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Título

Importancia de los Ríos Intermitentes ante el Cambio Climático: análisis de su resiliencia en el Río Lonquén

Tesis para optar al grado de

Doctor en Ciencias Ambientales con mención en Sistemas Acuáticos Continentales

Benigno Andiranel Banegas Medina

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2022

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La Tesis de Doctorado en Ciencias Ambientales con Mención en Sistemas Acuáticos continentales titulada "Importancia de los ríos intermitentes ante el cambio climático: análisis de su resiliencia en el Río Lonquén" del Sr. Benigno Andiranel Banegas Medina y realizada bajo la Facultad de Ciencias Ambientales, Universidad de Concepción, ha sido aprobada por la siguiente comisión de evaluación:

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Al tío y compadre José Puerto,

Mis padres, familia y amistades

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RESUMEN

Los ríos intermitentes y los arroyos efímeros son cursos de agua que cesan su caudal superficial en el tiempo y en el espacio, distinguiéndose entre períodos húmedos y secos. Se conoce que más del 50% de la red fluvial mundial son intermitentes, y son considerados como un mosaico de hábitats cambiante por pasar de un estado lóticos, lénticos a terrestres. Actualmente, estos ecosistemas se encuentran poco estudiados y no se reconocen como un objetivo prioritario para la conservación. El presente estudio se realizó en el Río Lonquén, perteneciente a la Zona Mediterránea Chilena, la cual se espera que ésta región bajo proyecciones de cambio climático, presente un aumento en la temperatura media del aire de 2º a 4º C y una reducción del caudal superficial de 30% a un 40% para finales del siglo XXI. Basamos nuestro estudio en 30 años de datos de caudal hidrológico, aplicando las herramientas como el IHA, las tendencias de Mann-Kendall y la herramienta TREHS. Nuestros resultados indicaron que el río Lonquén es un río intermitente con pozas. Se identificaron tendencias negativas en el caudal medio mensual al 95% de nivel de confianza ($Z = -2.08$; $S = -4641$; $p = 0.037$) equivalente a una disminución de 0.031 m^3/s por año). Por otro lado, se determinaron tendencias positivas a los días de flujo cero al 90% de nivel de confianza ($Z = 1{,}74$; $S = 148$; $p = 0{,}08$), aumentando en 3.5 días por año.

La Herramienta TREHS permitió determinar las dos métricas en la previsibilidad estacional de seis meses del período seco ($Sd6 = 0.9593$), y la medida de la permanencia del caudal ($Mf = 0.6559$) que revelan un régimen intermitente con

pozas para el río Lonquén. De igual manera, identificamos los estados acuáticos destacando un período seco entre diciembre a abril con predictibilidad de 78% a 100%. En cambio, el período húmedo se observó de junio a noviembre con una predictibilidad superior al 60 %. Durante la recesión y reanudación del caudal se identificaron cuatro estados acuáticos: desecación, seco con pozas desconectadas, reanudación y flujo base. Estos estados acuáticos nos permitieron evaluar la heterogeneidad ambiental de las variables ambientales y taxonómicas. Nuestros hallazgos mostraron variaciones significativas entre las condiciones ambientales y las comunidades de invertebrados. Durante la desecación, la abundancia, riqueza y diversidad (Índice de Shannon) se presentaron en valores altos en comparación al resto de los estados acuáticos, mientras que la rotación de especies fue máxima principalmente durante las condiciones de caudal base. Las pozas desconectadas y la reanudación del flujo se caracterizaron por presentar altas proporciones de taxones lénticos y no insectos, como las especies endémicas de bivalvos, gasterópodos y crustáceos, destacando la relevancia de las pozas desconectadas como refugios.

Las variaciones taxonómicas en los ríos intermitentes estuvieron determinadas por la abundancia de anélidos (*Nais* sp. y *Lumbricus* sp.), quironómidos, cladóceros (*Bosmina hagmanii*), copépodos (Cyclopoida), ostrácodos (*Herpetocypris reptans y Cypridopsis vidua*), efímeras (*Caenis* sp. y *Andesiops* sp.), el gasterópodo *Physa chilensis*, en el aporte de la disimilitud de las fases hidrológicas. Por otro lado, los rasgos de resiliencia y resistencia en las fases hidrológicas estuvieron constituidos por 14 modalidades, con una distinción por la duración del ciclo de vida corto y las muchas generaciones por año como parte de las categorías de resiliencia en la recesión del caudal. Los rasgos de resistencia destacaron la presencia de capullos y la respiración del plastrón en las pozas desconectadas. Los rasgos de resistencia y resiliencia fueron indicativos de estrategias ecológicas para sobrevivir y restaurar la biota después de la perturbación por sequía. Finalmente, el estudio global enfocado en los desechos vegetales terrestres, biopelículas y sedimentos del cauce seco de los ríos intermitentes, incluido el río Lonquén, reflejó un incremento en el consumo de oxígeno y liberación de dióxido de carbono con un aporte crítico del 4% de las emisiones globales de CO_2 de ríos intermitentes, además de una gran contribución de desechos de plantas y lixiviados hacia los sedimentos. Por lo tanto, se requieren más estudios para ampliar la comprensión del comportamiento de los invertebrados acuáticos para enfrentar escenarios de cambio climático y perturbaciones humanas.

ABSTRACT

The intermittent rivers and ephemeral streams are watercourses that cease to flow in time and or space, distinguishing between wet and dry periods. More than 50% of the global river network are intermittent, and they are considered a mosaic of lotic, lentic, and terrestrial habitats (shifting habitat mosaics). Currently, these ecosystems are understudied and a priority target for conservation because they are not recognized. We conducted our study in the Lonquen river from the Chilean Mediterranean zone. This zone is expected to increase the mean air temperature from 2 to 4º C under climate change projections, reducing the streamflow from 30 to 40% in the same period. We base our study on 30 years of hydrological streamflow data, applying tools such as IHA, Mann-Kendall trends, and the TREHS Tool. Our results indicated that the Lonquen river is an intermittent river with pools. Negative trends in the monthly mean streamflow at 95% confidence level (Z = -2.08; S = -4641; p = 0.037) equivalent to 0.031 m_3/s per year) was identified in the Lonquén river. On the other hand, positive trends were determined to the zero flow days at a 90% confidence level (Z = 1.74; S = 148; p = 0.08), increasing by 3.5 days per year.

The TREHS Tool allowed us to determine the two metrics in the six months seasonal predictability of dry period (Sd6 = 0.9593), and the measure of the flow permanence (Mf = 0.6559) that revealed a Regime Intermittent with pools to the Lonquén river. Similarly, we identified the aquatic states highlighting a dry period

between December to April with predictability from 78% to 100%. Instead, the wet period was observed from June to November with predictability higher than 60%. During the flow recession to consumption were identified four aquatic states: drying, dry (disconnected pools), rewetting, and baseflow. These aquatic states let us assess the environmental and taxonomical variables' environmental heterogeneity. Our findings showed significant variations between the environmental conditions and invertebrate communities. During the drying phase, abundance, richness, and diversity (Shannon Index) were highest, while species turn-over was highest mainly during the base flow conditions. The disconnected pools and the flow resumption phases were characterized by high proportions of lentic taxa and non-insects, such as the endemic species of bivalves, gastropods, and crustaceans, highlighting the relevance of disconnected pools as refuges.

The taxonomical variations in the intermittent rivers were determined by the abundance of annelids (*Nais* sp. and *Lumbricus* sp.), chironomids, cladocerans (*Bosmina hagmanii*), copepods (Cyclopoida), ostracods (*Herpetocypris reptans* and *Cypridopsis vidua*), mayflies (*Caenis* sp. and *Andesiops* sp.), the gastropod *Physa chilensis*, in the contribution of the dissimilarity of the hydrological phases. On the other hand, the resilience and resistance traits in the hydrological phases were constituted by 14 modalities with a distinction for short life cycle duration and the many generations per year as part of the resilience categories in the flowing recession. Resistance traits emphasized the presence of cocoons and the plastron respiration in the disconnected pools. The resistance and resilience traits were indicative of ecological strategies to survive and restore the biota after the drought disturbance. Finally, the global study focused on the terrestrial plant litters, biofilms, and sediments from the dry streambed in the intermittent rivers, including the Lonquén river, reflected an increase in oxygen consumption and release of carbon dioxide with a critical contribution of 4% of the global CO_2 emissions from intermittent dry rivers, besides a significant contribution from plant debris and leachate into sediments. Therefore further studies are required to expand the understanding of the aquatic invertebrates' behaviour to face climate change scenarios and human perturbations.

INTRODUCCIÓN

Debido a las condiciones de cambio climático actuales y a proyecciones futuras para finales del siglo XXI (2080-2100), se han estimado que existirá un incremento en las temperaturas promedio de 2 a 4° C y una reducción en las precipitaciones de un 20 hasta un 40% para la región centro-sur de Chile (Garreaud, 2011; Cabré et al. 2016; Araya-Osses et al. 2020). Estas proyecciones pueden tener impactos negativos para los ecosistemas dulceacuícolas, principalmente para la zona mediterránea Chilena (32°-40° latitud sur), la que forma parte de uno de los dos sitios reconocidos como *Hotspot de Biodiversidad* a nivel nacional (MMA, 2011; Fuentes-Castillo et al. 2019) y a nivel mundial (Myers et al. 2000; Klausmeyer & Shaw, 2009). Sin embargo, estos hábitats se encuentran muy degradados por actividades antrópicas como la extracción de agua y cambios en la cobertura y uso de suelo (agricultura, plantaciones forestales, urbanizaciones, etc.), por lo que la necesidad de planes de conservación debe ser una prioridad (Skoulikidis et al. 2017).

Frente a las predicciones de los efectos del cambio climático, se esperaría que a futuro se genere una mayor conversión o alteración del régimen hidrológico de ríos perennes a intermitentes o temporales, provocando una fragmentación de éstos ecosistemas fluviales con pérdida de biodiversidad y reducción de la integridad biótica (Datry et al. 2014; Shumilova et al. 2019). Asimismo, los ríos y arroyos de regiones con climas mediterráneos del mundo han sido considerados ecológicamente únicos y tal vez los más vulnerables a los daños ambientales por actividades antropogénicas (Bonada y Resh, 2013; Grantham et al. 2013; Cid et al. 2016). Sin embargo, en la zona mediterránea Chilena han sido generalmente ignorados en términos de investigación científica o relativamente poco estudiados con carencia de información, principalmente para invertebrados acuáticos (macroinvertebrados bentónicos y meiofauna) y peces; con conocimiento de biodiversidad extremadamente escasa y fragmentada (Fierro et al. 2019), ya que la mayor prioridad ha sido enfocada hacia los ecosistemas dulceacuícolas de la región sur del país, destacando el interés por interpretar la biogeografía desarrollada por los fenómenos de glaciación (CONAMA, 2006; Garreaud, 2011; Figueroa et al. 2013).

Es común entonces encontrar en estos ecosistemas, la formación de ríos intermitentes los cuales han sido considerados como un ecotono temporal (McDonough et al. 2011; Lobrera et al. 2019; Steward et al. 2022) por presentar una transición de ecosistemas acuáticos a terrestres, además de constituir un mosaico de hábitats cambiante, pasando de ambiente lótico (aguas en circulación) a léntico (aguas quietas) y posteriormente a terrestre, fenómeno que puede ir de días a semanas (Larned et al. 2010; Datry et al. 2014; Datry et al. 2016). Esta condición no impide que durante el periodo seco existan refugios para la biota acuática, como pozas y el hiporreos favoreciendo la permanencia de la meiofauna y macroinvertebrados bentónicos con capacidad de enterrarse y albergarse mientras se reestablece el flujo hídrico superficial (Datry et al. 2014; Bonada et al. 2020). A pesar de ello, los estudios en la zona hiporreica para caracterizar la composición físico-química del agua, así como la estructura de los ensambles de invertebrados acuáticos son escasos y poco explorados, en comparación a trabajos desarrollados en ríos con caudales permanentes o que involucran macroinvertebrados bentónicos (Clinton et al. 1996; Steward et al. 2012; Gomez-Gener et al. 2021).

Asimismo, los ríos intermitentes o temporales, no han sido considerados en los estudios de ecología acuática, ni en programas de conservación, proyectándose que a futuro exista una mayor proporción, debido a la acción del cambio climático y mayor demanda de agua (Larned et al. 2010; Gallart et al. 2012; Datry et al. 2014), necesitándose soluciones de sostenibilidad económica, social, ambiental y legal para su conservación y protección (Zhou et al. 2014). Por otro lado, se desconoce cómo se constituyen y comportan los ríos intermitentes en Chile, su composición biótica y condiciones ambientales, principalmente durante la estación seca, generándose en algunos casos (como ocurre en el río Lonquén) la instalación de punteras para la extracción de agua de uso doméstico y la agricultura (e.g. localidad de Buenos Aires, comuna de Portezuelo), los cuales van año a año incrementando su profundización para alcanzar la napa freática, requiriéndose por una parte de estudios enfocados a estos ecosistemas que contribuyan a programas de conservación de la biota acuática, y por otra parte, de uso sustentable de las comunidades aledañas mediante planes de gestión adecuados para estos sistemas (Julio et al. 2022). .

Ríos intermitentes o temporales

Existen varias consideraciones referidas a la conceptualización de ríos intermitentes o temporales, destacando principalmente el criterio de los cursos de agua que cesan su caudal de manera natural y periódica (Larned et al. 2010; Buttle et al. 2012; Steward et al. 2012; Datry et al. 2014), en algún punto o a lo largo de su curso en el tiempo y espacio y con alternancia, casi predecible de periodos húmedos y secos sobre ciclos anuales e interanuales (Sánchez-Montoya et al. 2011; Arthington et al. 2014). McDonough et al. (2011) destaca la condición de carecer de un caudal superficial durante una porción del año, mientras que Sánchez-Montoya et al. (2011) hace referencia a los cuerpos de agua dulce que se someten a una fase seca recurrente, de variación en longitud y que algunas veces es predecible en el tiempo y en duración.

Los ríos y arroyos temporales no están restringidos solamente a zonas áridas o semi-áridas, como se ha creído normalmente, sino que también pueden ocurrir en climas húmedos y subhúmedos (Larned et al. 2010; Buttle et al. 2012), ya que están presentes en gran parte de los biomas, climas y continentes del planeta (Larned et al. 2010; Datry, 2012). Asimismo, se ha despertado un mayor interés por estudiarlos a nivel mundial en los últimos años, con mayores esfuerzos encontrados para Norte América, Europa y Oceanía (Leigh et al. 2016), llegando a estimarse que a nivel global hasta un 60% de los ríos o arroyos cesan su caudal en al menos un día al año, presentando características de ríos intermitentes (Datry et al. 2014; Messager et al. 2021).

Países como Australia (50-70%), Estados Unidos (58-60%), Grecia (~43%), Francia (25-40%), Italia (Río Tagliamento ~50%) han estimado su representación y destacan la importancia en incluir estos sistemas fluviales en programas de conservación, especialmente por los servicios hidrológicos, ecológicos, ecosistémicos y culturales que se hace de ellos (Tooth, 2000; Larned et al. 2010; McDonough et al. 2011; Datry et al. 2014; Pastor et al. 2022). No obstante, para Chile se desconoce hasta el momento la proporción y estado de los ríos temporales dentro del territorio, solo algunas referencias, principalmente para la zona del norte árido con ríos de régimen esporádico que comprende las regiones de Tarapacá, Antofagasta y parte norte y nororiental de Atacama, donde impera gran áridez con un amplio número de sistemas con desarrollo endorreico, como las cuencas de la Alta Puna y de las zonas de elevaciones intermedia (la pampa del Tamarugal y los salares de Atacama y Punta Negra), además de los sistemas de cuencas arreicas o inactivas que se encuentran en el interior de la cordillera de la costa y el litoral de Tarapacá, siendo la mayoría salares, como salar Grande y Soronal (Niemeyer y Cereceda, 1984). Sin embargo, en recientes estudios se ha considerado la relevancia del río Lonquén (Región del Ñuble) por su comportamiento hidrológico y su interacción con sus componentes climáticos, ambientales y ecológicos que han permitido iniciar los primeros estudios en cuanto a su intermitencia y su posible degradación ante el cambio climático. (Duque & Vasquez, 2015; Stewart et al. 2015; Bouadila et al. 2020; Banegas et al. 2021).

Por otro lado, la importancia de los arroyos de cabeceras (efímeros e intermitentes) han sido destacados por su contribución en la recarga de los acuíferos subterráneos, protección de la erosión e inundaciones, reducción de la contaminación, reciclaje de nutrientes, hábitats para la vida silvestre acuática y terrestre (Bogan et al. 2014; Datry et al. 2016; Whol et al. 2017; White et al. 2018). Además, por su importancia económica en la contribución en la pesca y cacería, industria, minería, agricultura, ganadería, recreación, pero principalmente porque proveen de agua para los sistemas públicos de abastecimiento de agua para consumo humano (Leigh et al. 2016; Acuña et al. 2017; Kaletová et al. 2019); tal es el caso de la población de los Estados Unidos donde un tercio de ésta (117 millones de personas) obtienen o confían su agua de consumo total o parcial en arroyos efímeros o intermitentes (USEPA, 2008; USEPA, 2009).

Es por ello que desde finales de la década de 1980´s se ha expandido el interés por conocer el funcionamiento de éstos sistemas, integrando la evaluación ecológica e hidrológica (Leigh et al. 2016), por encima del interés en estudiar de manera aislada la biota de invertebrados, peces o inclusive la biogeoquímica, denotando un enfoque multidisciplinario para un mejor estudio de estos patrones y procesos distintivos (Busch et al. 2020). Ello ha permitido entender la importancia de proteger los ríos intermitentes, asociado a que parte de ellos forman parte de ecosistemas únicos o amenazados como las regiones mediterráneas, áridas y semi-áridas del planeta. La capacidad predictiva que permitan estos estudios facilitaran el desarrollo de modelos para responder a cambios y retos futuros como el cambio climático, cambio en el uso de suelo y demandas de agua para beneficio humano (Datry et al. 2016; Leigh et al. 2016; Sttubington et al. 2018; Borg-Galea et al. 2019).

A pesar de reconocerse la importancia del recurso agua como una fuente indispensable para sostener poblaciones humanas y otras especies, los requerimientos son cada vez mayores, teniéndose que incurrir al suministro y uso de los cuerpos de agua subterránea, estimándose que entre 1,5 y 3,0 billones de personas a nivel mundial se abastecen de aguas subterráneas, principalmente en áreas rurales, así como para actividades industriales (40%) e irrigación (20%), con costos muy elevados por su uso (Millennium Ecosystem Assessment, 2005). Esto genera nuevas amenazas por sobreextracción, introducción de contaminantes peligrosos, profundización de la napa freática y la intrusión de aguas salinas, tal como está afectando a 9 de 11 países mediterráneos de Europa (Millennium Ecosystem Assessment, 2005; Pastor et al. 2022). Información que para la zona mediterránea de Chile es desconocida.

Estado hidrológico, ecológico y químico de ríos intermitentes (The MIRAGE Toolbox)

De Girolamo et al*.* (2015), Costigan et al. (2017) y Nabih et al. (2021) reconocen que el régimen de caudal es uno de los principales controladores del estado ecológico de un río o arroyo, principalmente de los ríos temporales, encontrando variaciones en las características de la vida acuática y la disponibilidad temporal de los mesohábitats de acuerdo a su transición de húmedo a seco. Asimismo, existe una alta variabilidad de los caudales, con recurrente interrupción casi predecible de los mismos, hasta una completa desecación del canal en ríos temporales, los cuales determinan en gran medida los cambios en los estados acuáticos asociados a las condiciones hidrológicas (Gallart et al. 2012; de Girolamo et al. 2015).

Se entiende entonces, como *estado acuático* al conjunto de mesohábitats acuáticos que ocurren en tramos, en momentos particulares y que depende de las condiciones hidrológicas, permitiendo distinguir diversos niveles de fragmentación y conectividad, lo que ha permitido clasificar seis estados acuáticos: *Hiperheico*: descargas de agua inusualmente altas-inundaciones; *eurheico*: río completamente conectado y que fluye formando mesohábitats (pozas y rápidos), con abundancia de éste último; *oligorheico*: cuando las pozas dominan en los mesohábitats y continua conectado por un caudal superficial; *arheico*: pozas presentes pero totalmente desconectadas por cualquier flujo superficial; *hiporreico*: lecho del río desprovisto de agua o sin agua superficial, aunque con humedad del aluvión capaz de sostener la vida acuática hiporreica; y *edáfico*: lecho desprovisto enteramente de agua superficial, donde el aluvión está demasiado seco que impide la formación de vida acuática (Gallart et al. 2012; Prat et al. 2014; Gallart et al. 2016; Gallart et al. 2017).

En referencia al estado ecológico, los macroinvertebrados bentónicos han sido utilizados ampliamente como indicadores de calidad de agua, ya sea para evaluar cambios en el ambiente por condiciones naturales, como los inducidos por actividades humanas (Sánchez-Montoya et al. 2007). Los resultados obtenidos permiten ser comparables a nivel de la región mediterránea Europea, utilizando métricas de diversidad y riqueza (a nivel taxonómico de familias), la relaciones entre el número de taxones de Ephemeroptera, Plecoptera y Trichoptera (EPT) y de Odonata, Coleoptera y Hemiptera (OCH), las cuales son buenas indicadoras para identificar cambios estacionales en las comunidades de macroinvertebrados (Bonada et al. 2007), además de los cambios hidrológicos de acuático a terrestre (Sánchez-Montoya et al. 2007; Prat et al. 2014).

De igual manera, estos indicadores son una herramienta importante para medir el funcionamiento y la salud integral de un sistema acuático, que en conjunto con el estudio del régimen hidrológico y físico-químico, pueden acoplarse a la caja de herramientas del programa MIRAGE (proyecto para el Manejo de Ríos Intermitentes Mediterráneos de la Unión Europea, The MIRAGE Toolbox), como una herramienta esencial para la evaluación integrada para ríos temporales (Prat et al. 2014).

Por otro lado, Bonada et al. (2007), Arthington et al. (2014) and Lobrera et al. (2019) destacan que los ríos mediterráneos presentan una alta variabilidad espacial generada por perturbaciones estacionales predecibles (inundaciones y desecación), donde se pueden observar una considerable pérdida de la biodiversidad por la fragmentación de los ecosistemas, considerando que los ríos en su estado permanente no presentan rasgos significativos en función de pérdida de hábitats para la biota acuática, ya que existe una predominancia de rápidos y pozas presentes a través de todo el año. Mientras que para los estados temporales como los intermitentes y efímeros (pozas aisladas o lecho del río seco por algún periodo más largo) se destaca una fuerte contracción de éstos hábitats acuáticos, afectando principalmente las especies más susceptibles de las comunidades de macroinvertebrados (Bonada et al. 2020).

Al respecto, ciertos grupos han desarrollado rasgos históricos y biológicos (morfológicos, fisiológicos y de comportamiento) como una adaptación y resistencia ante dichas perturbaciones (tolerancia a la desecación), que les permiten utilizar las pozas y la zona hiporreica como refugio para su posterior recolonización, que, junto con habilidades de dispersión, una vez que se reconectan estos cuerpos de agua en la época húmeda (Bonada et al. 2007; Drummond et al. 2015). Por otro lado, la capacidad de resiliencia ante las perturbaciones por desecación, es soportada por parte de los invertebrados acuáticos, mediante su esperanza de vida, duración de vida, dispersión y locomoción con relación al sustrato. Mientras que la reproducción, las formas activas y estados inactivos de especies que forman bancos de semillas ya sea en lechos de ríos secos, pozas, humedales y hábitats de la llanura de inundación son destacados como mecanismos de resistencia. De esta manera, contribuyen en su recuperación a los niveles similares antes de la perturbación, una vez que los ríos se reconectan (Stubbington et al. 2013; Leigh et al. 2015; Stubbington et al. 2016; Crabot et al. 2020). Esta condición puede ser útil para desarrollar políticas de conservación frente a la amenaza del cambio climático (Busch et al. 2020).

Proyecciones de Cambio Climático en la Zona Mediterránea Chilena

Las proyecciones estimadas para finales del siglo XXI (2071 – 2100) bajo un escenario severo de calentamiento global (SRES A2 – emisiones muy elevadas de GEI) indican para el territorio de Chile, las magnitudes de calentamiento climático presentarán un incremento de 0,5 a 1º C sobre la costa, mientras que para la cordillera (tierras altas) del norte y centro de Chile el aumento se alcanzará hasta 5º C, con un promedio para Chile continental (región centro-sur) de 2 a 4° C. Se destaca nuevamente en las proyecciones futuras, las diferencias marcadas entre la región de la costa (menor calentamiento) y la cordillera de los Andes (mayor calentamiento), asociados a un aumento de los vientos del sur (CONAMA, 2006; Garreaud, 2011). Así para las precipitaciones, se presentará una fuerte disminución en la zona centro-sur de Chile, donde la región de la cordillera entre las regiones del Biobío a los Lagos, las precipitaciones anuales tendrán una disminución de 1000 mm/año, mientras que para la costa austral de Chile se generará un aumento de 500 mm/año y un leve aumento en el altiplano. Por lo tanto, se prevé una pérdida de pluviosidad de un 40% para la región de Chile central en comparación con los valores actuales (CONAMA, 2006; Garreaud, 2011; Valdes-Pineda et al. 2014).

Tomando en consideración dichas proyecciones futuras (incremento de las temperaturas y reducción de las precipitaciones), se estaría generando un aumento en los eventos extremos como las sequías, reflejando en una disminución en la cantidad y calidad de agua, con reducciones significativas de hasta un 20% de los caudales promedios superficiales de verano y un aumento de frecuencia de caudales bajos, siendo más acentuado en la región de Chile central y sur (Stehr et al. 2010; Garreaud, 2011; Ministerio del Medio Ambiente, 2011; Ministerio del Medio Ambiente, 2014; Valdez et al*.* 2014; Cabré et al. 2016). Esta incertidumbre estaría influyendo grandemente en la zona mediterránea Chilena (32-40° latitud Sur), debido al mal uso y aprovechamiento del recurso hídrico en la región, donde el 85% de las fuentes de agua son aprovechadas en la agricultura y el 70% de las aguas se pierden por evaporación o infiltración de los canales abiertos usados para la irrigación, con una considerable intervención por actividades agrícolas, forestales y la expansión urbana, donde además se presenta una menor proporción de áreas silvestres protegidas en la región (Figueroa et al. 2013), respecto el país.

Es así, que tomando en consideración las proyecciones y simulaciones climáticas para finales del siglo XXI en en la región centro-sur de Chile se propiciaría un incremento en la vulnerabilidad de los ríos temporales y mayor conversión de ríos perennes a temporales, con repercusiones en la disponibilidad de agua y relaciones tróficas, que conllevaría a un detrimento de la calidad de vida de la población y de los ecosistemas naturales, especialmente en la estructura comunitaria de invertebrados acuáticos, esperando se modifique y tiendan a desaparecer, en ciertos casos, especies bentónicas y en otras situaciones buscar refugiarse en pozas y en la zona hiporreica como un mecanismos de adaptación y resistencia a la desecación (Datry et al*.* 2014; Cid et al*.* 2015; Bonada et al. 2020).

Históricamente, los ríos intermitentes han experimentado variaciones climáticas, hidrológicas y de intervención humana que conllevan a procesos de flujo superficial y desconexión del mismo, generando procesos de adaptación por parte de la biota acuática en resistir y recuperarse ante las perturbaciones de desecación (Datry et al. 2013; Crabot et al. 2020). Muchas especies acuáticas han desarrollado mecanismos que facilitan la repoblación adaptativa que les han permitido sobreponerse ante las perturbaciones, de manera tal, que han podido recolonizar tramos alterados y dispersarse a través de mecanismos de vuelo, deriva de tramos superiores o incluso permanecer en pozas remanentes o desarrollar estados resistentes a la desecación, ante la pérdida de agua superficial (Bogan et al. 2017).

Alteraciones hidrológicas antropogénicas y naturales también han generado graves impactos hacia los ecosistemas Mediterráneos, siendo algunos de ellos: la construcción de represas, extracción de agua para usos domésticos, agrícolas o industriales, deforestación de la vegetación ripariana y extracción de arena, además de cambios en las temperaturas y precipitaciones, con reconocidos impactos en los procesos de resiliencia y resistencia ecológica en los ríos intermitentes (Malhi et al. 2019). Sumado a ello, la fragmentación de hábitats y la invasión de especies exóticas tienden a reducir la capacidad adaptativa de los ecosistemas, así como de la disponibilidad de absorber las perturbaciones y de aprender a adaptarse a las mismas, a través de los mecanismos de selección natural y las respuestas fisiológicas de los organismos acuáticos (Angeler et al. 2014).

Hoy en día, la compresión actual de cómo funcionan los ecosistemas ha evolucionado y se reconoce que estos son sistemas no lineales, dinámicos y fluctuantes que pueden volver a sus condiciones anteriores a las perturbaciones bajo procesos de mitigación y adaptación al cambio climático, generando la necesidad de comprender, administrar, restaurar y conservar los ecosistemas para una mejor respuesta ante el cambio climático y lograr mantener su integridad ecológica (Malhi et al. 2019; Cantonati et al. 2020; Pelletier et al. 2020). De igual manera, los ecosistemas naturales deben analizarse bajo un contexto ecológico y social para obtener una respuesta de adaptación ante las perturbaciones climáticas y antropogénicas, con un mejor entendimiento científico y una mayor conciencia pública para brindar beneficios y servicios ecosistémicos a la sociedad, con iniciativas de adaptación e influir en el comportamiento humano en la toma de decisiones, la innovación de nuevas tecnologías e infraestructura, políticas institucionales, gobernanza y manejo con reducción a la exposición de riesgo (Cantonati et al. 2020; Owen, 2020).

HIPÓTESIS

Proyecciones de cambio climático para finales del siglo XXI, indican que existirá una reducción significativa de caudal en la zona centro-sur de Chile, lo que generará mayor conversión de ríos perennes a temporales, con fragmentación de hábitats, pérdida de la biodiversidad acuática y un incremento en la extracción de agua subterránea; en ese sentido, se postulan las siguientes hipótesis:

1. Los ríos intermitentes presentan condiciones de refugio (pozas aisladas y lechos secos) para albergar parte de la biota acuática del río y sirven de foco de dispersión una vez que el río se conecte.

2. La reducción del hábitat acuático durante el proceso de desecación, condiciona la importancia relativa de cada uno de los refugios resaltando las adaptaciones de resiliencia y resistencia ante las perturbaciones por sequía por parte de la biota acuática de los ríos intermitentes.

OBJETIVOS

Objetivo General

Evaluar el papel del río intermitente Lonquén y su contribución en la resiliencia ante el cambio climático.

Objetivos Específicos

1. Determinar el tipo de río intermitente y su estado acuático mediante la evaluación del régimen hidrológico y de caudal del río Lonquén.

2. Caracterizar la comunidad de invertebrados bentónicos y variables ambientales en presencia de caudal superficial y durante la perturbación por desecación en el río Lonquén (pozas aisladas y lechos secos).

3. Determinar la importancia de las pozas aisladas y lechos secos como refugio y focos de dispersión de la fauna de invertebrados en los procesos de resiliencia y resistencia ante el cambio climático.

4. Estudiar si existen patrones de distribución anidado de especies de invertebrados acuáticos en el río Lonquén en relación al caudal superficial y pozas aisladas.

CAPÍTULO I

Hydrological, Environmental and Taxonomical Heterogeneity during the Transition from Drying to Flowing Conditions in a Mediterranean Intermittent River.

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Simple Summary: In recent decades, the riverine ecosystems have been considered to evaluate the aquatic biological diversity, hydrological variations, and ecosystem services. However, climatic change scenarios and anthropogenic interventions are expected to shift from perennial to intermittent rivers with possible repercussion on aquatic biodiversity and human well-being. Our study identified a significant reduction in the Mediterranean intermittent river streamflow with an increase of zero flow days in the last decades. Furthermore, the aquatic invertebrates showed variations during the transition from drying to rewetting with a significantly changing species adapted to the flowing conditions (rheophilic taxa) to non-flowing water. The importance of the disconnected pools as refuges during the dry condition was recognised to protect some endemic species and contribute to the recolonisation after the rewetting events. Include these important aquatic ecosystems in management and conservancy policies is a challenge that will contribute to preserving the freshwater resources and the biological diversity for our future generations.

Abstract: Intermittent rivers and ephemeral streams (IRES) are increasingly studied because of their often unique aquatic and terrestrial biodiversity, biogeochemical processes and associated ecosystem services. This study is the first to examine the hydrological, physicochemical and taxonomic variability during the dry-wet transition of an intermittent river in the Chilean Mediterranean Zone. Based on 30-years of river monitoring data and the TREHS tool, the hydrology of the river was characterised. Overall, the river shows a significant reduction in streamflow (-0.031 m^3/s per year) and a substantial increase of zero flow days (+3.5 days per year). During the transition of hydrological states, variations were observed in the environmental conditions and invertebrate communities. During the drying phase, abundance, richness, and diversity were highest, while species turn-over was highest during base flow conditions. The disconnected pools and the flow resumption phases were characterised by high proportions of lentic taxa and non-insects, such as the endemic species of bivalves, gastropods, and crustaceans, highlighting the relevance of disconnected pools as refuges. Future climatic change scenarios are expected to impact further the hydrology of IRES, which could result in the loss of biodiversity. Biomonitoring and conservation programmes should acknowledge these important ecosystems.

Keywords: Intermittent rivers and ephemeral streams; temporary rivers; TREHS Tool; aquatic invertebrates; Drying; Rewetting; Disconnected pools

Resumen: los ríos intermitentes y arroyos efímeros (IRES, por sus siglas en ingles) están siendo incrementado sus estudios debido a diversidad unica acuática y terrestre, además por sus procesos biogeoquímicos y encontrarse asociados a los servicios Ecosistémicos. El presente estudio es el primero en examinar la variabilidad hidrológica, físico-química y taxonómica durante la transición humeda-seca en la zona Mediterránea Chilena. El estudio fue basado en 30 años de monitoreo de datos hidrológicos del río Lonquén y en el uso de la herramienta THRES. La hidrología del río fue caracterizada encontrándose reducciones significaticas en el caudal (-0.031 m3/s por año) y un substancial lincremento de los días con caudal cero (`3.5 días por año). Durante la transición de los estados hidrológicos, variaciones fueron observadas en las condiciones ambientales y en las comunidades de invertebrados. Durante la fase de desecación, las abundancias, la riqueza y la diversidad fueron las más altas, en comparación a los otros estados acuáticos, mientras el reemplazo de las especies fue mucho mayor durante las condiciones de caudal base. Las pozas desconectadas y la fase de reanudación fueron caracterizadas por altas proprciones de taxones lénticos y grupos de no insectos (bivalvos, gastrópodos, crustáceos, resaltando la importancia de las pozas desconectadas como refugios. Futuros escenarios de cambio climático se esperan que presenten impactos hidrológicos de los IRES, los cuales podrían resultar en la perdida de biodiverisdad. Programas de monitoreos biológicos y conservación deben reconocer estos importantes ecosistemas.

Palabras claves: ríos intermitentes y arroyos efímeros, ríos temporales, THRES Tool, invertebrados acuáticos, desecación, reanudación, pozas desconectadas.

1. Introduction

Intermittent rivers and ephemeral streams (IRES) or non-perennial waterways are waterways that cease to flow at a particular space and time [1–3], hence having distinct wet and dry periods [4,5]. They are widely distributed and considered the most common fluvial ecosystems in the world [6,7]. More than 50% of the global river network are IRES [3,8–10], of which monitoring mainly takes place in the temperate and Mediterranean climate zones [10–12]. Perturbations in the flow regime reduce the availability of mesohabitats provoking a drastic loss of biodiversity [13,14]. Mosaics of lotic, lentic and terrestrial habitats (shifting habitat mosaics) in IRES provide a complex and dynamic system, variable in time and space [15]. In analogy with the temporary pond system, this hydrological variability may alter the composition and structure of the aquatic communities and their genetic structures [16]. During flow cessation and dry period, IRES accumulate a diversity of substrates, especially of terrestrial plant litter, biofilms, animal carcases, and sediments, considered as biogeochemical reactors or hot spot areas. These substrates generate high O_2 consumption and CO_2 release rates, with a notable impact on the global CO_2 flux through atmospheric emissions [17–21].

Mineralisation processes also result in the discharge of nutrients and suspended matter toward the coastal zone once the river gets reconnected [17,19]. In analogy with temporary pond systems, the dry riverbeds and hyporheic zone also store drought-resistant propagules, immature instars and adult stages of aquatic fauna surviving the dry conditions and recolonising the river when floods resume [22,23]. Despite some initiatives mainly in Europe, the USA and Australia that recognise the IRES, in many parts of the world, these aquatic systems remain understudied and not recognised as priority targets for conservation [6]. In the case of Chile, with an arid to semi-arid climate, there is limited knowledge of the aquatic ecology and the structure and functioning of rivers in general, despite the high demand for water in this area [24]. Although the Chilean Mediterranean Zone (ChMZ) experiences serious aridification, the increasing human population, intensification of agricultural irrigation practices, livestock farming, industrial activities and exotic forest plantations (pine and eucalyptus) demand huge freshwater volumes [24,25].

Currently, the National Water Agency (DGA, according to its initials in Spanish) is responsable for the management and administration of water resources carrying out the hydro-meteorological and water quality stations monitoring in the country. Systematic monitoring for the ecological quality is only persistent for six aquatic ecosystems (four rivers and two lakes) that count with surveillance plans associated with the secondary environmental quality standards [26]. However, more effort is necessary for monitoring the perennials or even the intermittent rivers, mainly in the ChMZ, that are very scarcely taken into account for their monitoring.

According to climate predictions, the central zone of Chile will experience an increase in summer mean air temperature from 2 to 4 _C, with a 20% to 40% reduction of precipitation and a 20% decrease in summer river streamflow [26–30]. The predicted hydrological changes under projected climate change and anthropogenic interventions (e.g., water abstraction) are also expected to induce perennial changes to intermittent rivers with possible repercussions for the aquatic biodiversity associated ecosystem functions [1,31–33]. Conventional hydro-ecological tools such as the "Indicators of Hydrologic Alteration IHA" [34] contribute to assessing flow predictability, but currently with weak applicability in IRES. The main reason is the absence of specific indicators for the three main flow phases (flow, disconnected pools and dry riverbed).

The novel TREHS Tool (Temporary Rivers Ecological and Hydrological Status) was specially developed to characterise the various aquatic states, investigate and manage temporary rivers and assess their ecological status [31]. It uses records of at least ten years of average monthly flow series from gauging stations to characterise the type of intermittent river: Permanent or perennial (P), Intermittent-pools (I-P), Intermittent-dry (I-D), Ephemeral (E), and the six aquatic states: Hyperrheic (overbank flood and drift of bedload and fauna), Eurheic (abundant riffles and mesohabitat available and connected), Oligorheic (slightly connected pools with lentic and lotic fauna), Arheic (disconnected pools and only lentic fauna), Hyporheic (no surface water and terrestrial fauna active), and Edaphic (alluvium moisture, terrestrial fauna and resistant stages of aquatic fauna) [7,8,13,31,35,36].

This study aims to assess the variability of hydrological, environmental and biotic conditions in response to flow intermittence in a river from the Chilean

Mediterranean zone. We based our approach on hydrological analysis and application of the TREHS tool to establish the aquatic states along the hydrological intermittence gradient and the relationship with physicochemical variables and taxonomic metrics in IRES. Furthermore, we will test to what extent the aquatic invertebrate communities use the disconnected pools as a refuge during the dry conditions and the ability to recolonise the different mesohabitats when flooding resumes. It is hypothesised that (1) the transition from flow recession to resumption will coincide with essential differences in environmental and taxonomical characteristics between the flow phases, and (2) the disconnected pools will serve as a refuge to a group of adapted taxa to the low or no flow conditions during the dry phase of the intermittent river.

2. Materials and Methods

2.1. Study area

The Lonquén river is located in the central-south of Chile and is part of the Itata river basin (Figure 1). The drainage area is about 1,178 km^2, and the river has a Strahler stream order four [37]. According to hydrological records, the annual mean precipitation is intensive and irregular in winter with an average of 835 mm per year (lowest: 400 mm; highest: 1,200 mm), mainly concentrated from June to September, with some sporadic additional rains in autumn and spring. The streamflow has a mean daily flow of 12.8 m^3/s, ceasing from days to weeks with complete drought in summer and autumn. The mean annual air temperature is 15°C (1 to 35°C). December to February are the warmest period with the highest potential evapotranspiration rates, varying from 944 to 1,244 mm and exceeding the average precipitation in the zone [38].

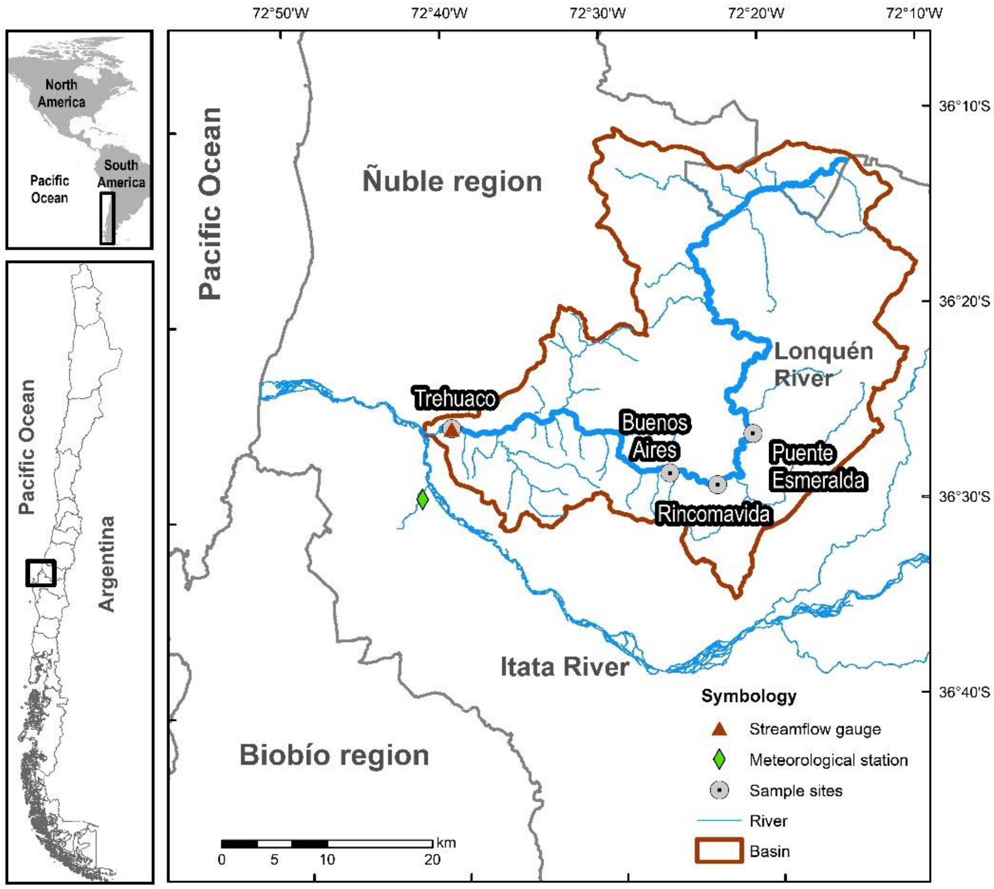


Figure 1. Map of the study area, the basin of the Lonquén River in Mediterranean Chile.

The Lonquén river originates from the coastal mountain range and is part of the interior dryland "secano interior" composed of granitic rocks from the Carboniferous period. The soils are predominantly shrink-swell clay soils, mostly degraded due to intense agricultural practices during the last centuries [39]. The land use in the basin is characterised by a cover of 20% forest (including native species and introduced plantations of pine and eucalyptus), 43% agriculture (vineyards, wheat, maise, potatoes and other vegetables), 36% meadows and thickets, and less than 1% is represented by urban, industrial and other areas without vegetation [38,40]. Rolling hills, mountains and temporary streams characterise the topography. At the same time, the geomorphology is constituted by granitic soils with low permeability. High capacity of moisture retention and low infiltration rates in the subsoil display a high superficial runoff in winter months and no runoff in summer, which rises and falls quickly after precipitation events [38].

2.2. Invertebrate sampling

Aquatic invertebrates were sampled during the dry season (December 2015 to May 2016) and the wet period (July to October 2016). Three replicate samples of aquatic invertebrates were collected on two occasions [41] at four sites along the Lonquén River (Puente Esmeralda, Rincomavida, Buenos Aires and Trehuaco) (Figure 1 and Table 1). We considered the presence of disconnected pools during the dry period, the river connectivity and the four different aquatic states identified with the TREHS Tool to evaluate the transition from drying to flowing condition or vice versa. The 96 samples were collected using a hand net with rectangular frame (240 x 160 mm; 250 µm of mesh size) following the semi-quantitative, multihabitat 3-minute kick sampling method [42-45] and preserved in 70% v/v ethanol solution. In the laboratory, samples were sorted, and the taxonomic identification of specimens was performed to family level using standard systematic identification keys [46-48] and counted using a binocular dissecting stereomicroscope (Olympus SZX12). The majority of invertebrates were identified to the family level, except for Hydracarina, Copepoda, and Collembola (order level), because of the identification difficulty.

Table 1. Location of the sampling sites of the Lonquén River and distance to source and downstream confluence.

Sampling sites / meteorological and gauge stations	**Geographic Coordinates**				**Distance to:**	
	Latitude	**Longitude**	**Altitude (masl)**	**max wet river wide (m)**	**Source (km)**	**downstream confluence (km)**
Puente Esmeralda	-36.442051	-72.351664	80	40	45.0	44.8
Rincomavida	-36.480823	-72.383816	65	40	52.9	36.9
Buenos Aires	-36.471718	-72.441632	60	70	59.6	30.2
Trehuaco	-36.427605	-72.663469	30	100	86.3	3.5
Coelemu	-36.491944	-72.698888	80	-o-	-o-	-o-
Río Lonquén en Trehuaco	-36.427665	-72.664110	30	-o-	-o-	-o-

Water samples were collected at the same time as the invertebrate samples. The pH, temperature, conductivity and dissolved oxygen were recorded *in situ* using a multi-probe HydroLab Quanta (Hydrolab Corporation®, Texas, USA). Suspended solids, dissolved solids, nitrate, nitrite, ammonia, total nitrogen, phosphate, and total phosphorus were analysed in the Environmental Sciences Centre EULA-Chile laboratory. Nitrite, ammonia and orthophosphate were excluded from the analysis because values were below detection limits.

2.3. Statistical analysis

Daily values of thirty years (1986-2015) of precipitation and streamflow records were obtained from the meteorological station *Coelemu* (0814002-K) and the gauge station *Río Lonquén en Trehuaco* (08144001-8), both available from the Dirección General de Aguas (Ministry of Public Works in Chile: https://dga.mop.gob.cl/servicioshidrometeorologicos/Paginas/default.aspx). The software "Indicators of Hydrologic Alteration- IHA" [34] was used to estimate ecologically relevant hydrological indexes such as mean and median flow, flow predictability, mean annual minimum and maximum n-day flow (MAM-n days), and the Environmental Flow Components (EFC). These indicators were determined with non-parametric (percentile) statistics. The high flow and low flow pulse thresholds and the median plus or minus 25% were also calculated with the IHA software. Additionally, the maximum flow data series of mean daily streamflow [49] was used to predict the flood quantiles according to the Log Pearson Type III method. Finally, significant trends in streamflow and the number of zero flow days per year (threshold zero m^3/s) were detected using the non-parametric Mann-Kendall (MK) test [50,51] and Sen's slope estimation [52]. A confidence level of 90% was used as a threshold to categorise a positive Z value, indicating an upward trend or negative Z value showing a downward trend [53-55]. MK test were implemented using R software (v2.6.2) [56] and Kendall package (v2.2) [57].

We used the open-access software for PC TREHS Tool (Temporary Rivers Ecological and Hydrological Status) developed by Gallart et al. [7,31,35] to identify the temporal pattern of aquatic states related to flow. The streamflow data of the Lonquén River were analysed with the software to deduce the type of intermittent river using two metrics (flow permanence and the predictability of periods without flow). Furthermore, we obtained an estimate of each aquatic state's percentage per month, the Temporary Regime Plot and the Aquatic States Frequency Graph. These results contributed to decide on the best period for biological monitoring and to detect variability in the invertebrate communities during drying and rewetting periods.

The environmental variables and the community composition (presence/absence) and structure (taxonomical abundance) of the aquatic invertebrates were compared among the aquatic states identified with the TREHS model. We estimated the local diversity of the aquatic invertebrates for each aquatic state using the following measures of alpha diversity: Shannon diversity index, taxonomic richness (at the family level) and abundance. Differences among aquatic states in richness and total abundance were confirmed by the one-way ANOVA F-statistic [44]. Also, we calculated the proportion of the main taxonomic groups for each aquatic state, based on the taxonomical categories: Annelida, Mollusca (bivalves and gastropods), Crustacea, EPT (Ephemeroptera, Plecoptera and Trichoptera), OCH (Odonata, Coleoptera and Hemiptera), Diptera, and others to identify the groups that were most sensitive to flow permanence [15,56]. Furthermore, we calculated the dissimilarities of community composition among aquatic states employing the analysis of beta diversity (turn-over and nestedness) based on Sørensen dissimilarity to examine the species replacement and species additions for each aquatic state [15,59,60].

Differences between aquatic states were examined using the one-way analysis of variance (ANOVA) F-statistic. In contrast, temporal differences between individual aquatic states were conducted using Tukey's post-hoc multiple comparisons test to identify significant differences [44]. We also compared the multivariate dispersions within the aquatic states for biological and environmental terms using the test of homogeneity of dispersion (PERMDISP; 61) and recognise statistical differences in the mean environmental and biological distances of observations to their group centroids. We tested the null hypothesis of no differences in environmental heterogeneity, community structure (taxonomical abundance) and community composition (presence/absence) among the aquatic states. To reduce the differences between the variables, abundance, and rare taxa; this analysis was based on the Euclidean distance matrix after standardisation of data (mean = 0, SD = 1). To the environmental heterogeneity, the Bray-Curtis dissimilarity matrix used the abundance data to the community structure and the Sørensen dissimilarity matrix for the presence/absence data to the community composition [62-64].

Finally, a redundancy analysis (RDA) allowed us to examine the community structure and association with the distinguished environmental conditions associated with aquatic states. This constrained ordination method was based on the Bray-Curtis distance matrix after the Hellinger transformation of the abundance data [63-65]. RDA analysis generates a set of environmental variables (final model) explaining the community structure variation among aquatic states. The final model was selected through a forward selection procedure. This method considered two stopping rules: critical *p*-value ($\alpha = 0.05$) and the value of reduced model adjusted R^2 [66]. The Shannon diversity index, PERMDISP and RDA analysis were performed using the *vegan* package [67], and beta diversity was calculated with the *betapart* package [68] using the R software [56].

3. Results

3.1. Hydrological variability

The precipitation variability shows that rainfall is concentrated between June to September with an annual mean of 831 mm (SD ±248 mm). In 1998 the lowest rainfall was recorded (357.2 mm) and the highest in 2006 (1,242.5 mm). The streamflow variability shows an annual mean daily of 12.8 m^3/s (SD ±8.0 m^3/s) with the lowest values of 0.8 m^3/s in 1998 and the highest of 29.1 m^3/s registered to 1992. Also, Figure 2a) shows a substantial reduction in the annual mean daily flow. In the cases of the more significant flows, the highest streamflow in the time series data was registered at 901 m^3/s (July 12th, 1987) and 909 m^3/s (July 29th, 1988).

Figure 2b displays the flood frequency illustrating the probability of extreme flood events in the river with a return period of 1,000 years. Peak floods exceeding 900 m^3/s are expected to take place about every 50 years in the studied river.

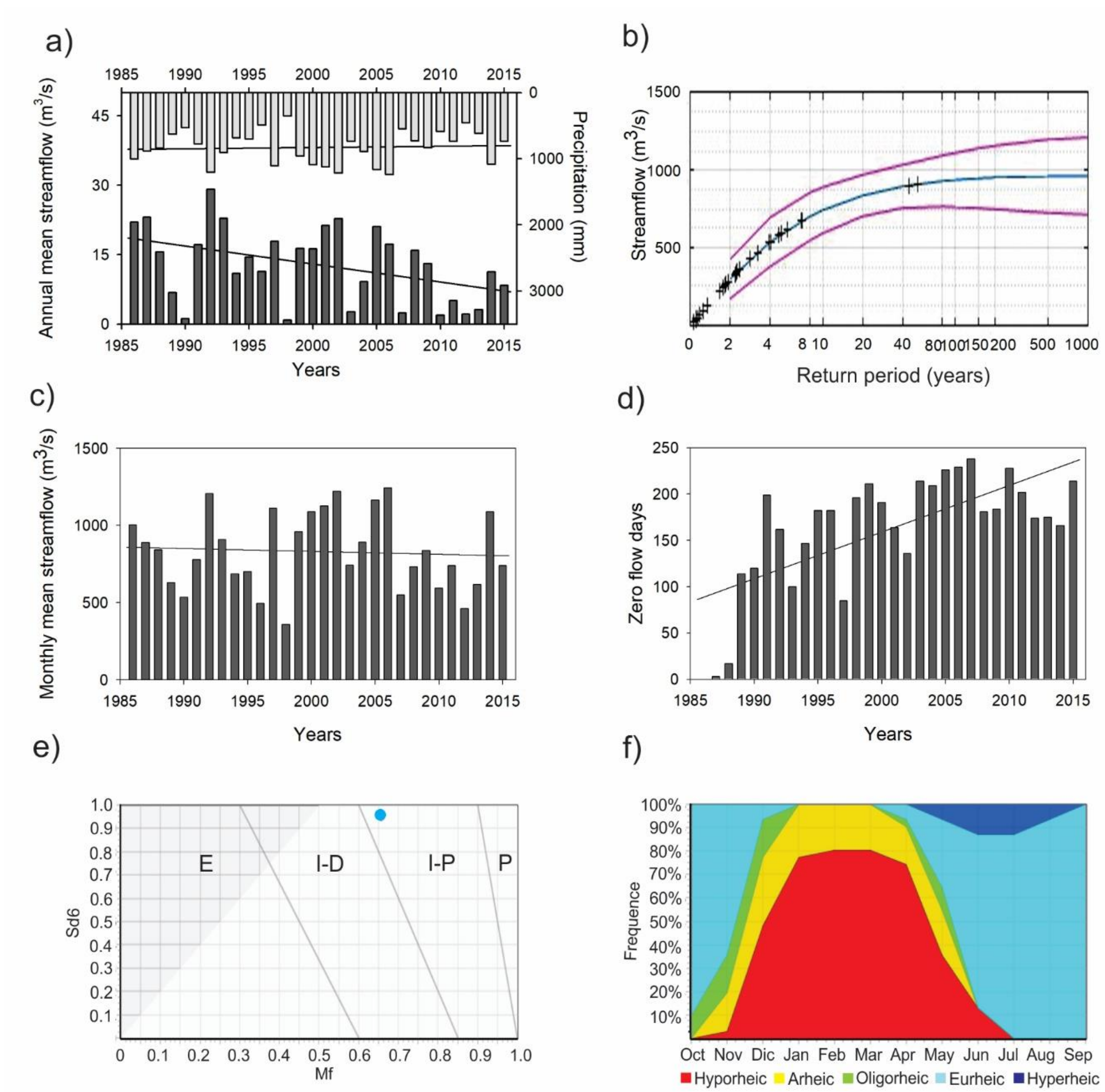


Figure 2. Annual mean streamflow and precipitation (a); probability of the extreme flood events (flood frequency analysis) (b); variation of the monthly mean streamflow (c); zero flow days (d); type of intermittent river (P: Perennial; I-P: Intermittent with pools; I-D: Intermittent-dry; E: Ephemeral) (e), and the aquatic states frequency graph (f) of the Lonquén River.

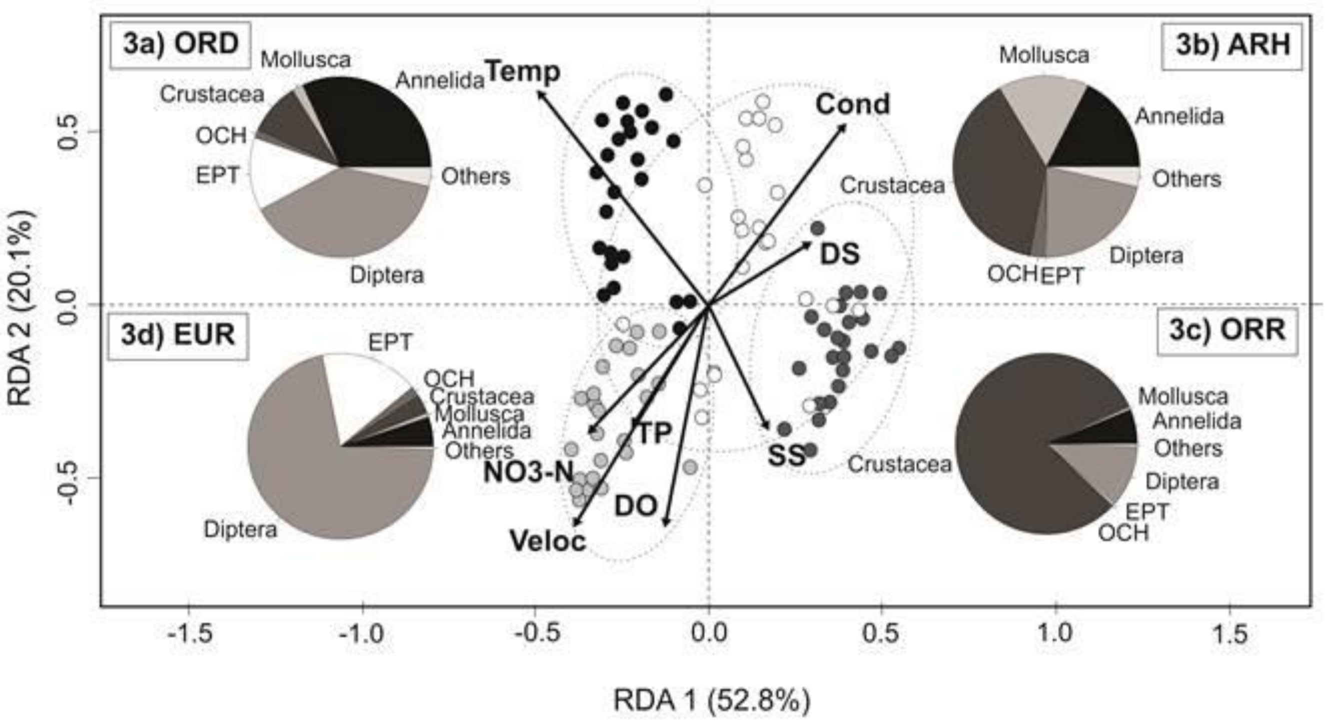
The IHA analysis was run twice: a) with the flow time-series including the 176 days of zero flow and b) replacing the zero values with the no-data symbol. The first simulation showed the highest median flow values (17.20 m^3/s) in August and zero flow (0.0 m^3/s) from December to May. The IHA simulation, in which the zero flow values were excluded prior to the analysis, showed the highest median flow values in August (16.7 m^3/s) and the lowest flow in January (0.1 m^3/s). The n-day minimum range from one to 90 days of the observations was between 0.04 to 0.13 m^3/s, respectively. In contrast, n-day maximum ranges (one to 90 days) were from 304.0 to 48.6 m^3/s. The base flow index was estimated at 0.005 m^3/s when zero flow values were excluded. Hence, the Environmental Flow Components (EFC) analysis revealed values of high flow peak of 19.15 m^3/s, small flood peak of 444.5 m^3/s and large flood peak of 901 m^3/s (Appendix A, Table S1).

The MK test shows a negative trend in the monthly mean streamflow at 95% confidence level (Z = -2.08; S = -4641; p = 0.037) equivalent to 0.031 m^3/s per year (Figure 2a). Instead, the zero flow days showed a positive trend at 90% confidence level (Z = 1.74; S = 148; p = 0.08), increasing with 3.5 days per year. The minimum of zero flow days was in 1986 (0 days) and the maximum (238 days) in 2007 with almost eight months of prolonged dry conditions (Figure 2d). These results display the considerable increased intermittence in the streamflow of the Lonquén River during the recorded time series. Additionally, the precipitation record shows no trend.
The application of the TREHS Tool revealed a *Regime I-P* (*intermittent with pools*) for the Lonquén River, as determined by the two calculated metrics: *the six months seasonal predictability of dry period* (Sd_6 = 0.9593), and *the measure of the flow permanence* (Mf = 0.6559), as presented in the Figure 2e. The Aquatic State Frequency Graphs (Figure 2f) illustrate the flow distribution related to the aquatic state at the Lonquén River. A dry period with no surface water determined from December to April (up 78% to 100%), where the river was under Arheic and Hyporheic conditions with the presence of some isolated pools (Appendix A, Table S2). The wet period occurred from June to November, with predictability higher than 60% (Eurheic and Hyperheic). The low flow situation where pools are connected by a small discharge of water (Oligorheic condition) was present in April and May (rewetting or flow resumption) and from October to December (drying or flow recession).

The distinct aquatic states were used to determine temporal variability (water quality and aquatic invertebrate composition and structure) during the transition from recession to the resumption of flow. The aquatic states were categorised according to flow permanence: Oligorheic during the drying phase or flow recession (ORD), Arheic with disconnected pools (ARH), Oligorheic during rewetting or flow resumption (ORR) and Eurheic with base flow conditions (EUR).

3.2. Environmental heterogeneity

Differences among environmental variables and aquatic states are summarised in Figure 3 and Table 2. The first two axes of the redundancy analysis (RDA1 and RDA2) significantly explained 72.9% of the total variation of environmental and taxonomical components (p < 0.001). RDA1 (52.8%) was mostly associated with velocity and temperature, the two variables that contributed most to environmental variability concomitant to the EUR and ORD, respectively. Conductivity and dissolved solids were the essential variables that explained the variability of the ARH states and were loaded toward the positive dimension of RDA1 and RDA2. The ORR state represented a transition between the dry and wet period with high values of dissolved oxygen and suspended solids, while the EUR state was also characterised by high values of dissolved oxygen, nitrates, total nitrogen and total



phosphorus.

Figure 3. Redundancy analysis (RDA) of the environmental variables: water temperature (Temp), conductivity (Cond), dissolved solids (DS), suspended solids (SS), dissolved oxygen (DO), water velocity (Veloc), nitrate-nitrogen (NO3-N) and total phosphorus (TP). The invertebrate community for the distinguished aquatic states is represented by the composition of the major invertebrate groups (pie charts) in the Lonquén River: (a) ORD (● Oligorheic-drying); (b) ARH (○ Arheic); (c) ORR (Oligorheic-rewetting), and (d) EUR (Eurheic).

Table 2. Summary of the environmental variables (mean ± standard deviation) measured in the different aquatic states at the Lonquén River (2015-2016) (see acronyms of aquatic states in Figure 3).

	ORD	ARH	ORR	EUR
Current velocity (m/s)	0.013±0.03	0.0±0.0	0.093±0.08	0.516±0.10
pH	7.64 ±0.40	7.52±0.68	6.65±0.24	7.80±0.27
Temperature (°C)	27.9±3.2	15.7±1.6	10.4±1.5	14.2±0.1
Conductivity (µS/cm)	232±48	289±28	226±38	120±4.5
Dissolved oxygen (mg/L)	5.48±1.53	5.96±2.74	8.72±2.05	10.81±0.23
Suspended solids (mg/L)	9.76±5.19	3.89±1.62	21.4±9.31	15.14±2.83

Dissolved solids (mg/L)	164±63	184±21	172±17	127±7
Nitrate-NO_3-N (mg/L)	0.06±0.10	0.12±0.07	0.02±0.01	0.17±0.02
Total Nitrogen (mg/L)	0.40±0.14	0.27+0.20	0.26±0.10	0.53±0.16
Total Phosphate (mg/L)	0.05±0.01	0.10±0.07	0.06±0.04	0.15±0.06

3.3. Taxonomical heterogeneity

A total of 66,392 individuals belonging to 49 families were collected in 96 samples. With respect to the aquatic states, the majority of individuals was obtained in the ORD state (absolute; relative abundance, 51,503; 77.6%), followed by the ORR (10,440; 15.7%), while the EUR (2,326; 3.5%) and ARH states (2,123; 3.2%) hosted the lowest numbers of individuals. These differences were statistically significant between the aquatic states (one-way ANOVA; F = 22.59, $p < 0.001$) with a significant increase marked to the ORD in comparison to the ARH (Tukey´s *post-hoc* test; F = 7.5, $p < 0.001$), ORR (Tukey´s *post-hoc* test; F = -5.8, $p < 0.001$) and EUR (Tukey´s *post-hoc* test; F = 6.5, $p < 0.001$) (Figure 4a). Similarly, family richness was most distinct during ORD in comparison to the rest of the aquatic states (one-way ANOVA; F = 8.995, $p < 0.001$), showing highest mean values (mean ±SD; 15.7±4.5; total = 40) in contrast with the ORR (10.0 ±3.2; total = 32) (Tukey´s *post-hoc* test; F = -1711, $p < 0.005$), EUR (9.2±2.8; total = 29) (Tukey´s *post-hoc* test; F = 2049, $p < 0.001$) and ARH states (8.2±3.0; total = 28) (Tukey´s *post-hoc* test; F = 2058, $p < 0.001$) (Figure 4b). The Shannon index (Figure 4c) revealed highest diversity in the drying condition (ORD), with decreasing values in the disconnected pools (ARH), rewetting phase (ORR) and base flow (EUR). The latter state was characterised by the highest beta diversity (Sørensen), with high percentages of species turn-over as compared to the other aquatic states (Figure 4d).

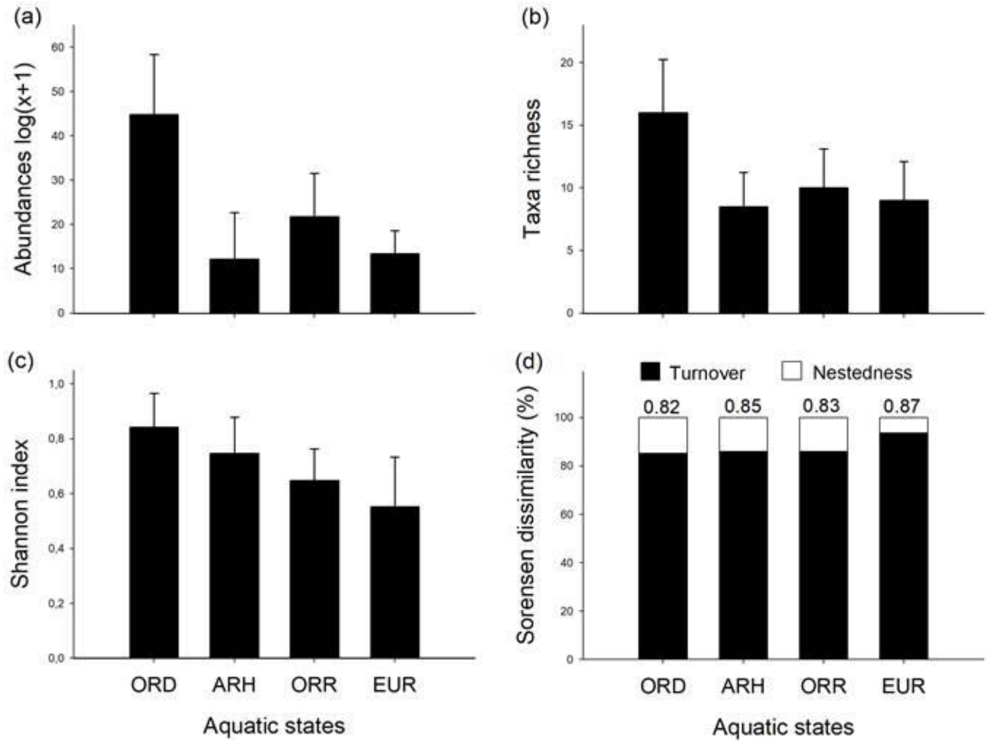


Figure 4. Mean of taxonomic metrics with standard deviation (-) for the distinguished aquatic states in the Lonquén River. Abundance log (x+1) (a); taxa richness (b); Shannon index (c); Sorensen dissimilarity (Turn-over %) (d), (see acronyms of aquatic states in Figure 3).

The aquatic invertebrate community was most distinguished in the ORD, with a high proportion of Annelida, crustaceans (cladocerans, copepods and ostracods), EPT (mainly mayflies) and Diptera (chironomids), superior to the rest of the aquatic states (Figure 3a). In the ARH state, the crustaceans, annelids, dipterans and molluscs were dominant in the stagnant pools (Figure 3b), as well as in the ORR, where microcrustaceans showed a higher abundance of individual species (Figure 3c). The EUR state was distinguished by the abundance of Diptera (chironomids) and Ephemeroptera (mayflies) with a reduced presence of Mollusca (gastropods), Ostracoda, Plecoptera (Grypopterigidae), Coleoptera (Dytiscidae) and non-chironomid dipterans (Figure 3d).

A high proportion of EPT and insect taxa were observed in the ORD and EUR states compared to the OCH and non-insect taxa (Figure 3a and 3d). The latter were mostly represented in the disconnected pools and during flow resumption (Figure 3b and 3c). The test of homogeneity (PERMDISP) evidenced the significant statistical differences in environmental heterogeneity among aquatic states (F= 7.087; p<0.001; Figure 5a). The same-pattern was revealed for the community composition (presence/absence; F= 9.026; p<0.001; Figure 5b) and the community structure (Bray-Curtis; F= 7.132; p<0.001; Figure 5c) among the aquatic states.

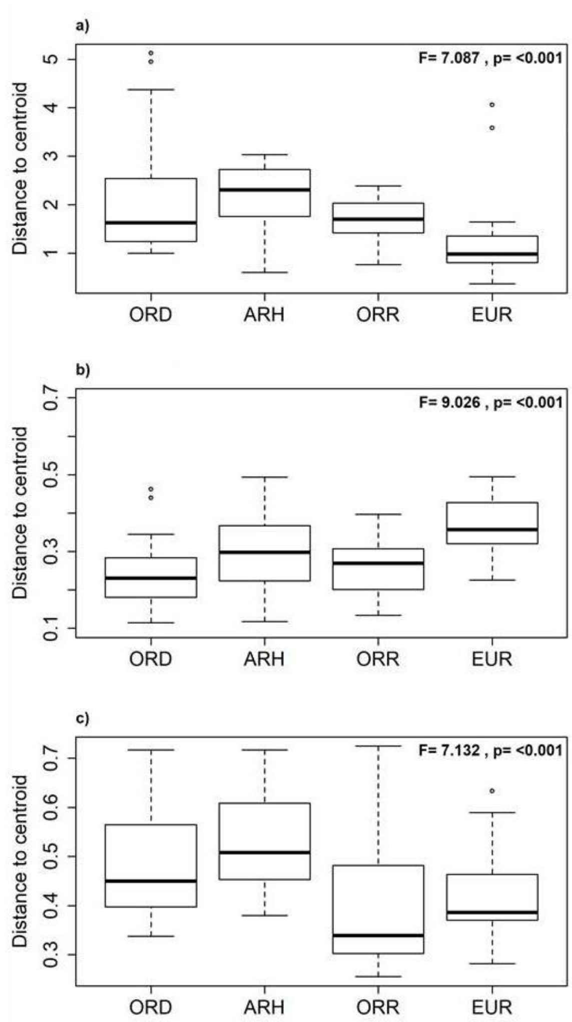


Figure 5. Boxplots of the test of homogeneity (PERMDISP) representing the mean distance from groups centroids of the environmental heterogeneity with Euclidean distance (a); taxonomical structure using abundance and Bray-Curtis dissimilarity (b), and taxonomical community using presence/absence and Sørensen dissimilarity (c) of the aquatic states (see acronyms of aquatic states in Figure 3).

4. Discussion

Here we present for the first time the integration of aquatic diversity and environmental conditions associated with different hydrological states - from drying to flow resumption - in an intermittent river from the Chilean Mediterranean. Significant patterns were revealed that are confirmed by several studies in other Mediterranean-climate regions of the world [10,14,69-73]. Besides, the open-access software TREHS Tool displayed an excellent response to the flow regime temporality in the Lonquén River compared to other hydrological indexes (e.g. Indicators of Hydrological Alterations – IHA). The tool included qualitative features such as the presence of flow, isolated pools or the lack of surface water, relevant to the biological communities [7]. Even though the Lonquén River is not a Mediterranean intermittent river from the Northern Hemisphere, the tool also proved to be applicable in our study region, as it reliably generated the two metrics and the different aquatic states. Further comparisons with other Mediterranean intermittent rivers could be considered, such as the Celone River (Puglia, Italy), which has similar seasonal predictability and flow permanence as compared to the Lonquén River (Figure 2e and 2f), for a better understanding on the functioning and structure of Mediterranean rivers in general [7,31,74].

Acuña et al. [75] and Buffagni et al. [76] 76observed a maximum habitat heterogeneity or diversification during streamflow reduction with the drying of the intermittent river. Drying of the river induced changes in the invertebrate community structure and composition with dominance of tolerant and adapted taxa to the low or no flow conditions and with the capacity to resist and recover from the drought period [72,76-79]. Our results confirmed this general pattern (Figure 3a). During the drying or recession period (ORD), there was a dominance of Diptera (chironomids), Annelida (*Nais* sp.) and Ephemeroptera (Baetidae and Caenidae) with a smaller but still considerable proportion of Ostracoda (Cyprididae), Hydracarina, Copepoda (Harpacticoida), Branchiopoda (*Daphnia ambigua*), Gastropoda (*Physa chilensis*), Hemiptera (Corixidae and Belastomatidae), Odonata (Aeshnidae and Coenagrionidae) and Coleoptera (Dytiscidae). All of these groups are recognised to be more adapted to the cessation of streamflow and to be able to survive lentic conditions [60,69]. The Ephemeroptera Baetidae family is also present during drying conditions and can resist prolonged harsh conditions while gaining tolerance to drought [80]. In our study, the Baetidae family (8%) and Caenidae (5%) also showed good representation during flow recession in the Lonquén River.

Prior studies conducted by Munné & Prat in 184 sites located in the Catalan Mediterranean Basins, NE Spain [70] and Hill & Milner in Manifold and Hamps rivers in the English Peak District of United Kingdom [60] reported that during the transition from the lotic to the lentic phase (disconnected, isolated or stagnant pools), many rheophilic taxa are replaced by others that are adapted to lentic habitats and that actively disperse when the river falls dry, such as Hemiptera (Corixidae) and Coleoptera (Dytiscidae and Helephoridae). A similar pattern was observed in our results, specifically illustrated by the higher presence of Hemiptera (Corixidae and Belastomatidae), Coleoptera (Heteroceridae, Hydrophilidae, Dytiscidae and Helephoridae) and Odonata (Coenagrionidae, Aeshnidae and Libelullidae) in comparison with the Ephemeroptera, Plecoptera and Trichoptera.

During drying and rewetting events, complex interactions take place between hydrological and physicochemical processes that expose the aquatic organisms to changing levels of abiotic variables, including chemical compounds [81]. Our results showed significant differences with a higher temperature during the drying period (ORD) (mean ±SD; 27.9±3.2°C) as part of the seasonal variability (summer). During the transition of drying to isolated pools (ARH), lower values of dissolved oxygen (5.95±2.74 mg/L), suspended solids (3.89±1.62 mg/L) and high conductivity values (289±28 µS/cm) were observed in the pools (Table 2). These changes associated with the loss of flow permanence also cause distinct variability in photosynthetic and respiration processes that may, in turn, result in high values of dissolved oxygen and pH on some occasions during the day and lower values at night [18,70]. These sometimes extreme environmental conditions affect the richness, abundance and diversity of aquatic invertebrates [76], as revealed here by the significant changes that were observed between the recession of flow to the disconnected pools phase (accept hypothesis 1; Figure 3 and 4).

When flow ceases in IRES, the presence of disconnected pools serves as an essential refuge to escape drought for a diverse and unique aquatic flora and fauna [18,82], which are adapted to survive even in the dry streambed through diverse strategies [60]. As a consequence, the density of lentic taxa increases, also including predator species, such as odonate larvae (Aeshnidae) and water scavengers beetles (dytiscids) [83]. Nevertheless, some fishes were present in the isolated pools of our study, which are also recognised to influence as predators and generate a significant change in the density and assemblages of the aquatic invertebrates [83].

Rest-pools in the streambed also provide habitat for newly colonising and dispersing taxa with the opportunity to survive and persist through flow cessation [18,60,82,84]. Although in our findings, some species of Diptera, Annelida and Ephemeroptera occurred in higher proportions during the drying period (Figure 3b). Peculiarly, high abundances were present in pools of taxa belonging to Gastropoda (*Physa chilensis*), Annelida (Lumbriculidae and Naididae), Ostracoda (Cyprididae), Copepoda (Cyclopoida and Harpacticoida) and Branchiopoda (Daphniidae) with fewer individuals counted for Coleoptera (Dytiscidae and Hydrophilidae) and Odonata (Aeshnidae). Decapoda (*Aegla* sp. and *Samastacus spinifrons*) and Bivalvia (*Diplodon chilensis*) were only represented in the isolated pools during the dry phase, where they have a low dispersal capacity and are protected from flow recession (accept hypothesis 2).

The flow resumption phase in intermittent rivers allows the recolonisation after the drought event. These routes have been distinguished by aerial dispersal, drift from upstream, redistribution from instream refugia or diapause (hyporheic zone) with increases in abundance and diversity of macroinvertebrates such as midges (chironomids) and blackflies (simulids) that are abundant in the early stage of flow resumption [62,85]. The invertebrate community structure in intermittent rivers typically recovers within a month after flow resumption, except for populations with low resilience, resulting in adverse effects on ecosystem functions (e.g. mollusc and some crustaceans) [79,86,87]. However, the resistant propagules in the sediment (often called seedbanks) of dry riverbeds and from the hyporheic zone are crucial for recolonisation after flow resumption and determine the aquatic invertebrate resilience level after drought [72,88-90]. In this study, a higher proportion of Branchiopoda (Bosminidae), Ostracoda (Cyprididae), Copepoda (Cyclopoida) and Annelida (Lumbriculidae) occurred during the rewetting, in contrast to the disconnected pools phase. Branchiopoda, Ostracoda and Copepoda produce drought-resistant dormant eggs or larval stages that survive long in the sediment and hatch after flow resumption. This process makes these species more resilient to drought than other taxa, which is in analogy with endorheic temporary pond systems [22].

During the wet season (base flow), recovery of flow permanence in the intermittent river contributes to the formation of spatial heterogeneity of mesohabitats, restoring the riffle habitats and promoting the recolonisation of riffles [71]. Rheophilic taxa (EPT) tends to be dominant in these mesohabitats, where especially a high correlation is reported between EPT and the increase of flow permanence [91]. In contrast, taxa adapted to low flow (OCH) disappear. Similar to Kelso and Entrekin [84], there is an increased richness and diversity of rheophilic taxa during rewetting. However, the richness and abundance during this (base flow) phase in our studied system were lower in comparison with the drying and rewetting conditions (Figure 4), which may be due to the disturbance by high flood in the river before the sampling dates (hyperrheic state). Such flooding events are recognised to cause intense but short-lived disturbance [31], causing a considerable scour of the aquatic invertebrates. In the Eurheic state, Leptophlebidae, Gripopterigidae, Simuliidae, Limoniidae and Tabanidae were recorded, representing riffle taxa adapted to flow [9292].

Our results also demonstrated that family taxon richness and abundance metrics were reliable indicators to compare between the aquatic states and unravel variations during the transition from drying to rewetting and base flow, similarly reported by Munné & Prat [7070]. Also, proportions of aquatic invertebrate groups (e.g. EPT%, OCH%, Diptera%, Non-insect%) and the diversity indices (alpha and beta) responded to the contraction and expansion of flow permanence in the Lonquén River (Table 3). We found higher richness, abundance and diversity during the drying period (flow recession) than during flowing conditions. These patterns will allow comparison with other IRES [71,72,93].

Table 3. Taxonomic metrics selected by relevance to intermittent flows and expected response to the transitional variability from flow recession to the resumption in IRES.

Metric	Definition	Relevance to intermittent flows	Reference
Richness	The number of species of a given taxon in the chosen assemblage. The number of species or taxa in the unit of study (Magurran, 1988).	Lower values are expected in intermittent flow rivers than in permanent ones. It is decreasing after the disconnection of the river in isolated pools with lentic-like and resistance taxa colonising in the dry period.	Drummond et al. 2015; Dolédec et al. 2017; Skoulikidis et al. 2017; Soria et al. 2017; Hill & Milner, 2018; Wilding et al. 2018
Abundance	Number of individuals (density or biomass) of each specie or community (Magurran, 1988).	Lower values are expected in intermittent flow rivers than in permanent ones.	Stubbington et al. 2009; Cid et al. 2017; Dolédec et al. 2017. Acuña et al. 2005
		Increased abundance (and richness) is possible to find soon after flow ceased with a rapid decrease when the isolated pools are constituted.	Present study
Shannon diversity	Mathematical index to measure the diversity in a natural systems and it assumes that individuals are randomly sampled from an	Higher values are expected in perennial sites than intermittent.	Drummond et al. 2015
		It is expected to find high values in the drying condition or pools when the river is recently disconnected.	Present study

	infinitely large community and that all species are represented in the sample (Magurran, 1988).		
Beta diversity	Difference in species composition (and sometimes species abundance) among sites, or turn-over between two or more habitats or localities (Magurran 1988).	Change in community composition along hydrological intermittence gradients is driven by loss (nestedness) and turnover (replacement) of taxa due to increasing fragmentation or environmental harshness.	Datry et al.2016b; Datry et al. 2017; Hill & Milner, 2018
	Turn-over: Replacement of some species by others between sites Nestedness: smaller numbers of species are subsets of the biota at richer sites (Baselga 2010).	Community structure may vary sharply during the different hydrological phases. During the phases dominated by dispersal (flowing), the nestedness may be observed, particularly for weak to moderate dispersers. In contrast, when species sorting or environmental filtering dominates in IRES, the taxa turn-over may be observed more commonly during the non-flowing or dry phase.	Datry et al. 2017; Present study
		High beta diversity (turn-over) is expected to find in the perennial sites after the high flood perturbation. However, the nestedness is possible to be moderate in intermittent sites and disconnected pools than perennials.	

Some studies state that the loss of freshwater biodiversity at a global scale is expected to be higher in Mediterranean basins, especially considering climate change and associated anthropogenic threats, with habitat loss as the prime factor resulting in species extinction [33,71,94]. The predictions of climate change for central Chile include extreme climatic events, such as the increase in summer mean air temperature (2° to 4° C), reduction of precipitation (20 to 40%) and decrease in summer river streamflow (20%) [26-30], especially in the Mediterranean zone [28,29]. Already in our study, a reduction of streamflow and an increase in the number of zero flow days were revealed in the Lonquén River during a period of about 30 years. It is expected that this pattern will continue, further affecting the flow permanence in the region under future climatic change and land-use scenarios. These predicted harsh conditions are expected to decrease the percentages of Eurheic and Oligorheic states, while at the same time to increase the prevalence of Arheic and Hyporheic (dry period) conditions.

Future reductions in water permanence may lead to increased habitat heterogeneity with contraction of flow and formation of pools with the need of migration and prolonged exposure of aquatic organisms to predation and competition in isolated pools or even the disappearance of these refugees by completely drying-out [87,95-98]. Some resistant species could become more dominant in the dry riverbeds. For example, zooplankton resists dry periods by producing resistant dormant eggs that can be distributed by birds and winds and that hatch when floods return [16]. Indeed, branchiopods and ostracods were observed in higher proportions in the Oligorheic state after flow resumption (ORR) in our results, indicating the importance of resistance traits to the dry conditions, which may even become more intense with possible scenarios of climate change [99]. Furthermore, the extent and duration of drying events and water abstraction will further lower the water table and affect the colonisation and resilience of the invertebrate communities in IRES from the hyporheic zone that is also used as a refuge and to survive during the drying events [88].

Although the central Chile Mediterranean basin (ChMZ) is recognised as a global hotspot of biodiversity with extraordinary endemism in plants and fauna [94,100], only limited research is taking place on IRES, essential ecosystems in the region. Studies on freshwater biodiversity are scarce, and numerous Mediterranean rivers in Chile remain completely unexplored or not including an ecological approach [24]. Unfortunately, as for most of the worldwide Mediterranean systems, the IRES have not yet been included in conservation management despite the ecosystem services that provide for the human-well being [101], where the standards for water quality and biodiversity conservation are only determined for perennial rivers [71], especially concerning their vulnerability to climate change and anthropogenic stressors [102].

However, limited knowledge, availability of resources for research and development in most Mediterranean countries have generated ineffective conservation and management strategies of IRES [10]. It is necessary that public and private institutions relevant to water monitoring and management in Chile, such as the DGA, can recognise the ecosystem services provided by IRES and extend the ecological monitoring to these streams. Establishing reference conditions of IRES in the ChMZ will be an essential asset for conservation and management in response to the climate change, considering the decline of endemic populations, the loss of freshwater biodiversity and fragmentation of the aquatic ecosystems. Some of the bivalves, gastropods and crustacean species in our study are endemics for Chile, should be considered in adaptative and conservation strategies for their low capability to migrate to other basins under harsh climate conditions [24,103]. These considerations are especially important for the species *Diplodons chilensis, Littoridina cumingii, Chilina dombeyana, Physa chilensis, Biomphalaria chilensis, Gundlachia gayana, Hyalella costera, Aegla sp.* and *Samastacus spinifrons*, additionally to the microcrustacean groups (cladocerans, copepods and ostracods) identified in our samples (Appendix A, Table S3). This is especially relevant, considering the expectation that more perennial rivers will convert to temporal or intermittent ones by the impact of land use and climate change in the region [32].

5. Conclusions

This study is the first on IRES integrating hydrological, environmental and aquatic diversity variables during the transition from drying to flowing condition in a Mediterranean intermittent river in South America. Significant patterns revealed that help to understand the response of aquatic invertebrates to shifting temporal habitats. Our findings revealed that a substantial reduction of the streamflow and a clear trend towards increasing zero flow days in the last decades in the Mediterranean climates could cause lost sensible species with low capability to migrate on the riverine ecosystems. Furthermore, it is expected to find alterations in biological diversity and their biotic interactions. It was also possible to affirm the importance of disconnected pools as refuges for a diverse and unique set of aquatic flora and fauna and provide habitat for colonisation after flow resumption. During the transition from recession to the resumption of flow, the biological diversity significantly changed from species adapted to flowing conditions (rheophilic taxa) to non-flowing water such as the OCH taxa and the non-insect species (bivalves, gastropods and crustacean). Further long-term biological, hydro-meteorological and water quality monitoring studies are necessary to provide a site-specific history that allows the integration of temporal and spatial variability to define the conservation status and identify climatic change effects.

Supplementary Materials: Table S1: Indicators of Hydrologic Alteration- IHA in the Lonquén River. Table S2: Percentage of the aquatic states frequency of the Lonquén River. Table S3: Aquatic invertebrate taxa (Family and taxon) recorded in the Lonquén River, according to aquatic states and sampling sites (PE: Puente Esmeralda; RM: Rincomavida; BA: Buenos Aires; TR: Trehuaco).

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CAPÍTULO II

RESISTANCE AND RESILIENCE TRAITS COMPOSITION OF THE AQUATIC INVERTEBRATES COMMUNITY IN A MEDITERRANEAN INTERMITTENT RIVER

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Abstract: The hydrological process controls the non-perennial waterways, where the cessation of the surface water tends to regulate the ecological processes. It is known that more than half of the global river network are non-perennials, and it is expected to increase in the future by anthropogenic and climate change scenarios. A hydrological analysis was conducted in the Lonquen river focused on 30 years of streamflow records. A dry period between November to April with an increase of zero flow days was recognised. Four sites were sampled for the aquatic invertebrates analysis, besides four hydrological phases (drying, dry with pools, rewetting and baseflow) identified. No significant differences were detected between the spatial variability, while to the hydrological phases, the ANOSIM analysis showed a statistical difference between these phases (ANOSIM: R= 0.79; 0.001). The SIMPER results indicated the abundance of annelids (Nais sp. and Lumbricus sp.) chironomids, cladocerans (Bosmina hagmanii), copepods (Cyclopoida), ostracods (Herpetocypris reptans and Cypridopsis vidua), mayflies (Caenis sp. and Andesiops sp.), the gastropod Physa chilensis, in the contribution of the dissimilarity of the hydrological phases. The resilience and resistance traits in the hydrological phases were constituted by 14 modalities with a distinction for short life cycle duration and the many numbers of generations per year as part of the resilience categories in the flowing recession. The resistance traits emphasised the presence of cocoons and the plastron respiration in the disconnected pools. The resistance and resilience traits are indicative of ecological strategies to survive and restore the biota after the drying perturbation. So that, further studies are required to expand the understanding of the aquatic invertebrates behaviour to face climate change scenarios and human

ABSTRACT

The hydrological process controls the non-perennial waterways, where the cessation of the surface water tends to regulate the ecological processes. It is known that more than half of the global river network are non-perennials, and it is expected to increase in the future by anthropogenic and climate change scenarios. A hydrological analysis was conducted in the Lonquen river focused on 30 years of streamflow records. A dry period between November to April with an increase of zero flow days was recognised. Four sites were sampled for the aquatic invertebrates analysis, besides four hydrological phases (drying, dry with pools, rewetting and baseflow) identified. No significant differences were detected between the spatial variability, while to the hydrological phases, the ANOSIM analysis showed a statistical difference between these phases (ANOSIM: R= 0.79; 0.001). The SIMPER results indicated the abundance of annelids (*Nais* sp. and *Lumbricus* sp.) chironomids, cladocerans (*Bosmina hagmanii*), copepods (Cyclopoida), ostracods (*Herpetocypris reptans* and *Cypridopsis vidua*), mayflies (*Caenis* sp. and *Andesiops* sp.), the gastropod *Physa chilensis*, in the contribution of the dissimilarity of the hydrological phases. The resilience and resistance traits in the hydrological phases were constituted by 14 modalities with a distinction for short life cycle duration and the many numbers of generations per year as part of the resilience categories in the flowing recession. The resistance traits emphasised the presence of cocoons and the plastron respiration in the disconnected pools. The resistance and resilience traits are indicative of ecological strategies to survive and restore the biota after the drying perturbation. So that, further studies are required to expand the understanding of the aquatic invertebrate behaviour to face climate change scenarios and human perturbations.

Keywords: *non-perennial waterways, biological traits, intermittent rivers, flow cessation, flow resumption, disconnected pools.*

1. Introduction

The non-perennial waterways are characterised by a temporary lack of surface flow that leads to isolated pools or dry channels (Busch et al. 2020). They are controlled by the magnitude and intensity of the rainfall (hydrological regime), high rates of evaporation, geology (type of soil) and the deep groundwater that influence in the hydrological and ecological processes (Smeti et al. 2019; Fortesa et al. 2021; Shanafield et al. 2021). Similarly, the non-perennial waterways can also be recognised as intermittents when they are referred to as a seasonal flow during a part of the year, and the ephemerals just have continuous surface flow immediately following the precipitation (Fritz et al. 2020; Shanafield et al. 2021).

The intermittent rivers and ephemeral streams are represented over half of the global river network length (Datry et al. 2016; Shumilova et al. 2019) even up to 60% of all rivers and streams of the world cease to flow at least one day per year

(Messager et al. 2020). Several studies have revealed that the occurrence of non-perennial rivers will increase in the future due to shifts in global climate, land cover change and increase of water abstractions with an urgent need to assess the hydrological and ecological conditions worldwide to face climate change (Cid et al. 2016; Datry et al. 2017; Yu et al. 2018; Busch et al. 2020).

The aquatic invertebrate communities of the intermittent rivers that historically experience drying events have a high capacity to recover when flow resume and persist through periods without surface water (resistance). Similarly, they also can return to their previous conditions soon after flow resumes (resilience), involving physiological, behavioural, and dispersal adaptations that allow the organisms to persist through the drying disturbances (Datry et al. 2013; Kelso & Entrekin, 2018; Crabot et al. 2020). Dispersal, substrate relation and resilience form provide essential information to assess resistance and resilience conditions into the structure and functioning of stream communities in non-perennial rivers (Usseglio_Polaterra et al. 2000; Bonada et al. 2007).

The recovery of the aquatic invertebrate composition in the intermittent rivers after the drought disturbance depends on the recolonisation process from desiccation-resistant dormant stages (hyporheic refuges), aerial dispersal and drift from the refuge or perennial reaches. These conditions are critical to the recolonisation processes from upstream reaches or neighbouring basins and passive or slower instream dispersal to the recovery or restoration of the aquatic community from weeks to several months (Hay et al. 2017; Bogan et al. 2018). The desiccation-resistant eggs conform to the invertebrate seedbanks, cocoons, cysts, and larval and adult invertebrates in diapause conformed mainly by a large number of protistans, nematodes, rotifers and microcrustaceans that emerge from the dry sediments annually-inundated sections during the flow resumption (Boulton et al. 1993; Hay et al. 2017).

Predictions of climate change indicate that drought events may increase in some regions with a higher frequency of dry conditions, becoming unknown the response of the aquatic invertebrates to face the transition from wet-dry cycles with a harsh climate in the future (Stubbington et al. 2016). Furthermore, it is expected that more perennial rivers change to intermittent or temporary states affected by the climatic change scenarios and anthropogenic interventions with a considerable prediction that could disturb the hydrology and aquatic biodiversity in the non-perennial rivers (Datry et al. 2014).

Historically, there has existed a perception of the non-perennial waterways to devaluate and underestimate them because they are not considered as relevant to the ecological processes, habitat for biodiversity, and human well-being with a relative lack of scientific attention (Arscott et al. 2010; Rodriguez-Lozano et al. 2020). Nevertheless, some initiatives are recovering more attention in recent years, where the intermittent rivers and ephemeral streams have been positioned into the conservation status in some areas of the Mediterranean climates (Leigh et al. 2016; Acuá et al. 2017; Stubbington et al. 2018). Besides, exists a significant challenge to conducting these ecosystems to a legal, regulatory and conservation status worldwide (Nikolaidis et al. 2013; Skoulikidis et al. 2017).

We focus on the composition of the aquatic invertebrate community collected in the Lonquén intermittent river, identifying biological traits that represent the characteristics of adaptation and recovery to the dry phase in the annual flow regime. We aimed to identify the resistance and resilience traits of the aquatic invertebrates in the intermittent Lonquen river, according to the adaptations from flow cessation to resumption conditions. We also predict that the variation of the flowing conditions in the Lonquen river shows a fluctuation of the resistance and resilience traits that allow to recolonise and establish the biotic assemblage in the intermittent river.

MATERIALS AND METHODS

2.1 Study area

The Lonquen river basin is part of the coastal mountain range from the Chilean Mediterranean Zone in the central-south of Chile. It has an area of 1,178 km^2, and it is characterised by a marked Mediterranean seasonal climate with precipitation that varies from 400 to 1200 mm and evapotranspiration from 944 to 1244 mm. The mean annual air temperature was 15ºC (1 to 35ªC) with an annual mean daily streamflow of 12.8 m^3/s and a variation in the monthly mean streamflow showing an increase of 3.5 zero flow days per year, corresponding to data between 1985 to 2015 (Uribe et al. 2004, Banegas et al. 2021). According to the THRES Tool (Gallart et al. 2016), the Lonquen river is an intermittent river with pools determined by the six months seasonal predictability of the dry period (Sd6 = 0.9593) and the measure of the flow permanence (Mf = 0.6559). In addition, the TREHS Tool also displayed the flow distribution related to the aquatic states showing a dry period with no surface water from December to April and a wet period that occurred from June to November. (Banegas et al. 2021).

The basin of the Lonquen river is conformed by rolling hills, mountains and temporary streams with low permeability, high capacity of moisture retention and low infiltration rates in the subsoil. The landscape of the river basin is covered mainly by agricultural areas in 43% (vineyards, wheat, maise, potatoes and other vegetables), meadows and thickets (36%), forest (native species and introduced pine and eucalyptus plantations) being 20% and less than 1% is represented by urban, industrial and other areas without vegetation (Uribe et al. 2004; Duque & Vasquez, 2015).

2.2 Invertebrate sampling

The sampling of the aquatic invertebrates was conducted from December 2015 to October 2016. We selected four sites in the Lonquen river (Puente Esmeralda, Rincomavida, Buenos Aires and Trehuaco) because they were characterised by the presence of riffles in the wet period and disconnected pools during the dry period (Figure 1). A total of 192 samples were collected in the four sites, based on a multihabitat 3-min kick sampling method using a hand net with a rectangular frame (240 x 160 mm; 250 µm of mesh size). In all four study reaches we collected six replicates samples in two sampling occasions during the *drying* (slightly connected pools with lentic and lotic fauna), *dry with the presence of disconnected pools* (no surface water), *rewetting* (disconnected pools with only lentic fauna) and *base flow* (abundant riffles and mesohabitat available and connected) conditions in the river (Gallart et al. 2012; Garcia et al. 2017). All the samples were preserved in 70% ethanol and sorted in the laboratory. All the specimens were counted and identified to the lowest taxonomical level possible (usually genus) (Suarez et al. 2017; White et al. 2017; Crabot et al. 2020).

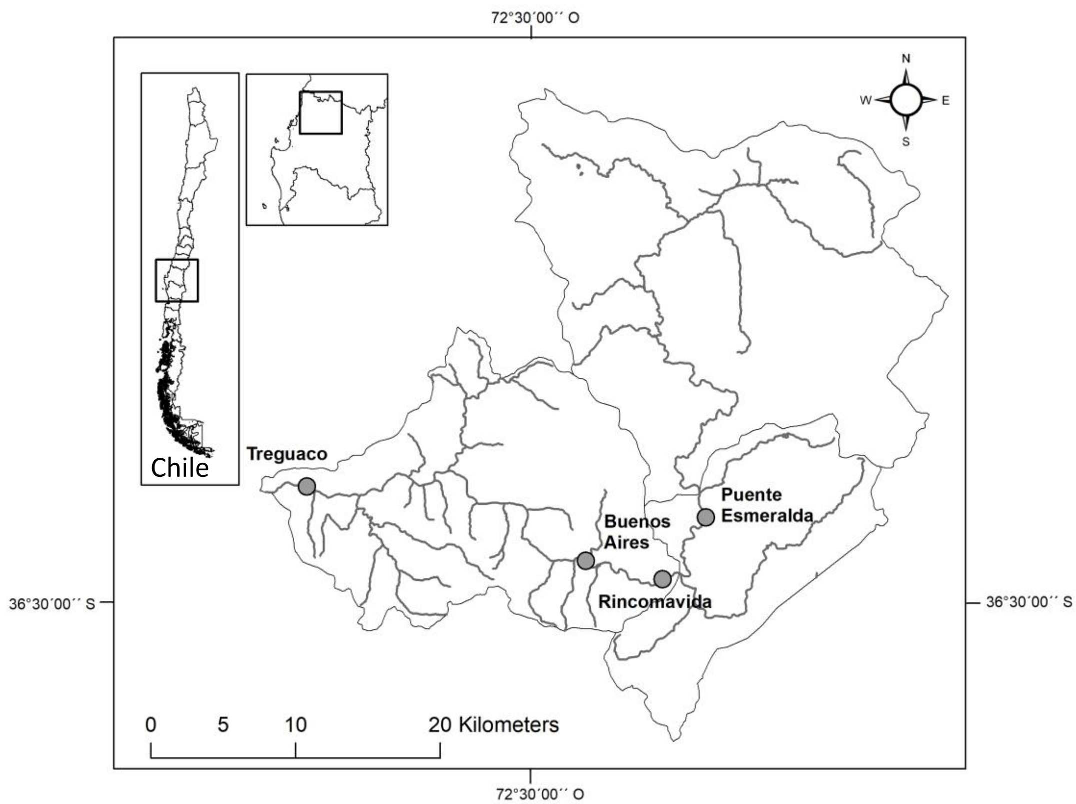

Figure 1. Map of the Lonquen river showing the sampled sites.

2.3 Statistical analysis

The monthly streamflow records (1986-2015) were collected from the gauge station *Río Lonquén en Trehuaco* (08144001-8) available from the Dirección General de Aguas (Ministry of Public Works in Chile: http://snia.dga.cl/BNAConsultas/reportes). The physico-chemical variables in water and the community structure of the aquatic invertebrates were analysed to identify variations among the sites. Similarly, we identified four flowing conditions according to the presence of surface water in the waterway of the Lonquen river, identifying four flowing conditions: drying, dry with pools, rewetting and baseflow (Lobrera et al. 2019). The total taxonomical richness, abundance (log x+1) and Shannon diversity index were analysed using the univariate diversity indices (DIVERSE) for each sampling site and the seasonal flowing conditions in the Lonquen river. Differences between the flowing conditions across all sites sampled and the flowing conditions were determined by the two-way crossed analysis of similarities (ANOSIM) with a significance level of 0.1% (Lobrera et al. 2019)

The richness and Shannon diversity were calculated using the raw abundance (Beche et al. 2006). Consequently, the biological data was overall transformed to square root to down weight the high abundances before applying the Bray-Curtis dissimilarity matrix to the community structure. Similarly, a non-metric multidimensional scaling (nMDS) was conducted to order the variation patterns of the aquatic invertebrates assemblages ranked among the hydrological phases of the Lonquen river (Stubbington et al. 2016; Lobrera et l. 2019). All analyses were calculated using the PRIMER-E v.6 software (Clarke & Gorley, 2006).

The description of the resistance and resilience biological traits composition was determined by seven categories across fourteen modalities for the resilience and resistance traits, according to Usseglio-Polaterra et al. (2000) and Tatchet et al. (2010). We only considered biological traits related to drying and rewetting conditions as resistance and resilience features in the Lonquen river based on the lifespan, reproduction, dispersal, resistance, respiration and locomotion as described by Crabott et al. (2020) to specify the adaptation to variation in the flowing conditions in the intermittent river selecting the strongest affinity of each taxon to each category.

RESULTS

The streamflow of the Lonquen river has shown variation during the studied period from 1985 to 2015. The highest concentrations were observed between June and October, reducing in recent years. It showed the highest values of 29.1 m^3/s to 1992, while the lowest was registered in 1998 (0.8 m^3/s). The annual mean daily streamflow was 12,8 m^3/s (SD $\pm$ 8 m^3/s). Similarly, a recognised period of dry conditions is evidenced during November to April, coinciding with the summer and autumn seasons in the Mediterranean zone of Chile (Figure 2).

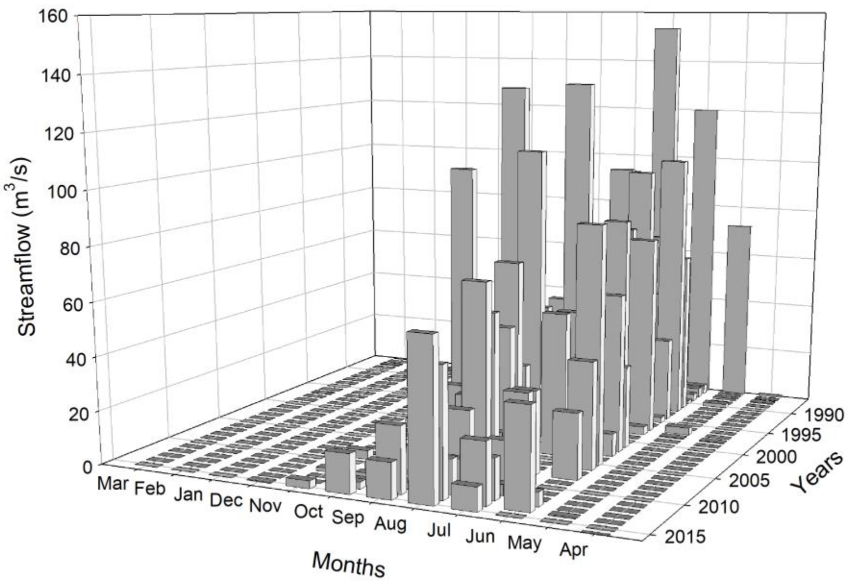

Figure 2. variation of the monthly mean streamflow of the Lonquen river.

Spatial and temporal variations in the taxonomic composition

A total of 55 taxa were identified at the four sites in the Lonquen river with a total of 187,356 individuals. The taxonomic composition evidenced no significant differences between sites (ANOSIM: Global R= 0.399; *p*-value < 0.001) that were represented by Puente Esmeralda (mean ±SD of richness; abundance; Shannon diversity: 9.55±5.5; 282±378; 0.665±0.69), Rincomavida (11±4.8; 634±822; 0.684±0.16), Buenos Aires (8.9±3.8; 441±731; 0.669±0.17), and Trehuaco (9.53±4.6; 1764±3126; 0.573±0.17). The hydrological phases were represented by the drying (13.7±4.1; 112.6±487.6; 0.756±0.19), dry with pools (6.4±2.9; 11.8±23.1; 0.644±0.21); rewetting (8.5±3.2; 45.8±200; 0.629±0.13) and baseflow (6.4±2.4; 13.04±34.18; 0.455±0.15) that were representative of the flowing conditions in the Lonquen river (Figure 3a and 3b).

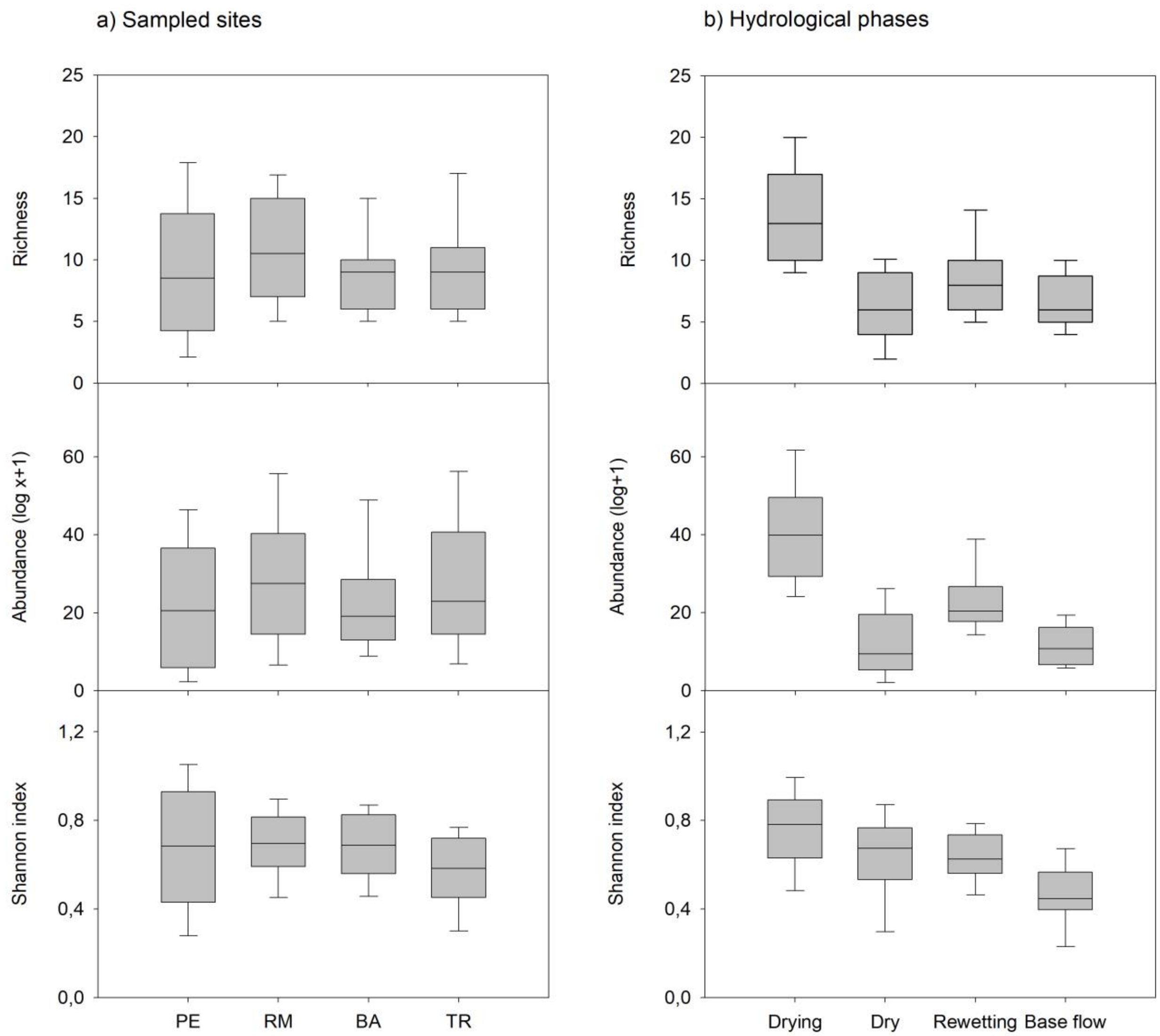

Figure 3. spatial and temporal variations across the sampled sites (a) PE: Puente Esmeralda, RM: Rincomavida, BA: Buenos Aires, TR: Trehuaco and the hydrological phases (drying, dry with pools, rewetting and baseflow) in the Lonquen river. Median values (horizontal central line), 5^{th} and 95^{th} percentiles as vertical boxes with error bars.

The nMDS displayed the patterns of the assemblage of the aquatic invertebrates grouped by the hydrological phases being the drying, rewetting and baseflow phases grouped by similarity of the aquatic invertebrates. In contrast, the dry with pools displayed a major scattering compared to the other flowing conditions. Besides, the ANOSIM (R= 0.79; 0.001) showed significant differences between the hydrological phases evidenced in Figure 4.

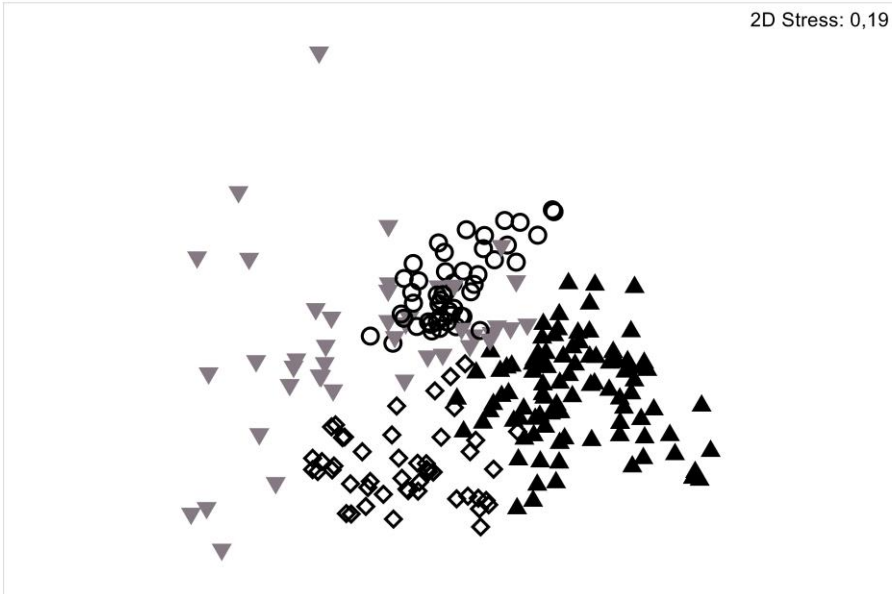

Figure 4. non-metric multidimensional scaling of the hydrological phases in the Lonquen river. (▲ Drying; ▼ Dry with pools; ○ Rewetting; ◇ Baseflow.)

Functional composition variations in the taxonomic composition

The values of the similarity percentage (SIMPER) taxa that contribute most to the significant differences were limited to the taxa that contributed ≥5% to the total dissimilarity (Table 1). The Chironomidae taxon was represented in all the groups with a contribution higher than 17% in Rewetting & Baseflow until 38.8% of the contribution to the Dry & Baseflow phases. The *Nais* taxon was represented in four groups of the hydrological phases with a percentage of around 10%, except for the *Dry & Baseflow* that was represented with 6%. Cyclopoida was relevant to the *Dry & Rewetting* and *Rewetting & Baseflow* groups with a contribution of up to 23%. Similarly, *Bosmina* and *Cypridopsis* contributed to the same groups in 15% and 13%, respectively. At the same time, *Andesiops* supplied to the groups *Drying & Dry*, *Drying & Rewetting* and *Drying & Baseflow* 10% of its contribution. In less proportion, it was expressed *Lumbricus*, Hydracarina, *Herpetocypris*, *Caenis* and *Physa* with a notable contribution to the groups of the hydrological phases.

Table 1. Percentage of contribution (%) of the taxa that contribute more than 5% to the dissimilarity of the aquatic invertebrates community composition between the hydrological phases (Drying, Dry with pools, Rewetting and Baseflow). The overall average dissimilarity is presented in brackets for each group of the hydrological phases.

Drying & Dry (90.4%)		**Drying & Rewetting (85.0%)**		**Drying & Base flow (84.4%)**		**Dry & Rewetting (82.4%)**		**Dry & Base flow (83.1%)**		**Rewetting & Base flow (81.3%)**	
Taxon	%	Taxon	%	Taxon	%	Taxon	%	Taxon	%	Taxon	%
Chironomidae	28.72	Chironomidae	21.19	Chironomidae	27.46	Cyclopoida	23.65	Chironomidae	38.76	Cyclopoida	23.88
Nais	10.76	*Nais*	9.66	*Nais*	11.39	Chironomidae	16.22	*Caenis*	8.53	Chironomidae	17.85
Andesiops	9.63	Cyclopoida	9.02	*Andesiops*	10.17	*Bosmina*	15.72	*Nais*	5.94	*Bosmina*	15.48
Hydracarina	7.1	*Andesiops*	8.98	Hydracarina	7.44	*Cypridopsis*	14.13	*Lumbricus*	5.82	*Cypridopsis*	13.53
Herpetocypris	5.86	*Bosmina*	8.44	*Caenis*	6.1	*Lumbricus*	9.23	*Herpetocypris*	5.38	*Lumbricus*	9.64
Caenis	5.71	*Cypridopsis*	6.08	*Herpetocypris*	5.82			*Physa*	5.13		
		Hydracarina	5,54								

Resistance and Resilience traits relevant in the hydrological phases

Resilience and resistance biological traits were identified in the aquatic Invertebrates of the Lonquen river. Four categories (*Life cycle duration*, *Potential number of cycles per year*, *Dispersal*, *Locomotion and substrate relation*) with seven modalities represented the Resilience characteristics. Meanwhile, the Resistance traits were constituted by three categories (*Reproduction*, *Resistance form* and *Respiration*) and seven modalities (Table 2).

Table 2. Resistance and Resilience traits and modalities for the hydrological phases in the Lonquen river according to Usseglio-Polaterra et al. (2000), Tatchet et al. (2010) and Crabott et al. (2020).

Resilience traits		**Resistance traits**	
Traits	Modalities	Traits	Modalities
2. Life cycle duration	< 1 year	5. Reproduction	Clutches (in vegetation) Clutches (terrestrial)
3. Potential number of cycles per year	≥ 1 (multivoltine)	7. Resistance forms	Eggs, statoblasts Cocoons Diapause or dormancy
6. Dispersal	Aquatic passive Aquatic active Aerial active	8. Respiration	Plastron Spiracle
9. Locomotion and substrate relation	Surface swimmer Full water swimmer Interstitial		

The Resilience traits of the hydrological phases in the Lonquen river (Drying, Dry with pools, the Rewetting and Baseflow) showed a major abundance for the traits of Life cycle duration with a short modality of less than one year and the multivoltine modality. The aerial active dispersal and the aquatic passive traits were represented in a considerable abundance to the Drying, Drying with pools and Baseflow condition. Moreover, the locomotion and substrate relation showed very low proportions in the flowing conditions (Figure 5a).

In the case of the Resistance traits (Figure 5b), the modality of clutches in the vegetation of the Reproduction traits was predominant in the hydrological phases, except for the baseflow condition that was represented in similar proportion with the clutches terrestrial. The resistance forms were characterised by the prevalence of cocoons in all the hydrological phases, while the eggs, statoblast and gemmules were just in the Drying and baseflow conditions. The diapause and dormancy modality was present in the Drying and Baseflow with a low proportion. However, the Respiration traits were represented by plastron in all the flowing conditions with the presence of the spiracles in Drying and Baseflow hydrological phases.

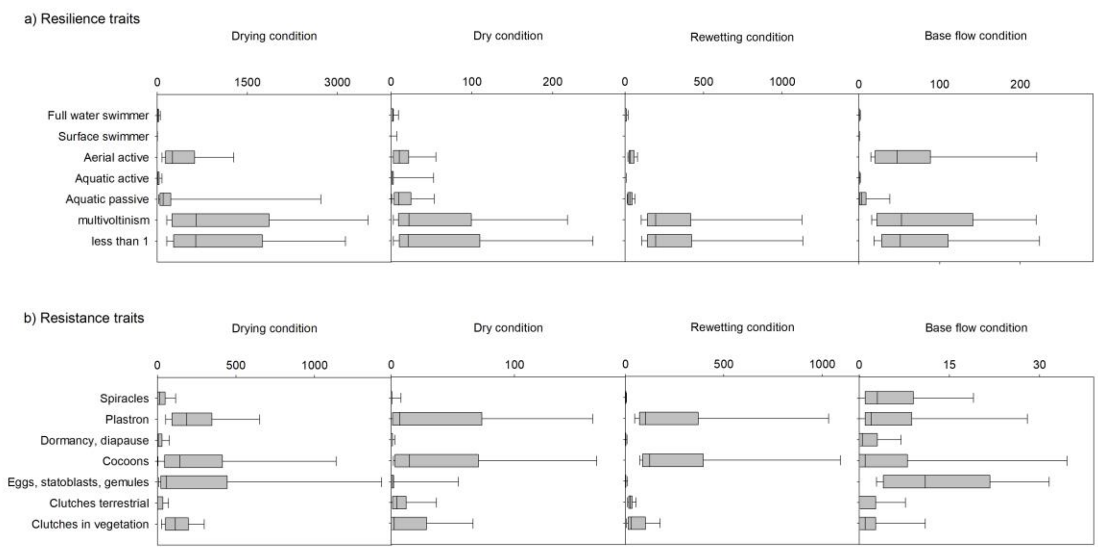

Figure 5. Traits and modalities of the hydrological phases (Drying, Dry with pools, Rewetting and Baseflow) to (a) Resistance and (b) Resilience traits in the Lonquen river.

DISCUSSION

The non-perennial waterways are characterised by a reduction of the flowing water until to show a longitudinal surface discontinuous when the river gets dry. This condition prevents the transport of nutrients, sediments, materials and biota in the surface waters (Allen et al. 2020). The present study performed a recognised dry period in the Lonquen river between November and April in 30 years of streamflow data (1985-2015) with a substantial reduction in the monthly mean streamflow in the most recent years. Fragmented surface water was observed in the river through its basin with some disconnected pools during the dry period. Similarly, the Lonquen river has been identified as an intermittent river with a trend to decrease the monthly mean streamflow equivalent to 0.03 m3/s per year and increase the zero flow days by 3.5 days per year (Banegas et al. 2021). Also, high streamflow records have been registered in the Lonquen river up to 900 m^3/s monthly mean streamflow to 1987 and 1988. Considerations referred to as high flows influence in the river channel characteristics and even in the invertebrate community within the riverine ecosystems (Arscott et al. 2010).

Hydrological connectivity plays an essential role in the aquatic habitats formation in the riverine ecosystems contributing to the channel form. Nevertheless, a reduction in precipitation with an increase in evapotranspiration and climate change scenarios can generate sporadic flows with a decrease in the habitat for biodiversity in riverine ecosystems, especially the non-perennials rivers ((Fritz et al. 2020; Shanafield et al. 2021). However, the shifting habitats between flowing, isolated pools and dry phases are part of the intermittence in non-perennial waterways. Our results showed significant differences between the hydrological phases (drying, dry with pools, rewetting and baseflow) with recognised grouping by the similarity of the taxonomical variations between the flowing conditions (ANOSIM and nMDS analyses), represented in Figure 4.

The predominance of habitat heterogeneity also supported the high proportion of the taxonomical variations during the flow cessation. A space where converge adapted species to flowing and low flow conditions was produced to shelter the aquatic biodiversity from the drying perturbation (Acuña et al. 2005, Buffagni et al. 2020, Doledec et al. 2020). However, the richness, abundance, and alpha diversity (Shannon index) prevalence was demonstrated during the drying condition identified in the Lonquen river (Figure 3b and Figure 4). A high proportion of gastropods (*Physa chilensis*), annelids (*Nais* sp. and *Lumbricus* sp.), microcrustaceans (*Daphnia ambigua*, Harpacticoida, ostracods (*Herpetocypris reptans* and *Cypridiopsis vidua*), mayflies (*Caenis* sp. and *Andesiops* sp.), hemipterans (*Sigara* sp. and *Belostoma elegans*) and dipterans (Chironomidae, Ceratopogonidae and Simulium sp.) were predominant during the flowing cessation. Instead, the isolated, stagnant or disconnected pools served as a transitional habitat of major ecological relevance that supported the aquatic ecosystems during no flowing periods (Bonada et al. 2020). They were represented mainly by *Physa chilensis*, *Daphnia ambigua*, the copepods of Cyclopoida and Harpacticoida), ostracods (*Herpetocypris reptans* and *Cypridiopsis vidua*) and the chironomids.

After the dry disturbance in the non-perennial waterways, the richness and the aquatic community composition depends on its recovery by the severity of the drying disturbance and biogeographical history (Crabot et al. 2016; Schriever et al.

2016). Recolonisation from rewetted reaches advance according to the capacity to withstand drying and recover after flow resumes originated by external sources (Acuña et al. 2005; Stubbington et al. 2016). In the same way, the surface-subsurface exchange is important by the contribution of the hyporheic zone of the benthic invertebrates that refuge during the dry phase (Allen et al. 2020). Our results showed an outstanding contribution of the aquatic invertebrates to the community assemblages during the flow resumption, conformed mainly by *Lumbricus* sp., *Bosmina hagmanni* (cladocerans), the copepod of Cyclopoida, *Cypridiopsis vidua* (ostracods) and the midges of chironomids. These invertebrates are characterised to resist the dry conditions, recolonising and dispersing after the rewetting conditions appear to be adapted to produce drought-resistant dormant eggs under harsh conditions (Brendonck et al. 2003). The chironomids and mayflies (*Caenis* sp. and *Andesiops* sp.) were abundant in the baseflow condition but with low richness, abundance and diversity in contrast with the hydrological phases that can be affected by flooding events that cause short and intense disturbance on the aquatic biota (Gallart et al. 2012; Banegas et l. 2021).

The non-perennial waterways present an apparent harshness during the drying condition with the predictability of flow recession. Besides, resistance and resilience are conferred by physiological, morphological and life-history traits related to the organisms involving a range of adaptations to survive within dry riverbed sediments (Crabot et al. 2019; Bruno et al. 2020). Our results selected a set of traits related to resistance and resilience, identifying a total of 14 modalities in the aquatic invertebrates of the Lonquen river. Resilience traits demonstrated dominance in the modalities with a short (less than one year) and a potential number of cycles per year (multivoltine) in the annual flow regime. High abundance of *Physa chilensis,* Hydracarina, *Daphnia ambigua*, Harpacticoidea, *Herpetocypris reptans*, *Cypridiopsis vidua*, *Caenis* sp., *Andesiops* sp. and the dipterans of chironomids, ceratopogonids and *Simulium* sp. prevalence in all hydrological phases. Instead, the cladoceran *Bosmina hagmanii* was exclusively in the disconnected pools and the rewetting phase.

The dominance of resilience traits in the hydrological phases shows tolerance to dry conditions that influence in the responses of the aquatic community and are always dominant along intermittence gradient along with the hydrological phases (Crabot et al. 2020). Moreover, Crabot et al. (2019) highlighted the influence of the fragmentation on intermittent rivers generating a selective pressure on the aerial dispersers provoking a loss of habitat connectivity. Alternately, our results displayed that the aerial dispersion was preponderant in the baseflow condition with the existence of mayflies (*Caenis* sp. Leptophlebiidae), the beetles (*Tropistemus lateralis* and *Ranthus* sp.) and chironomids in the aquatic community.

The resistance traits for the Lonquen river performed a major proportion of clutches in vegetation than terrestrial in the hydrological phases (ostracods and odonates), with a presence of cocoons in all the flowing conditions (annelids, cladocerans, copepods and ostracods). The resistance form of diapause or dormancy presented low values with a recognised abundance in the baseflow of gastropods (*Chilina dombeyana*, *Littoridina cumingii*, *Sigara* sp. and *Notonecta* sp.) and some dipterans such as *Ephydra* sp. and *Escatella* sp.). Instead, the eggs, statoblasts and gemmules were distinguished in the drying and baseflow phases by a predominance of mayflies.

The plastron conformed to the respiration traits with an outstanding contribution of bivalves (Diplodon chilensis), gastropods (Physa chilensis), cladocerans, copepods, ostracods. However, this trait was present in the drying condition in minor proportions, in contrast with the baseflow phases characterised by the presence of hemipterans, coleopterans, and dipterans in all hydrological phases. The respiration by spiracles was present in baseflow conditions with the abundance of *Physa chilensis*, Hydracarina, cladocerans, copepods and ostracods,

Furthermore, Leigh et al. (2015) suggest that resistance traits are important to conserve the assemblages in the intermittent sites. In contrast, the permanent sites are a source of taxa with resilience to recolonise the intermittent sites when flow returns. Nevertheless, both mechanisms are responsible for the recovery of the aquatic invertebrates after the disturbance of dry conditions. The resilience modalities of short life cycle duration and the multivoltine commanded in the hydrological phases, besides the aerial dispersion that contributes to drying and baseflow conditions (Gauthier et al. 2020). However, the presence of cocoons and the respiration by plastron were important to resistant mechanisms to the disconnected pools. Nevertheless, the baseflow phase highlighted the major resistance modalities that could be associated with the predominance of taxa adapted to constitute the aquatic assemblage in the intermittent river (Bogan et al. 2014).

CONCLUSIONS

The present study remarks on the importance of assessing the hydrological and ecological characteristics in a non-perennial waterway from the Mediterranean zone of Chile. Hydrological phases were identified according to the temporal patterns from the hydroperiod gradient of the Lonquen river, which showed significant differences based on the composition of the aquatic invertebrates in the Lonquen river. Moreover, we based our characterisation on biological traits that help expose the possible impact of harsh conditions derived from the anthropogenic and climate stressors on the intermittent river. Resilience and resistance traits were determined to confirm the response of the aquatic invertebrates to low flowing as a mechanism to resist and recover from the disturbance of dry conditions. Physiological, behavioural, and dispersal adaptations were indicative of the ecological strategies to survive and restore the aquatic invertebrate community after seasonal or supra-seasonal drying events. Further studies are required on the non-perennial waterways in Mediterranean climates from South America to understand the behaviour of the aquatic invertebrates to face climate change scenarios and human perturbation on riverine ecosystems that contribute to take actions to manage and conserve the intermittent rivers and ephemeral streams.

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CAPÍTULO III

A GLOBAL ANALYSIS OF TERRESTRIAL PLANT LITTER DYNAMICS IN NON-PERENNIAL WATERWAYS

Datry, T.; Foulquier, A.; Corti, R.; von Schiller, D.; Tockner, K.; Mendoza-Lera, C.; Clément, J.C.; Gessner, M.O.; Moleón, M.; Stubbington, R.; Gücker, R.; Albariño, R.; Allen, D.C.; Altermatt, F.; Arce, M.I.; Arnon, S.; Banas, D.; **Banegas-Medina, A**.; Beller, E.; Blanchette, M.L.; Blanco-Libreros, J.F.; Blessing, J.J.; Boëchat, I.J.; Boersma, K.S.; Bogan, M.T.; Bonada, N.; Bond, N. R.; Brintrup Barría, K.C.; Bruder A.; Burrows, R.M.; Cancellario; T.; Canhoto, C.; Carlson, S.M.; Cauvy-Fzraunié, S.; Cid, N.; Danger, M.; de Freitas, M.; Terra; De Girolamo, .A.M.; de La Barra, E.; del Campo, R.; Diaz-Villanueva, V.D.; Dyer, F.; Elosegi, A.; Faye, E.; Febria, C.; Four, B.; Gafny, S.; Ghate, S.D.; Gómez, R.; Gómez-Gener, L.; Graça, M.A.S; Guareschi, S.; Hoppeler, F.; Hwan, J.L.; Jones, J.I.; Kubheka, S.; Laini, A.; Langhans, S.D.; Leigh, C.; Little, C.J.; Lorenz, S.; Marshall, J.C.; Martín, E.; McIntosh, A.R.; Meyer, E.I.; Miliša, M.; Mlambo, M.C.; Morais, M.; Moya, N.; Negus, P.M.; Niyogi, D.K.; Papatheodoulou, A.; Pardo, I.; Pařil, P.; Pauls, S.U.; , Pešić V.; Polášek M., Robinson; C.T., Rodríguez-Lozano P.; Rolls R.J., Sánchez-Montoya; M.M., Savić A.; Shumilova, O.; Sridhar, K.R.; Steward, A.L.; Storey, R.; Taleb A., Uzan A.; Vander Vorste R., Waltham; N.J., Woelfle-Erskine; C., Zak D.; Zarfl, C.; Zoppini A.

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SIMULATING REWETTING EVENTS IN INTERMITTENT RIVERS AND EPHEMERAL STREAMS: A GLOBAL ANALYSIS OF LEACHED NUTRIENTS AND ORGANIC MATTER

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SEDIMENT RESPIRATION PULSES IN INTERMITTENT RIVERS AND EPHEMERAL STREAMS

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INTRODUCTION

In recent years, intermittent rivers and ephemeral streams have had a greater interest in being included in research, management and conservation programs, demonstrating the concern to know even more about their hydrology, ecology, ecosystem services and how to face the scenarios of climate change (Leigh et al. 2016; Shanafield et al. 2021). Currently, some definitions in reference to intermittent rivers, temporary streams, and non-perennial waterways highlight the coincide that they are waterways that cease their surface flow at some point in time and space (Larned et al. 2010, Acuña et al. 2014, Datry et al. 2014). They represent more than 50% of the global network of river systems, reaching even higher percentages in regions with arid and semi-arid climates (Datry et al. 2014; Prat et al. 2014; Shumilova et al. 2019). On the other hand, intermittent rivers are recognised for accumulating a great diversity of invertebrates adapted to disturbances by desiccation and overlapping once the bodies of water have been reconnected again (Kelso & Entrekin, 2018; Crabot et al. 2020).

Likewise, they involve a mineralisation process considered as biogeochemical reactors "hot spot areas" because they host a large number of sediments, nutrients, organic matter, litter, biofilms, carcasses and eggs of invertebrates that are subsequently flushed downstream or transported to coastal areas with the flow resumption (Datry et al. 2018; Shumilova et al. 2019; von Schiller et al. 2019). As part of the recent interest in the study of non-perennial river waterways, some initiatives have arisen to further deepen the knowledge of intermittent rivers, mainly in the European Mediterranean region, North America and Oceania. Some of these initiatives are known as the Mediterranean Intermittent River Management (MIRAGE), the Intermittent Rivers, Biodiversity, Analysis and Synthesis project (IRBAS), the Science and Management of Intermittent Rivers and Ephemeral Streams (SMIRES) and currently the "1000 intermittent rivers project", which have generated scientific contributions in the study of these ecosystems for their correct management, conservation and protection (Prat et al. 2014; Leigh et al. 2016; Datry et al. 2017; Datry et al. 2018; Shumilova et al. 2019).

The project of the 1,000 intermittent rivers has tried to carry out a global coverage in terms of the study and analysis of the most significant number of these ecosystems, in which a total of 205 intermittent rivers and temporary streams were studied, constituted in 27 countries and five continents, could be sampled (Figure 1). Similarly, the purpose of the project was to quantify the coarse particulate organic matter collected from the beds during the dry period and understand the main drivers of the variations in organic matter. Besides, to evaluate the ecological consequences of the flow pulses received. In addition, the nutrient leaching and carbon dioxide concentration that is released in these ecosystems.

Figure 1. Global map of the sampled sites across five climate zones (Koppen-Geiger classes).

As a local scale of the 1000 intermittent rivers project initiative, the participation was carried out with the sampling of six tributaries of the Lonquén River with characteristics of being intermittent or temporary, which provided the necessary conditions for their sampling. The temporary streams considered for the study are described in Table 1.

The terrestrial plant litter plays an important role in the contribution of organic carbón (C) produced by terrestrial plants annually. Almost a half is respired by the plants, but only a small fraction is removed by herbivores, and a great proportion enters the dead organic matter pool (Boyero et al. 2011) or contributes to the atmospheric CO_2 emissions (Raymond et al. 2013). This contribution is particularly apparent in perennial rivers and streams, in which water and nutrient availability stimulate a rapid decomposition by microbes and invertebrate detritivores (Gessner et al. 2010; Boyero et al. 2011; Raymond et al. 2013). Similarly, the terrestrial plant litter deposited in freshwaters and the release of its decomposition products are critical energy sources that support food webs and ecosystem processes, which include key C-cycling pathways (Gessner et al. 2010; Boyero et al. 2011).

Tabla 1. Características de los arroyos (esteros) muestreados dentro de la cuenca del Río Lonquén (1,000 Intermittent River Project).

River Name	Estero Goropeumo	Estero Caña Dulce	Estero Arrayán	Estero Cocinero	Estero Coiquencillo	Estero Virquinco	Río Lonquén
Catchment area (km^2)	3,8396	7,0256	12,418	28,85	19,89	56,89	44,49
Stream order	1	1	1	1	1	1	1
Mean annual flow (m^3/s)	0,047	0,085	0,151	0,351	0,242	0,692	0,541
Average slope (°/00) **degree**	8,58*	9,43	7,96	2,29	10,82	5,08	4,39
Average slope (°/00) **percent rise**	15,19	16,71	14,05	5,11	19,39	9,01	7,78
Stream lentgh (km)	4.91 km	4.10 km	5.98 km	12.65 km	10.19 km	11.58 km	14.92 km
Distance to source (km)	1.71 km	1.67 km	1.37 km	2.35 km	7.47 km	6.61 km	5.69 km
Distance to downstream confluence (km)	3.2 km	2.43 km	4.61 km	10.3 km	2.82 km	4.97 km	9.23 km
% of the catchment being intermittent	100%	100%	100%	100%	100%	100%	100%
Total length of the river being intermittent	4.91 km	4.10 km	5.98 km	12.65 km	10.19 km	11.58 km	14.92 km
Number of active flow recorder in the catchment	1	1	1	1	1	1	1
Distance to the closest flow recorder (if any, in km)	3.50 km	10.9 km	12.5 km	32.2 km	25.5 km	39.4 km	43.6 km
Flow recorder time serie length (if any, in year)	35 years	35 years	35 years	35 years	35 years	35 years	35 years
Climate zone (following the Koppen system)	Csb Warm-summer mediterranean climate	Csb Warm-summer mediterranean climate	Csb Warm-summer mediterranean climate	Csb Warm-summer mediterranean climate	Csb Warm-summer mediterranean climate	Csb Warm-summer mediterranean climate	Csb Warm-summer mediterranean climate
Annual precipiation (mm)	897,9 mm	897,9 mm	897,9 mm	897,9 mm	897,9 mm	897,9 mm	897,9 mm

A major shortcoming of current estimates of the contribution of rivers and streams to global C cycling have been observed in the study of aquatic ecology (Raymond et al. 2013). Moreover, the intermittent streams (IRES), in which drying and rewetting events create ecosystems that transition between terrestrial and aquatic phases. IRES are widespread ecosystems that drain a large proportion of the terrestrial biomes across all continents and climate types (Larned et al. 2010; Datry et al. 2014; Acuña et al. 2014). Moreover, IRES are increasing in extent due to global change (Datry et al. 2016; Jaeger et al. 2014). During the dry phase, the terrestrial plant litter deposited on the riverbed accumulates, decomposing only slowly through photodegradation and terrestrial decomposer activity (Austin & Vivanco, 2006). Then, when flow resumes, the accumulated material is mobilized and transported downstream (Corti & Datry, 2012; Rosado et al. 2015).

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On the other hand, perturbations presented by anthropogenic pressures and climate change in non-perennial waterways promote riverine ecosystems' spatial and temporal intermittence. However, during the dry phase, a diversity of substrates (leaf litter, epilithic biofilms, wood, animal carcasses and sediments) accumulated on the dry riverbed are available to the decomposition processes once the rewetting condition return in the streams or rivers (Corti & Datry, 2012; Datry et al., 2018).

The first flush pulses make available a considerable amount of nutrients, organic matter released into the river channel that can be used as fuel to primary producers and heterotrophic organisms (Austin et al., 2004; Corti et al. 2012; Bernal et al. 2013). Eutrophication and hypoxia processes are recognized to generate consequences for the excess of nutrients transported to downstream lakes, reservoirs, and coastal areas, altering the aquatic ecosystems' ecological functioning (Bunn et al. 2006; Hladyz et al. 2011; Whitworth et al. 2012; Datry et al. 2016).

Recycling nutrients and dissolved organic matter as part of the biogeochemical processes that occurred in the streambed of intermittent rivers has been studied to understand the role in ecosystem performance (Datry et al. 2014; Datry et al. 2018). Similarly, the quantity and quality of the dissolved compound released after the rewetting is referred to as leaching that depends on physicochemical of the substrates accumulated on riverbeds rich in soluble sugars, carbonic and amino acids, phenolic substances, proteins, and inorganic nutrients such as phosphorus, nitrogen, potassium) (Nykvist, 1963; Gessner, 1991; Bärlocher, 2005; Harris et al. 2016).

Finally, in the non-perennial waterways, most streams are heterotrophic ecosystems that retain organic matter and emit large quantities of carbon dioxide into the atmosphere. The processes of drying to rewetting in the intermittent rivers are similar to that in soils (Arce et al., 2019; Gallo et al., 2013; Marcé et al., 2019 and represent a large pulse of CO_2 as part of the respiration in the sediments during the resumption (Gallo et al., 2013; Marcé et al., 2019).

MATERIALS AND METHODS

The global study comprised a total of 205 intermittent rivers or ephemeral streams in 27 countries representing the five major Köppen–Geiger climate classes. The samples of leaf litter, epilithic biofilms (biofilms), and sediments were collected during the dry phase according to the protocol of the 1,000 Intermittent Rivers Project (Datry et al. 2016). The leaching experiment was directed by the simulation of the rewetting conditions in the laboratory, exposing dried substrates to leaching solutions as a proxy. The leaf litters were cut into pieces 0.5 X 0,5 cm and homogenized in glass beakers filled with 200 ml of NaCl (200 mg/L) solution.

According to leaching techniques for the leaf litter, the samples were put at 20º C for four hours. The substrate and the leaching solution were shaken at 100 rpm in darkness and filtered through 8.0 µm cellulose acetate and 0.45 µm cellulose nitrate membrane filters. The filtered leachates were collected in 200 ml glass flasks. The leachates solutions were analyzed to determine the organic carbon (C) and total nitrogen (N) content of substrates. Sediment texture descriptors (fractions [%] of sand, silt, clay were determined, and the DOC, soluble reactive phosphorus (SRP), ammonium (N-NH4+), nitrate(N-NO3−), and phenolics.

The quadrants of one square meter selected the samples collected for the sediment respiration pulses during the dry period were conformed by the presence of litter, branches, fruits, fresh vegetation, sediments and biofilm. The samples from the micro basins were collected from the reconnection of the surface flow during the dry streambed were present in the river or stream. Subsequently, the samples were oven-dried at 60 ° C for a period of 12 hours. Instead, the sediments were sieved on a 2 mm mesh, placed in the oven to dry. Separately, 200 grams of dry sediments were weighed and packed in plastic bags (Datry et al. 2015). The humidity percentage of the collected samples was estimated. The samples were sent to the National Institute of Research in Sciences and Technologies for Environment and Agriculture in Lyon, France (IRSTEA).

In the case of the Samples of sediments were collected, preserved, and transported according to Datry et al. (2015). Afterwards, the samples were incubated for 24 hours at 20ºC. Demand oxygen was measured at control (beginning of the analysis) and at the end of the incubation to obtain the total CO_2 production (nmolCO2 · g−1 dry mass · hr−1). Besides, the MicroRespTM was used to examine the response of the sediments' respiration to rewetting.

The organic carbon and total nitrogen content (%) from the sediment samples were determined using an elemental analyzer (TruSpec Micro CHNS, Leco Corp., St. Joseph, MI, USA) after grinding and acidification with 2M HCl. The sediment respiration assays were measured in the laboratory under standardized conditions. Fort he dry conditions, the measure of the respiration was using the commercial MicroRespTM device (Macaulay Scientific Consulting Ltd., UK). In contrast, respiration was measured with the MicroRespTM system and the decline of dissolved oxygen (DO) concentrations in sealed incubation bottles in wet conditions. Finally, the percentage change of CO2 in the headspace was converted to a respiration rate (nmol CO_2 · g−1 dry mass · hr−1) considering the incubation time and temperature, gas constant, headspace volume, and sediment mass, as described in the MicroRespTM technical manual. The mean values of the analytical replicates were used in further data analyses.

RESULTS AND DISCUSSION

In the non-perennial waterways is common to find an accumulation of plant litter from riparian vegetation stored in the dry streambed. It contributes to the carbon and nitrogen cycling that were transported downstream when the flow resumes (Stanley et al. 1997; Larned et al. 2010; Corty et al. 2012; Datry et al. 2016). The contribution of the plant litters in the global rivers studied was ranged from 0 to 8,291 g dry mass/m^2 mean and SD (277±796 g dry mass/m^2) comprised mainly by leaf litter and wood (41%), herbs and fruits and catkins (around 20%). The major proportion of the terrestrial material was reported to rivers of the first order, forested and from temperate the non-perennial waterways with an organic matter accumulation. Besides, due to the biological activity and physical abrasion absent in intermittent rivers let the transportation of the material stored downstream when flow resume (Larned et al. 2010; Corti et al. 2016).

The dry period delays the leaf litter decomposition from the dry riverbeds affecting downstream transportation. Similarly, the scenarios of climate change could increase the low quality of the organic matters and nutrients with repercussions on detrital food webs (Corti et al. 2012; Jaeger et al. 2014). The respiration process and CO_2 release (oxygen consumption) after the flow resumption was ranged from 0.004 to 0.97 mg O_2 g dry mass/h (0.29±0.20) reported from coarse particulate organic matter. These results were conducted to identify a proportion of high O_2 consumption and CO_2 release rates after the leaf litter in the flow resumption in temperate regions (Figure 2).

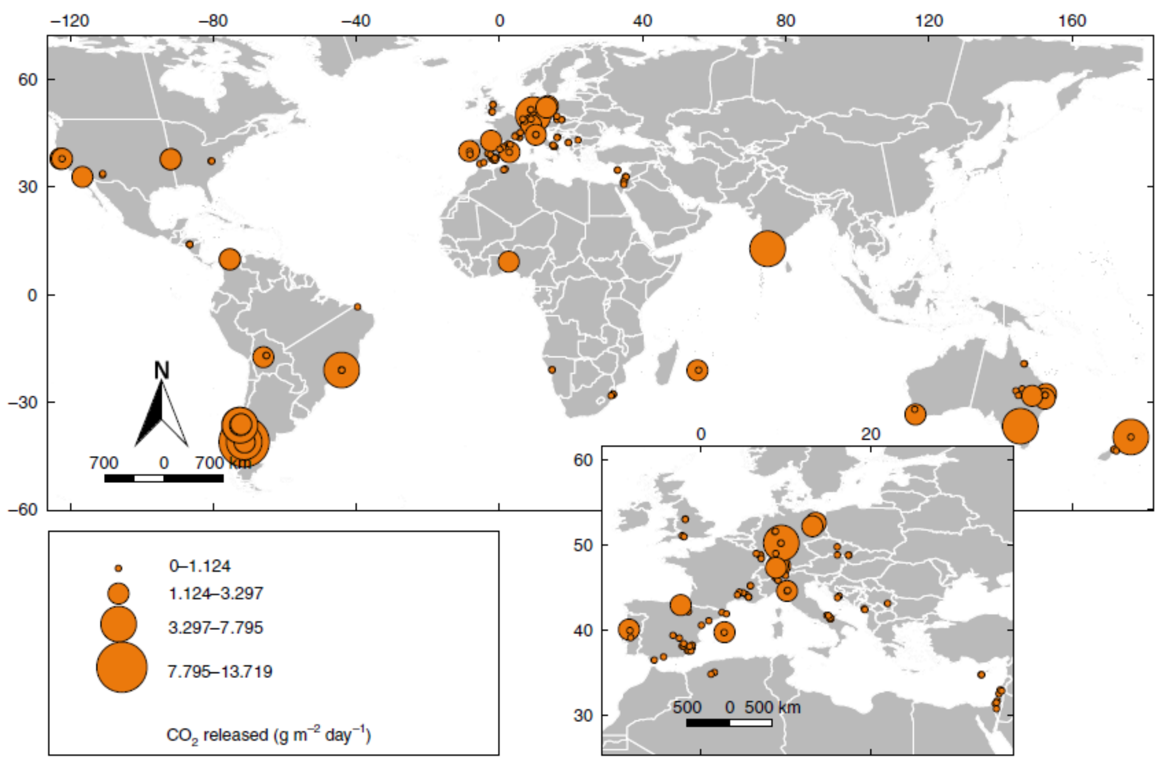

Figure 2. Global map of the potential CO_2 released according to the original sampling reaches.

Considering that the study was conducted in 212 rivers, reflexing the importance of the intermittent rivers as biogeochemical reactors characterised varying with the morphology and magnitude of flow pulse (Corti et al. 2012). Moreover, in extreme flow conditions, the leaf litter remain in the river channels and riparian areas decomposing at similar rates to the perennial rivers. Finally, the CO_2 released from the intermittent rivers and ephemeral streams during the dry phases and rewetting events contribute to the global CO_2 emissions. The intermittent river could increase the global CO_2 emissions from 7 to 152% during a single rewetting event that would increase the consequences of global climate change, mainly when the dry period becomes more prolonged in many regions (Larned et al. 2010; Datry et al. 2014; Jaeger et al. 2014).

Leaching rates

The highest values of total leached amounts and dissolved organic matter were found in leaves, followed by biofilms and sediments. The amounts of N-NO3− were highest for biofilms, and no significant difference was found between leaves and sediments. Leached amounts of DON from leaves and biofilms were not significantly different.

The total leached amounts of nutrients and DOM from leaves and biofilms decreased in a similar sequence: DOC > phenolics > DON > SRP > N-NH4+ > N-NO3− (based on median values). The total leached amounts from sediments decreased in the following order: DOC > phenolics > N-NO3− > N-NH4+ ≈ DON > SRP.

Table 2. Total and relative rates of nutrients and organic matter species from leaves of IRES according to the arid, continental, temperate and tropical climate zones.

			Leaves			
Parameter	Unit	Leaching rate	Arid	Continental	Temperate	Tropical
DOC	mg/g dry mass	Total	30.98	47.40	25.30	22.90
	mg/g C	Relative	86.28	108.86	58.10	66.50
$N\text{-}NH_4^+$	mg/g dry mass	Total	0.06	0.14	0.08	0.105
	mg/g N	Relative	7.80	11.70	6.60	8.20
$N\text{-}NO_3^-$	mg/g dry mass	Total	0.004	0.006	0.002	0.008
	mg/g N	Relative	0.43	0.32	0.27	0.59
DON	mg/g dry mass	Total	0.30	0.22	0.14	0.29
	mg/g N	Relative	22.03	17.80	12.50	28.80
SRP	mg/g dry mass	Total	0.11	0.24	0.15	0.16
Phenolics	mg of GAE/g of substrate	Total	9.08	20.18	8.38	8.92
	mg of GAE/g of C	Relative	0.23	0.51	0.20	0.24
$SUVA_{254}$	mg C/L		1.60	1.44	1.57	1.88

Continuation Table 2. Total and relative rates of nutrients and organic matter species from bed sediments of IRES according to the arid, continental, temperate and tropical climate zones.

			Sediments			
Parameter	Unit	Leaching rate	Arid	Continental	Temperate	Tropical
DOC	mg/g dry mass	Total	0.06	0.25	0.07	0.08
	mg/g C	Relative	14.66	13.30	12.24	19.92
N-NH_4^+	mg/g dry mass	Total	0.001	0.004	0.0015	0.002
	mg/g N	Relative	6.01	4.30	4.51	6.36
N-NO_3^-	mg/g dry mass	Total	0.003	0.01	0.004	0.005
	mg/g N	Relative	13.03	10.57	10.48	18.32
DON	mg/g dry mass	Total	0.001	0.007	0.002	0.002
	mg/g N	Relative	6.10	4.90	4.80	2.30
SRP	mg/g dry mass	Total	0.0004	0.002	0.0005	0.0007
Phenolics	mg of GAE/g of substrate	Total	0.003	0.010	0.005	0.007
	mg of GAE/g of C	Relative	0.008	0.006	0.005	0.009
$SUVA_{254}$	mg C/L		1.21	2.01	1.75	1.78

Note. GAE: gallic acid equivalent.

The relative leached amounts of DOC and phenolics (mg/g C) and DON (mg/g N) were highest for leaves, followed by biofilms and sediments (Figure 3). However, there were no significant differences for the amounts of DON between leaves and biofilm leachates, nor for phenolics between biofilms and sediments. Relative leached amounts of N-NH4+ were highest for biofilms, followed by leaves and bed sediments, with a significant difference between leaves and sediments.

For all substrates, we observed large variations in the total and relative leached amounts of nutrients and DOM (Figure 3). The highest variability in total and relative leached amounts of DOC, N-NO3−, and SRP was observed for biofilms, which was up to 10 times higher than for sediments and leaves. Sediments had the highest variability in the total leached amounts of DON and relative leached amounts of N-NH4+ and phenolics. For leaves, the highest variability was found in the relative leached amounts of DON.

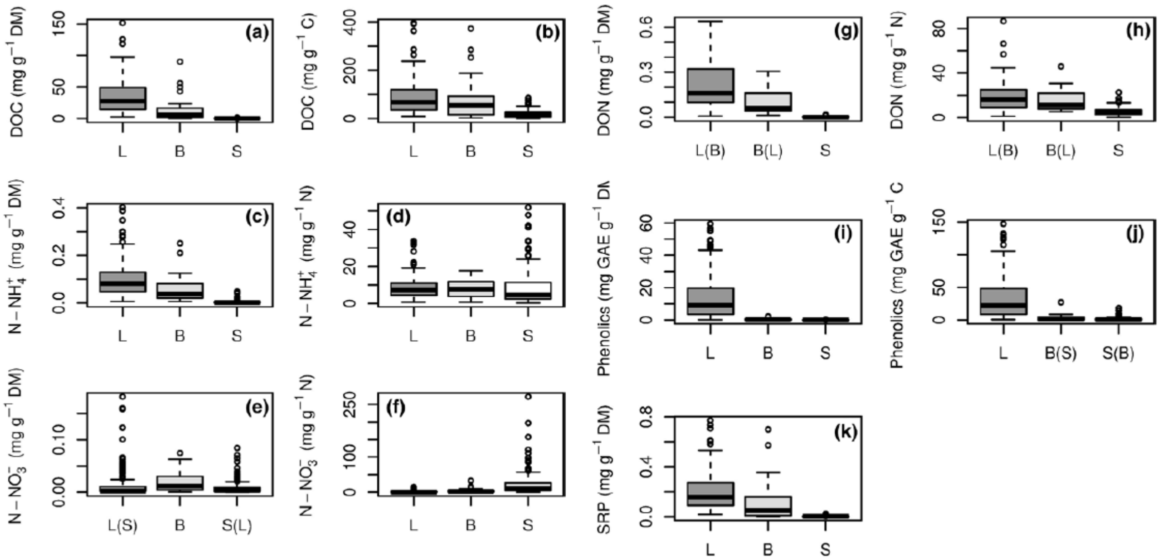

Figure 3. Total (left) and relative (right) leached amounts of nutrients and dissolved organic matter from leaves (L), biofilms (B), and sediments (S) of IRES globally. Box: median, interquartile range (25%–75%), and outliers (i.e. values that exceed 1.5 interquartile range).

Effects on the amounts of leached nutrients and DOM

On a global scale, 25% of the variance in the amounts of nutrients and DOM leached from sediments could be explained by selected variables (fraction [a + b + c]), which was more than twice that for leaves (11%) (Figure 4). For sediments, around 23% of the variance could be explained by the effect of substrate characteristics (fraction [a + b]), around 15% by the effect of environmental variables (fraction [b + c]), and 13% by the effect of environmental variables on substrate characteristics (fraction [b]) (Figure 4a). Instead, the substrate characteristics and the environmental variables explained approximately an equal percentage of variance, 8% and 6%, respectively, which was much lower than sediments.

Environmental variables and substrate characteristics accounted for 3% of the variance in the quantitative composition of leaf leachates. For both substrates, the most influential (variable influence on projection: VIP >1) were the C fraction, N fraction, PET, and in the case of leaves, C:N and pasture cover within the river catchment. For both sediments and leaves, the highest percentage of variance in amounts of leached nutrients and DOM was explained for the continental and tropical zones (59% and 46% for sediments, 39% and 40% for leaves, respectively Figure 4). Substances leached from sediments from these regions were explained mainly by the environmental variables and their effect on substrate characteristics. High VIP was found for the dry period duration, N fraction and textural classes (both zones), river width and forest cover (continental), PET, urban cover, and a fraction of C (tropical).

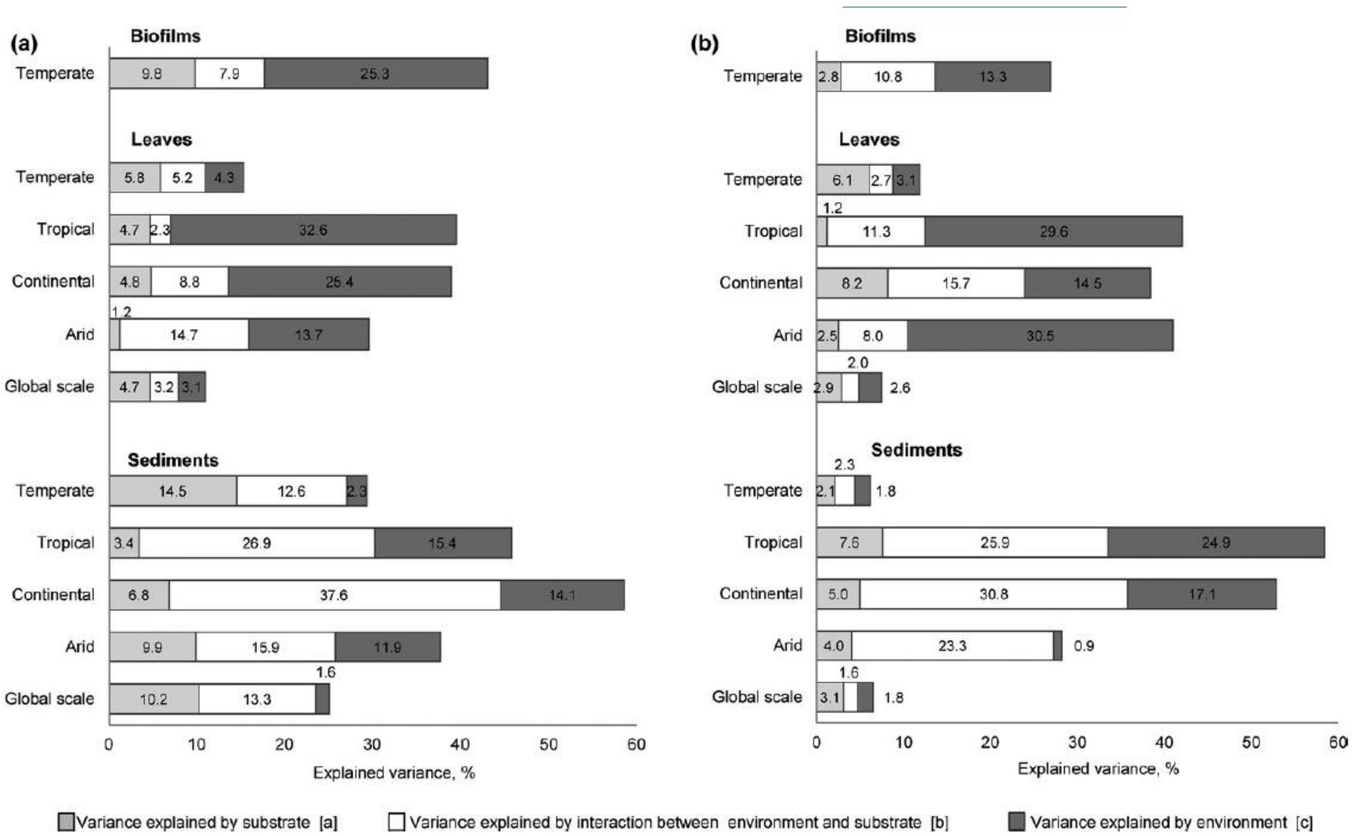

Figure 4. Partitioning of variance in quantitative composition (a) and qualitative characteristics (b) of leachates on global and regional scales (values indicate percentage of variance explained

In contrast, most of the variance was explained by environmental variables alone and not by their effect on the substrates for leaves in these zones. Environmental variables with high VIP in these zones were the potential evapotranspiration (PET) and aridity (in both). The total variance in leachates was best explained for biofilms (48%), followed by sediments (30%) and leaves (15%). In contrast to sediments and leaves, the variance in biofilm leachates was better explained by environmental variables (VIP >1 for aridity and altitude) than by substrate characteristics.

Sediment respiration pulses in the intermittent rivers and ephemeral streams
The results of the sediment respiration using the MicroRespTM method in dry conditions ranged from 0.01 to 14.1 nmol CO2 · g−1 dry mass · hr−1. In earlier studies, these low respiration rates are similar to other ex situ dry stream sediments (0.2–4.5 nmol CO2 · g−1 dry mass · hr−1 (Gómez-Gener et al., 2015). This consideration indicated that the dry sediments from the intermittent rivers and ephemeral streams like soils support a moderate active microbial community. On the other hand, the sediments under rewetting conditions increase the respiration rates from 0.01 to 147 nmol CO2 · g−1 dry mass · hr−1, and from 0 to 411 nmol CO2 · g−1 dry mass · hr−1 for the bottle incubations method.

These values are in the upper range of respiration rates reported from perennial stream sediments (range = 0–356 nmol CO2 · g−1 dry mass · hr−1 suggesting that rewetting events after dry phases in IRES are associated with rapid recovery of metabolic activity by heterotrophic organisms present in the sediments. Finally, The higher sediment respiration upon rewetting, with a mean 32-fold (MicroRespTM) or 66-fold (bottle incubation) increase in wet compared to dry conditions (Figure 5).

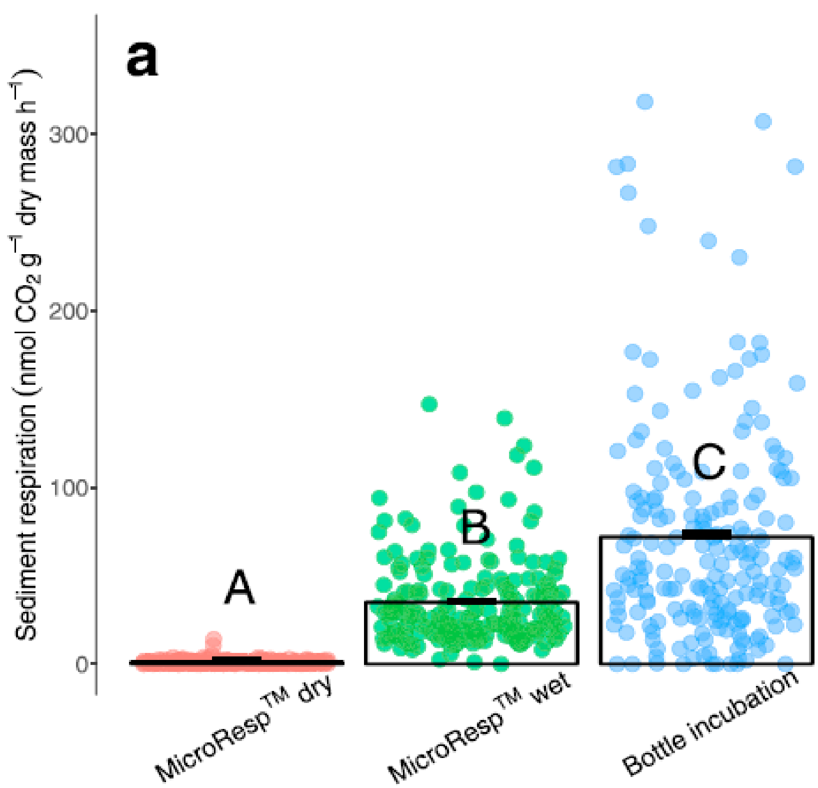

Figure 5. Sediment respiration in dry and rewetted conditions in three types of standardized assays. Differences between types are significant (analysis of variance, $F2$, 398 =748.6, p < 0.001).

After rewetting from both streams and soils, the upper range of increases was reported. The CO_2 flux from soils can increase 0.4-fold to 130-fold after rewetting, with the highest increases typically reported from deserts (Kim et al., 2012). Similarly, in dry IRES of the semiarid southwestern United States, the CO_2 flux increased 6-fold to 33-fold immediately following experimental rewetting (Gallo et al., 2013).

The magnitude and drivers of sediment respiration pulses upon rewetting reported in this study should be viewed with caution because respiration was measured in small samples, disconnected from their structural matrix, and under standardized laboratory conditions. For instance, the incubation temperature and the nutrient concentration in the water used for rewetting may have differed from those found at ambient conditions at the sampling sites.

These findings showed a high sediment respiration rate in IRES upon rewetting might significantly contribute to CO_2 emissions from the global stream network (Datry et al., 2018). Similarly, the estimations of release rate from rewetted sediments of 10.0 (0.0–56.9) g C · m^{-2} · day^{-1} exceed the release rates from rewetted leaf litter collected from the same IRES sites (mean = 0.24 g C · m^{-2} · day^{-1}, range = 0–3.7). The sediments are critical contributors to CO_2 emissions, and a global upscaling of this release rate resulted in a global CO_2 flux from a single rewetting in IRES sediments. This contribution represents a mean of 4% of the global CO_2 emissions from dry IRES (0.124 PgC/year according to Marcé et al., 2019) and between 0.2% (0.0–1.4%) and 0.8% (0.0–4.5%) of the global CO_2 emissions from perennial streams (0.56–1.8 Pg C/year according to Raymond et al., 2013.

IRES are often subject to multiple rewetting events (i.e., due to rain and flow reconnection) per year (Corti & Datry, 2012; Jacobson et al., 2000; von Schiller et al., 2017). The obtained results suggest that emissions from IRES during rewetting episodes may be a dominant term in the annual CO_2 balance in many stream networks where IRES and rewetting episodes are frequent. In any case, we are far from producing a robust global estimate of CO_2 emissions from IRES during rewetting events because our calculations rely on several assumptions that need to be considered with caution. The number of rewetting events varies significantly in space and time (von Schiller et al., 2017). Future research is needed to clarify the relevance of these uncertainties and processes, including the influence of antecedent flow conditions and type of rewetting (i.e., fed by groundwater and Surface water or rainwater) on respiration response to rewetting.

CONCLUSION

The most variability in quantity and decomposition of plant litter found in the intermittent rivers at the global scale was determined by the aridity, riparian vegetation cover, channel width, and dry-phase duration. Similarly, the CO_2 emissions upon litter rewetting contribute up to 10% of the daily CO_2 emission from the perennial rivers, particularly in temperate climates. It is recommended to include the intermittent rivers and ephemeral streams in the global carbon cycle assessment for the contribution to the global CO_2 emission and consider them in the climate change scenarios.

The intermittent rivers and ephemeral streams are good performers as pulsed biogeochemical reactors (Larned et al., 2010) at a global scale. The findings of this study serve as modelling of the processes observed in the laboratory to address ecological implications of rewetting events at catchment scales. Potential implications for the functioning of rivers could be determined by the effect of leached substances on the degree of nutrient limitation of microorganisms downstream, and therefore community composition (Demi, Benstead, Rosemond, & Maerz, 2018) as well as on the fate of refractory substances and intensification of their decomposition through the so-called “priming effect” (Guenet, Danger, Abbadie, & Lacroix, 2010). The results of our study support the recent call for developing effective strategies for the management of IRES to avoid negative consequences for downstream ecosystems caused by excessive nutrient and organic matter load.

The global study in the intermittent rivers and ephemeral streams spanning 200 reaches across six continents and covering a wide range of environmental conditions enabled us to assess the magnitude and environmental drivers of respiration pulses in IRES sediments upon arrival rewetting. These data indicate that rewetting greatly increases sediment respiration, supporting the view of IRES as coupled aquatic-terrestrial ecosystems that function as “punctuated biogeochemical reactors” in response to spatiotemporal fluctuations in drying and rewetting (Larned et al., 2010). The results also demonstrate that key sediment properties drive the response of respiration to rewet and, in turn, are influenced by climate and catchment conditions. Specifically, we found that organic-rich, low C/N, and coarse sediments experience a larger respiration pulse upon rewetting, with greater riparian cover in more natural and humid catchments leading to higher respiration pulses by increasing the sediment OC content.

These results expand our understanding of metabolism and C cycling in stream networks with implications for large-scale modelling efforts. Furthermore, our findings support research demonstrating that rewetting events represent “hot moments” (McClain et al., 2003) or “control points” (Bernhardt et al., 2017) of CO_2 release in IRES, that is, short periods of high biogeochemical activity that may contribute significantly to the emissions of CO_2 from the global stream network.

Therefore, an update of respiration and CO_2 emissions in the global stream network is needed, mainly because the spatial extent of IRES and the frequency of wetting-drying cycles are increasing due to climate change and other anthropogenic pressures.

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DISCUSIÓN GENERAL

Este trabajo recoge los registros hidrológicos colectados en un periodo de 30 años (1985-2015) en el Río Lonquén, el cual pertenece a la Zona del Mediterráneo Chileno. Se caracteriza por poseer estaciones climáticas bien marcadas con un periodo húmedo y frio en invierno y seco con altas temperaturas en verano, peculiar de los climas Mediterráneos (Figueroa et al. 2013; Valdés-Pineda et al. 2014). Se conoce además que los ecosistemas Mediterráneos se encuentran amenazados principalmente por las actividades antropogénicas y climáticas (cambio climático), con reducción de los caudales superficiales y perdida de la biodiversidad (Bonada & Resh, 2013; Figueroa et al. 2013; Grantham et al. 2013).

El presente estudio es el primero en realizarse en la región Latinoamericana que incluye la integración de la diversidad de invertebrados acuáticos, condiciones ambientales y estados hidrológicos (Río Lonquén del Mediterráneo Chileno), tomando en consideración las condiciones de desecación a reconexión y con la identificación de patrones significativos que sustentaron nuestros hallazgos.

En referencia a los caudales superficiales del Río Lonquén (PAPER I), se pudo constatar que existe una reducción de los mismos, determinada por una tendencia negativa en los caudales promedio mensuales (0.031 m^3/s por año) y una tendencia positiva en los días con cero caudales superficiales (3.5 días por año) (Banegas et al. 2021). Estas variaciones significativas también han sido observadas en otros ecosistemas Mediterráneos en donde se evidencian las amenazas y perturbaciones a las que se encuentran sometidos actualmente los ríos intermitentes (Monroy et al. 2017; Skoulikidis et al. 2017; Soria et al. 2019).

Una herramienta desarrollada por parte de las iniciativas europeas para el estudio de los ríos temporales (intermitentes y efímeros) Mediterráneos, ha sido la elaboración e implementación del programa *Estados Hidrológicos y Ecológicos de Ríos Temporales TREHS Tool* (Temporary Rivers Ecological and Hydrological Status) (Gallart et al. 2012). Este fue aplicado en el presente estudio, encontrándose buena resolución de los caudales, con la identificación del tipo de río intermitente (Intermitente con pozas) y la estimación de las métricas de predictibilidad estacional de seis meses y la medida de la permanencia de caudal, respondiendo de esta manera al Objetivo 1, permitiendo establecer comparaciones entre ecosistemas Mediterráneos, de acorde a las métricas empleadas (de Girolamo et al. 2014; Gallart et al. 2017).

En base a los estados acuáticos identificados con el programa TREHS Tool, se destaca un periodo seco de diciembre a abril con una predictibilidad del 78% al 100% de ocurrencia. Dichos valores resaltan una estacionalidad seca con un reconocido periodo sin caudales superficiales, constituidos por los estados *Arreico* (pozas desconectadas y la presencia de fauna léntica) e *Hiporreico* (sin agua superficial y fauna activa terrestre) (Gallart et al. 2012; Gallart et al. 2017; Tzoraki et al. 2016).

En referencia a las comunidades de invertebrados acuáticos del río Lonquén (Objetivo 2), éstos mostraron una heterogeneidad máxima de los hábitats durante la reducción de los caudales (Banegas et al. 2021). Dichos cambios son inducidos por la dominancia de especies adaptadas y tolerantes a los bajos caudales o sin caudales superficiales, y con la capacidad de resistir y recuperarse (resistencia y resiliencia) de los periodos de sequias (Boersma et al. 2014; Warfe et al. 2016; Vander Vorste et al. 2016; Doledec et al. 2017). Además, se observó dominancia de especies adaptadas a la recesión de los caudales y capaces de sobrevivir en condiciones de aguas lénticas (Garcia-Roger et al. 2011; Hill & Miller, 2018), como los quironómidos, anélidos (*Nais* sp.), efemerópteros (*Baetis* sp. y *Caenis* sp.), ostrácodos (Ciprididae), cladóceros (*Daphnia ambigua*), gastrópodos (*Physa chilensis*), hemípteros (Corixidae y Belastomatidae), odonatos (Aeshnidae y Coenagrionidae) y coleópteros (Dytiscidae).

Durante los periodos de transición de condiciones lóticas a lénticas, la presencia de pozas aisladas o desconectadas se vuelven más evidentes, con un sobresaliente cambio en las comunidades de invertebrados (Munné & Prat, 2011; Hill & Miller, 2018). Se destaca en nuestro estudio la presencia predominante en las pozas aisladas de los taxones de OCH: Odonata (Coenagrionidae, Aeshnidae y Libelullidae), Coleoptera (Heteroceridae, Hydrophilidae, Dytiscidae y Helephoridae), Hemiptera (Corixidae y Belastomatidae), los cuales sobresalieron en comparación con las especies EPT (Ephemeroptera, Plecoptera y Trichoptera) por estar más adaptados a condiciones sin flujo de corriente y una mejor aceptación a variables ambientales de ecosistemas estancados (Doledec et al. 2017; Lobrera et a. 2019; Bonada et al. 2020).

Por otro lado, las interacciones encontradas en los valores hidrológicos y físico-químicos en los eventos de desecación y reconexión mostraron variaciones en valores de temperatura superiores en los estados de desecación. Mientras que las pozas aisladas presentaron valores más bajos de oxígeno disuelto, sólidos suspendidos y alta conductividad, debido a los procesos fotosintéticos y de respiración dentro las pozas aisladas (Arenas-Sánchez et al. 2016). En cambio, estas condiciones no fueron limitantes para favorecer a las pozas desconectadas como albergues esenciales para refugiarse o escapar ante las sequias beneficiando a nuevos procesos de colonización, una vez que los hábitats fluviales se han recuperado (Bonada et al. 2006). Nuestro estudio reflejó (Paper I; Figura 3) altas abundancias de Gastropodos (*Physa chilensis*), anelidos (Lumbriculidae and Naiididae), ostracodos (Cyprididae), copepodos (Cyclopoida and Harpacticoida) y cladoceros (Daphniidae) con pocos individuos de Coleoptera (Dytiscidae e Hydrophilidae) y Odonata (Aeshnidae). Las especies de Decapoda (*Aegla* sp. y *Samastacus spinifrons*) y Bivalvia (*Diplodon chilensis*) solamente estuvieron presentes en las pozas aisladas, mostrando una baja capacidad de dispersión y de recuperación de sus poblaciones después de las perturbaciones (Oertli et al. 2002; Fuentealba et al. 2010; Bogan et al. 2015; Leigh et al. 2016; Vander Vorste et al. 2016; Bonada et al. 2020).

Procesos de reconexión en el río intermitente Lonquén permitieron la recolonización de los microhábitats después del periodo seco, destacando el papel de los lechos secos y del hiporreos en los procesos de distribución de los refugios a lo largo del río y de los estados de diapausa o dormancia que permanecieron como propágulos resistentes a las sequias, principalmente para los branquiopodos (*Bosmina hagmanni*), ostrácodos (*Herpetocypris reptans* and *Cypridiopsis vidua*) y copépodos (Cyclopoida) que contribuyeron en el incremento de las riquezas, abundancia y diversidad de los invertebrados acuáticos en nuestros resultados y que han sido reportados por diversos autores (Vander Vorste et al. 2015; Doledec et al. 2017; Lobrera et al. 2019; Lobrera et al. 2021). Similarmente, condiciones de patrones de anidamiento de especies fueron observados en los estados acuáticos de desecación y reconexión en el Río Lonquén (Objetivo 4; Paper I; Figura 4) con un mayor reemplazo para el estado acuático de caudal base, el cual se encuentra principalmente marcado por perturbaciones asociadas a las condiciones de sequias (Shriever et al. 2016; Aspin et al. 2018). Dicha condición además respondió a patrones de recolonización de refugios perennes en la reconexión como la vía dominante en la recuperación de las comunidades de invertebrados acuáticos en ríos intermitentes (Datry et al. 2016).

Predicciones de cambio climático proyectan para Chile central un incremento de las temperaturas medias de 2º a 4º C con reducción de las precipitaciones de un 20 a 40% y una reducción de un 20% para los caudales de verano (CONAMA 2006; Garreaud 2013; Valdés-Pineda et al. 2014; Cabré et al. 2016). Sin embargo, la región de Chile central, ya se encuentra experimentando una condición de megasequía reportada desde el 2010, lo cual ha experimentado un déficit de las precipitaciones anuales que van desde un 25 a un 40% y una anomalía en promedio de +1ª C (Garreaud et al. 2020). En nuestro estudio fue identificada una reducción de los caudales superficiales en el Río Lonquén, evidenciado en el incremento de los días con caudal cero. Si estos patrones se mantienen en el tiempo bajo escenarios de megasequías, cambio climático y cambio de uso de suelo se estaría esperando una pérdida de las pozas aisladas, profundización del nivel freático (hiporreos) y la consecuente pérdida de la biodiversidad y funcionalidad ecológica de estos delicados sistemas acuáticos (Oertli et al. 2002; Heirshkovitz et al. 2013; Datry et al. 2017; Wilding et al. 2018).

Como respuesta al Objetivo 3, se resalta la importancia de los refugios encontrados en las pozas aisladas, en donde aquellas especies que tienen baja capacidad de migrar a otras cuencas requieren de estrategias adaptativas y de conservación para hacer frente las condiciones extremas. Sin embargo, estos refugios brindan condiciones para sobrepasar las sequias y recolonizar posterior a la reanudación de los caudales (Myers et al. 2000; Figueroa et al. 2013). Asimismo, las pozas desconectadas dentro de los ríos intermitentes requieren ser considerados en programas de manejo y conservación, porque albergan una diversidad endémica que requiere ser atendida con preocupación especial, encontrándose especies relevantes para la región Mediterránea Chilena, como: *Diplodons chilensis, Littoridina cumingii, Chilina dombeyana, Physa chilensis,* *Biomphalaria chilensis, Gundlachia gayana, Hyalella costera, Aegla sp., Samastacus spinifrons* y algunos grupos de los microcrustáceos (cladóceros, copépodos y ostrácodos) (Paper I) donde se espera que a futuro bajo los impactos de cambio climático y uso de suelo exista una mayor conversión de ríos perennes a intermitentes (Datry et al. 2014).

Aquí la conectividad ecológica juega un papel relevante en el desarrollo de adaptaciones fisiológicas, morfológicas y de rasgos de historia de vida relacionados a la sobrevivencia bajo condiciones de sequias que favorecen las adaptaciones de rasgos de resistencia y resiliencia en el ecosistema acuático (Crabot et al. 2019; Bruno et al. 2020). Al respecto, en el río Lonquén se identificaron 14 modalidades de rasgos de resiliencia y resistencia (Paper II), donde destacan en alta abundancia para las especies de *Physa chilensis,* Hydracarina, *Daphnia ambigua*, Harpacticoidea, *Herpetocypris reptans*, *Cypridiopsis vidua*, *Caenis* sp., *Andesiops* sp. y los quironómidos, ceratopogónidos y *Simulium* sp., prevalenciendo en las fases hidrológicas. En cambio, el cladócero *Bosmina hagmanii* fue exclusivo de las pozas desconectadas y de la fase de reconexión (Objetivo 3, Paper II).

Las modalidades de resiliencia de duración de ciclos de vida cortos y multivoltinismo comandan en las fases hidrológicas, además de la dispersión que contribuyen a la desecación y condiciones de caudal base (Gauthier et al. 2020). Sin embargo, la presencia de capullos y la respiración por plastrón son importante en los mecanismos de resistencia para las pozas desconectadas. Las condiciones de caudal base resaltaron una mayor resistencia que podría estar asociada a la predominancia de especies adaptadas dentro de los ensambles de invertebrados acuáticos presentes en el río intermitente (Bogan et al. 2014). Rasgos de Resistencia son importantes para conservar los ensambles de la biota acuática en sitios intermitentes, mientras que los sitios permanentes son importantes como fuente de recolonización de taxones para sitios intermitentes cuando los caudales se reconectan (Objetivo 3) (Leigh et al. 2015).

Los lechos secos de los ríos intermitentes, además de invertebrados alojan una gran cantidad de material orgánico, hojas y restos de madera provenientes de la vegetación ripariana, que son almacenados durante el periodo seco. Estos restos se integran al ciclo del carbón y nitrógeno cuando se re-humectan y transportan hacia aguas abajo contribuyendo a las emisiones globales de CO_2 desde un 7% hasta 152% con relevantes consecuencias al cambio climático global (Objetivo 3), principalmente cuando el periodo seco se prolongue por la influencia del cambio climático (Larned et al. 2010; Datry et al. 2014; Jaeger et al. 2014).

Por otro lado, cantidades de lixiviados que se pueden presentar en los lechos secos de los ríos intermitentes pueden liberar cantidades importantes de materia orgánica disuelta presente en las hojas, biofilm o sedimentos (Shumilova et al. 2019). Por ello, las tasas de respiración de los sedimentos una vez que se rehumedecen contribuyen a las emisiones de CO_2 a nivel global durante los múltiples eventos que varían significativamente en el tiempo y espacio (von Schiller et al., 2017). Valores de emisiones pueden llegar alcanzar un 4% de las emisiones globales de ríos intermitentes secos, valores por encima del aporte por parte de ríos perennes (0.8). Sin embargo, se requiere de futuras investigaciones que clarifiquen la relevancia de los procesos y las condiciones que generen un caudal que posibilite la reconexión, ya sea por precipitaciones, alimentación de aguas subterráneas o escorrentía superficial, con respuesta en los procesos de respiración (Von Schiller et al. 2019).

Adaptaciones fundamentales son necesarias implementar dentro de los sistemas ecológicos Mediterráneos de Chile, principalmente para los ríos intermitentes donde se pueda desarrollar el ajuste de comportamientos, acciones y toma de decisiones dentro de un contexto biológico y social con respuestas ante el cambio climático. Medidas de adaptación, capacidad, vulnerabilidad y resiliencia son necesarias para la articulación de ideas colaborativas con los tomadores de decisiones que simultáneamente mejoren el bienestar humano, las relaciones interinstitucionales y la seguridad ambiental (Owen, 2020). Por consiguiente, dichas acciones se esperan sean incorporadas como una contribución a la conservación de la cuenca del Río Lonquén y por ser parte de un sistema importante para la producción agropecuaria y de alta vulnerabilidad ante los efectos del cambio climático en la región.

CONCLUSIONES

1. Durante muchos años, el estudio de los cuerpos de agua no perennes, ríos intermitentes o arroyos efímeros han sido desestimados en programas de manejo, conservación y protección. Sin embargo, algunas iniciativas han surgido en regiones como el Mediterráneo Europeo, Norte América y Oceanía que han permitido conocer el comportamiento de sus procesos hidrológicos, la ecología de los invertebrados acuáticos, los servicios ecosistémicos y su interrelación, principalmente ante los escenarios de cambio climático. A nivel de Latinoamérica, son escasos los estudios en este campo, en donde se pueden resaltar los trabajos realizados en el Río Lonquén, el cual forma parte de la Zona Mediterránea Chilena y que a contribuido ha posicionarse dentro de algunas iniciativas globales, como el proyecto de los 1000 ríos intermitentes para el entendimiento de la ecología de dichos ecosistemas.

2. El Río Lonquén presenta características hidrológicas, ambientales y acuáticas en los procesos de transición de desecación a rehumectación relevantes para la región Mediterránea Chilena, revelando significativos patrones hidroclimáticos para lograr entender la respuesta de los invertebrados acuáticos en los cambios de hábitats temporales.

3. Nuestros resultados permitieron determinar que la primera hipótesis **“Los ríos intermitentes presentan condiciones de refugio (pozas aisladas y**

lechos secos) para albergar parte de la biota acuática del río y sirven de foco de dispersión una vez que el río se conecta“ es aceptada, ya que las reducciones de los caudales superficiales observadas en el río Lonquén permitieron destacar la importancia de las pozas aisladas o desconectadas, las cuales han servido como refugio para especies sensibles con baja capacidad de migrar, principalmente para especies endémicas de bivalvos, gastrópodos y crustáceos como: *Diplodons chilensis, Littoridina cumingii, Chilina dombeyana, Physa chilensis, Biomphalaria chilensis, Gundlachia gayana, Hyalella costera, Aegla* sp. y *Samastacus spinifrons*, quiénes contribuyendo al enriquecimiento de la diversidad, abundancia y recolonizando de nuevo los microhábitats en condiciones de caudal base una vez que se reanudan los caudales superficiales.

4. Especies adaptadas a soportar las condiciones adversas ocasionadas por los procesos de desecación, han desarrollado capacidades para recuperar sus comunidades acuáticas mediante adaptaciones fisiológicas, de comportamiento y/o de dispersión contribuyendo a los procesos de recolonización. En ese sentido, nuestros resultados permitieron aceptar la segunda hipótesis **“La reducción del hábitat acuático durante el proceso de desecación condiciona la importancia relativa de cada uno de los refugios, resaltando las adaptaciones de resiliencia y resistencia ante las perturbaciones por sequía por parte de la biota**

acuática de los ríos intermitentes” en donde se pudo identificar que las comunidades de invertebrados acuáticos del río Lonquén mostraron estrategias ecológicas representadas por rasgos de resistencia (huevos atados a la vegetación, prevalencia de capullos y estados de diapausa y dormancia) y resiliencia (ciclos de vida cortos, muchas generaciones dentro de un año y dispersión activa aérea), caracterizando los principales rasgos prevalecientes en las distintas etapas de desecación y destacando la importancia de cada uno de los refugios para restablecer las poblaciones de la comunidad de invertebrados acuáticos.

5. Nuevos aportes fueron registrados a través del presente estudio en relación a la hidrología y ecología de los invertebrados acuáticos en la región mediterránea Chilena, donde servirán de línea base esencial para programas de manejo y conservación, tanto a nivel local como a nivel regional.

6. El presente estudio remarca además el papel de los lechos secos de los ríos intermitentes en cuanto almacenar una diversidad de sustratos, como restos de plantas terrestres, animales y sedimentos considerados como reactores biogeoquímicos o áreas hot spot responsables de altos niveles de consumo de oxígeno, liberación de dióxido de carbono con un notable impacto en los flujos globales y de emisiones atmosféricas, así como de

liberación de lixiviados de materia orgánica, principalmente en la fase de rehumectación de los lechos.

7. Futuros estudios son requeridos en la región Mediterránea Chilena para entender el comportamiento de los invertebrados acuáticos y sus interacciones con su ambiente ante los escenarios de cambio climático y su resiliencia que favorezcan la toma de decisiones para el manejo y conservación de los ríos intermitentes, en base a los aportes generados por parte de la presente tesis.

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