (19) *Camponatus foreli* from riparian, (20) *Aphodius distinctus* from shoreline/dry bed, (21) *Camponatus silvaticus* from shoreline/dry bed, (22) *Cataglyphis iberica* from shoreline/dry bed, (23) Grilloidea from riparian, (24) *Pseudocleonus grammicus* from riparian, (25) *Messor bouveri* from riparian, (26) *Arctosa personata* from riparian, (27) *Devade tenella* from riparian, (28) Calillepis from riparian, (29) Cephalota from riparian, (30) *Arctosa perita* from riparian, (31) *Haplodrassus rufipes* from riparian, (32) Berlandina from riparian, (33) *Zodarion pseudoelegans* from riparian, (34) *Heser nilicola* from riparian, (35) Trombidium from riparian, (36) *Pheidole pallidula* from riparian, (37) *Plagiolepis pygmaea* from riparian, (38) *Gnaphosa causieus* from riparian, (39) Eresus from riparian, (40) *Oxyopes mediterraneus* from riparian, (41) *Gnaphosa zeugitana* from riparian, (42) *Gnaphosa zeugitana* from shoreline/dry bed, (43) *Syrdenus gralli* from shoreline/dry bed, (44) *Devade tenella* from shoreline/dry bed, (45) *Pheidole pallidula* from shoreline/dry bed, (46) *Devade indistincta* from shoreline/dry bed, (47) *Gnaphosa alacris* from shoreline/dry bed, (48) Cephalota from shoreline/dry bed, (49) *Drasterius bimmaculatus* from shoreline/dry bed. More detailed list of nodes in Table S1 from Supplementary material.

rely primarily on terrestrial resources during the three hydrological phases. This finding suggests the need to distinguish different terrestrial compartments (shoreline and riparian), and their respective consumers, to better understand the cross-habitat subsidies flows in temporary inland waters.

Previous empirical data in perennial ecosystems have already confirmed the dietary composition difference in the shoreline and riparian. Contribution of aquatic subsidies in terrestrial diets are usually concentrated near the aquatic habitat; that is 20–40 % are within the first 10 m in streams (Sanzone et al., 2003) and <1 % are at 50 m in lakes (Briers et al., 2005). Specifically, in the studied stream and lake, before drying (wet phase), shoreline communities exhibited a higher dietary composition of aquatic subsidies than riparian consumers. These observed differences were more marked at the onset of drying (contraction phase), when terrestrial invertebrate communities easily colonized the extended shoreline (e.g., Sánchez-Montoya et al., 2020; Steward et al., 2022; Freixinos et al., 2024). It is worth highlighting that in the contraction phase while the main aquatic resource for shoreline predators was macroinvertebrates in the studied stream, this community consumed mainly biofilm in the studied lake. These differences could be explained by the significative higher biofilm biomass in the lake as well as the influence of the body size in predator-prey interactions (Cohen et al., 1993; Schmid-Araya et al., 2002), given the small size of rotifers that compose the aquatic community in the contraction phase in the lake.

On the other hand, the flow of terrestrial subsidies from shoreline and riparian habitats to the aquatic habitat decreased in the contraction phase, particularly in Muerte Lake, as predicted. This decline is likely due to the shrinking aquatic habitat, which increased the distance from the riparian habitat, thus reducing the input of terrestrial subsidies (Dolabela et al., 2022). At the same time, we detected in both ecosystems an increase in the contribution of aquatic resources (mainly macroinvertebrate) to aquatic consumers. This result aligns with previous findings, which highlight an increase in biotic interactions in the contraction phase, especially predation, due to the abiotic stress imposed by the aquatic habitat reduction (Boulton and Lake, 2008; Stubbington et al., 2017; Karagianni et al., 2018). In the case of Serranos stream, an aquatic habitat reduction and shifts from riffles to pools in the contraction phase might have created favorable conditions for aquatic predators, which in turn benefit from the high density of prey trapped in pools and tolerance to harsh drying conditions (Boulton and Lake, 1992; Bonada et al., 2006, 2020). In fact, we reported an increase in predator diversity in Serranos stream in the contraction phase, mainly due to Odonata and Coleoptera. However, in Muerte lake, characterized by the absence of aquatic predators throughout the hydrological phases, the increase of aquatic resources to aquatic consumer is attributed to the filtering of dead animal detritus and their feces by detritivores (Alcorlo, 1999).

Finally, in the dry phase, with the total absence of aquatic habitat, interactions between the two terrestrial study habitats (dry bed and riparian) markedly increased, as expected, in both study ecosystems. The contribution of terrestrial resources to terrestrial communities increased in the dry phase compared to the two previous phases. This fact led to a similar dietary composition for both dry bed and riparian terrestrial communities, as had been previously suggested (Steward et al., 2022). Interestingly, in Muerte lake the contribution of biofilm to terrestrial consumers increased in the dry phase compared to the previous two hydrological phases. This points to the fact that biofilm may serve as a resource subsidy to terrestrial invertebrates, as it has been occasionally described. For example, Bastow et al. (2002) demonstrated how the Pygmy grasshopper feed almost exclusively on algae along the shoreline of streams; Rueda and Montes (1988) highlighted the importance of terrestrial beetles for recycling stranded aquatic organic matter along the shoreline of the aquatic habitat in lakes.

On the other hand, this study is focused solely on ground-dwelling arthropods, because they have recently been pointed out as key component for temporary inland waters (e.g., Sánchez-Montoya et al., 2016; Steward et al., 2022; Freixinos et al., 2024). However, flying taxa may also act as an important element for the meta-ecosystem food web, as reported in previous studies (Muehlbauer et al., 2014). Therefore, we consider that future research should include flying arthropods to provide a more comprehensive understanding of cross-habitat subsidy flows in temporary inland waters.

4.3. Effect of drying on meta-ecosystem food webs

In both Serranos stream and Muerte lake, we observed the profound effects drying has on the structure of the meta-ecosystem food webs. The integration of both aquatic and terrestrial habitats in temporary inland waters has allowed us to expand the knowledge about global pattern of diversity and subsidy consumption in this type of ecosystems along with factors governing the meta-ecosystem food webs.

We observed an increase in food-web complexity (nodes, links, and connectance) during drying, although this occurred at different hydrological phases depending on the ecosystem. This rise in complexity was primarily due to the increased diversity of terrestrial invertebrates as drying progressed. A similar increase in terrestrial invertebrate diversity in streams and lakes during drying has been previously described (Sánchez-Montoya et al., 2016; Steward et al., 2022; Freixinos et al., 2024).

In Serranos stream, the highest food web complexity was observed during the contraction phase, with the lowest complexity occurring during the dry phase, according to our initial hypothesis. The increased complexity in the contraction phase, indicated by a higher number of nodes, links, links per species, and connectance, can be attributed to the reported peaks of both aquatic and terrestrial diversity. Firstly, this high aquatic diversity in the contraction phase has been previously reported in temporary streams and mainly attributed to the presence of connected pools (Bonada et al., 2006). Secondly, the high terrestrial diversity at the onset of drying has been previously explained in temporary ecosystems (Sánchez-Montoya et al., 2020; Steward et al., 2022; Freixinos et al., 2024). In addition, the elevated grade of omnivory, which drastically increased links and connectance between trophic levels (Schmid-Araya et al., 2002; Rooney and McCann, 2012), could explain the highest complexity at the onset of drying. When compared to the contraction phase, in the dry phase we observed the lowest complexity, which responds to both the absence of aquatic communities and lower terrestrial invertebrate diversity (as described Steward et al., 2022).

In Muerte lake, however, the highest complexity was reported in the dry phase. Unlike Serranos stream, Muerte lake showed an unexpected high terrestrial diversity in the dry phase compared to the contraction phase. This suggest that the global pattern of terrestrial communities observed in lotic ecosystems during drying (see Sánchez-Montoya et al., 2020; Steward et al., 2022; Freixinos et al., 2024) may not be reliable for some lentic ecosystems.

Finally, the length of the meta-ecosystem food webs showed different dynamics depending on the study ecosystem type. In Muerte lake, as we hypothesized the highest length was detected in the contraction and the lowest in the dry phase. Conversely, in Serranos stream, lower variation of length was observed across the hydrological phases; the longest food web was in the wet phase. Although multiple factors (i.e. species composition, resource availability, prey-predator interactions and disturbances) have been suggested as drivers for food web length dynamics in temporary inland waters (Post et al., 2000), the complexity of these patterns is still not fully understood and continues to be a challenge for ecologists. Therefore, additional research in temporary inland waters is required to reveal the mechanisms involved in the shortening and lengthening of food web length.

It is important to note that, despite the relatively low-diversity of invertebrate communities in saline environments and their expected weak response to environmental changes due to low diversity and limited trophic interactions (McCann, 2000), we observed significant changes in the structure of the meta-ecosystem food web in both studied ecosystems in response to drying. However, while our findings are noteworthy, future studies are needed to expand the study of temporary inland saline waters. Such research would allow for a broader understanding of these unique environments and facilitate meaningful comparisons not only between different saline systems, but also with freshwater ecosystems. This comparative approach is essential to gain insights into the ecological mechanisms governing biodiversity and ecosystem processes under varying temporality and salinity conditions.

5. Conclusions

The current findings shed insights into aquatic-terrestrial food webs dynamics of saline inland waters undergoing drying phases such as streams and lakes. We reported that the drying of aquatic habitat, and the subsequent expansion of terrestrial habitat, significantly influenced the cross-habitat subsidies flows and the meta-ecosystem food web of both temporary saline inland waters. Despite the low diversity of saline communities and their expected weak responses to environmental changes limited trophic interactions, significant alterations in the meta-ecosystem food web structure have been observed in both studied ecosystems in response to drying. Also, despite the different spatial drying patterns between lotic and lentic ecosystems, we confirmed in both cases that the importance of aquatic subsidies to terrestrial consumers is modulated by the distance to the aquatic habitat. We also demonstrated in both cases that the contraction phase implies a higher consumption of aquatic resources by aquatic and shoreline invertebrates, but not for riparian invertebrates. Moreover, the drying of both temporary saline inland waters types led to an increase of the complexity of the meta-ecosystem food web given that the increase invertebrate diversity and omnivory. However, the dynamic in the length of the food webs along the drying depend on the type of inland waters, which in turn is possibly influenced by their contrasting spatial drying patterns. Additionally, in lentic ecosystems, we reported that biofilm can be an important resource for terrestrial invertebrate communities during drying. We conclude that in order to understand the subsidy flows and food webs of temporary inland waters it is necessary to incorporate the terrestrial component and the hydrological variability. This is crucial in the face of climate change, because an increase in the frequency and duration of dry periods, along with higher salinity levels, are expected.

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CRediT authorship contribution statement

Zeus Freixinos: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation. **Paloma Alcorlo:** Writing – review & editing, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Rosa Gómez:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jesús Miñano:** Validation, Supervision, Methodology. **Judit Boadella:** Writing – review & editing, Writing – original draft. **María Mar Sánchez-Montoya:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Zeus Freixinos reports financial support was provided by Spanish

Ministry of Science, Innovation and Universities. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.177516.

Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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