Universidad de Concepción

Facultad de Ciencias Ambientales
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RESILIENCIA DE ECOSISTEMAS FLUVIALES:

ANÁLISIS MEDIANTE RASGOS EMPÍRICOS DE ENSAMBLES DE PECES

Tesis para optar al grado de

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PAULINA ANDREA VEGA IBÁÑEZ

Profesor Guía: Dra. Evelyn Habit Conejeros

Profesor Co-Guía: PhD Konrad Górski

Dpto. de Sistemas Acuáticos, Facultad de Ciencias Ambientales

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RESUMEN

Los ecosistemas de agua dulce están experimentando una alarmante disminución en la biodiversidad debido a una combinación de efectos locales y alteraciones a escala de cuenca, lo que impide su capacidad para mantener la resiliencia frente a los disturbios antropogénicos. Las cuencas hidrográficas Andinas del Centro-sur de Chile enfrentan múltiples disturbios antropogénicos, como extracción de agua, energía hidroeléctrica, minería, efluentes domésticos e industriales, que afectan su capacidad de adaptarse a nuevos disturbios y de seguir proporcionando contribuciones a la sociedad. Además, la variación en la intensidad de estos disturbios resulta en un marcado gradiente, desde altos disturbios (Maipo, Rapel, Biobío, Maule), medios (Mataquito, Itata) y bajos (Imperial y Toltén). El objetivo de este estudio fue evaluar la resiliencia de los ríos en ocho cuencas hidrográficas del Centro-sur de Chile utilizando los ensambles de peces como indicadores ecosistémicos y siguiendo el marco de "las 3Rs de la resiliencia de ecosistemas fluviales". Se estudió la resiliencia ecosistémica utilizando índices taxonómicos y de rasgos funcionales de los ensambles de peces, evaluando los tres mecanismos de resiliencia: recursos, reclutamiento y refugio, que influyen colectivamente en las respuestas de los ensambles a los disturbios. Los índices taxonómicos capturaron cambios en la riqueza de especies, abundancia, diversidad, equidad y diversidad beta, mientras que los rasgos funcionales reflejaron las características de las especies de peces que promueven la resiliencia. Los test estadísticos revelaron diferencias significativas en los índices de resiliencia entre las cuencas, exhibiendo diferentes niveles de resiliencia. El reclutamiento fue el mecanismo de resiliencia más afectado, revelado por el indicador de diversidad beta, vinculado a la fragmentación en las cuencas de los ríos Maipo, Rapel y Biobío. En tanto, en la cuenca del río Toltén también se encontró un efecto significativo en el mecanismo de resiliencia, pero evidenciado por rasgos funcionales de menor resiliencia, vinculados a salmónidos no nativos. El mecanismo de recursos también se vio afectado, principalmente por cambios en el uso del suelo y contaminación del agua, en las cuencas de los ríos Maipo, Rapel, Mataquito y Maule, reflejado por el indicador de baja riqueza de especies. Notablemente, se observaron respuestas no lineales de resiliencia a los disturbios antropogénicos en varias cuencas, lo que desafía las suposiciones sobre los patrones de disturbios-resiliencia. De hecho, las cuencas hidrográficas caracterizadas por disturbios medios mostraron una alta resiliencia, indicando adaptación a las disturbios y conservación de resiliencia. Este estudio destaca la importancia de utilizar múltiples indicadores para entender la resiliencia de los ecosistemas y enfatiza la necesidad de estrategias integradas para abordar los desafíos complejos que enfrentan los ecosistemas de agua dulce

ÍNDICE DE CONTENIDO

ÍNDICE DE TABLAS

ÍNDICE DE FIGURAS

ÍNDICE TABLAS MATERIAL SUPLEMENTARIO

ÍNDICE FIGURAS MATERIAL SUPLEMENTARIO

1. MARCO TEÓRICO

1.1. RESILIENCIA ECOLÓGICA

Uno de los principales desafíos que enfrenta la humanidad es la gestión sostenible de los ecosistemas, que implica equilibrar su uso actual con su capacidad para continuar proporcionando contribuciones y recursos en el futuro (Parsons et al., 2016). Este desafío requiere comprender los ecosistemas como sistemas socioecológicos, en los cuales los seres humanos son componentes interdependientes (Elmqvist et al., 2003). Sin embargo, las actividades antropogénicas (o disturbios antropogénicos) han alterado las dinámicas naturales de estos sistemas, lo que conlleva repercusiones directas en el bienestar del ser humano. En este sentido, las actividades antropogénicas han reducido la capacidad de los ecosistemas para amortiguar nuevos disturbios, haciéndose cada vez más inciertas sus respuestas (Elmqvist et al., 2003; Scheffer et al., 2001).

La capacidad de un ecosistema para absorber disturbios y permanecer dentro del mismo régimen con la misma estructura, función y retroalimentación se conoce como “resiliencia” (Holling, 1973; Walker and Salt, 2006; Westman, 1978). Esta es una característica ecológica importante que refleja la complejidad de los procesos homeostáticos de un ecosistema (Westman, 1978), incluye el grado en que el sistema es capaz de auto organizarse y, también, expresa una capacidad de aprendizaje y adaptación (Elmqvist et al., 2003). En este sentido, la gestión de los ecosistemas basada en la resiliencia considera la capacidad de adaptación de los sistemas socioecológicos para prevenir transformaciones a estados indeseables (Chapin et al., 2009). Esta capacidad de los ecosistemas para restaurar su estructura después de un disturbio ya sea natural o inducido por el hombre, es fundamental para su funcionamiento y, por lo tanto, de las contribuciones que entregan a los seres humanos (Parsons et al., 2016).

Un concepto relevante en el estudio de la resiliencia de los ecosistemas es el umbral o punto de inflexión (Chapin et al., 2009; Standish et al., 2014; Walker and Salt, 2006). La pérdida de resiliencia acerca el ecosistema a un límite, que, ante un nuevo disturbio podría empujarlo sobre este umbral a un estado alternativo, es decir, a un estado indeseable o degradado (Chapin et al., 2009). Por lo tanto, los umbrales proporcionan un medio para cuantificar cuánto disturbio puede absorber un ecosistema antes de cambiar a otro estado (Standish et al., 2014). Además, podrían indicar cuándo sería necesario intervenir para promover la recuperación del ecosistema a un estado anterior al disturbio (Suding and Hobbs, 2009).

1.2. RESILIENCIA EN ECOSISTEMAS FLUVIALES

La resiliencia en ecosistemas fluviales requiere que las comunidades biológicas persistan frente a variaciones hidrológicas y geomorfológicas altamente dinámicas (Van Looy et al., 2019). Los disturbios naturales producidos por procesos como el régimen de caudal, regulan y confieren estructura a las comunidades biológicas de los ecosistemas fluviales (Poff and Ward, 1989). En este sentido, las variaciones temporales naturales en mecanismos tales como la productividad de los ríos, la conectividad física y la heterogeneidad ambiental, son características claves que promueven la resiliencia en ecosistemas fluviales (Van Looy et al., 2019). Sin embargo, tales mecanismos de resiliencia están siendo afectados por los disturbios antropogénicos. Un ecosistema sujeto a un único disturbio generalmente se recupera, pero, si sufre múltiples disturbios antes de la recuperación, entonces el efecto combinado puede conducir a un cambio a largo plazo y el ecosistema puede entrar en un nuevo dominio ecológico (Jaiswal et al., 2021). En particular, los ríos son unos de los ecosistemas más impactados a nivel mundial; principalmente por la contaminación del agua, fragmentación y destrucción de hábitat, invasión de especies exóticas, sobreexplotación de los recursos hídricos y biológicos, y por el cambio climático (Arthington et al., 2018; Chapin et al., 2009; Dudgeon et al., 2006; Jaiswal et al., 2021). Estos impactos están relacionados y exacerbados por la modificación del régimen de caudal de los ríos. El cambio de uso de suelo, los embalses, la extracción de aguas superficiales y subterráneas, y las transferencias de aguas entre cuencas son los principales impulsores de los cambios en el régimen hídrico en ecosistemas fluviales (Arthington et al., 2018). Este escenario implica nuevos desafíos en la gestión de los ecosistemas fluviales a nivel mundial (Van Looy et al., 2019).

El enfoque que se ha mantenido por un largo tiempo en la gestión de ecosistemas dulceacuícolas y, en especial de ecosistemas fluviales, se basa principalmente en el monitoreo de calidad de agua o de concentración de contaminantes específicos (Jaiswal et al., 2021; Jaiswal and Pandey, 2021). Si bien estos análisis proporcionan un marco para medir los cambios cualitativos cuando son realizados en una escala espacio-temporal adecuada, también tienen limitaciones significativas, ya que no se pueden interpretar los mecanismos internos que mantienen el equilibrio ecológico, incluida la resiliencia (Jaiswal et al., 2021). En general, los parámetros utilizados en evaluaciones de calidad del agua proporcionan información útil sobre el estado de un río, en términos fisicoquímicos, pero no sobre su resiliencia frente al cambio (Parsons et al., 2016).

La gestión de los ecosistemas fluviales bajo un enfoque de resiliencia requiere poder detectar, con cierta confianza, si estos mantienen su resiliencia y su capacidad para suministrar contribuciones a la sociedad (Parsons et al., 2016). En este sentido, algunos autores proponen que medir el umbral de disturbio de un ecosistema es fundamental en el estudio de resiliencia (Standish et al., 2014; Suding and Hobbs, 2009). Sin embargo, esta propuesta también presenta dificultades, ya que los umbrales no son permanentes en el tiempo, es decir, se mueven a medida que los ecosistemas evolucionan en respuesta a los cambios globales (Standish et al., 2014). A pesar de la sólida base teórica de la resiliencia ecológica, entendida como una propiedad emergente de los sistemas adaptativos complejos, es bastante difícil de cuantificar (Jaiswal and Pandey, 2021; Quinlan et al., 2016; Standish et al., 2014)

No obstante, en los últimos años han surgido aproximaciones integradas para medir la resiliencia ecológica de ecosistemas fluviales. Van Looy et al. (2019) proponen un modelo específico para estos ecosistemas, el modelo de “Las tres Rs”. Este modelo identifica tres mecanismos centrales para evaluar la resiliencia ecológica: recursos, reclutamiento y refugio (Van Looy et al., 2019).

Se proponen estos tres mecanismos debido a que un disturbio altera el ecosistema y la estructura de las comunidades biológicas, a través de cambios en la provisión y productividad de los recursos, la conectividad espacial (reclutamiento) y la heterogeneidad del hábitat (refugio) (White and Pickett, 1985 en Van Looy et al., 2019).

En primer lugar, los recursos y la productividad del ecosistema son los principales determinantes del potencial de recuperación de una comunidad después de un disturbio. Así, en respuesta a una cambio en la disponibilidad de los recursos, el mecanismo de resiliencia a nivel de comunidad implica la reorganización interna, la cual está basada en interacciones bióticas como la competencia y la facilitación (Connell and Ghedini, 2015). En otras palabras, los pulsos de recursos inducen respuesta tróficas a nivel comunitario en relación a la nueva dinámica de recursos (Van Looy et al., 2019).

En segundo lugar, el mecanismo de reclutamiento se basa en la dinámica de las metacomunidades, entendiéndose metacomunidad como el conjunto de comunidades locales que están relacionadas por la dispersión de múltiples especies, las cuales potencialmente pueden interactuar entre ellas (Leibold et al., 2004). Este mecanismo incluye la conectividad del hábitat, la capacidad de dispersión de los organismos y el tamaño del grupo regional de especies (Van Looy et al., 2019). En este sentido, la configuración de la red hídrica puede afectar la estructura de las comunidades. Por ejemplo, la posición de un sitio dentro de la red hídrica puede influir en la velocidad en que ese sitio es recolonizado o reclutado después de un disturbio. Los sitios más aislados río arriba pueden experimentar tasas de reclutamiento más bajas después de un disturbio. Esto se debe a su menor conexión con el grupo de especies a nivel regional en comparación con aquellos sitios ubicados en áreas centrales de la red hídrica (Tonkin et al., 2016). En este aspecto, la recuperación de las comunidades bióticas fluviales está influenciada en gran medida en la capacidad de dispersión de los organismos que componen metacomunidades. Esta capacidad afecta no solo la tasa de reclutamiento o recolonización después de un disturbio, sino también su dispersión para evitarlos (Van Looy et al., 2019).

Por último, los ecosistemas fluviales ofrecen refugios ante disturbios, a través de mosaicos de parches de hábitats que le confieren heterogeneidad al ecosistema (Van Looy et al., 2019). Esta heterogeneidad de hábitats proporciona resiliencia ecológica a las comunidades a través del mecanismo de redundancia funcional, impulsado simultáneamente por la diversidad de respuestas de los organismos y la especialización del hábitat (Angeler and Allen, 2016; Van Looy et al., 2019). El concepto de redundancia funcional implica que la pérdida de especies se compensa con otras especies que contribuyen de manera similar al funcionamiento ecosistémico (Biggs et al., 2020; Fetzer et al., 2015). Por lo tanto, es una propiedad comunitaria que juega un papel importante en la prevención de cambios funcionales en ecosistemas bajo presión (Muntadas et al., 2016). La importancia recae en la similitud funcional de las especies en un rasgo, pero su especiación o diferenciación en otros (Van Looy et al., 2019). Así, los organismos funcionalmente similares podrían responder de manera diferente a los disturbios, y por lo tanto, mantendrían la estructura y la función de las comunidades en el espacio y tiempo, confiriéndole resiliencia a los ecosistemas fluviales (Nash et al., 2016).

De acuerdo con Van Looy et al. (2019) se pueden calcular distintos índices taxonómicos, filogenéticos o basados en rasgos funcionales de las comunidades fluviales para determinar cuantitativamente los mecanismos de resiliencia descritos anteriormente (Tabla 1). Por ejemplo, para el mecanismo de recursos los índices taxonómicos, como la riqueza o diversidad de Shannon, permiten dilucidar los efectos comunitarios ante una fluctuación de recursos. En el caso de los índices filogenéticos, la relación de especies supone que especies estrechamente relacionadas se superpongan en el uso del hábitat y de los recursos (Poff et al., 2006), generando respuestas competitivas o facilitadoras a la nueva dinámica. Por último, rasgos funcionales relacionados con los hábitos alimenticios reflejarán directamente los cambios en la disponibilidad de recursos en el ecosistema fluvial (Van Looy et al., 2019).

Tabla 1. Índices taxonómicos, filogenéticos y de rasgos funcionales para los mecanismos de resiliencia en ecosistemas fluviales.

ÍNDICES	RECURSOS	RECLUTAMIENTO	REFUGIO
Taxonómicos	Riqueza/abundancia Diversidad de Shannon	Similitud taxonómica Diversidad Beta	Riqueza taxonómica
Filogenéticos	Relación de especies	Similitud comunitaria	Distinción y diversidad
Rasgos funcionales	Hábitos alimenticios Grupos tróficos	Rasgos de dispersión Rasgos de reproducción	Gremios de hábitat y rasgos de historia de vida específicos

1.3. PECES COMO INDICADORES DE LA INTEGRIDAD ECOLÓGICA DE LOS RÍOS

Una herramienta fundamental para establecer el estado ecológico de los ecosistemas es el monitoreo biológico (Hughes et al., 1998; Parsons et al., 2016). Las comunidades biológicas reflejan las condiciones de los ecosistemas, puesto que son sensibles a los cambios en un amplio espectro de factores ambientales (Karr, 1981), integrándolos en el espacio y en el tiempo. En especial, en los ecosistemas fluviales, la biota acuática puede integrar las características físicas, químicas y biológicas de estos cuerpos de agua, así como también los efectos de las múltiples actividades antropogénicas (Fierro et al., 2019).

Se han utilizado diversos organismos para el monitoreo biológico de ecosistemas fluviales, siendo los peces uno de los más comunes (Parsons et al., 2016). Este grupo ha sido utilizado desde hace más de 100 años para evaluar los impactos de las actividades antropogénicas en los ríos (Simon, 1999 en de Carvalho et al., 2017), ya que pueden ser afectados por disturbios tanto a escala local, como a escala de cuenca hidrográfica, e incluso ambos (Fierro et al., 2019). Los ensambles de peces son un grupo funcionalmente diverso, los cuales representan una variedad de niveles tróficos; incluyendo especies omnívoras, herbívoras, insectívoras, planctívoras y piscívoras (Karr, 1981). Además, al ser el eslabón final de la red trófica en los ecosistemas fluviales, a diferencia de organismos como las microalgas o los macroinvertebrados, los peces proporcionan una visión íntegra de la salud de los ecosistemas. Esto se debe a que dependen de una variedad de funciones y procesos para sobrevivir, crecer y reproducirse (Karr, 1981).

Otras ventajas de utilizar los ensambles de peces como indicadoras de la integridad ecológica incluyen su relativa longevidad en comparación con otras especies de agua dulce. Además, al ser especies móviles, tienen el potencial de integrar los efectos de los disturbios en escalas espaciales y temporales más largas (Parsons et al., 2016). Por ejemplo, son sensibles a los disturbios continuos, como cambios en el régimen de caudal, invasión de especies exóticas o fragmentación del hábitat (de Carvalho et al., 2017; Fierro et al., 2019). Por último, muchas especies de peces ya han sido estudiadas en términos de sus requisitos ambientales y sus historias de vida, lo que facilita la interpretación de la presencia o ausencia de taxa (Parsons et al., 2016).

1.4. SÍNTESIS DEL ECOSISTEMA FLUVIAL

Los ríos constituyen sistemas complejos y jerárquicos que operan en múltiples niveles de organización y escalas (Thoms et al., 2018). Su forma y comportamiento refleja una interacción de procesos geomorfológicos, hidrológicos y ecológicos (Dollar et al., 2007). Por lo tanto, para comprender y gestionar los ríos como ecosistemas, se requiere un enfoque holístico e interdisciplinario (Delong and Thoms, 2016; Dollar et al., 2007), que también considere la resiliencia y la gestión adaptativa (Van Looy et al., 2019). Esta perspectiva cobra relevancia particular en el contexto del cambio climático y las múltiples presiones que afectan los ecosistemas fluviales.

La Síntesis del Ecosistema Fluvial (RES por sus siglas en inglés) propuesta por Thorp et al. (2006), surge como un marco para comprender los patrones, en su mayoría discontinuos, a lo largo de las dimensiones longitudinales y laterales de las redes fluviales (Thorp et al., 2008). RES considera las dimensiones de los ecosistemas fluviales en un modelo jerárquico y físico, reconociendo que relaciones hidrogeomorfológicas y ecológicas operan a múltiples escalas (Delong and Thoms, 2016). A diferencia del Concepto de Río Continuo, que describe los ríos como gradientes continuos de condiciones físicas que regulan los procesos ecológicos dentro del río (Vannote et al., 1980), RES describe la organización longitudinal de los ríos en grandes parches hidrogeomorfológicos, determinados por la geomorfología de la cuenca y las características del régimen de caudal (Thorp et al., 2008). Además, considera la influencia de las condiciones climáticas al incidir en la escorrentía, vegetación ripariana y vegetación acuática (Thorp et al., 2006). Estos parches hidrogeomorfológicos denominados Zonas de Procesos Funcionales (ZPFs), difieren en su estructura geomorfológica y patrones hidrológicos, su ubicación no es completamente predecible y pueden encontrarse reiteradamente a lo largo de la red fluvial (Delong and Thoms, 2016).

La relevancia de las ZPFs recae en que sus diferencias geomorfológicas tienen profundos impactos en la estructura y función de los ecosistemas (Thorp et al., 2008). Se ha evidenciado que a mayor variabilidad física dentro de una ZPF, entendida como heterogeneidad geomorfológica, se relaciona con una mayor complejidad ecológica (Maasri et al., 2021). Por ejemplo, las ZPFs físicamente más complejas se han asociado con una mayor diversidad de especies y una mayor longitud de la cadena trófica (Thoms et al., 2017).

La ventaja del modelo RES radica en que proporciona un marco teórico fundamentado en el estudio de las características hidrogeomorfológicas de los ríos, permitiendo predecir la distribución de especies y la estructura de las comunidades bióticas, es decir, el funcionamiento ecológico del río (Thorp et al., 2008). Al ser aplicable tanto en ecosistemas fluviales prístinos como degradados, RES se convierte en una herramienta valiosa para la gestión, monitoreo y restauración de los ecosistemas de agua dulce alterados (Thorp, 2009). Además, posibilita el estudio de cómo los disturbios antropogénicos afectan los ecosistemas fluviales a una escala adecuada (Dollar et al., 2007; Parsons et al., 2016), permitiendo abordar el estudio de los ríos y sus comunidades con un enfoque de resiliencia.

1.5. CUENCAS ANDINAS DEL CENTRO SUR DE CHILE

Las cuencas hidrográficas Andinas del Centro-sur de Chile (Figura 1) se caracterizan por formar parte de una continuidad geomorfológica a lo largo de la pendiente occidental de la Cordillera de Los Andes (Rojas et al., 2019). Estas cuencas presentan ríos cortos de alta pendiente, que llevan sus aguas desde la Cordillera de Los Andes hacia el Océano Pacífico, es decir, son cuencas exorreicas (Habit et al., 2019). Además, pertenecen al *hotspot* de biodiversidad de Chile, debido esencialmente a su combinación excepcional de una alta concentración de especies endémicas y un alto nivel de amenaza (Myers et al., 2000).

Sin embargo, estas cuencas hidrográficas están sujetas a distintos disturbios antropogénicos, como extracción de agua, fragmentación física, regulación de caudal, efluentes domésticos e industriales, entre otras (Habit et al., 2019). Así, las cuencas desde el río Maipo hasta el río Toltén muestran un gradiente de intervención antropogénica, desde cuencas con un alto grado de intervención (Rapel, Maipo, Maule y Biobío), pasando por un nivel medio (Mataquito e Itata), hasta un bajo nivel de intervención (Imperial y Toltén).

Los ríos Andinos del Centro-sur de Chile se caracterizan por un amplio rango de elevaciones, sosteniendo una diversidad de ZPFs a lo largo de las cuencas andinas. De hecho, Habit et al. (2022) aplicaron el modelo de estudio de ZPFs en las ocho cuencas de estudio. Se delimitaron las redes hídricas de cada cuenca en base a 16 variables geomorfológicas a escala de cuenca, de valle y de canal (Table S1). Estas variables incorporan características geológicas, climáticas y topográficas fundamentales de los paisajes fluviales (Thoms et al., 2017). Se obtuvieron ocho ZPFs, distribuidas sin seguir un patrón longitudinalmente ordenado (Figura 2), dentro de las cuales tres ZPFs presentan una alta representatividad en las ocho cuencas, estas son las ZPFs:

Sinuosa de Canal Único, Sinuosa Multicanal y Suave Pendiente Trenzada Aguas Abajo (SSC, SMC y BGDS, respectivamente por sus siglas en inglés) (Fig. S1).

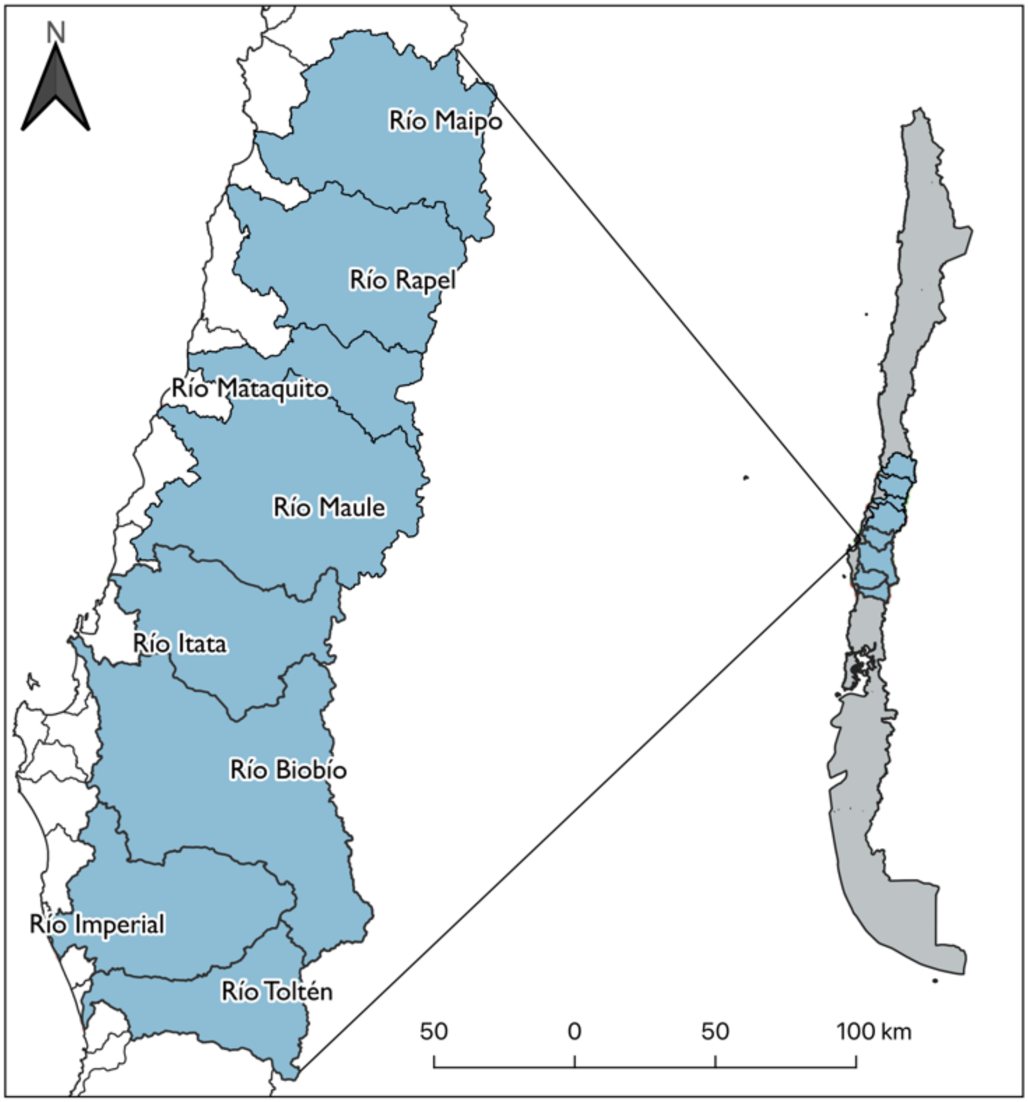

Figura 1. Cuencas andinas del Centro-sur de Chile.

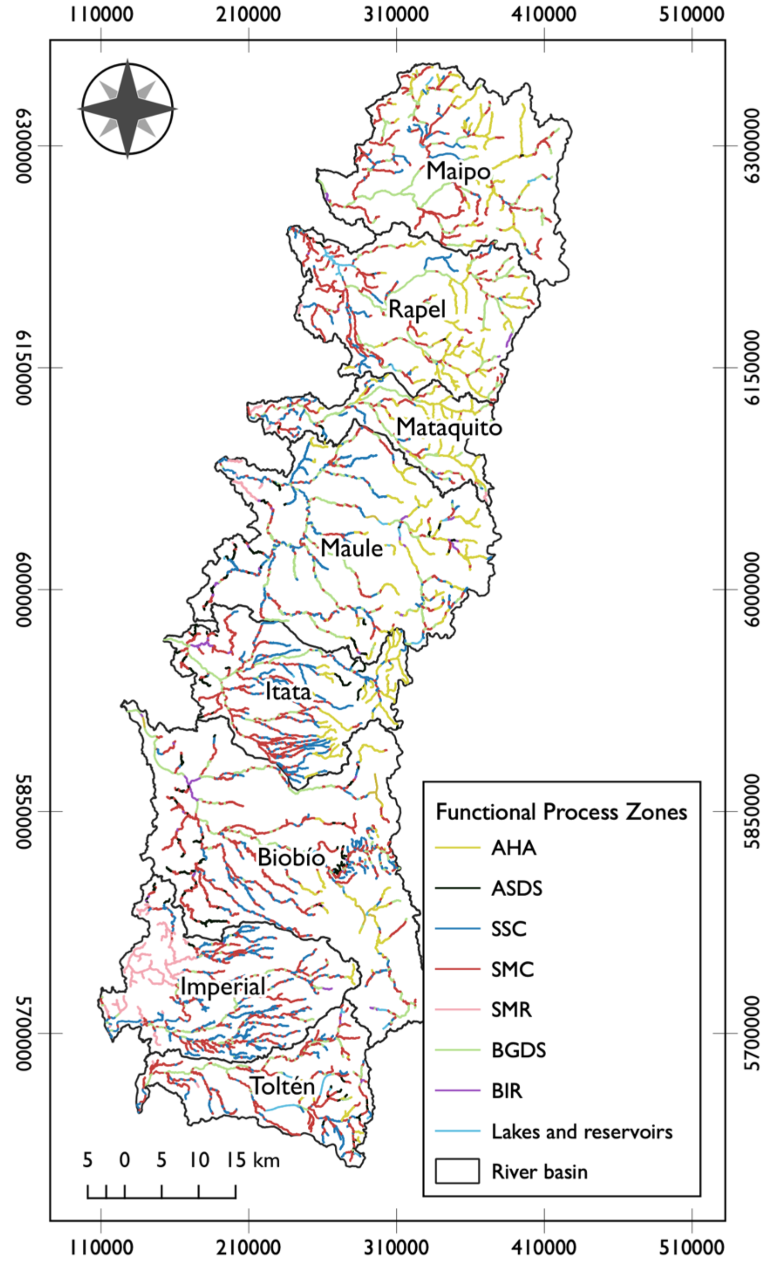

Figura 2. Zonas de Procesos Funcionales (ZPFs) en las cuencas de estudio. AHA, Andean High Altitude; ASDS, Andean Steep Downstream Slope; SSC, Sinuous-Single Channel; SMC, Sinuous-Multi Channel; SMR, Sinuous Metamorphic Rock; BGDS, Braided Gentle Downstream Slope; BIR, Braided Intrusive Rock.

Estas tres ZPFs presentan una distinta complejidad en términos de variabilidad geomorfológica, siendo la ZPF SSC la de menor complejidad, la ZPF SMC de mediana complejidad y la ZPF BGDS de mayor complejidad. En este estudio se considerarán sólo las ZPFs SSC y BGDS, las cuales difieren principalmente por la cantidad de canales y la clase de forma de canal. La ZPF SSC presenta un canal ancho y un valle angosto (Figura 3), mientras que la ZPF BGDS presenta un valle ancho, multicanales de alta densidad y más de tres canales (Figura 4).

Figura 3. Ejemplo de ZPF SSC.

Figura 4. Ejemplo de ZPF BGDS.

2. PREGUNTA DE INVESTIGACIÓN E HIPÓTESIS

Considerando la distinta complejidad física que presentan las Zonas de Procesos Funcionales (ZPFs) de las cuencas Andinas del Centro-sur de Chile, surgen las siguientes **preguntas de investigación:** ¿Son las ZPFs más complejas, más resilientes a los disturbios antropogénicos? ¿Son las cuencas hidrográficas con mayores disturbios menos resilientes?

De las preguntas anteriores se desglosan las siguientes hipótesis:

Si las ZPFs representan la escala espacial más apropiada para evaluar la resiliencia: De acuerdo con los mecanismos de resiliencia de ecosistemas fluviales, las ZPFs físicamente más complejas (BGDS) son más resilientes a los disturbios antropogénicos que las menos complejas (SSC).

Si las ZPFs no son la escala apropiada: Las cuencas hidrográficas con mayores disturbios presentarán menor resiliencia.

3. OBJETIVOS

El **objetivo general** de este proyecto de tesis es evaluar la resiliencia del ecosistema fluvial en cuencas Andinas del Centro-sur de Chile.

Los **objetivos específicos** son:

1. Describir la composición y estructura comunitaria de ensambles de peces en dos ZPFs de distinto nivel de complejidad.
2. Determinar la escala más apropiada para el estudio y evaluación de la resiliencia ecosistémica.
3. Evaluar los mecanismos de resiliencia del ecosistema fluvial basándose en ensambles de peces mediante índices cuantitativos.

4. CAPÍTULO 1. RIVER RESILIENCE: ASSESSMENT USING EMPIRICAL FISH ASSEMBLAGE TRAITS

Este capítulo está basado en:

Vega, P., Górski, K., and Habit, E.

River resilience: Assessment using empirical fish assemblage traits.

Enviado a: Freshwater Biology.

ABSTRACT

1. Freshwater ecosystems are experiencing an alarming decline in biodiversity due to a combination of local effects and basin-scale disturbances, disrupting their ability to maintain resilience in the face of anthropogenic alterations. The Andean river basins of Central-southern Chile face multiple anthropogenic disturbances, such as water extraction, hydropower, mining, domestic and industrial discharges that affect their ability to adapt to new disturbances, and to continue providing contributions to society. Furthermore, the variation in intensity of disturbances in these basins results in a marked gradient, from highly disturbed (Maipo, Rapel, Biobío, Maule), through medium (Mataquito, Itata) to low (Imperial and Toltén).
2. The aim of this study was to evaluate resilience in eight river basins in Central-southern Chile based on fish assemblages following the framework of three Rs of river ecosystem resilience. The assessment was performed using taxonomic and functional trait indices, considering three resilience mechanism: resources, recruitment and refugia, that collectively influence assemblage responses to disturbances. Taxonomic indices captured changes in species richness, abundance, diversity, evenness, and beta diversity, while functional traits reflected fish species' characteristics promoting resilience.
3. Statistical tests revealed significant differences in resilience indices among basins, with some exhibiting higher or lower resilience levels. Recruitment was the most affected resilience mechanism revealed by beta diversity indicator linked to river fragmentation in the Maipo, Rapel and Biobío river basins, whereas in the Toltén River basin functional traits of lower resilience were linked to non-native salmonids. Resources mechanism was also impacted, primarily by land use changes and water pollution in the Maipo, Rapel, Mataquito and Maule river basins reflected by low species richness indicator. Interestingly, non-linear responses of resilience to anthropogenic disturbances were observed across several basins, challenging assumptions about disturbance-resilience patterns. Indeed, river basins characterised by medium disturbances, revealed high resilience, indicating adaptation to disturbances and resilience retainment.
4. This study offered valuable insights regarding the indicators that promote resource, recruitment and refugia resilience mechanisms in river ecosystems. Fish assemblages proved to be suitable indicators of river resilience, representing diverse responses to anthropogenic disturbances among basins. Furthermore, this study underscores the importance of using multiple indicators to understand ecosystem resilience and emphasises the need for integrated strategies to address the complex interactions of climate change, intensified land use, species invasion and population growth that face freshwater ecosystems.

Keywords: Andean rivers; Resilience mechanisms; Anthropogenic disturbances; Functional Process Zones; Resilience trait

4.1. INTRODUCTION

Freshwater ecosystems present an alarming biodiversity decline caused by combination of local effects and disturbances across catchments that is challenging to manage (Linke et al., 2011). Indeed, river ecosystems are often modified and impacted to the point that their contributions to society are severely affected (Wohl, 2014). Furthermore, anthropogenic modifications may prevent river ecosystems from adapting to new disturbances that cause shifts in demographic rates of aquatic organisms (Mouillot et al., 2013). Some anthropogenic disturbances can significantly erode ecological resilience of river ecosystems making them more vulnerable to new disturbances (Mori et al., 2013). Resilience is ecosystem's ability to absorb disturbances and remain within the same regime i.e., structure, function and feedbacks (Holling, 1973; Parsons et al., 2016; Walker and Salt, 2006; Westman, 1978). As such, resilience also encompasses the ability to reorganise itself and adapt to change (Elmqvist et al., 2003). In river ecosystems, resilience implies the persistence of biological communities in highly dynamic hydrological and geomorphological regimes (Van Looy et al., 2019). Indeed, anthropogenic activities such as fragmentation, flow regime alteration, water pollution, habitat degradation, species invasions and climate change pose significant challenges to maintenance of river ecosystems' resilience (Arthington et al., 2018; Dudgeon et al., 2006; Jaiswal et al., 2021; Van Looy et al., 2019).

Van Looy et al. (2019) proposed an integrated framework to assess resilience of river ecosystems. This framework recognises flow-related disturbances as dominant forces shaping riverine communities and suggests three major resilience mechanisms based on responses of aquatic communities to disturbances in productivity (resources mechanism), spatial connectivity (recruitment mechanism) and habitat heterogeneity (refugia mechanism). For the resources mechanism, the potential recovery of an altered ecosystem rely on food availability and variables such as light, oxygen, substrate, and temperature (Van Looy et al., 2019). Consequently, this mechanism operates at the community level, involving internal reorganisation driven by biotic interactions such as competition and facilitation (Connell and Ghedini, 2015). The recruitment mechanism is based on metacommunity dynamics and depends on habitat connectivity, species dispersal capacity and regional species pool size (Leibold et al., 2004). As such, the river network configuration strongly affects community structure i.e., site position in the river network affects post-disturbance recolonisation or recruitment rates (Tonkin et al., 2016). Therefore, the community recovery is largely influenced by the species dispersal capacity since it affects not only the rate of recruitment or recolonisation after a disturbance but also dispersal to avoid disturbances (Van Looy et al., 2019). The refugia mechanism operates through mosaic of patches of habitats that confer heterogeneity to the ecosystem (Van Looy et al., 2019). This habitat heterogeneity provides ecological resilience to communities through mechanisms of functional redundancy, driven simultaneously by the diversity of responses of organisms and habitat specialisation (Angeler and Allen, 2016). The concept of functional redundancy implies that the loss of species is compensated for by others that contributes similarly to ecosystem functioning i.e., the functional similarity of species in one trait and their differentiation in other (Biggs et al., 2020; Fetzer et al., 2015; Van Looy et al., 2019). Thus, functionally similar organisms could respond differently to disturbances and would therefore maintain the structure and function of communities in space and time, conferring resilience to river ecosystems (Nash et al., 2016).

Fish are excellent indicators of the ecological status of river ecosystems as they can integrate the effects of disturbances over long spatial and temporal scales since they are relatively long-lived and mobile organisms and their assemblages are functionally diverse (Parsons et al., 2016). Furthermore, as top predators in food webs, fish offer a comprehensive view of the ecological status of river ecosystems. Their survival, growth and reproduction rely on a diversity of functions and processes directly related to river connectivity (Karr, 1981; Schiemer, 2000). For example, in the upper Mississippi River, dam constructions altered fish trophic positions indicating a loss of functional diversity and consequently resilience (Delong et al., 2011; Delong and Thoms, 2016b). This decline likely stemmed from diminishing habitat heterogeneity (refugia mechanism) near the dams (Van Looy et al., 2019).

The comprehension and management of river ecosystems requires an interdisciplinary and holistic approach that acknowledges the intricate interplay between their physical and biological components (Delong and Thoms, 2016a; Dollar et al., 2007; Thorp et al., 2008). Furthermore, it necessitates an understanding of resilience and adaptive management strategies (Parsons et al., 2016). The interplay of physical and biological components within river ecosystems generates distinct spatial patterns noticeable across multiple scales (Elgueta et al., 2019; Thoms et al., 2017). The Riverine Ecosystem Synthesis (RES) emerged as a framework to elucidate hydrogeomorphological and ecological relationships that operate at these multiple scales (Delong and Thoms, 2016a; Thorp et al., 2008). This framework conceptualises river networks as a series of river zones, named Functional Process Zones (FPZs). Each FPZ delineates a large section of river characterised by relatively uniform geological histories and channel morphologies, thereby promoting similar functional ecological organisations (Habit et al., 2022). The physical attributes of FPZs influence ecological traits both within and across river sections (Thorp et al., 2008). Furthermore, geomorphological differences among FPZs have profound impacts on ecosystem structure and function (Thorp et al., 2008). Research has demonstrated that increased geomorphological heterogeneity, indicative of greater physical variability in a FPZ, is correlated with higher ecological complexity e.g., biodiversity and food chain length increases with greater FPZ's physical complexity (Maasri et al., 2021; Thoms et al., 2017),.

Andean rivers of Central-southern Chile provide an excellent model for evaluating the resilience of fish assemblages and its relationship with FPZs. These rivers are characterised by a diverse range of elevation across basins that supports a diversity of FPZs (Elgueta et al., 2019; Habit et al., 2022). Each Andean exorheic basin features short, steep rivers that flow from 3,000 m.a.s.l. in the Andes Cordillera to the Pacific Ocean (Habit et al., 2019). Furthermore, they remained isolated for more than 10,000 years (Charrier et al., 2015) and are characterised by fish assemblages with low species diversity, but with high levels of endemism, explained by basins' geological history and geomorphological characteristics (Campos et al., 1998; Habit et al., 2006). Presently, these rivers are affected by various anthropogenic disturbances, e.g. water extraction for human consumption, irrigation, domestic and industrial discharges, hydropower (flow regulation and physical fragmentation), mining, and recreation. Consequently, increasing anthropogenic disturbances threaten the ability of these rivers to continue provisioning contributions to society (Habit et al., 2022, Habit et al., 2019).

The aim of this study was to assess resilience in eight Andean River basins of Central-southern Chile in two FPZs of contrasting geomorphological complexity, based on the evaluation of fish assemblages as indicators of ecological resilience. We postulated that physically more complex FPZs are more resilient to anthropogenic disturbances than less complex FPZs. We described the composition and structure of fish assemblages in two FPZs of different levels of complexity in each basin. Subsequently, we assessed resilience mechanisms (resources, recruitment and refugia) of each basin through quantitative indices based on fish assemblages (taxonomic and functional traits) following the three Rs of river ecosystem resilience (Van Looy et al., 2019). Evaluation of ecological resilience plays a vital role in identifying human impacts on the biophysical components of ecosystems. Thus, monitoring resilience indicators allows a better understanding of the river ecosystem's capacity to adapt and transform in response to anthropogenic disturbances, informing adaptative management strategies (Parsons et al., 2016).

4.2. METHODOLOGY

4.2.1. STUDY SITE

This study was carried out across eight Andean River basins in Central-southern Chile, between 32º 55' and 39º 40' Lat. S. (Fig. 1). These rivers are characterised by relatively short length (<380 km), steep slopes, pluvio-nival flow regimes, and average annual discharges ranging from 100 to 1,000 m^3/s (Díaz et al., 2021). The prevailing climate is warm-summer Mediterranean climate (Csb) according to the Köppen-Geiger classification (Table 1). Studied river basins are located in the "Chilean winter rainfall-Valdivian forest" biodiversity hotspot (Arroyo et al., 2004; Myers et al., 2000) and belong to the Chilean ichthyogeographic province that accommodates the highest fish species richness and seven endemic species: *Bullockia maldonadoi, Cheirodon galusdae, Diplomystes incognitus, Diplomystes nahuelbutaensis, Diplomystes arratie, Percilia irwini* and *Trichomycterus chiltoni*. The latter three are endemic to the Biobío River basin, Chile's most diverse river basin (Dyer, 2000; Muñoz-Ramírez et al., 2023; Vila and Habit, 2015).

This study area represents an anthropogenic disturbance gradient from North to South, with a high level of disturbances due to fragmentation, land use changes, and water pollution in the Maipo, Rapel, Biobío and Maule rivers, through moderate disturbances in the Mataquito and Itata rivers, and less altered and non-fragmented Imperial and Toltén rivers (Habit et al., 2022; Habit et al., 2019). Some of the basins are highly populated e.g., the Metropolitan region in the Maipo River basin is inhabited by 7 million people, the Gran Concepción area in the Biobío River basin is inhabited by 1.5 million people, and the Maule region is inhabited by 1 million people (INE, 2024). Consequently, Maipo, Biobío and Maule rivers receive wastewater from multiple sources. The Maipo River basin has been described as the most polluted in Chile (Vega-Retter et al., 2014). In addition, the Maipo and Rapel river basins accommodate copper mining industry in their headwaters causing water extraction, damming and channelisation, and changes in the physical and chemical water quality (Habit et al., 2019). Forestry activity and pulp mill industry with industrial effluents discharging directly to rivers are present in the Biobío River basin (three pulp mills), and, to a lesser extent, in the Itata River basin (one pulp mill). The primary industrial discharge that flows into the Biobío River comes from the pulp mill industry, which generates 80% of the 5 billion tons per year of the pulp produced in Chile, and water consumption reaches up to 127 m^3/ton of product (Figueroa et al., 2020). Most of the studied basins had undergone a pervasive land use change, especially the Mataquito, Maule, Itata, Biobío river basins, with 22.3% of land use for forest plantations dominated by *Pinus radiata* and *Eucalyptus globulus,* and 20.7% for agriculture and livestock (Habit et al., 2024). Large reservoirs that store water for irrigation are located mainly in the Rapel and Maule river basins (Díaz et al., 2019). In addition, the Maipo, Rapel, Biobío, and Maule river basins host between 9 and 19 hydropower plants including large dams with reservoirs and hydropeaking as well as run-of-river dams (Ministerio de Energía, 2018). Indeed, the Rapel River basin accommodates the oldest reservoir in Chile, built in 1968, and is the most fragmented basin in the country (Table 1). Imperial and Toltén river basins are significantly less affected by anthropogenic activities with primary disturbances being the aquaculture farms and non-native salmonids that affect native species through predation and competition (Habit et al., 2015).

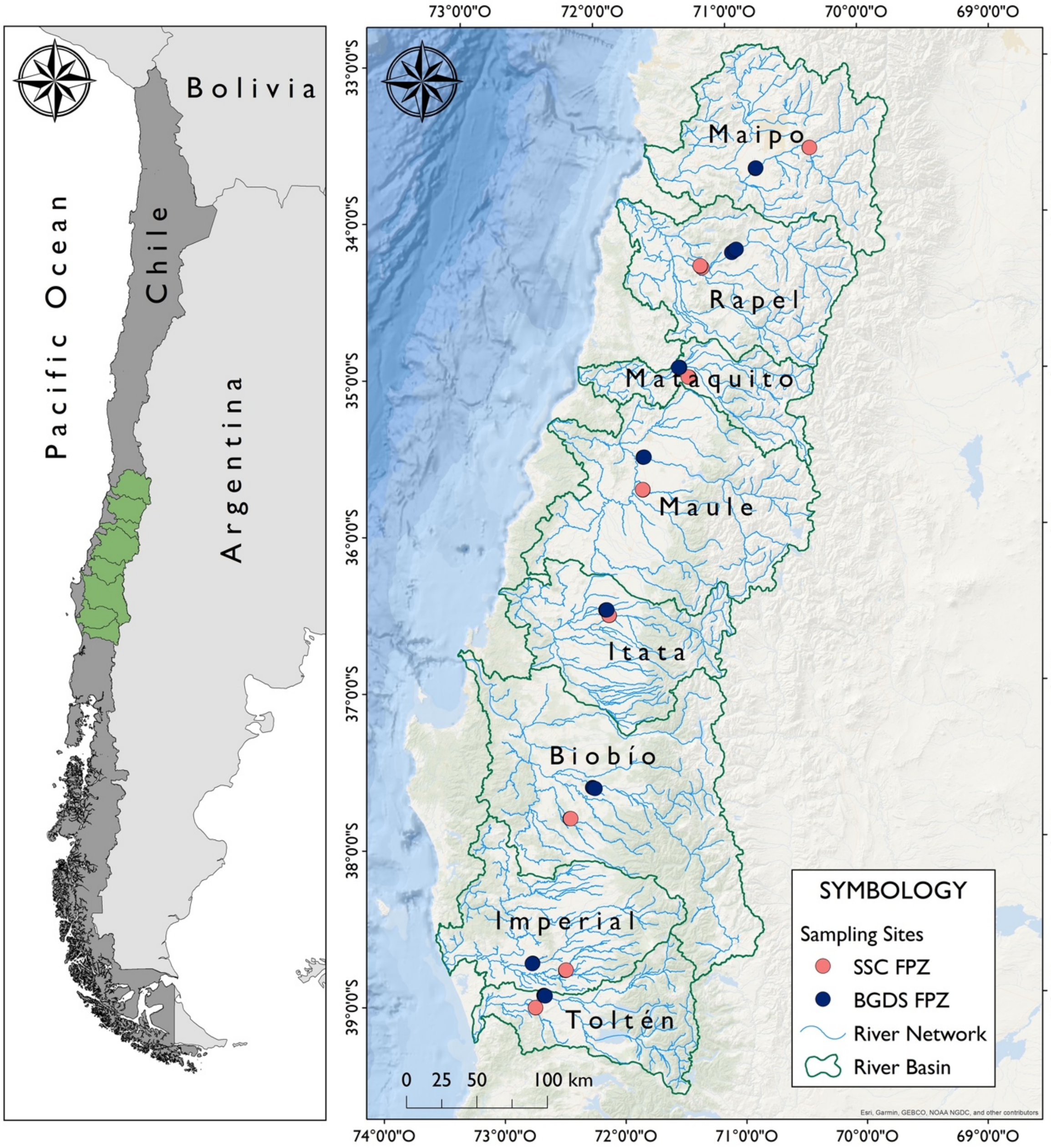

Fig. 1. Geographic location of the eight studied basins and location of sampling sites associated with two Functional Process Zones (FPZs). SSC, Sinuous Single Channel; BGDS, Braided Gentle Downstream Slope.

Table 1. Geographic position, catchment area, predominant climate, flow regime, mean, annual precipitation, mean annual discharge at the mouth of the eight river basins and Fragmentation Index (Díaz et al., 2021; Habit et al., 2022). Csa, hot-summer Mediterranean climate; Csb, warm-summer Mediterranean climate; Cfb, Oceanic climate (Marine west coast).

Basin	Latitude (º ')	Longitude (º ')	Area (km^2)	Maximum Altitude (m)	Predominant Climate	Flow Regime	PP_{MA} (mm)	Q_{MA} (m^3/s)	Fragmentation Index
Maipo	32◦ 55′ – 34◦ 18′ S	69◦ 48′ – 71◦ 38′ W	15,273	6,546	Csa-Csb	Snowmelt	650	134	0.393
Rapel	33◦ 54′ – 35◦ 00′ S	70◦ 01′ – 71◦ 51′ W	13,766	5,138	Csa-Csb	Snowmelt-rain	882	169	0.463
Mataquito	34◦ 48′ – 35◦ 38′ S	70◦ 24′ – 72◦ 11′ W	6,332	4,058	Csb	Snowmelt-rain	1373	113	0.080
Maule	35◦ 06′ – 36◦ 35′ S	70◦ 21′ – 72◦ 27′ W	21,052	3,931	Csb	Snowmelt-rain	1400	495	0.361
Itata	36◦ 12′ – 37◦ 20′ S	71◦ 02′ – 72◦ 52′ W	11,326	3,178	Csb	Snowmelt-rain	1764	331	0.044
Biobío	36◦ 52′ – 38◦ 54′ S	70◦ 50′ – 73◦ 12′ W	24,369	3,487	Csb	Rain	1873	971	0.436
Imperial	37◦ 49′ – 38◦ 58′ S	71◦ 27′ – 73◦ 30′ W	12,668	3,066	Csb-Cfb	Rain	2056	264	0.002
Toltén	38◦ 36′ – 39◦ 38′ S	71◦ 24′ – 73◦ 14′ W	8,448	3,710	Cfb	Rain	2062	540	0.016

4.2.2. FUNCTIONAL PROCESS ZONES

The characterisation of river landscape to identify groups of river sections with similar hydrogeomorphic character (FPZs) was carried out by Habit et al. (2022), based on 16 hydrogeomorphic variables corresponding to three spatial scales: river basin, valley, and channel. Seven FPZs were obtained, and these showed a patchy distribution within and among the river networks. Within the eight study basins, three FPZs were more abundant: Sinuous Single-Channel (SSC), Sinuous Multi-Channel (SMC) and Braided Gentle Downstream Slope (BGDS). The SSC and BGDS FPZs are contrasting in terms of geomorphological complexity, differing mainly by the number of channels and the channel planform. SSC FPZ is characterised by sinuous rivers with wide single channel and a narrow valley, whereas BGDS FPZ is characterised by braided gentle downstream slopes with a wide channel and valley.

4.2.3. FISH SAMPLING

Between January and April 2021, 46 sites were sampled in the Maipo, Rapel, Mataquito, Maule, Itata, Biobío, Imperial, and Toltén river basins under low flow conditions (Fig. 1). Of these, 23 sites were located in the SSC FPZ, and 23 in the BGDS FPZ. Within each river basin, each FPZ had three sampling sites, except for the BGDS FPZ in the Maule River basin and the SSC FPZ in the Toltén River basin, each represented by two sampling sites. At each site, sampling was conducted using a Halltech HT-2000 (Halltech, Guelph, Canada) backpack electrofisher for approximately 30 minutes, depending on the available habitat area. In addition, fish were captured in shallow water habitats (<1 m depth), characterised by gravel and sand patches, using 6-meter-long beach seines (1.5-meter-height and 10 mm stretched mesh size), between two and four seine hauls per sampling site. Hence, sampling was performed in every microhabitat within each site, covering riffles, pools, and runs. Captured specimens were anaesthetised, identified to the species level using specialised identification keys (Ruiz and Marchant, 2004; Salas et al., 2012), counted, weighed and then returned to their habitats.

4.2.4. DATA ANALYSIS

Non-metric multidimensional scaling (NMDS) analysis was performed to explore changes in the composition and structure of fish assemblages between FPZs (SSC and BGDS). NMDS was based on Bray-Curtis dissimilarity matrix on the square root transformed abundance (Clarke and Warwick, 2001). Subsequently, differences in composition and structure of fish assemblages between FPZs and among basins were tested by permutational multivariate analysis of variance (PERMANOVA; Anderson et al., 2015). Threshold was stablished at $P<0.05$. Subsequently, Canonical Analysis of Principal Coordinates (CAP) was used to visualise overall patterns of dispersion in fish species composition and assemblage structure among the eight study basins and to assess the level of singularity of each fish assemblage based on the Bray-Curtis dissimilarity matrix. This method allows a constrained ordination on the basis of a distance or dissimilarity measure and discriminate between FPZs and among basins (Anderson and Willis, 2003). Additionally, an Analysis of Similarity Percentages (SIMPER) was used to estimate the contribution of each fish species to the similarity among basins (Clarke, 1993). PRIMER-E v7.0 program (Anderson et al., 2015) was used for data treatment and analyses.

River resilience for eight river basins was assessed using taxonomic and functional trait indices based on fish assemblages for each resilience mechanism. For the classification of functional traits for each species see Table S2. Table 2 and 3 show the expected trend for higher or lower resilience for each index. For the resources mechanism, taxonomic indices capture changes in the species richness, abundance, diversity, and evenness that, in turn, allow to infer disturbance consequences at the community level. For the recruitment mechanism, taxonomic indices such as beta diversity based on Sørensen, and Bray-Curtis coefficient capture the recruitment recovery at the basin level (Van Looy et al., 2019). For the refugia mechanism, changes in taxonomic richness, in this case richness by taxonomic order, diversity by taxonomic order and evenness by taxonomic order represent redundancy response to disturbances, i.e. what is suitable for one species will also be for closely related ones (Mouillot et al., 2013).

The functional traits correspond to species characteristics that promote resilience for each mechanism. For example, a fish species belonging to the omnivorous trophic guild adds more resilience to the assemblage than an invertivores-piscivorous, invertivores or detritivores species, or one that uses the floodplain is more resilient than one that does not, due to the higher number of resources available to cope with disturbances. In this study, phylogenetic indices were not used due to the lack of information on the phylogeny of several native fish species. Taxonomic indices for the resources and refugia mechanisms were estimated using the Diverse routine of PRIMER-E v7.0 (Clarke and Gorley, 2015). Taxonomic indices of the recruitment mechanism were based on a distance-based approach to obtain beta diversity (see Díaz et al. 2021). The homogeneity dispersion test (PERMIDSP) was used to assess the multivariate dispersion within each river basin (Anderson et al., 2006). PERMDISP provided a measure of total beta diversity based on both presence-absence (Sørensen coefficient) and abundance data (Bray-Curtis coefficient).

Table 2. Taxonomic and functional traits indices used for each resilience mechanism. ↑ indicates resilience increase as the value of the index increases; ↓ indicates resilience decrease as the value of the index increases. † indicates indices and traits proposed in this study.

Mechanism	Resources	Recruitment	Refugia
Taxonomic indices	Richness ↑	Beta diversity (Sørensen) ↓	†Richness by taxonomic order ↑
	Total Abundance ↑		†Shannon diversity index by taxonomic order ↑
	Shannon diversity index ↑	Beta diversity (Bray-Curtis) ↓	†Pielou evenness index by taxonomic order ↑
	†Pielou evenness index ↑		
Functional traits	Trophic guilds	Migratory life history	†Vertical position
		†Abundance-Weighted Average Size	
		†Sexual maturity	
		Fecundity	
	†Floodplain use	†Spawning	†Velocity preference
		†Egg size	
		†Parental care	

Table 3. Functional traits used to assess fish assemblages' resilience mechanisms in each basin. These traits were selected based on the available knowledge about fish species captured in the eight basins (Table S2). ↑ indicates resilience increase as biomass of fish in a particular trait category increase. ↓ indicates resilience decrease as the biomass of fish in a particular trait category increase.

Trait type	Trait	Categories	Categorical – Value
Ordinal	Trophic guilds	Detritivore ↓	1
		Invertivore ↓	2
		Inv-Piscivore ↓	3
		Omnivore ↑	4
Ordinal	Floodplain use	Scarcely↓	1
		Frequently ↑	2
Ordinal	Migratory Life History	Non-migratory ↑	1
		Amphidromous facultative ↓	2
		Catadromous facultative ↓	3
		Anadromous ↓	4
Continuous	Maximum length	Species maximum size recorded in literature ↓	-
Ordinal	Sexual Maturity	Rapid (1st year) ↑	1
		Late (after 1st year) ↓	2
Ordinal	Fecundity	Low ↓	1
		High (>1000 oocytes or eggs) ↑	2
Ordinal	Spawning	Single ↓	1
		Multiple ↑	2
Ordinal	Egg size	Small ↑	1
		Large (> 2 mm) ↓	2
Ordinal	Parental care	Absent ↓	1
		Present ↑	2
Ordinal	Vertical position	Benthic ↓	1
		Benthopelagic ↑	2
		Pelagic ↓	3
Ordinal	Velocity preference	Limnophilic ↓	1
		Eurytopic ↑	2
		Reophilic ↓	3

Fish biomass was calculated for the functional trait that represents more resilience (indicated with ↑ in Table 3, i.e. omnivorous, frequently floodplain use, rapid sexual maturity, high fecundity, multiple spawning, small egg size, parental care, benthopelagic, eurytopic) resulting in a functional trait index based on biomass. For functional traits with more than two ordinal categories (Table 3), Principal Component Analysis (PCA) was performed using the first principal component as a proxy for the functional trait index in software PRIMER-E v7.0 (Table S3). Subsequently, statistically significant differences in taxonomic and functional trait indices among basins were assessed. One-way ANOVAs were conducted for normally distributed indices with homogenous variances. For indices with non-normal distribution but homogeneous variance Kruskal-Wallis test was used. Post hoc Tukey's (HSD) and Dunn tests (Bonferroni method) were carried out in cases of significant differences. The normality distribution and variance homogeneity were assessed using the Shapiro-Wilk test and the Levene test, respectively. All analysis were performed in R version 4.0.3 (R Core Team, 2020). For Beta diversity based on Sørensen and Bray Curtis coefficients, PERMANOVA was used to test significant differences among basins (Anderson et al., 2015). The differences were considered significant at $P<0.1$. Finally, to assess the resilience for each river basin, the post-hoc analyses (significant differences) results were used to estimate the percentage of low resilience indices out of the total significant indices. Therefore, river basins with 50 to 100% of low resilience indices were considered as 'low resilience'; river basins with 20 to 50% significant indices of low resilience were classified as 'medium resilience', and river basins with 0 to 20% of significant indices of low resilience were classified as 'high resilience'.

4.3. RESULTS

4.3.1. FUNCTIONAL PROCESS ZONES' FISH COMPOSITION

A total of 3,094 fish specimens was captured, corresponding to fifteen native and five non-natives species. Eighteen species were found in the SSC FPZ, while sixteen were captured in the BGDS FPZ (Table S4). Both evaluated FPZs were dominated by *Basilichthys microlepidotus, Percilia gillissi* and *Trichomycterus areolatus*. Also, rare species were found in both FPZs e.g., from the Diplomystidae family, *D. incognitus* was found in BGDS FPZ in the Rapel River basin, *D. arratie* in SSC FPZ in the Biobío River basin, and *Diplomystes camposensis* in BGDS FPZ in the Toltén River basin. Regarding non-native species, *Gambusia holbrooki, Oncorhynchus mykiss* and *Salmo trutta* were found in both FPZs in some basins (Table S4). It is noteworthy that in one replicate of the SSC FPZ of the Maipo River basin, no fish specimens were found. Species richness increased with increasing latitude, independently of the FPZ, from the northern Maipo River basin with a medium of two species in the SSC FPZ, to the southern Toltén River basin with a median of seven species in both FPZ (Fig. 2). NMDS based on the Bray-Curtis dissimilarity matrix on fish abundance at each sampling site did not present any clear similarity pattern for FPZs fish assemblages (Fig. S2). Fish composition and abundance was significantly different among basins and FPZs nested within river basins (Table 4).

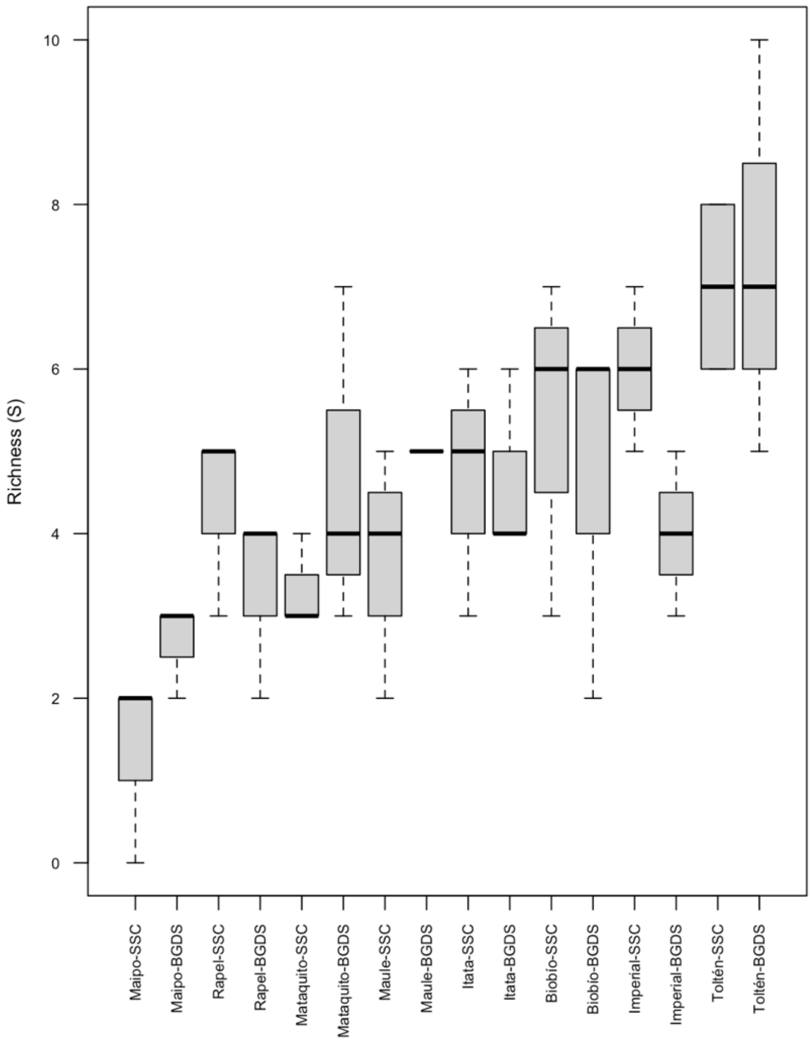

Fig. 2. Fish species richness in both FPZs in each river basin. SSC, Sinuous Single Channel; BGDS, Braided Gentle Downstream Slope FPZ.

Table 4. Results of PERMANOVA conducted on Bray-Curtis similarity matrix based on fish abundance data. df, degrees of freedom; SS, sums of squares; Pseudo-F, distance-base pseudo-F-statistic; P, probability values (obtained using 9999 permutations of residuals under a reduced model). Significant effects are indicated in bold.

Factor	df	SS	Pseudo-F	P(perm)	Unique perms
Basin	7	55789	2.9212	**0.0001**	9885
FPZ (Basin)	8	21840	2.0736	**0.0003**	9861
Res	30	39496	-	-	-

4.3.2. CAP FPZ-BASIN

Although PERMANOVA revealed significant differences between the FPZs nested within river basins, the CAP analysis (Fig. 3) indicated poor classification of the Basin-FPZ factor. Only 23 out of 46 sites were classified correctly, resulting in a classification error of 50%. The Maipo-BGDS, Itata-SSC and Itata-BGDS variables achieved 100% correct classification, while the Mataquito-BGDS, Biobío-SSC and Biobío-BGDS variables showed no correct classification (Table S5).

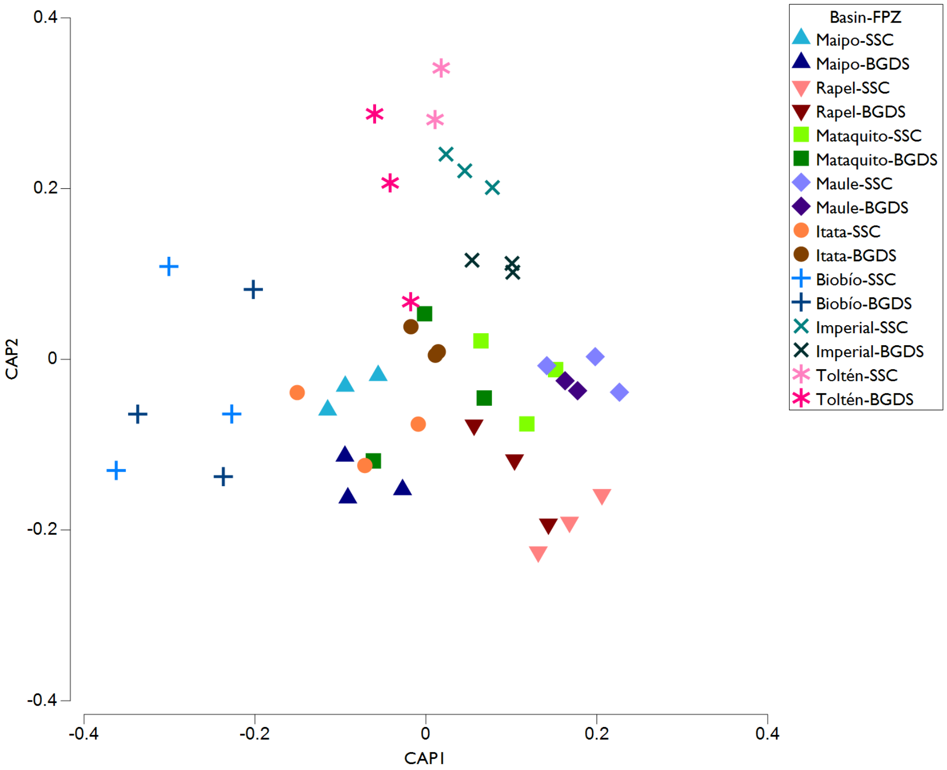

Fig. 3. Canonical Principal Coordinate Analysis (CAP) on fish abundance data in each FPZ of the eight basins. SSC, Sinuous Single Channel; BGDS, Braided Gentle Downstream Slope.

4.3.3. BASIN IDENTITY

CAP analysis conducted on fish abundance data across the eight study basins revealed a classification accuracy of 78% (Table 5). The Mataquito River basin exhibited the lowest classification percentage, together with a substantial dispersion of its data meaning that sampling sites within the Mataquito River basin present higher similarities with the Maipo, Rapel and Itata river basins (Table 5). However, seven out of the eight study basins showed high percentages of correct classification (>60%). The Maule and Itata river basins reached 100% classification accuracy. Overall, these results revealed a strong basin identity based on fish species presence and abundance. Each basin significantly differed in fish assemblage composition and abundance (Table 4). Based on SIMPER analysis, the dominant species were *T. areolatus* and *P. gillissi* in the Rapel, Mataquito, Itata, Imperial, and Toltén river basins, while in the Biobío River basin *P. irwini* and *Percichthys trucha* were dominant (Fig. 4). *Percichthys trucha* was abundant also in the Itata River basin, and to a lesser extent in the Maipo and Mataquito river basins. Among non-native species *G. holbrooki* was abundant in the Rapel and Maule river basins, whereas *O. mykiss* was abundant in Maipo River basin and southern basins such as Imperial and Toltén (Fig. 4).

Native fish species richness exceeded non-native species richness in all basins (Table S4). The central-southern river basins, Biobío, Imperial and Toltén hosted the highest number of native species, accommodating nine, seven and ten species, respectively. In contrast, the presence of non-native species appeared relatively uniform across the eight evaluated basins, ranging from one to two introduced species per basin (Table S4). The non-native species found correspond to *Cnesterodon decemmaculatus*, *Cyprinus carpio, G. holbrooki*, *O. mykiss* and *S. trutta.*

Table 5. Canonical Principal Coordinate Analysis (CAP) on fish abundance data in the eight basins.

Original Group	Maipo	Rapel	Mataquito	Maule	Itata	Biobío	Imperial	Toltén	Total	% Correct
Maipo	5	0	1	0	0	0	0	0	6	83.3
Rapel	0	4	1	1	0	0	0	0	6	66.7
Mataquito	1	1	2	0	2	0	0	0	6	33.3
Maule	0	0	0	5	0	0	0	0	5	100.0
Itata	0	0	0	0	6	0	0	0	6	100.0
Biobío	1	0	0	0	0	5	0	0	6	83.3
Imperial	0	0	0	0	0	0	5	1	6	83.3
Toltén	0	0	1	0	0	0	0	4	5	80.0

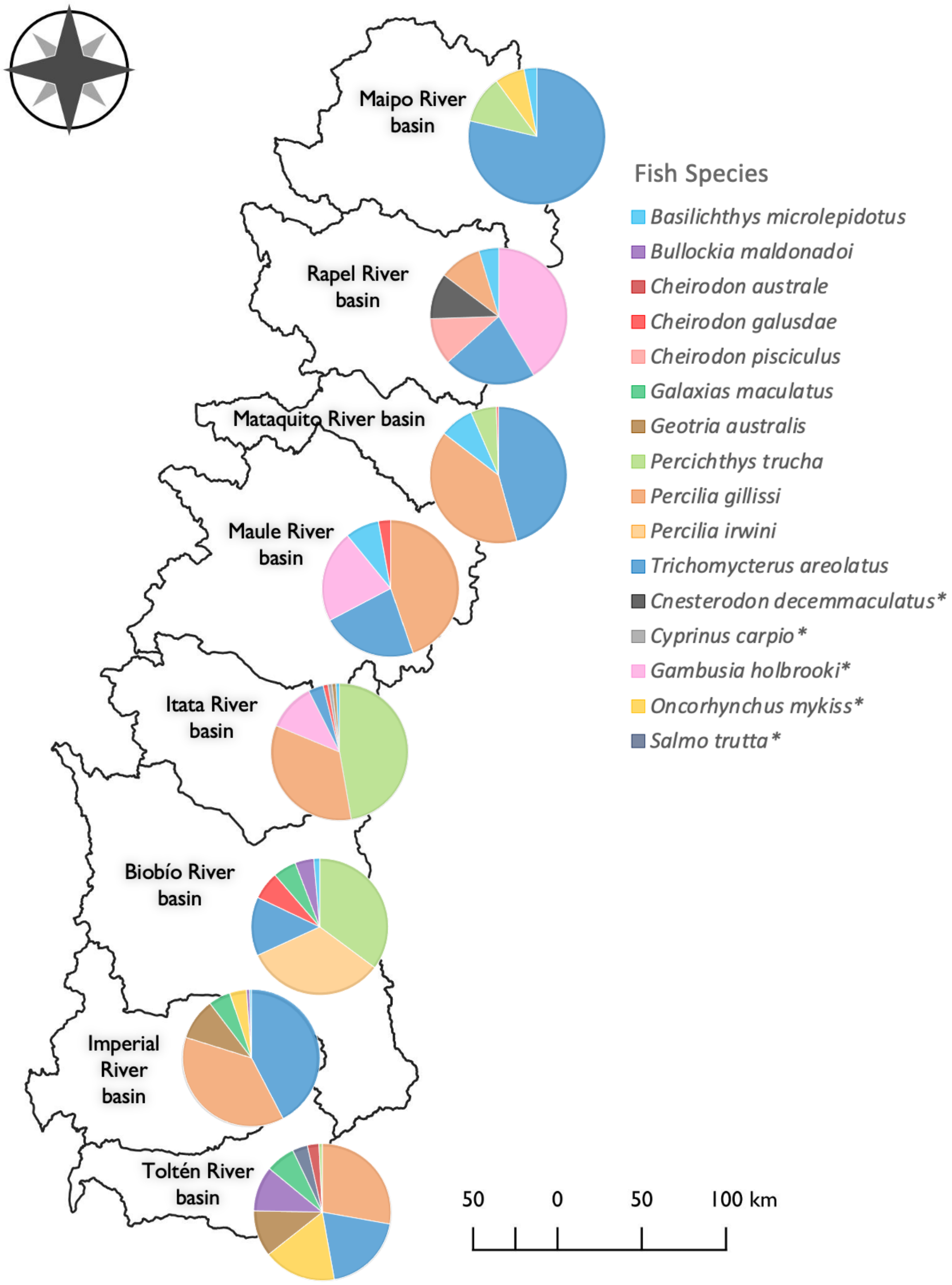

Fig. 4. Fish assemblage composition in eight Andean river basins. The pie chart represents the percentage of contribution of each species to the differences among basins (similarity percentage analysis). Species marked with * are non-native.

4.3.4. RESILIENCE MECHANISMS

4.3.4.1. RESOURCES MECHANISM

Fish species richness, total abundance and Shannon diversity index showed significant differences among the eight studied basins (Table 6; Fig. 5; Table S6 and S7). A clear pattern of richness increase with increasing latitude was observed where the Maipo River basin had the lowest richness (median=2) and the Toltén River basins the highest richness (median=7; Fig. 5a). Total abundance also increased with increasing latitude and in the Mataquito River basin exhibited notably high variability in comparison with the rest of the basins (Fig. 5b). Shannon diversity index also increased with increasing latitude (Fig. 5c). In contrast, the Pielou evenness index (J'), trophic guilds and floodplain use did not show significant differences among studied basins (Table 6).

Table 6. Effects of Basin factor on resources mechanisms' variables based on ANOVA and Kruskal-Wallis' analyses (see Table S6 and S7 for details). Significant differences (*P*<0.1) are indicated in bold. F, F value; H, chi-squared.

Resources Mechanism	F/H	p-value
Richness (S)	F=5.2840	**0.000282**
Total Abundance (N)	H=16.888	**0.018130**
Shannon Diversity Index (H')	F=2.9800	**0.013600**
Pielou Equitability Index (J')	H=3.0509	0.880300
Trophic Guilds	F=1.5590	0.178000
Floodplain Use	H=4.2598	0.749400

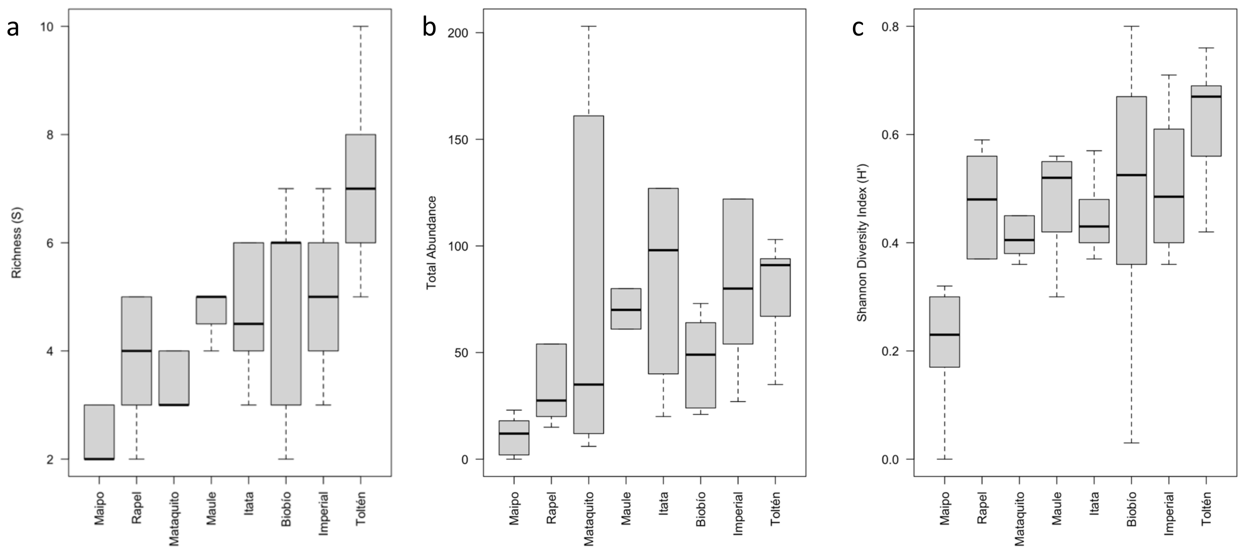

Fig. 5. Boxplot of a) Richness (S), b) Total Abundance, c) Shannon Diversity Index (H'), for eight studied basins. The lower end of the whisker represents the minimum value, the upper end the maximum value, the black line in the boxplot represents the median and the dotted line represents the standard deviation.

4.3.4.2. RECRUITMENT MECHANISM

Beta diversity (Sørensen), abundance-weighted average size, rapid sexual maturity, high fecundity, multiple spawning, small egg size and parental care showed significant differences among basins (Table 7). Beta diversity based on presence-absence (Sørensen) was higher in highly fragmented Maipo, Rapel and Biobío river basins (Fig. 6a, Table 1; Table S8). The abundance-weighted average size generally increased with increasing latitude except for the Maipo River basin that exhibited considerable variability (Fig. 6b). No clear pattern of differences among basins was observed for rapid sexual maturity, however, the Rapel, Mataquito, and Maule river basins showed the same fish biomass values for this trait that were higher compared to other basins (Fig.6c). Similarly, high fecundity showed no clear pattern of differences among basins (Fig. 6d), however Biobío and Imperial river basins showed higher variation compared to other studied basins. Maipo and Toltén river basins exhibited the lowest biomass for multiple spawning trait (Fig. 6e; Table S9). Maipo River basin presented the highest variation in small egg size trait, whereas egg size was significantly lower in the Toltén River basin (Fig. 6f; Table S10). Lastly, all river basins were characterised by high variation of the parental care trait, except for the Maipo River basin with zero biomass for this trait (Fig. 6g). Beta diversity based on the Bray-Curtis index and migratory life history did not show significant differences among studied basins (Table 7).

Table 7. Effects of Basin factor on recruitment mechanisms' variables based on ANOVA and Kruskal-Wallis' analyses. Significant differences (*P*<0.1) are indicated in bold (see Table S6, S7 and S8 for details). F, F value; H, chi-squared.

Recruitment Mechanism	**F/H**	***P***
Beta Diversity (Sørensen)	F=2.8644	**P(perm)= 0.0819**
Beta Diversity (Bray-Curtis)	F=2.3564	P(perm)= 0.1855
Migratory Life History	F=6.1954	0.5060000
Abundance Weighted Average Size	H=24.641	**0.0008784**
Rapid Sexual Maturity	H=20.374	**0.0048150**
High Fecundity	H=21.502	**0.0030940**
Multiple Spawning	F=6.1770	**0.0000797**
Small Egg Size	H=15.264	**0.0327600**
Parental Care	H=18.024	**0.0118600**

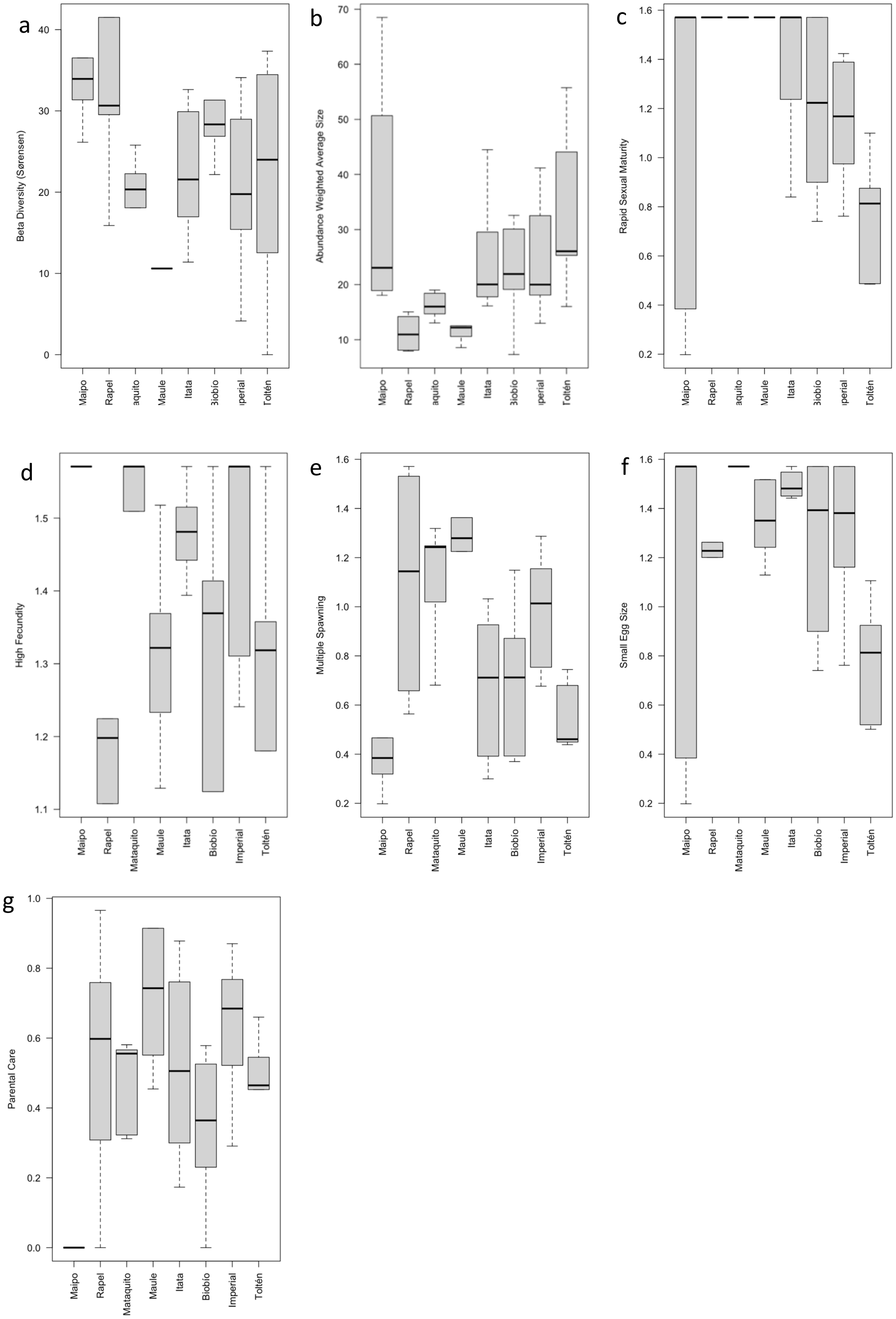

Fig. 6. Boxplot of a) Beta Diversity (Sørensen), b) Abundance Weighted Average Size, c) Rapid Sexual Maturity, d) High Fecundity, e) Multiple Spawning f) Small Egg Size, g) Parental care for eight studied basins. The lower end of the whisker represents the minimum value, the upper end the maximum value, the black line in the boxplot represents the median and the dotted line represents the standard deviation.

4.3.4.3. REFUGIA MECHANISM

Richness by taxonomic order, Shannon diversity index by taxonomic order and velocity preference showed significant differences among the eight studied basins (Table 8). Similarly to species richness (resources mechanism), richness by taxonomic order showed a clear pattern of increase with increasing latitude (Fig. 7a; Table S6). Shannon diversity index by taxonomic order also showed a clear increase with increasing latitude (Fig. 7b). Lastly, velocity preference showed a pattern of increase in velocity preference with increasing latitude with Maipo and Itata river being high value outliers indicating higher eurytopic fish biomass (Fig. 7c). Pielou evenness index by taxonomic order and vertical position did not show significant differences among studied basins (Table 8).

Table 8. Effects of Basin factor on refugia mechanisms' variables based on ANOVA and Kruskal-Wallis' analyses (see Table S6 and S7 for details). Significant differences (*P*<0.1) are indicated in bold. F, F value; H, chi-squared.

Refugia Mechanism	F/H	p-value
Richness by taxonomic order	F=3.5410	**0.00503**
Shannon Diversity Index by taxonomic order	F=2.3450	**0.04300**
Pielou Evenness Index by taxonomic order	H=2.3511	0.93790
Vertical Position	F=1.5230	0.18900
Velocity Preference	F=2.9840	**0.01350**

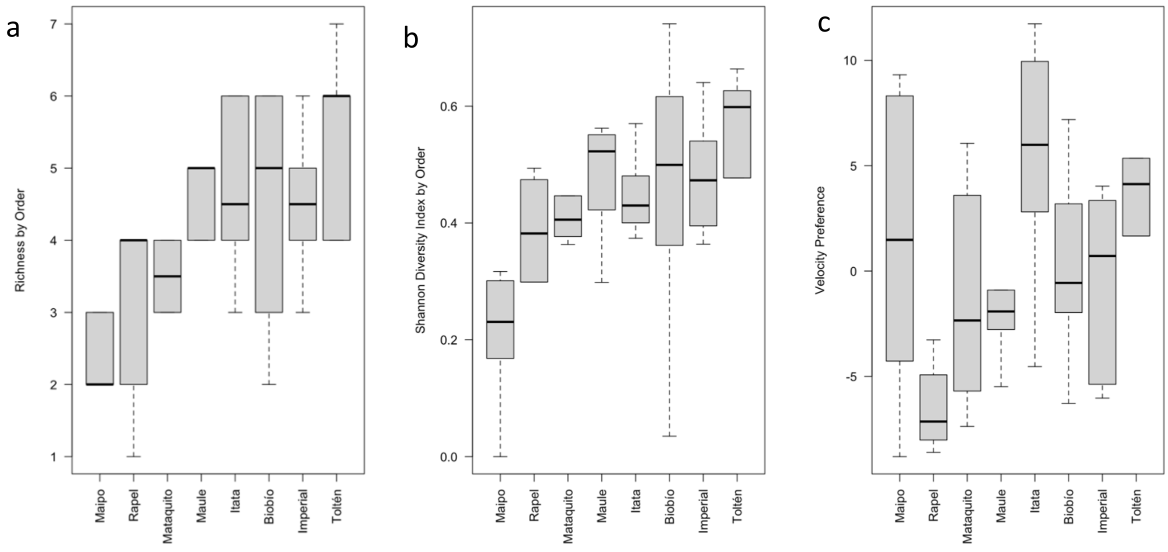

Fig. 7. Boxplot of a) Richness by taxonomic order, b) Diversity Index by taxonomic order, c) Velocity for eight studied basins. The lower end of the whisker represents the minimum value, the upper end the maximum value, the black line in the boxplot represents the median and the dotted line represents the standard deviation.

4.3.5. RESILIENCE PER BASIN

Among the eight studied basins, the Maipo and Rapel river basins exhibited the lowest resilience. The Biobío and Toltén river basins were classified as having medium resilience, whereas Mataquito, Maule, Itata and Imperial river basins showed the highest resilience (Fig. 8a). The Maipo River basin showed ten significant indices, nine of these are of lower resilience, of which six indices correspond to taxonomic and three to functional traits (Fig. 8b; 8c). The Rapel River basin showed seven significant indices, of which four are of lower resilience (two taxonomic and two functional traits). The Mataquito and Maule river basins only exhibited one significant index of low resilience each, a taxonomic index (low richness; Fig. 8b; 8c). For the Itata River basin, the significant index of low resilience corresponds to a functional trait (multiple spawning). The Biobío River basin showed two low resilience indices out of five significant ones, one taxonomic (high beta diversity based on Sørensen index) and one functional trait (multiple spawning). Notably, the Imperial River basin presented all its significant indices of high resilience (Fig. 8b). Lastly, the Toltén River basin was characterised by 10 significant indices, among which four (corresponding to functional traits) represent low resilience (Fig. 8b; 8c).

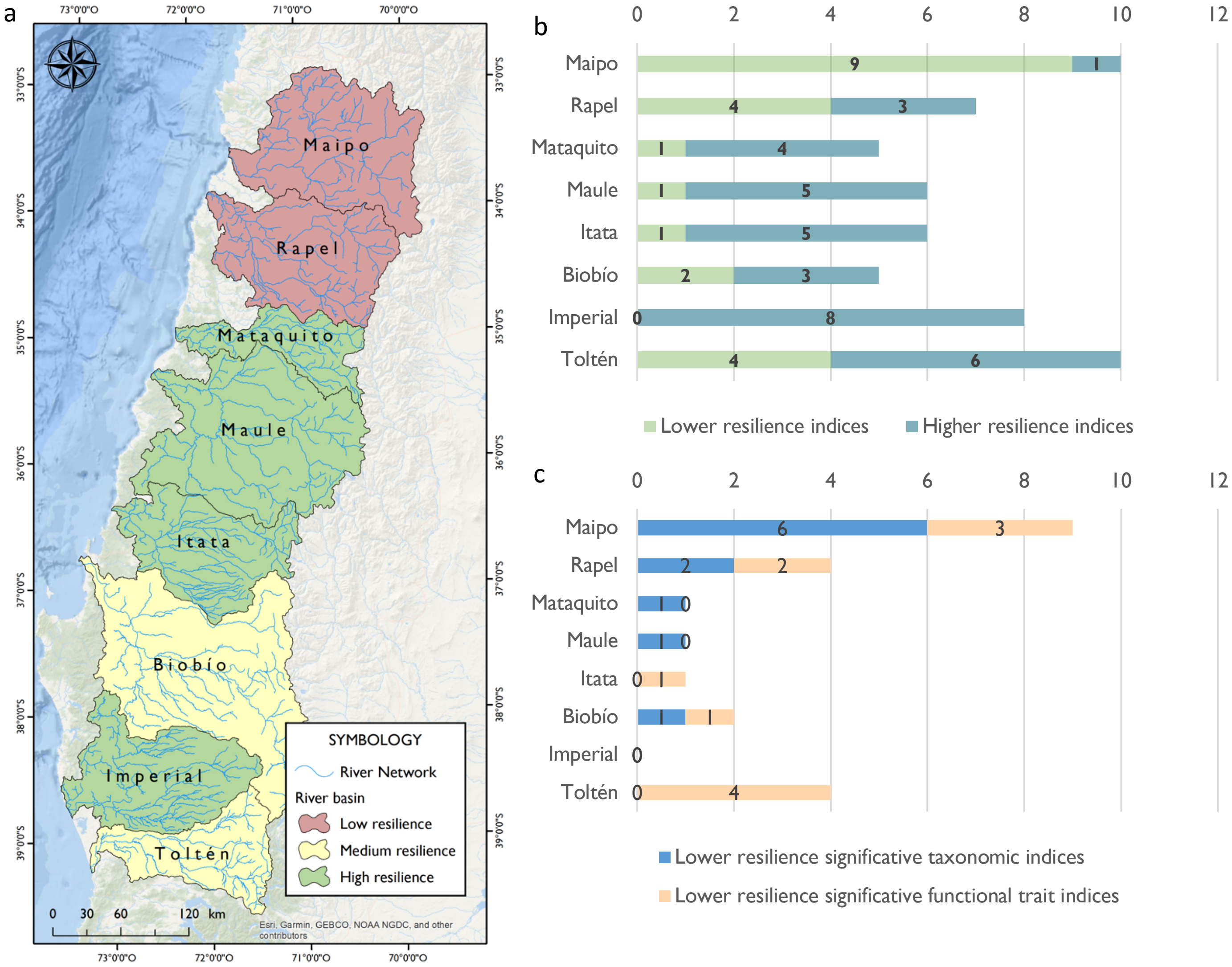

Fig. 8. a) Resilience classification for studied basins based on evaluated indices; b) The number of significant resilience indices per basin; c) The number of significant lower resilience taxonomic and functional trait indices per basin.

4.4. DISCUSSION

Fish assemblages identified in each of the eight river basins allowed assessment of resources, recruitment and refugia resilience mechanisms evaluated through taxonomic and functional trait indices. The most affected resilience mechanism was recruitment (linked to beta diversity indicator), related to the high fragmentation level of rivers such as the Rapel, Biobío and Maipo (Díaz et al., 2019; Habit et al., 2022). Fragmentation in these river basins is caused primarily by hydropower plants, water-diverting structures, and reservoirs for irrigation. Furthermore, functional trait analyses also revealed significant alteration of recruitment mechanism by the invasion of non-native trout in the Toltén River basin. The second most affected mechanism was resources (linked to species richness indicator), mostly due to land use changes and water pollution, evidenced in the Maipo, Rapel, Mataquito and Maule river basins. Lastly, the refugia mechanism was mostly affected in the most disturbed Maipo River basin.

Ecological resilience in river ecosystems, while theoretically well founded, faces substantial challenges in quantification due to the intricate and dynamic nature of these ecosystems (Jaiswal and Pandey, 2021; Quinlan et al., 2016; Standish et al., 2014). Some of the most common difficulties are the presence of multiple environmental stressors, spatial and temporal variability, and scarcity of long-term data (Parsons et al., 2016; Tracy et al., 2022). Despite these difficulties, few empirical approaches that may allow measurement of resilience in river ecosystems have been suggested (Downing and Leibold, 2010; Jaiswal and Pandey, 2019, 2021; Tracy et al., 2022). Downing and Leibold (2010) experimentally assessed resilience in aquatic food webs, evaluating how species richness and composition responded to a disturbance. Tracy et al. (2022) focused on creating a river resilience index for a river basin that includes multiple relevant natural and anthropogenic impact factors, such as landscape features, connectivity, heterogeneity, land use and water extraction, whereas Jaiswal and Pandey (2019, 2021) created a river resilience risk index focused on biochemical processes as resilience feedbacks to characterise tipping points in large disturbed rivers. As such, there are different approaches to understand river ecosystem resilience, some based on the ecological components, while others based on biochemical processes. In the present study we employed an empirical approach based on fish assemblage taxonomic and functional trait indices adapted and expanded from the original proposal of Van Looy et al. (2019). Data availability is a common issue when working with functional traits and there is a growing disconnect between trait-based ecology and the actual availability and interpretability of trait data (Kremer et al., 2017). To address this issue, we combined extensive literature review and expert knowledge to obtain most comprehensive trait database for Chilean river fish species. Despite the conceptual framework provided by Van Looy et al. (2019), identifying and measuring ecologically relevant traits remains a challenge (Kremer et al., 2017). Not all functional traits are equally useful, and their utility depends on their ecological relevance (Streit and Bellwood, 2023). Indeed, in this study functional traits such as trophic guild, floodplain use, migratory life history and vertical position were not significantly different among river basins. Therefore, we suggest further exploration of functional traits that are ecologically meaningful for assessing resilience based on fish assemblages.

Another concern to measure resilience is finding an appropriate spatial scale. RES conceptual framework suggests FPZ as an appropriate scale to assess river functioning processes and resilience (Parsons and Thoms, 2018; Thorp et al., 2008). Our results support a strong identity of fish assemblages at the river basin scale that overarches differences at the hydrogeomorphological FPZ scale for eight studied river basins. However, our results are based on limited samples for each FPZ in each basin and as such we recognise the necessity for further research to elucidate the effects of type, size, and location (both longitudinal and lateral) of FPZs within each basin. Indeed, advance in understanding the critical factors influencing resilience in river ecosystems is often hindered by a limited focus on spatial dimensions (Thorp et al., 2023). Strong fish assemblage river basin identity revealed in the present study is associated with geological isolation of assessed basin for over 10,000 years (Charrier et al., 2015) that resulted in native fish assemblages characterised by multiple early-diverged and highly endemic species (Habit et al., 2006). River basins evaluated in the present study are located in two of the three areas of endemism described for the Chilean ichthyographic province. The Central area, which includes the Maipo and Rapel river basins, with two endemic species: *Diplomystes chilensis* (extinct) and *Cheirodon pisciculus*; and the South-central area, between Maule and Imperial river basins, with five endemic species: *C. galusdae, D. nahuelbutaensis, D. arratie, T. chiltoni* and *P. irwini.* The latter three species are endemic to the Biobío River basin (Arratia and Quezada-Romegialli, 2020; Dyer, 2000; Muñoz-Ramírez et al., 2023; Vila and Habit, 2015).

In this study, recruitment appeared to be the resilience mechanism most affected by anthropogenic disturbance. Beta diversity index was an effective indicator of lower resilience related to recruitment mechanism and strongly associated with high fragmentation of several studied basins. Indeed, beta diversity has been shown to be a good predictor of river fragmentation (Baldan et al., 2023; Edge et al., 2017; Gauthier et al., 2020). Barriers cause fish assemblages to become increasingly different because of the loss of longitudinal connectivity, causing a higher turnover of species or higher beta diversity between the local fish assemblages (Díaz et al., 2021; Xia et al., 2022). Fragmentation is one of the major threats to riverine ecosystems and this is most explicitly expressed by the decline in numbers of migratory fish species (van Puijenbroek et al., 2019). In fact, the most fragmented Maipo, Rapel and Biobío river basins were characterised by the highest beta diversity indices (Díaz et al., 2019). In the case of the Maipo River basin, this is not only due to the presence of barriers, but there also sections of the river that have lost longitudinal connectivity due to water scarcity (Fuster, 2021). Indeed, fragmentation driven loss of resilience linked to recruitment mechanism in the Maipo and Rapel river basins seems to be related to impediment of recolonisation after disturbance and resulting extirpation of migratory species such as *Mordacia lapicida, G. australis* and *Galaxias maculatus* (Díaz et al., 2023).

An interesting finding was that the recruitment mechanism appears to be also affected by lower resilience functional traits, such as large body size, late sexual maturity, single spawning, and large egg size, in less impacted and non-fragmented basins. These functional traits are dominant in non-native trout *O. mykiss* and *S. trutta* (Arismendi et al., 2011; Estay et al., 2021; Gonzalez et al., 2012; Tyler et al., 1996). The Toltén River basin resulted as an example of this effect because the recruitment mechanism is altered by the high abundance of non-native trout. Salmonid invasion is the most important threat to native biodiversity in southern Chilean river basins. Indeed, trout negatively impact native fish assemblages, leading to a decline in their abundances, due to predation and competition (Arismendi et al., 2009; Habit et al., 2015). Furthermore, trout affect the trophic position of native fish changing natural food webs (Belk et al., 2014; Correa et al., 2012; Habit and Victoriano, 2012). Here, these effects of trout and lower resilience traits that trout contribute to fish assemblage are reflected in lower resilience in the recruitment mechanism and specifically in functional trait indicators. Furthermore, in less intervened Toltén River basin the functional traits indices captured the effects of biological disturbances that in other river basins with higher number of physical disturbances did not emerge.

The resources mechanism linked to species richness indicator was the second most affected by anthropogenic disturbances in the studied basins. A major driver of species richness decline worldwide is land use change (Allan et al., 2015; Cardinale et al., 2012; Gossner et al., 2016; Murphy and Romanuk, 2014; Powers and Jetz, 2019; Simkin et al., 2022). Conversion of natural landscape into other productive systems affects integrity of river ecosystems in terms of nutrient cycling, increase surface runoff and reduced water quality (Esse et al., 2021; Fierro et al., 2019; Miserendino et al., 2011). Therefore, land use changes can modify the consumer-resource interactions and reconfigure the flow of energy through the entire river ecosystem food web altering the resources mechanism (Price et al., 2019). Water pollution from domestic and industrial effluents is also a major threat to biodiversity in river ecosystems (Bassem, 2020; Dudgeon et al., 2006; Gomez et al., 2014; Groh et al., 2022), it reduces the abundance and diversity of native fish fauna and other organisms (Magurran and Phillip, 2001; Ngor et al., 2023; Paruch et al., 2019; Sun et al., 2019). Loss of resilience in relation to the resources mechanism due to extensive land use changes in the Maipo, Rapel, Mataquito and Maule river basins was reflected in significantly lower species richness compared to the rest of the studied basins. During the last decades land use has changed from native forest to agriculture and urbanisation, as well as exotic plantations of *P. radiata* and *E. globulus* for pulp production in the Central-southern basins (Mataquito and Maule river basins) (Aguayo et al., 2009; Henríquez-Dole et al., 2018; Hermosilla-Palma et al., 2021; Puertas et al., 2014). For example, in the Rapel River basin, land use changes have caused high loads of organic matter and nutrients in the Rapel reservoir located in the lower basin, causing several algal blooms, hypoxia and anoxia events, and associated fish mortalities (Vila et al., 2000). The Maipo River basin is the most disturbed among studied basins and this is reflected in other resources mechanism's indicators such as low abundance and low Shannon's diversity. It is also the only river basin within the study area with low resilience taxonomic indicators for the refugia mechanism, such as low richness by taxonomic order and low Shannon's diversity by taxonomic order. Indeed, apart from fragmentation, land use changes and pollution, Maipo River basin concentrates 40% of Chilean population (7 million people; INE, 2024) and it has been described as one of the most contaminated river basins in Chile (Habit et al., 2024). Indeed, these anthropogenic disturbances seem to have profound impact on the availability and quality of refuges for fish assemblages. As a consequence, it seems to have reduced ability to facilitate the survival of fish species and possibly other aquatic organisms under these adverse conditions (Keppel et al., 2012; Van Looy et al., 2019).

Relationships between anthropogenic disturbances and river resilience assessed by fish assemblage indicators resulted in non-linear responses across river basins, i.e. a highly disturbed river basin did not always result in lower resilience. Indeed, medium resilience was detected in river basins with different levels of anthropogenic disturbances. These results have different local explanations, such as the unexpected case of the Toltén River basin that is a representation of the significance of biological invasions in physically well-conserved ecosystems (Bernery et al., 2022; Costantini et al., 2023; Hou et al., 2023). Meanwhile, the highly disturbed Biobío River basin still hosts a naturally highly diverse fish assemblage, indicating higher resilience (Habit et al., 2007). Also, the cases of the Itata and Mataquito river basins, with medium levels of disturbances, showed high resilience. These basins possibly exemplify that at medium level of disturbances fish assemblages can adapt to these disturbances and resilience of the river ecosystem could be maintained. This diversity and non-linearity of responses highlights the complexity of river resilience mechanisms, where the influence of disturbances varies across basins, challenging assumptions about disturbance-resilience patterns.

The resilience assessment based on fish assemblages of Andean River basins of Central-southern Chile provided insights into resources, recruitment and refugia resilience mechanisms in river ecosystems. Fish assemblages resulted to be suitable indicators of river ecosystem resilience that could be related to different anthropogenic disturbance levels at basin scale. The use of several resilience indicators revealed different responses of the fish assemblages to anthropogenic disturbances associated with each resilience mechanism. Recruitment indices (beta diversity Sørensen and functional traits) revealed low resilience due to fragmentation and presence of non-native trout. Meanwhile, resources indices (richness, abundance, and Shannon's diversity) revealed the effects of land use changes and water pollution. Thus, these indices emerged as key indicators of river resilience in the studied basins. Integrated strategies, such as the one used here, are necessary in the current environmental scenario since the interplay between climate change, land use intensification, species invasion and human population growth bring new challenges to the global management and conservation of freshwater ecosystems. This highlights the need to continue understanding adaptive management approaches for ecosystem resilience and measures to improve resilience of river ecosystems.

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5. CONCLUSIÓN GENERAL

En este estudio se evaluó la resiliencia fluvial en ocho cuencas Andinas del Centro-sur de Chile: Maipo, Rapel, Mataquito, Maule, Itata, Biobío, Imperial y Toltén. La escala espacial de ZPFs no fue adecuada para estudiar la resiliencia, dado que los ensambles de peces respondieron a una escala de cuenca por sobre una escala hidrogeomorfológica. Por ello, se evaluaron los mecanismos de resiliencia de recursos, reclutamiento y refugio a escala de cuenca utilizando el marco conceptual de "Las tres Rs" propuesto por Van Looy et al. (2019). El mecanismo de reclutamiento fue el más afectado por disturbios antropogénicos, particularmente en cuencas con alta fragmentación (Maipo, Rapel y Biobío) y presencia de especies invasoras como los salmónidos (Toltén). Este mecanismo fue representado principalmente por indicadores como diversidad beta (Sørensen) y rasgos funcionales de menor resiliencia asociados a salmónidos. Por otro lado, el cambio de uso de suelo y la contaminación del agua afectaron significativamente el mecanismo de recursos en las cuencas de los ríos Maipo, Rapel, Mataquito y Maule, representado por indicadores como la riqueza de especies. La cuenca del río Maipo, el caso más crítico en relación a los disturbios antropogénicos que presenta, la pérdida de resiliencia en el mecanismo de recursos también se vio reflejado en una baja abundancia y baja diversidad de Shannon. Por último, los casos de las cuencas de los ríos Itata y Mataquito, caracterizados por niveles de disturbios medios, exhibieron una notable resiliencia. Estos ejemplos sugieren que, en condiciones de disturbios medios, los ensambles de peces pueden adaptarse, lo que contribuye a mantener la resiliencia del ecosistema fluvial. Este estudio destaca la complejidad de los patrones de resiliencia a los disturbios y la importancia de utilizar diversos indicadores para evaluar la resiliencia, proporcionando conocimientos relevantes para la gestión adaptativa de los ecosistemas fluviales.

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7. MATERIAL SUPLEMENTARIO

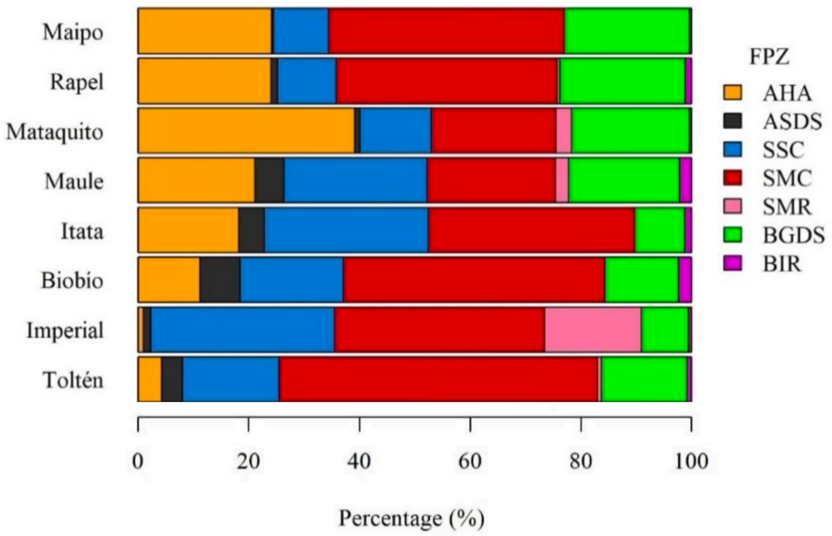

Fig. S1. Porcentaje de abundancia de cada ZPF en cada cuenca de estudio. AHA, Andean High Altitude; ASDS, Andean Steep Downstream Slope; SSC, Sinuous-Single Channel; SMC, Sinuous-Multi Channel; SMR, Sinuous Metamorphic Rock; BGDS, Braided Gentle Downstream Slope; BIR, Braided Intrusive Rock.

Table S1. Variables geomorfológicas a escala de cuenca, valle y canal.

Escala	Variable geomorfológica	Unidad
Cuenca	Elevación	m
	Geología dominante	-
	Precipitación anual	mm
Valle	Pendiente a la derecha del valle	grados
	Pendiente a la izquierda del valle	grados
	Pendiente aguas abajo del valle	grados
	Ancho promedio del fondo del valle	m
	Ancho promedio del valle	m
	Relación entre el ancho valle y el ancho del fondo del valle	m
Canal	Ancho promedio del canal	m
	Sinuosidad del cauce	-
	Sinuosidad de la banda del canal	-
	Longitud promedio de la banda del canal	m
	Tipo de Confinamiento: confinado, parcialmente confinado, no confinado	-
	Clase de forma del canal: canal único, multicanal de baja densidad, multicanal de alta densidad, reservorio.	-
	Cantidad de canales	-

Table S2. Classification of functional traits for each species.

Information was extracted from different sources (Baker et al., 2017; Campos, 1969; Campos, 1970; Chiang et al., 2012; Estay et al., 2021; Ferriz et al., 1999; Golusda, 1927; Habit & Victoriano, 2005; Habit et al., 2009; Manríquez et al., 1998; Montoya et al., 2012; Oyanedel et al., 2018; Patimar, 2010; Prochelle & Campos, 1985; Ruiz, 1993; Ruiz & Marchant, 2004; Serezli et al., 2010) and expert knowledge. *Non-native species.

Species	Trophic guild	Floodplain use	Migratory life history	Maximum size	Sexual maturity	Fecundity	Spawning	Egg size	Parental care	Velocity preference	Vertical position
Aplochiton taeniatus	2	1	3	36,1	1	2	1	1	1	2	3
Bullockia maldonadoi	2	1	1	8,6	1	1	1	1	1	3	1
Basilichthys microlepidotus	3	2	1	40	1	2	1	1	1	1	3
*Cyprinus carpio**	4	2	1	120	2	2	2	1	1	1	2
*Cnesterodon decemmaculatus **	4	2	1	3,8	1	1	2	2	2	1	3
Cheirodon australe	4	1	1	7	1	1	2	1	1	1	3
Cheirodon galusdae	4	1	1	6,7	1	1	2	1	1	1	3
Cheirodon pisciculus	4	1	1	6,8	1	1	2	1	1	1	3
Diplomystes camposensis	2	1	1	24,9	2	1	1	2	1	3	1
Diplomystes incognitus	2	1	1	17,9	2	1	1	2	1	3	1
Diplomystes arratie	2	1	1	35	2	1	1	2	1	3	1
Geotria australis	1	2	4	57	2	2	1	1	2	3	1
*Gambusia holbrooki**	4	1	1	8	1	1	2	2	2	1	2
Galaxias maculatus	2	1	2	12	1	2	1	1	1	1	3
*Oncorhynchus mykiss**	3	1	1	122	2	2	1	2	1	2	3
Percilia gillissi	2	1	1	9	1	2	2	1	2	2	2
Percilia irwini	2	1	1	9,6	1	2	2	1	2	2	2
Percichthys trucha	3	1	1	45	1	2	1	1	1	2	3
*Salmo trutta**	3	1	1	140	2	2	1	2	1	2	3
Trichomycterus areolatus	2	1	1	15	1	2	2	1	1	3	1

Table S3. Scores of Principal Coordinate Analysis (PCA) for Trophic Guilds, Migratory Life History, Vertical Position and Velocity Preference

Trophic Guilds				**Migratory Life History**				**Vertical Position**			**Velocity Preference**		
SCORE1	SCORE2	SCORE3	SCORE4	SCORE1	SCORE2	SCORE3	SCORE4	SCORE1	SCORE2	SCORE3	SCORE1	SCORE2	SCORE3
-7,9018124	-5,0923596	-1,3306215	-0,8751661	-6,0487367	1,13868338	-0,0895643	0,0401241	-4,5731169	-7,3199068	6,0525745	8,3138126	-1,5433542	-2,6351661
-1,6611649	-6,8534163	-1,0370659	-0,4383727	-0,1447563	0,81163657	-0,0579688	0,02684599	0,39076354	-7,0962409	1,85330904	3,0515796	-4,5953739	-0,3290774
9,87612574	-3,8490673	-1,1360313	-0,0200208	11,7665769	0,15181672	0,00577524	5,7274E-05	10,2641082	-1,6995932	-2,1106863	-8,8100502	-5,836686	-0,0446789
-8,5143932	-6,338433	-1,2139925	-0,8298322	-6,7807363	1,17923197	-0,0934816	0,04177037	-5,2182324	-8,4713666	5,60360011	9,31386622	-2,2413335	-1,9596446
-0,4067189	-3,7281993	-1,3346844	-0,5668599	1,48251625	0,72149496	-0,0492604	0,02318623	1,77563841	-4,2817565	3,12078709	-0,0935239	-0,3806692	0,54187811
4,04333835	-1,5111779	-1,4813254	-0,4712817	5,46682431	0,50078704	-0,0279382	0,01422548	5,70162363	-1,3578527	2,23407471	-4,2753177	-1,8881245	-1,956501
3,26443498	-3,7669313	1,39011424	-0,1518832	4,69798455	0,54337637	-0,0320527	0,01595461	3,49879724	-3,6270225	-2,9079216	-6,4574522	-1,6649905	5,16897999
1,83261952	-2,6681475	1,65122646	-0,2621577	3,18220778	0,62734175	-0,0401644	0,01936361	1,96358538	-3,2450665	-3,733287	-4,9298916	-1,1397884	6,02191177
8,21217609	-0,215967	1,94150758	-0,0446801	6,73057414	0,43078251	-0,0211752	0,0113833	7,1785506	2,23326539	-1,4384085	-8,6063918	-0,8025636	0,19224931
-0,1649963	5,98675908	2,63006161	-0,7472972	-2,780708	0,95765324	-0,0720753	0,03277427	0,26434329	5,28773761	5,85561208	-7,8325571	8,3654922	-3,1467171
6,58386478	2,91860471	-1,8893686	-0,6134146	4,19148689	0,57143345	-0,0347632	0,01709373	8,29497505	2,83007931	3,64818352	-8,0235078	-0,1218252	-4,9723272
4,91370752	-0,6469055	1,30963851	-0,2419771	5,38038235	0,50557543	-0,0284008	0,01441989	4,47551218	-0,9070316	-4,7133776	-3,2700874	-4,2208568	2,71356473
-5,5782346	-0,3069217	-1,7790499	-1,0507874	-4,1103875	1,0313099	-0,0791911	0,03576473	-5,5945502	-1,0381565	-1,1486803	6,0608804	-0,2584177	0,72884933
5,22973202	-0,9112429	-1,5213297	-0,4463519	6,24792485	0,45751853	-0,0237581	0,01246878	5,40912647	0,43461614	-0,553669	-5,6992487	-1,268578	0,0281436
3,37076792	2,75795765	-1,9311041	-0,7719517	2,44453764	0,66820447	-0,0441121	0,02102264	3,27265322	3,70045738	0,91073901	-3,269083	1,40522657	-2,0502672
-3,5580418	6,35941998	17,337478	0,27895005	-13,215694	1,53569189	-0,1279186	0,05624266	-11,268955	10,7527878	-4,8153833	-1,4270882	16,0346606	9,6086143
8,01262447	-1,6658287	-1,3935736	-0,2534825	8,87968484	0,31173405	-0,0096741	0,00654992	8,49983365	-0,03252	-0,5396349	-7,3773562	-3,896436	-1,6393004
-2,3762935	8,62196975	-1,5565268	-1,3484185	-5,7445264	1,12183186	-0,0879363	0,03943993	-3,0728613	8,37434434	3,20260134	3,59401968	4,54304187	-6,8262937
8,35248005	-0,6176761	0,13096905	-0,1660502	7,97903188	0,36162508	-0,014494	0,0085755	8,1679407	0,39740699	-4,4768376	-5,4857471	-4,9274998	1,54037294
-1,7861627	1,60513727	0,71175999	-0,7537434	-1,2405423	0,87233686	-0,063833	0,02931042	-1,7440638	1,25827063	1,98380342	-2,7803458	5,55796498	1,83004594
2,77064658	5,30719156	-1,5852781	-0,910676	0,15186615	0,79520538	-0,0563815	0,02617888	2,4996655	6,01200512	1,83452354	-1,9179838	2,75858484	-3,7784089
-1,3245087	7,09558948	1,46831321	-0,9621804	-4,1119572	1,03139685	-0,0791995	0,03576826	-2,8428257	7,05241358	0,01549847	2,02420274	5,79191087	-0,596673
2,97608291	3,63391562	1,46501137	-0,5575639	1,26335025	0,7336355	-0,0504333	0,02367914	1,72920389	4,43935067	-2,4695405	-0,9032049	1,07214091	0,5955614

-7,2340621	-8,9475093	6,07578512	1,18706848	-7,5105754	0,22546205	-0,7713338	0,04564758	-8,1073102	-7,5908146	-2,1777599	8,74656592	-1,1012239	6,4020744
-1,7271819	-5,7647082	0,21372642	-0,3964866	-0,0586587	0,80686725	-0,0575081	0,02665235	-0,6303908	-6,3444559	-2,1824038	2,80774958	-5,4757698	2,22830758
5,56600743	-4,5815368	2,35545349	1,62494195	6,08153041	-0,7979131	-0,8819273	0,01568699	4,46097037	-1,2329571	-2,4510422	-4,5374642	-2,5191987	2,13460687
-7,7068453	7,66712962	-1,4572636	-1,5605234	-9,2782816	1,31758172	-0,1068474	0,04738738	-9,1549872	6,42116424	-1,0097626	9,94847115	3,33164794	-2,9290383
-1,036704	1,76849201	-0,3243856	-0,8102148	-0,5403373	0,8335495	-0,0600858	0,02773565	-1,5353992	0,8404545	-4,6106429	3,23471372	-3,3182407	0,67023022
-11,302514	2,36169803	-2,1562791	-1,5169173	-10,343905	1,37661117	-0,1125501	0,04978398	-11,669584	-0,8611503	-5,0432913	11,7338292	0,82429998	4,85126683
1,70012671	1,4504384	0,71283028	-0,5677342	1,93423263	-0,2528581	1,34922943	0,07990649	1,19271087	1,30367358	0,59858284	-1,9699001	1,36403884	-0,1538029
-2,0866165	-4,8596196	-1,2491411	-0,5846332	-0,2339747	0,81657876	-0,0584463	0,02704664	-1,2586283	-5,0292669	-1,3362076	3,18873964	-5,1768185	0,18687467
-0,0273393	0,1248268	-2,003748	2,91027141	1,15548659	-2,6836659	-1,5979794	0,05270903	0,14316673	1,01812171	1,54862643	0,39738623	-0,5104424	-3,2170981
-6,3886165	-4,1900243	-0,218001	-0,7542738	-4,5189147	1,05393997	-0,0813774	0,03668351	-5,6089264	-5,3062063	-1,0718814	7,19200428	-3,0693695	1,47723141
7,15477947	-4,4214485	5,2808913	0,40395884	4,77099378	0,53933208	-0,031662	0,01579041	4,71490181	-5,772674	-0,8044237	-6,2821811	-1,7725457	5,07221877
1,26149738	-1,0026175	-1,5838444	-0,6488016	2,80153539	-0,399085	1,49825782	0,08392721	2,26969332	-1,0650675	2,20170378	-1,5268457	-0,6089194	-1,6369692
-4,4437048	6,69292153	-3,0441156	6,0477744	-5,1588209	-8,217109	0,29517281	0,24138965	-5,636017	5,41827781	5,18122237	3,34610571	8,27744838	-3,1541939
-3,4794266	0,36850176	-1,8102644	-0,9826952	-2,2071053	-0,1306524	1,48471485	0,09574012	-3,4706376	0,005611	0,33656465	4,03038969	-0,3104899	-1,5021627
1,72290031	3,52475628	-2,1104397	0,02655316	1,05308226	-1,7050956	1,89166001	0,12791816	0,49579292	3,29187548	-0,9002083	0,10531111	0,58550068	-1,079981
-0,8316387	2,32540008	-2,1345193	1,29251672	-0,558728	-1,7089008	-0,3396026	0,07288182	0,6176845	1,71316916	5,01669492	-5,3791413	6,11741365	-0,9548248
8,08425042	-0,2536777	-1,6688786	1,39717009	7,77165139	-1,0642793	-0,9899815	0,01227436	8,00470374	1,75596287	-0,934156	-6,034102	-3,2777458	-2,0881898
2,22446598	5,2566633	-2,3415857	0,77017631	-0,1413943	-0,6449181	-1,0451922	0,03011356	1,11480402	6,01694985	-1,5766487	1,32519997	-0,6984056	-3,8413588
-0,7450635	1,39586346	-0,0683	1,89073583	-0,0527685	-2,1361826	-0,4090156	0,07805374	-1,2265888	1,39940501	-0,2478676	1,66206819	-0,0008082	-1,2225015
-4,4090843	-3,2631186	-1,5742976	0,76570308	-2,3552698	-1,2022876	0,26725489	-1,9726256	-3,7260806	-4,7661753	-2,4118377	5,3563825	-4,3697247	1,49811362
-3,4422289	-0,1823163	0,58729061	-0,7525019	-2,0432947	-0,3741183	1,83028464	0,10962689	-3,6233055	-1,2423398	-0,9878951	4,12780867	-0,699322	0,69646796
-11,492452	-1,5895891	-0,6168803	2,51949117	-9,662528	-2,8377848	-0,5238537	0,12351488	-11,024898	-3,1082396	1,52715846	11,8774231	0,46772071	-0,894917
2,47317714	0,00520362	-1,7101616	-0,0563801	3,40914026	0,12462435	-0,37121	0,0199555	4,58660985	-0,5615388	3,92759533	-4,550038	1,1984292	-1,5774704

Table S4. Fish composition in each FPZ by basin. SSC, Sinuous Single Channel; BGDS, Braided Gentle Downstream Slope.

Order	**Family**	**Species**	**Maipo**		**Rapel**		**Mataquito**		**Maule**		**Itata**		**Biobío**		**Imperial**		**Toltén**	
			SSC	**BGDS**	**SSC**	**BGDS**	**SSC**	**BGDS**	**SSC**	**BGDS**	**SSC**	**BGDS**	**SSC**	**BGDS**	**SSC**	**BGDS**	**SSC**	**BGDS**
Native species																		
Atheriniformes	Atherinopsidae	*Basilichthys microlepidotus*	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1
Centrarchiformes	Perciliidae	*Percilia gillissi*	0	0	1	1	1	1	1	1	1	1	0	0	1	1	0	0
		Percilia irwini	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Characiformes	Characidae	*Cheirodon australe*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
		Cheirodon galusdae	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0
		Cheirodon pisciculus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Osmeriformes	Galaxiidae	*Aplochiton taeniatus*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
		Galaxias maculatus	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
Perciformes	Percichthyidae	*Percichthys trucha*	0	1	0	1	1	1	0	0	1	1	1	1	0	1	0	1
Petromyzontiformes	Geotriidae	*Geotria australis*	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	1
Siluriformes	Diplomystidae	*Diplomystes camposensis*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
		Diplomystes incognitus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
		Diplomystes arratie	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
	Trichomycteridae	*Bullockia maldonadoi*	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1
		Trichomycterus areolatus	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1
Non-native species																		
Cypriniformes	Cyprinidae	*Cyprinus carpio*	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Cyprinodontiformes	Poeciliidae	*Cnesterodon decemmaculatus*	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
		Gambusia holbrooki	0	0	1	1	0	1	1	1	1	1	0	0	0	0	0	0
Salmoniformes	Salmonidae	*Oncorhynchus mykiss*	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1
		Salmo trutta	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1

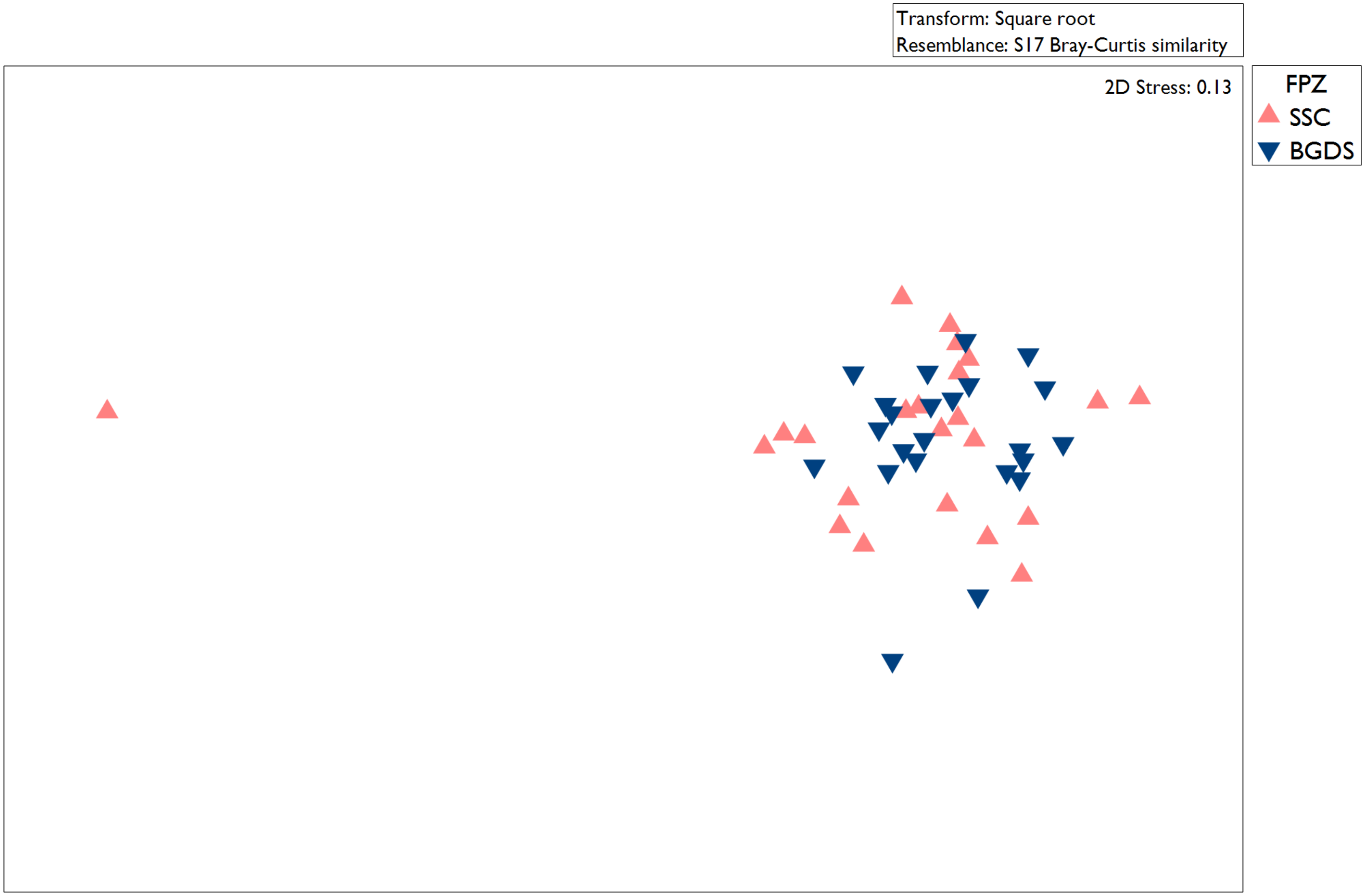

Fig. S2. Non-metric multidimensional scaling (NMDS) based on the Bray-Curtis dissimilarity matrix of fish abundance at each sampling site. SSC, Sinuous Single Channel FPZ; BGDS, Braided Gentle Downstream Slope FPZ.

Table S5. Canonical Principal Coordinate Analysis (CAP) on fish abundance data in Basin-FPZ. SSC, Sinuous Single Channel; BGDS, Braided Gentle Downstream Slope.

Original Group	**Maipo**		**Rapel**		**Mataquito**		**Maule**		**Itata**		**Biobío**		**Imperial**		**Toltén**		**Total**	**% Correct**
	SSC	BGDS	SSC	BGDS	SSC	BGDS	SSC	BGDS	SSC	BGDS	SSC	BGDS	SSC	BGDS	SSC	BGDS		
Maipo-SSC	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	3	66.67
Maipo-BGDS	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	100.00
Rapel-SSC	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	3	66.67
Rapel-BGDS	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	3	33.33
Mataquito-SSC	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	3	66.67
Mataquito-BGDS	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	3	0.00
Maule-SSC	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	3	0.00
Maule-BGDS	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	2	50.00
Itata-SSC	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	3	100.00
Itata-BGDS	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	3	100.00
Biobío-SSC	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	3	0.00
Biobío-BGDS	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	3	0.00
Imperial-SSC	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	3	66.67
Imperial-BGDS	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	3	66.67
Toltén-SSC	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	2	50.00
Toltén-BGDS	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	3	33.33

Mis-classification error: 50%

Table S6. ANOVA results for Richness, Shannon Diversity Index, Trophic Guilds, Migratory Life History, Multiple Spawning, Richness by Taxonomic order, Shannon Diversity Index by Taxonomic Order, Vertical Position, Velocity Preference.

RESOURCES MECHANISM	**Df**	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
Richness					
Basin	7	81.54	11.648	5.284	0.000282
Residuals	38	83.77	2.204		
Shannon Diversity Index					
Basin	7	0.5297	0.07567	2.98	0.0136
Residuals	38	0.9651	0.02540		
Trophic Guilds					
Basin	7	289	41.29	1.559	0.178
Residuals	38	1006	26.49		
RECRUITMENT MECHANISM	**Df**	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
Migratory Life History					
Basin	7	197.1	28.16	0.915	0.506
Residuals	38	1170.9	30.81		
Multiple Spawning					
Basin	7	3.380	0.4829	6.177	0.0000797
Residuals	37	2.892	0.0782		
REFUGIA MECHANISM	**Df**	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
Richness by taxonomic order					
Basin	7	43.81	6.259	3.541	0.00503
Residuals	38	67.17	1.768		
Shannon by taxonomic order					
Basin	7	0.3980	0.05686	2.345	0.043
Residuals	38	0.9214	0.02425		
Vertical position					
Basin	7	298.8	42.69	1.523	0.189
Residuals	38	1065.1	28.03		
Velocity preference					
Basin	7	531.4	75.91	2.984	0.0135
Residuals	38	966.6	25.44		

Table S7. Kruskal-Wallis results for Abundance, Pielou Evenness Index, Floodplain Use, Abundance Weighted Average Size, Rapid Sexual Maturity, High Fecundity, Small Egg Size, Parental Care and Pielou by Taxonomic Order.

RESOURCES MECHANISM	**chi-squared**	**df**	**p-value**
Abundance	16.888	7	0.01813
Pielou Evenness Index	30.509	7	0.8803
Floodplain Use	42.598	7	0.7494
RECRUITMENT MECHANISM	**chi-squared**	**df**	**p-value**
Abundance Weighted Average Size	24.641	7	0.0008784
Rapid Sexual Maturity	20.374	7	0.004815
High Fecundity	21.502	7	0.003094
Small Egg Size	15.264	7	0.03276
Parental Care	18.024	7	0.01186
REFUGIA MECHANISM	**chi-squared**	**df**	**p-value**
Pielou by taxonomic order	23.511	7	0.9379

Table S8. PERMANOVA results for Beta Diversity (Sørensen) and Beta Diversity (Bray-Curtis).

Beta Diversity (Sørensen)		
DEVIATIONS FROM CENTROID		
F: 2.8644	df1: 7	df2: 38
P(perm): 0.0819		
Number of permutations: 9999		
PAIRWISE	COMPARISONS	
Groups	t	P(perm)
(Maipo,Rapel)	0.37476	0.6751
(Maipo,Mataquito)	2.5285	0.0044
(Maipo,Maule)	2.6819	0.0773
(Maipo,Itata)	2.128	0.0545
(Maipo,Biobío)	1.0476	0.5401
(Maipo,Imperial)	2.1735	0.066
(Maipo,Toltén)	1.7066	0.2495
(Rapel,Mataquito)	2.2304	0.0183
(Rapel,Maule)	2.4438	0.0539
(Rapel,Itata)	1.7935	0.1543
(Rapel,Biobío)	0.63404	0.6263
(Rapel,Imperial)	1.8536	0.1579
(Rapel,Toltén)	1.4143	0.2377
(Mataquito,Maule)	0.69599	0.6262
(Mataquito,Itata)	0.82231	0.4673
(Mataquito,Biobío)	2.4856	0.0229
(Mataquito,Imperial)	0.44421	0.6698
(Mataquito,Toltén)	0.5135	0.6322

(Maule,Itata)	1.4631	0.1749
(Maule,Biobío)	2.8726	0.0483
(Maule,Imperial)	1.0339	0.4737
(Maule,Toltén)	0.94753	0.3865
(Itata,Biobío)	1.8557	0.0668
(Itata,Imperial)	0.27417	0.7579
(Itata,Toltén)	0.0229	0.9912
(Biobío,Imperial)	1.8439	0.1146
(Biobío,Toltén)	1.2341	0.3588
(Imperial,Toltén)	0.16579	0.8718
Beta Diversity (Bray-Curtis)		
DEVIATIONS FROM CENTROID		
F: 2.3564	df1: 7	df2: 38
P(perm): 0.1855		
Number of permutations: 9999		

Table S9. Post-hoc Tukey test results for Richness, Shannon Diversity Index, Multiple Spawning, Richness by Taxonomic Order, Shannon Diversity Index by Taxonomic Order, Velocity Preference.

Richness	diff	lwr	upr	p adj
Rapel-Maipo	1,83333333	-0,914396773	4,58106344	0,409919761
Mataquito-Maipo	2,00000000	-0,747730106	4,747730106	0,302987667
Maule-Maipo	2,20000000	-0,681843648	5,081843648	0,249036036
Itata-Maipo	2,66666667	-0,08106344	5,414396773	0,062592901
Biobío-Maipo	3,00000000	0,252269894	5,747730106	0,023985648
Imperial-Maipo	3,00000000	0,252269894	5,747730106	0,023985648
Toltén-Maipo	5,20000000	2,318156352	8,081843648	2,90288E-05
Mataquito-Rapel	0,16666667	-2,58106344	2,914396773	0,999999349
Maule-Rapel	0,36666667	-2,515176981	3,248510315	0,999895694
Itata-Rapel	0,83333333	-1,914396773	3,58106344	0,975717510
Biobío-Rapel	1,16666667	-1,58106344	3,914396773	0,868746788
Imperial-Rapel	1,16666667	-1,58106344	3,914396773	0,868746788
Toltén-Rapel	3,36666667	0,484823019	6,248510315	0,012558961
Maule-Mataquito	0,20000000	-2,681843648	3,081843648	0,999998345
Itata-Mataquito	0,66666667	-2,08106344	3,414396773	0,993339667
Biobío-Mataquito	1,00000000	-1,747730106	3,747730106	0,936465235
Imperial-Mataquito	1,00000000	-1,747730106	3,747730106	0,936465235
Toltén-Mataquito	3,20000000	0,318156352	6,081843648	0,020548766
Itata-Maule	0,46666667	-2,415176981	3,348510315	0,999482652
Biobío-Maule	0,80000000	-2,081843648	3,681843648	0,985267508
Imperial-Maule	0,80000000	-2,081843648	3,681843648	0,985267508
Toltén-Maule	3,00000000	-0,009987522	6,009987522	0,051294486
Biobío-Itata	0,33333333	-2,414396773	3,08106344	0,999924317
Imperial-Itata	0,33333333	-2,414396773	3,08106344	0,999924317
Toltén-Itata	2,53333333	-0,348510315	5,415176981	0,120537170
Imperial-Biobío	8,88178E-16	-2,747730106	2,747730106	1,000000000
Toltén-Biobío	2,20000000	-0,681843648	5,081843648	0,249036036
Toltén-Imperial	2,20000000	-0,681843648	5,081843648	0,249036036
Shannon Diversity Index	diff	lwr	upr	p adj
Rapel-Maipo	0,211666667	-0,083259539	0,506592872	0,319689553
Itata-Maipo	0,238333333	-0,056592872	0,533259539	0,190985881
Mataquito-Maipo	0,241666667	-0,053259539	0,536592872	0,178037126
Maule-Maipo	0,261666667	-0,047654547	0,57098788	0,150282649
Biobío-Maipo	0,276666667	-0,018259539	0,571592872	0,079543721

Imperial-Maipo	0,3	0,005073795	0,594926205	0,043743191
Toltén-Maipo	0,411666667	0,102345453	0,72098788	0,002915059
Itata-Rapel	0,026666667	-0,268259539	0,321592872	0,99998976
Mataquito-Rapel	0,03	-0,264926205	0,324926205	0,999977086
Maule-Rapel	0,05	-0,259321214	0,359321214	0,999488672
Biobío-Rapel	0,065	-0,229926205	0,359926205	0,99629725
Imperial-Rapel	0,088333333	-0,206592872	0,383259539	0,977347397
Toltén-Rapel	0,2	-0,109321214	0,509321214	0,449866584
Mataquito-Itata	0,003333333	-0,291592872	0,298259539	1
Maule-Itata	0,023333333	-0,28598788	0,332654547	0,999997056
Biobío-Itata	0,038333333	-0,256592872	0,333259539	0,99987964
Imperial-Itata	0,061666667	-0,233259539	0,356592872	0,997332084
Toltén-Itata	0,173333333	-0,13598788	0,482654547	0,626296555
Maule-Mataquito	0,02	-0,289321214	0,329321214	0,999998986
Biobío-Mataquito	0,035	-0,259926205	0,329926205	0,999934755
Imperial-Mataquito	0,058333333	-0,236592872	0,353259539	0,998120302
Toltén-Mataquito	0,17	-0,139321214	0,479321214	0,648373261
Biobío-Maule	0,015	-0,294321214	0,324321214	0,999999862
Imperial-Maule	0,038333333	-0,27098788	0,347654547	0,99991262
Toltén-Maule	0,15	-0,173075471	0,473075471	0,80872879
Imperial-Biobío	0,023333333	-0,271592872	0,318259539	0,99999591
Toltén-Biobío	0,135	-0,174321214	0,444321214	0,852065565
Toltén-Imperial	0,111666667	-0,197654547	0,42098788	0,938984382
Multiple Spawning	diff	lwr	upr	p adj
Toltén-Maipo	0,11356	-0,454125215	0,681245215	0,997952569
Itata-Maipo	0,237833333	-0,30568388	0,781350547	0,849278862
Biobío-Maipo	0,260066667	-0,283450547	0,80358388	0,783208445
Imperial-Maipo	0,5421	-0,001417214	1,085617214	0,051011069
Rapel-Maipo	0,6609	0,117382786	1,204417214	0,008340763
Mataquito-Maipo	0,6843	0,140782786	1,227817214	0,005688748
Maule-Maipo	0,82484	0,257154785	1,392525215	0,00094409
Itata-Toltén	0,124273333	-0,41924388	0,667790547	0,99529495
Biobío-Toltén	0,146506667	-0,397010547	0,69002388	0,98742146
Imperial-Toltén	0,42854	-0,114977214	0,972057214	0,214408899
Rapel-Toltén	0,54734	0,003822786	1,090857214	0,047361088
Mataquito-Toltén	0,57074	0,027222786	1,114257214	0,033754901
Maule-Toltén	0,71128	0,143594785	1,278965215	0,006006806
Biobío-Itata	0,022233333	-0,495989996	0,540456663	0,99999994

Imperial-Itata	0,304266667	-0,213956663	0,822489996	0,56926972
Rapel-Itata	0,423066667	-0,095156663	0,941289996	0,18085593
Mataquito-Itata	0,446466667	-0,071756663	0,964689996	0,135245496
Maule-Itata	0,587006667	0,043489453	1,13052388	0,026502042
Imperial-Biobío	0,282033333	-0,236189996	0,800256663	0,657641652
Rapel-Biobío	0,400833333	-0,117389996	0,919056663	0,234167087
Mataquito-Biobío	0,424233333	-0,093989996	0,942456663	0,178333259
Maule-Biobío	0,564773333	0,02125612	1,108290547	0,036839026
Rapel-Imperial	0,1188	-0,39942333	0,63702333	0,995219085
Mataquito-Imperial	0,1422	-0,37602333	0,66042333	0,986054008
Maule-Imperial	0,28274	-0,260777214	0,826257214	0,705579645
Mataquito-Rapel	0,0234	-0,49482333	0,54162333	0,999999915
Maule-Rapel	0,16394	-0,379577214	0,707457214	0,976174968
Maule-Mataquito	0,14054	-0,402977214	0,684057214	0,990139539

Richness by taxonomic order	diff	lwr	upr	p adj
Rapel-Maipo	1,166666667	-1,293787918	3,627121251	0,792067687
Mataquito-Maipo	2,000000000	-0,460454585	4,460454585	0,185465011
Maule-Maipo	2,200000000	-0,380546539	4,780546539	0,143938516
Biobío-Maipo	2,500000000	0,039545415	4,960454585	0,044132018
Imperial-Maipo	2,500000000	0,039545415	4,960454585	0,044132018
Itata-Maipo	2,666666667	0,206212082	5,127121251	0,025621488
Toltén-Maipo	3,400000000	0,819453461	5,980546539	0,003297153
Mataquito-Rapel	0,833333333	-1,627121251	3,293787918	0,955992432
Maule-Rapel	1,033333333	-1,547213206	3,613879872	0,899308668
Biobío-Rapel	1,333333333	-1,127121251	3,793787918	0,663976589
Imperial-Rapel	1,333333333	-1,127121251	3,793787918	0,663976589
Itata-Rapel	1,500000000	-0,960454585	3,960454585	0,524400793
Toltén-Rapel	2,233333333	-0,347213206	4,813879872	0,132128921
Maule-Mataquito	0,200000000	-2,380546539	2,780546539	0,999996452
Biobío-Mataquito	0,500000000	-1,960454585	2,960454585	0,997769699
Imperial-Mataquito	0,500000000	-1,960454585	2,960454585	0,997769699
Itata-Mataquito	0,666666667	-1,793787918	3,127121251	0,987193457
Toltén-Mataquito	1,400000000	-1,180546539	3,980546539	0,662732142
Biobío-Maule	0,300000000	-2,280546539	2,880546539	0,999943234
Imperial-Maule	0,300000000	-2,280546539	2,880546539	0,999943234
Itata-Maule	0,466666667	-2,113879872	3,047213206	0,998939765
Toltén-Maule	1,200000000	-1,495292955	3,895292955	0,839008148
Imperial-Biobío	0,000000000	-2,460454585	2,460454585	1,000000000

Itata-Biobío	0,166666667	-2,293787918	2,627121251	0,999998600
Toltén-Biobío	0,900000000	-1,680546539	3,480546539	0,948782613
Itata-Imperial	0,166666667	-2,293787918	2,627121251	0,999998600
Toltén-Imperial	0,900000000	-1,680546539	3,480546539	0,948782613
Toltén-Itata	0,733333333	-1,847213206	3,313879872	0,983153376
Shannon diversity index by taxonomic order	diff	lwr	upr	p adj
Rapel-Maipo	0,130546568	-0,157640066	0,418733202	0,826975516
Itata-Maipo	0,239468323	-0,04871831	0,527654957	0,16552013
Mataquito-Maipo	0,242111765	-0,046074869	0,530298399	0,15605976
Biobío-Maipo	0,250799515	-0,037387118	0,538986149	0,127928735
Maule-Maipo	0,263365193	-0,038887498	0,565617884	0,127007821
Imperial-Maipo	0,272988694	-0,01519794	0,561175327	0,074384014
Toltén-Maipo	0,295083119	-0,007169573	0,59733581	0,059925677
Itata-Rapel	0,108921755	-0,179264878	0,397108389	0,923470775
Mataquito-Rapel	0,111565197	-0,176621437	0,399751831	0,914108726
Biobío-Rapel	0,120252947	-0,167933686	0,408439581	0,878500393
Maule-Rapel	0,132818625	-0,169434066	0,435071316	0,847685194
Imperial-Rapel	0,142442126	-0,145744508	0,430628759	0,756327318
Toltén-Rapel	0,164536551	-0,137716141	0,466789242	0,658992335
Mataquito-Itata	0,002643442	-0,285543192	0,290830075	1,000000000
Biobío-Itata	0,011331192	-0,276855442	0,299517826	0,999999968
Maule-Itata	0,02389687	-0,278355822	0,326149561	0,999995929
Imperial-Itata	0,03352037	-0,254666263	0,321707004	0,999943035
Toltén-Itata	0,055614795	-0,246637896	0,357867487	0,998814748
Biobío-Mataquito	0,00868775	-0,279498883	0,296874384	0,999999995
Maule-Mataquito	0,021253428	-0,280999263	0,323506119	0,999998187
Imperial-Mataquito	0,030876929	-0,257309705	0,319063562	0,999967366
Toltén-Mataquito	0,052971354	-0,249281338	0,355224045	0,999134223
Maule-Biobío	0,012565678	-0,289687014	0,314818369	0,999999953
Imperial-Biobío	0,022189178	-0,265997455	0,310375812	0,999996609
Toltén-Biobío	0,044283603	-0,257969088	0,346536295	0,999732489
Imperial-Maule	0,009623501	-0,292629191	0,311876192	0,999999993
Toltén-Maule	0,031717926	-0,283974715	0,347410566	0,999978938
Toltén-Imperial	0,022094425	-0,280158266	0,324347116	0,99999763
Velocity preference	diff	lwr	upr	p adj
Imperial-Biobío	-0,600906677	-9,934544429	8,732731075	0,999999015
Itata-Biobío	5,155777022	-4,177860731	14,48941477	0,642664721
Maipo-Biobío	1,083527224	-8,250110528	10,41716498	0,99994378

Mataquito-Biobío	-1,519513205	-10,85315096	7,814124547	0,999464261
Maule-Biobío	-1,979149636	-11,7683515	7,810052223	0,997840554
Rapel-Biobío	-6,686515209	-16,02015296	2,647122543	0,321868771
Toltén-Biobío	3,528195015	-6,261006845	13,31739687	0,939481999
Itata-Imperial	5,756683699	-3,576954053	15,09032145	0,509798103
Maipo-Imperial	1,684433901	-7,649203851	11,01807165	0,998953704
Mataquito-Imperial	-0,918606528	-10,25224428	8,415031224	0,999981706
Maule-Imperial	-1,378242959	-11,16744482	8,410958901	0,999794669
Rapel-Imperial	-6,085608532	-15,41924628	3,24802922	0,439212514
Toltén-Imperial	4,129101692	-5,660100168	13,91830355	0,872517089
Maipo-Itata	-4,072249798	-13,40588755	5,261387955	0,852270868
Mataquito-Itata	-6,675290227	-16,00892798	2,658347525	0,323885232
Maule-Itata	-7,134926658	-16,92412852	2,654275202	0,301403023
Rapel-Itata	-11,84229223	-21,17592998	-2,508654479	0,005150614
Toltén-Itata	-1,627582007	-11,41678387	8,161619853	0,999385249
Mataquito-Maipo	-2,60304043	-11,93667818	6,730597323	0,98487025
Maule-Maipo	-3,062676861	-12,85187872	6,726524999	0,971190191
Rapel-Maipo	-7,770042433	-17,10368019	1,563595319	0,163913459
Toltén-Maipo	2,444667791	-7,344534069	12,23386965	0,992079943
Maule-Mataquito	-0,459636431	-10,24883829	9,329565429	0,99999989
Rapel-Mataquito	-5,167002004	-14,50063976	4,166635748	0,64020487
Toltén-Mataquito	5,04770822	-4,74149364	14,83691008	0,716013956
Rapel-Maule	-4,707365573	-14,49656743	5,081836287	0,780407368
Toltén-Maule	5,507344651	-4,71714323	15,73183253	0,670557506
Toltén-Rapel	10,21471022	0,425508364	20,00391208	0,035538045

Table S10. Post-hoc Dunn test results for Abundance, Abundance Weighted Average Size, Rapid Sexual Maturity, High Fecundity, Small Egg Size and Parental Care.

Abundance	Z	P.unadj	P.adj
Biobío - Imperial	-1,16175159	0,245336385	1,000000
Biobío - Itata	-1,15099463	0,249734446	1,000000
Imperial - Itata	0,01075696	0,991417354	1,000000
Biobío - Maipo	2,07609311	0,03788534	1,000000
Imperial - Maipo	3,2378447	0,001204364	0,033722
Itata - Maipo	3,22708774	0,001250571	0,035016
Biobío - Mataquito	0,02151392	0,982835701	1,000000
Imperial - Mataquito	1,1832655	0,236703939	1,000000
Itata - Mataquito	1,17250855	0,240992943	1,000000
Maipo - Mataquito	-2,05457919	0,039919667	1,000000
Biobío - Maule	-0,70563744	0,480413636	1,000000
Imperial - Maule	0,40204924	0,68764779	1,000000
Itata - Maule	0,39179288	0,695211256	1,000000
Maipo - Maule	-2,68511455	0,007250495	0,203014
Mataquito - Maule	-0,72615015	0,467746725	1,000000
Biobío - Rapel	0,44103532	0,659187424	1,000000
Imperial - Rapel	1,60278691	0,108981708	1,000000
Itata - Rapel	1,59202995	0,111377975	1,000000
Maipo - Rapel	-1,63505779	0,102036934	1,000000
Mataquito - Rapel	0,41952141	0,674835114	1,000000
Maule - Rapel	1,12614812	0,260102829	1,000000
Biobío - Toltén	-1,0625587	0,287982125	1,000000
Imperial - Toltén	0,04512798	0,964005303	1,000000
Itata - Toltén	0,03487162	0,972182113	1,000000
Maipo - Toltén	-3,04203582	0,002349839	0,065796
Mataquito - Toltén	-1,08307142	0,278776725	1,000000
Maule - Toltén	-0,34172609	0,732557035	1,000000
Rapel - Toltén	-1,48306938	0,138055978	1,000000
Abundance Weighted Average Size	Z	P.unadj	P.adj
Biobío - Imperial	0,00000000	1,00000000	1,00000000
Biobío - Itata	-0,1098967	0,912491264	1,0000000
Imperial - Itata	-0,1098967	0,912491264	1,0000000
Biobío - Maipo	-0,6496511	0,515917617	1,0000000
Imperial - Maipo	-0,6496511	0,515917617	1,0000000

Itata - Maipo	-0,5448687	0,585843849	1,0000000
Biobío - Mataquito	1,3187609	0,187249044	1,0000000
Imperial - Mataquito	1,3187609	0,187249044	1,0000000
Itata - Mataquito	1,4286577	0,153102644	1,0000000
Maipo - Mataquito	1,9070403	0,056515366	1,0000000
Biobío - Maule	2,3932308	0,016700731	0,4676205
Imperial - Maule	2,3932308	0,016700731	0,4676205
Itata - Maule	2,4980133	0,012489152	0,3496963
Maipo - Maule	2,9133376	0,003575877	0,1001246
Mataquito - Maule	1,1358416	0,256022863	1,0000000
Biobío - Rapel	2,7254393	0,006421599	0,1798048
Imperial - Rapel	2,7254393	0,006421599	0,1798048
Itata - Rapel	2,835336	0,004577751	0,1281770
Maipo - Rapel	3,2482555	0,00116115	0,0325122
Mataquito - Rapel	1,4066783	0,15952279	1,0000000
Maule - Rapel	0,2053736	0,837280265	1,0000000
Biobío - Toltén	-0,77539	0,438109229	1,0000000
Imperial - Toltén	-0,77539	0,438109229	1,0000000
Itata - Toltén	-0,6706076	0,502470548	1,0000000
Maipo - Toltén	-0,1203859	0,904177498	1,0000000
Mataquito - Toltén	-2,0327793	0,04207483	1,0000000
Maule - Toltén	-3,0337235	0,002415557	0,0676356
Rapel - Toltén	-3,3739944	0,000740859	0,0207440
Rapid Sexual Maturity	Z	P.unadj	P.adj
Biobío - Imperial	0,7158368	0,474092111	1,00000000
Biobío - Itata	-1,049894	0,293766846	1,00000000
Imperial - Itata	-1,7657308	0,077441017	1,00000000
Biobío - Maipo	-0,1638057	0,869884127	1,00000000
Imperial - Maipo	-0,8463293	0,397369064	1,00000000
Itata - Maipo	0,837229	0,402463865	1,00000000
Biobío - Mataquito	-1,3242981	0,185404053	1,00000000
Imperial - Mataquito	-2,040135	0,041336886	1,00000000
Itata - Mataquito	-0,2744041	0,78377408	1,00000000
Maipo - Mataquito	-1,098863	0,271827806	1,00000000
Biobío - Maule	-1,9110662	0,055996078	1,00000000
Imperial - Maule	-2,5935898	0,009497973	0,26594325
Itata - Maule	-0,9100315	0,362805892	1,00000000
Maipo - Maule	-1,6728746	0,094351992	1,00000000

Mataquito - Maule	-0,6483975	0,516727919	1,00000000
Biobío - Rapel	-1,7060778	0,087993602	1,00000000
Imperial - Rapel	-2,4219146	0,015438979	0,43229140
Itata - Rapel	-0,6561838	0,511705899	1,00000000
Maipo - Rapel	-1,4628757	0,143501407	1,00000000
Mataquito - Rapel	-0,3817796	0,702624822	1,00000000
Maule - Rapel	0,2843848	0,77611547	1,00000000
Biobío - Toltén	1,6244062	0,104289135	1,00000000
Imperial - Toltén	0,9418826	0,346252743	1,00000000
Itata - Toltén	2,6254409	0,008653683	0,24230312
Maipo - Toltén	1,7120826	0,086881454	1,00000000
Mataquito - Toltén	2,887075	0,003888416	0,10887564
Maule - Toltén	3,3849571	0,000711894	0,01993302
Rapel - Toltén	3,2510876	0,001149644	0,03219004
High Fecundity	Z	P.unadj	P.adj
Biobío - Imperial	-1,65292844	0,098345429	1,0000000
Biobío - Itata	-1,25937405	0,207895259	1,0000000
Imperial - Itata	0,39355439	0,693910061	1,0000000
Biobío - Maipo	-2,64811796	0,008094128	0,2266356
Imperial - Maipo	-1,07211253	0,283669489	1,0000000
Itata - Maipo	-1,44735192	0,147798384	1,0000000
Biobío - Mataquito	-2,05772724	0,039616324	1,0000000
Imperial - Mataquito	-0,4047988	0,685625411	1,0000000
Itata - Mataquito	-0,79835319	0,424665559	1,0000000
Maipo - Mataquito	0,68615202	0,492617249	1,0000000
Biobío - Maule	0,14366308	0,885766527	1,0000000
Imperial - Maule	1,71966851	0,085492716	1,0000000
Itata - Maule	1,34442912	0,178809663	1,0000000
Maipo - Maule	2,67292685	0,007519265	0,2105394
Mataquito - Maule	2,10562902	0,03523659	0,9866245
Biobío - Rapel	0,88830848	0,37437484	1,0000000
Imperial - Rapel	2,54123691	0,011046104	0,3092909
Itata - Rapel	2,14768253	0,031738985	0,8886916
Maipo - Rapel	3,49508686	0,000473908	0,0132694
Mataquito - Rapel	2,94603572	0,003218752	0,0901251
Maule - Rapel	0,70330582	0,481865183	1,0000000
Biobío - Toltén	0,13079773	0,895935319	1,0000000
Imperial - Toltén	1,70680316	0,087858646	1,0000000

Itata - Toltén	1,33156377	0,183003578	1,0000000
Maipo - Toltén	2,66060921	0,007799943	0,2183984
Mataquito - Toltén	2,09276367	0,036370257	1,0000000
Maule - Toltén	-0,01231764	0,990172198	1,0000000
Rapel - Toltén	-0,71617117	0,473885661	1,0000000
Small Egg Size	Z	P.unadj	P.adj
Biobío - Imperial	-0,06719131	0,9464294	1,00000000
Biobío - Itata	-0,43674354	0,662297348	1,00000000
Imperial - Itata	-0,36955223	0,711716152	1,00000000
Biobío - Maipo	0,07687729	0,938721168	1,00000000
Imperial - Maipo	0,14094169	0,887916007	1,00000000
Itata - Maipo	0,49329591	0,621803516	1,00000000
Biobío - Mataquito	-1,57899588	0,114337002	1,00000000
Imperial - Mataquito	-1,51180457	0,130583587	1,00000000
Itata - Mataquito	-1,14225234	0,253349146	1,00000000
Maipo - Mataquito	-1,58239079	0,113560387	1,00000000
Biobío - Maule	0,3331349	0,739032454	1,00000000
Imperial - Maule	0,39719931	0,691220494	1,00000000
Itata - Maule	0,74955353	0,453523647	1,00000000
Maipo - Maule	0,24534799	0,806186997	1,00000000
Mataquito - Maule	1,8386484	0,065966917	1,00000000
Biobío - Rapel	0,85108998	0,394719372	1,00000000
Imperial - Rapel	0,91828129	0,358471619	1,00000000
Itata - Rapel	1,28783352	0,197803921	1,00000000
Maipo - Rapel	0,73460517	0,462579989	1,00000000
Mataquito - Rapel	2,43008586	0,015095246	0,42266690
Maule - Rapel	0,47834755	0,632402857	1,00000000
Biobío - Toltén	2,15256398	0,031352962	0,87788293
Imperial - Toltén	2,21662839	0,026648496	0,74615789
Itata - Toltén	2,56898261	0,010199758	0,28559321
Maipo - Toltén	1,98731871	0,046887089	1,00000000
Mataquito - Toltén	3,65807748	0,000254114	0,00711520
Maule - Toltén	1,74197072	0,081513567	1,00000000
Rapel - Toltén	1,34108153	0,179893983	1,00000000
Parental Care	Z	P.unadj	P.adj
Biobío - Imperial	-1,7616003	0,07813686	1,0000000
Biobío - Itata	-1,0569602	0,290529772	1,0000000
Imperial - Itata	0,7046401	0,481034234	1,0000000

Biobío - Maipo	1,6376294	0,101499017	1,0000000
Imperial - Maipo	3,3172494	0,000909084	0,0254544
Itata - Maipo	2,6454014	0,008159406	0,2284634
Biobío - Mataquito	-0,9248401	0,35504907	1,0000000
Imperial - Mataquito	0,8367601	0,402727416	1,0000000
Itata - Mataquito	0,13212	0,894889362	1,0000000
Maipo - Mataquito	-2,5194299	0,011754504	0,3291261
Biobío - Maule	-2,1667097	0,030256994	0,8471958
Imperial - Maule	-0,4870898	0,626194706	1,0000000
Itata - Maule	-1,1589378	0,246481555	1,0000000
Maipo - Maule	-3,6423775	0,000270132	0,0075637
Mataquito - Maule	-1,2849093	0,198823995	1,0000000
Biobío - Rapel	-1,2771602	0,201545699	1,0000000
Imperial - Rapel	0,4844401	0,628073586	1,0000000
Itata - Rapel	-0,2202	0,825715371	1,0000000
Maipo - Rapel	-2,8553539	0,00429889	0,1203689
Mataquito - Rapel	-0,3523201	0,724598252	1,0000000
Maule - Rapel	0,9489853	0,342628104	1,0000000
Biobío - Toltén	-0,5290803	0,596749759	1,0000000
Imperial - Toltén	1,1505397	0,249921668	1,0000000
Itata - Toltén	0,4786917	0,632157983	1,0000000
Maipo - Toltén	-2,0744666	0,038035995	1,0000000
Mataquito - Toltén	0,3527202	0,724298223	1,0000000
Maule - Toltén	1,5679108	0,116901945	1,0000000
Rapel - Toltén	0,6886442	0,491047213	1,0000000

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8. ANEXO: MANUSCRITO ENVIADO A FRESHWATER BIOLOGY

Freshwater Biology

RIVER RESILIENCE: ASSESSMENT USING EMPIRICAL FISH ASSEMBLAGE TRAITS

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RESEARCH ARTICLE

RIVER RESILIENCE:
ASSESSMENT USING EMPIRICAL FISH ASSEMBLAGE TRAITS

Paulina Vega[1], Konrad Górski[2,3], Evelyn Habit[1,4]

[1]Departamento de Sistemas Acuáticos, Facultad de Ciencias Ambientales, Universidad de Concepción, Concepción 4030000, Chile
[2]Instituto de Ciencias Marinas y Limnológicas, Facultad de Ciencias, Universidad Austral de Chile, Valdivia, Chile
[3]Facultad de Ciencias, Universidad Católica de la Santísima Concepción, Concepción, Chile
[4]Centro EULA-Chile, Universidad de Concepción, Concepción, Chile

Konrad Górski
Email: konrad.gorski@uach.cl
Evelyn Habit
Email: ehabit@udec.cl

Correspondence
Paulina Vega, Departamento de Sistemas Acuáticos Facultad de Ciencias Ambientales, Universidad de Concepción, Concepción 4030000, Chile.
Email: paulinavegaibanez@gmail.com

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ABSTRACT

1. Freshwater ecosystems are experiencing an alarming decline in biodiversity due to a combination of local effects and basin-scale disturbances, disrupting their ability to maintain resilience in the face of anthropogenic alterations. The Andean river basins of Central-southern Chile face multiple anthropogenic disturbances, such as water extraction, hydropower, mining, domestic and industrial discharges that affect their ability to adapt to new disturbances, and to continue providing contributions to society. Furthermore, the variation in intensity of disturbances in these basins results in a marked gradient, from highly disturbed (Maipo, Rapel, Biobío, Maule) through medium (Mataquito, Itata) to low (Imperial and Toltén).
2. The aim of this study was to evaluate resilience in eight river basins in Central-southern Chile based on fish assemblages following the framework of three Rs of river ecosystem resilience. The assessment was performed using taxonomic and functional trait indices, considering three resilience mechanism: resources, recruitment and refugia, that collectively influence assemblage responses to disturbances. Taxonomic indices captured changes in species richness, abundance, diversity, evenness, and beta diversity, while functional traits reflected fish species' characteristics promoting resilience.
3. Statistical tests revealed significant differences in resilience indices among basins, with some exhibiting higher or lower resilience levels. Recruitment was the most affected resilience mechanism revealed by beta diversity indicator linked to river fragmentation in the Maipo, Rapel and Biobío river basins, whereas in the Toltén River basin functional traits of lower resilience were linked to non-native salmonids. Resources mechanism was also impacted, primarily by land use changes and water pollution in the Maipo, Rapel, Mataquito and Maule river basins reflected by low species richness indicator. Interestingly, non-linear responses of resilience to anthropogenic disturbances were observed across several basins, challenging assumptions about disturbance-resilience patterns. Indeed, river basins characterized by medium disturbances, revealed high resilience, indicating adaptation to disturbances and resilience retainment.
4. This study offered valuable insights regarding the indicators that promote resource, recruitment and refugia resilience mechanisms in river ecosystems. Fish assemblages proved to be suitable indicators of river resilience, representing diverse responses to anthropogenic disturbances among basins. Furthermore, this study underscores the importance of using multiple indicators to understand ecosystem resilience and emphasizes the need for integrated strategies to address the complex interactions of climate change, intensified land use, species invasion and population growth that face freshwater ecosystems.

1. INTRODUCTION

Freshwater ecosystems present an alarming biodiversity decline caused by combination of local effects and disturbances across catchments that is challenging to manage (Linke et al., 2011). Indeed, river ecosystems are often modified and impacted to the point that their contributions to society are severely affected (Wohl, 2014). Furthermore, anthropogenic modifications may prevent river ecosystems from adapting to new disturbances that cause shifts in demographic rates of aquatic organisms (Mouillot et al., 2013). Some anthropogenic disturbances can significantly erode ecological resilience of river ecosystems making them more vulnerable to new disturbances (Mori et al., 2013). Resilience is ecosystem's ability to absorb disturbances and remain within the same regime i.e., structure, function and feedbacks (Holling, 1973; Parsons et al., 2016; Walker and Salt, 2006; Westman, 1978). As such, resilience also encompasses the ability to reorganize itself and adapt to change (Elmqvist et al., 2003). In river ecosystems, resilience implies the persistence of biological communities in highly dynamic hydrological and geomorphological regimes (Van Looy et al., 2019). Indeed, anthropogenic activities such as fragmentation, flow regime alteration, water pollution, habitat degradation, species invasions and climate change pose significant challenges to maintenance of river ecosystems' resilience (Arthington et al., 2018; Dudgeon et al., 2006; Jaiswal et al., 2021; Van Looy et al., 2019).

Van Looy et al. (2019) proposed an integrated framework to assess resilience of river ecosystems. This framework recognizes flow-related disturbances as dominant forces shaping riverine communities and suggests three major resilience mechanisms based on responses of aquatic communities to disturbances in productivity (resources mechanism), spatial connectivity (recruitment mechanism) and habitat heterogeneity (refugia mechanism). For the resources mechanism, the potential recovery of an altered ecosystem rely on food availability and variables such as light, oxygen, substrate, and temperature (Van Looy et al., 2019). Consequently, this mechanism operates at the community level, involving internal reorganisation driven by biotic interactions such as competition and facilitation (Connell and Ghedini, 2015). The recruitment mechanism is based on metacommunity dynamics and depends on habitat connectivity, species dispersal capacity and regional species pool size (Leibold et al., 2004). As such, the river network configuration strongly affects community structure i.e., site position in the river network affects post-disturbance recolonisation or recruitment rates (Tonkin et al., 2016). Therefore, the community recovery is largely influenced by the species dispersal capacity since it affects not only the rate of recruitment or recolonisation after a disturbance but also dispersal to avoid disturbances (Van Looy et al., 2019). The refugia mechanism operates through mosaic of patches of habitats that confer heterogeneity to the ecosystem (Van Looy et al., 2019). This habitat heterogeneity provides ecological resilience to communities through mechanisms of functional redundancy, driven simultaneously by the diversity of responses of organisms and habitat specialisation (Angeler and Allen, 2016). The concept of functional redundancy implies that the loss of species is compensated for by others that contributes similarly to ecosystem functioning i.e., the functional similarity of species in one trait and their differentiation in other (Biggs et al., 2020; Fetzer et al., 2015; Van Looy et al., 2019). Thus, functionally similar organisms could respond differently to disturbances and would therefore maintain the structure and function of communities in space and time, conferring resilience to river ecosystems (Nash et al., 2016).

Fish are excellent indicators of the ecological status of river ecosystems as they can integrate the effects of disturbances over long spatial and temporal scales since they are relatively long-lived and mobile organisms and their assemblages are functionally diverse (Parsons et al., 2016). Furthermore, as top predators in food webs, fish offer a comprehensive view of the ecological status of river ecosystems. Their survival, growth and reproduction rely on a diversity of functions and processes directly related to river connectivity (Karr, 1981; Schiemer, 2000). For example, in the upper Mississippi River, dam constructions altered fish trophic positions indicating a loss of functional diversity and consequently resilience (Delong et al., 2011; Delong and Thoms, 2016b). This decline likely stemmed from diminishing habitat heterogeneity (refugia mechanism) near the dams (Van Looy et al., 2019).

The comprehension and management of river ecosystems requires an interdisciplinary and holistic approach that acknowledges the intricate interplay between their physical and biological components (Delong and Thoms, 2016a; Dollar et al., 2007; Thorp et al., 2008). Furthermore, it necessitates an understanding of resilience and adaptive management strategies (Parsons et al., 2016). The interplay of physical and biological components within river ecosystems generates distinct spatial patterns noticeable across multiple scales (Elgueta et al., 2019; Thoms et al., 2017). The Riverine Ecosystem Synthesis (RES) emerged as a framework to elucidate hydrogeomorphological and ecological relationships that operate at these multiple scales (Delong and Thoms, 2016a; Thorp et al., 2008). This framework conceptualizes river networks as a series of river zones, named Functional Process Zones (FPZs). Each FPZ delineates a large section of river characterized by relatively uniform geological histories and channel morphologies, thereby promoting similar functional ecological organisations (Habit et al., 2022). The physical attributes of FPZs influence ecological traits both within and across river sections (Thorp et al., 2008). Furthermore, geomorphological differences among FPZs have profound impacts on ecosystem structure and function (Thorp et al., 2008). Research has demonstrated that increased geomorphological heterogeneity, indicative of greater physical variability in a FPZ, is correlated with higher ecological complexity e.g. biodiversity and food chain length increases with greater FPZ's physical complexity (Maasri et al., 2021; Thoms et al., 2017),.

Andean rivers of Central-southern Chile provide an excellent model for evaluating the resilience of fish assemblages and its relationship with FPZs. These rivers are characterized by a diverse range of elevation across basins that supports a diversity of FPZs (Elgueta et al., 2019; Habit et al., 2022). Each Andean exorheic basin features short, steep rivers that flow from 3,000 m.a.s.l. in the Andes Cordillera to the Pacific Ocean (Habit et al., 2019). Furthermore, they remained isolated for more than 10,000 years (Charrier et al., 2015) and are characterised by fish assemblages with low species diversity, but with high levels of endemism, explained by basins' geological history and geomorphological characteristics (Campos et al., 1998; Habit et al., 2006). Presently, these rivers are affected by various anthropogenic disturbances, e.g. water extraction for human consumption, irrigation, domestic and industrial discharges, hydropower (flow regulation and physical fragmentation), mining, and recreation. Consequently, increasing anthropogenic disturbances threaten the ability of these rivers to continue provisioning contributions to society (Habit et al., 2022, Habit et al., 2019).

The aim of this study was to assess resilience in eight Andean River basins of Central-southern Chile in two FPZs of contrasting geomorphological complexity, based on the evaluation of fish assemblages as indicators of ecological resilience. We postulated that physically more complex FPZs are more resilient to anthropogenic disturbances than less complex FPZs. We described the composition and structure of fish assemblages in two FPZs of different levels of complexity in each basin. Subsequently, we assessed resilience mechanisms (resources, recruitment and refugia) of each basin through quantitative indices based on fish assemblages (taxonomic and functional traits) following the three Rs of river ecosystem resilience (Van Looy et al., 2019). Evaluation of ecological resilience plays a vital role in identifying human impacts on the biophysical components of ecosystems. Thus, monitoring resilience indicators allows a better understanding of the river ecosystem's capacity to adapt and transform in response to anthropogenic disturbances, informing adaptative management strategies (Parsons et al., 2016).

2. METHODOLOGY

2.1. STUDY SITE

This study was carried out across eight Andean River basins in Central-southern Chile, between 32º 55' and 39º 40' Lat. S. (Fig. 1). These rivers are characterized by relatively short length (<380 km), steep slopes, pluvio-nival flow regimes, and average annual discharges ranging from 100 to 1,000 m^3/s (Díaz et al., 2021). The prevailing climate is warm-summer Mediterranean climate (Csb) according to the Köppen-Geiger classification (Table 1). Studied river basins are located in the "Chilean winter rainfall-Valdivian forest" biodiversity hotspot (Arroyo et al., 2004; Myers et al., 2000) and belong to the Chilean ichthyogeographic province that accommodates the highest fish species richness and seven endemic species: *Bullockia maldonadoi, Cheirodon galusdae, Diplomystes incognitus, Diplomystes nahuelbutaensis, Diplomystes arratie, Percilia irwini* and *Trichomycterus chiltoni*. The latter three are endemic to the Biobío River basin, Chile's most diverse river basin (Dyer, 2000; Muñoz-Ramírez et al., 2023; Vila and Habit, 2015).

This study area represents an anthropogenic disturbance gradient from North to South, with a high level of disturbances due to fragmentation, land use changes, and water pollution in the Maipo, Rapel, Biobío and Maule rivers, through moderate disturbances in the Mataquito and Itata rivers, and less altered and non-fragmented Imperial and Toltén rivers (Habit et al., 2022; Habit et al., 2019). Some of the basins are highly populated e.g., the Metropolitan region in the Maipo River basin is inhabited by 7 million people, the Gran Concepción area in the Biobío River basin is inhabited by 1.5 million people, and the Maule region is inhabited by 1 million people (INE, 2024). Consequently, Maipo, Biobío and Maule rivers receive wastewater from multiple sources. The Maipo River basin has been described as the most polluted in Chile (Vega-Retter et al., 2014). In addition, the Maipo and Rapel river basins accommodate copper mining industry in their headwaters causing water extraction, damming and channelisation, and changes in the physical and chemical water quality (Habit et al., 2019). Forestry activity and pulp mill industry with industrial effluents discharging directly to rivers are present in the Biobío River basin (three pulp mills), and, to a lesser extent, in the Itata River basin (one pulp mill). The primary industrial discharge that flows into the Biobío River comes from the pulp mill industry, which generates 80% of the 5 billion tons per year of the pulp produced in Chile, and water consumption reaches up to 127 m^3/ton of product (Figueroa et al., 2020). Most of the studied basins had undergone a pervasive land use change, especially the Mataquito, Maule, Itata, Biobío river basins, with 22.3% of land use for forest plantations dominated by *Pinus radiata* and *Eucalyptus globulus,* and 20.7% for agriculture and livestock (Habit et al., 2024). Large reservoirs that store water for irrigation are located mainly in the Rapel and Maule river basins (Díaz et al., 2019). In addition, the Maipo, Rapel, Biobío, and Maule river basins host between 9 and 19 hydropower plants including large dams with reservoirs and hydropeaking as well as run-of-river dams (Ministerio de Energía, 2018). Indeed, the Rapel River basin accommodates the oldest reservoir in Chile, built in 1968, and is the most fragmented basin in the country (Table 1). Imperial and Toltén river basins are significantly less affected by anthropogenic activities with primary disturbances being the aquaculture farms and non-native salmonids that affect native species through predation and competition (Habit et al., 2015).

2.2. FUNCTIONAL PROCESS ZONES

The characterisation of river landscape to identify groups of river sections with similar hydrogeomorphic character (FPZs) was carried out by Habit et al. (2022), based on 16 hydrogeomorphic variables corresponding to three spatial scales: river basin, valley, and channel. Seven FPZs were obtained, and these showed a patchy distribution within and among the river networks. Within the eight study basins, three FPZs were more abundant: Sinuous Single-Channel (SSC), Sinuous Multi-Channel (SMC) and Braided Gentle Downstream Slope (BGDS). The SSC and BGDS FPZs are contrasting in terms of geomorphological complexity, differing mainly by the number of channels and the channel planform. SSC FPZ is characterized by sinuous rivers with wide single channel and a narrow valley, whereas BGDS FPZ is characterized by braided gentle downstream slopes with a wide channel and valley.

2.3. FISH SAMPLING

Between January and April 2021, 46 sites were sampled in the Maipo, Rapel, Mataquito, Maule, Itata, Biobío, Imperial, and Toltén river basins under low flow conditions (Fig. 1). Of these, 23 sites were located in the SSC FPZ, and 23 in the BGDS FPZ. Within each river basin, each FPZ had three sampling sites, except for the BGDS FPZ in the Maule River basin and the SSC FPZ in the Toltén River basin, each represented by two samapling sites. At each site, sampling was conducted using a Halltech HT-2000 (Halltech, Guelph, Canada) backpack electrofisher for approximately 30 minutes, depending on the available habitat area. In addition, fish were captured in shallow water habitats (<1 m depth), characterized by gravel and sand patches, using 6-meter-long beach seines (1.5-meter-height and 10 mm stretched mesh size), between two and four seine hauls per sampling site. Hence, sampling was performed in every microhabitat within each site, covering riffles, pools, and runs. Captured specimens were anaesthetized, identified to the species level using specialized identification keys (Ruiz and Marchant, 2004; Salas et al., 2012), counted, weighed and then returned to their habitats.

2.4. DATA ANALYSIS

Non-metric multidimensional scaling (NMDS) analysis was performed to explore changes in the composition and structure of fish assemblages between FPZs (SSC and BGDS). NMDS was based on Bray-Curtis dissimilarity matrix on the square root transformed abundance (Clarke and Warwick, 2001). Subsequently, differences in composition and structure of fish assemblages between FPZs and among basins were tested by permutational multivariate analysis of variance (PERMANOVA; Anderson et al., 2015). Threshold was stablished at $P<0.05$. Subsequently, Canonical Analysis of Principal Coordinates (CAP) was used to visualize overall patterns of dispersion in fish species composition and assemblage structure among the eight study basins and to assess the level of singularity of each fish assemblage based on the Bray-Curtis dissimilarity matrix. This method allows a constrained ordination on the basis of a distance or dissimilarity measure and discriminate between FPZs and among basins (Anderson and Willis, 2003). Additionally, an Analysis of Similarity Percentages (SIMPER) was used to estimate the contribution of each fish species to the similarity among basins (Clarke, 1993). PRIMER-E v7.0 program (Anderson et al., 2015) was used for data treatment and analyses.

River resilience for eight river basins was assessed using taxonomic and functional trait indices based on fish assemblages for each resilience mechanism. For the classification of functional traits for each species see Table S1. Table 2 and 3 show the expected trend for higher or lower resilience for each index. For the resources mechanism, taxonomic indices capture changes in the species richness, abundance, diversity, and evenness that, in turn, allow to infer disturbance consequences at the community level. For the recruitment mechanism, taxonomic indices such as beta diversity based on Sørensen, and Bray-Curtis coefficient capture the recruitment recovery at the basin level (Van Looy et al., 2019). For the refugia mechanism, changes in taxonomic richness, in this case richness by taxonomic order, diversity by taxonomic order and evenness by taxonomic order represent redundancy response to disturbances, i.e. what is suitable for one species will also be for closely related ones (Mouillot et al., 2013)**.**

The functional traits correspond to species characteristics that promote resilience for each mechanism. For example, a fish species belonging to the omnivorous trophic guild adds more resilience to the assemblage than an invertivores-piscivorous, invertivores or detritivores species, or one that uses the floodplain is more resilient than one that does not, due to the higher number of resources available to cope with disturbances. In this study, phylogenetic indices were not used due to the lack of information on the phylogeny of several native fish species. Taxonomic indices for the resources and refugia mechanisms were estimated using the Diverse routine of PRIMER-E v7.0 (Clarke and Gorley, 2015). Taxonomic indices of the recruitment mechanism were based on a distance-based approach to obtain beta diversity (see Díaz et al. 2021). The homogeneity dispersion test (PERMIDSP) was used to assess the multivariate dispersion within each river basin (Anderson et al., 2006). PERMDISP provided a measure of total beta diversity based on both presence-absence (Sørensen coefficient) and abundance data (Bray-Curtis coefficient).

Fish biomass was calculated for the functional trait that represents more resilience (indicated with ↑ in Table 3, i.e. omnivorous, frequently floodplain use, rapid sexual maturity, high fecundity, multiple spawning, small egg size, parental care, benthopelagic, eurytopic) resulting in a functional trait index based on biomass. For functional traits with more than two ordinal categories (Table 3), Principal Component Analysis (PCA) was performed using the first principal component as a proxy for the functional trait index in software PRIMER-E v7.0 (Table S2). Subsequently, statistically significant differences in taxonomic and functional trait indices among basins were assessed. One-way ANOVAs were conducted for normally distributed indices with homogenous variances. For indices with non-normal distribution but homogeneous variance Kruskal-Wallis test was used. Post hoc Tukey's (HSD) and Dunn tests (Bonferroni method) were carried out in cases of significant differences. The normality distribution and variance homogeneity were assessed using the Shapiro-Wilk test and the Levene test, respectively. All analysis were performed in R version 4.0.3 (R Core Team, 2020). For Beta diversity based on Sørensen and Bray Curtis coefficients, PERMANOVA was used to test significant differences among basins (Anderson et al., 2015). The differences were considered significant at $P<0.1$. Finally, to assess the resilience for each river basin, the post-hoc analyses (significant differences) results were used to estimate the percentage of low resilience indices out of the total significant indices. Therefore, river basins with 50 to 100% of low resilience indices were considered as 'low resilience'; river basins with 20 to 50% significant indices of low resilience were classified as 'medium resilience', and river basins with 0 to 20% of significant indices of low resilience were classified as 'high resilience'.

3. RESULTS

3.1. FUNCTIONAL PROCESS ZONES' FISH COMPOSITION

A total of 3,094 fish specimens was captured, corresponding to fifteen native and five non-natives species. Eighteen species were found in the SSC FPZ, while sixteen were captured in the BGDS FPZ (Table S3). Both evaluated FPZs were dominated by *Basilichthys microlepidotus, Percilia gillissi* and *Trichomycterus areolatus*. Also, rare species were found in both FPZs e.g., from the Diplomystidae family, *D. incognitus* was found in BGDS FPZ in the Rapel River basin, *D. arratie* in SSC FPZ in the Biobío River basin, and *Diplomystes camposensis* in BGDS FPZ in the Toltén River basin. Regarding non-native species, *Gambusia holbrooki, Oncorhynchus mykiss* and *Salmo trutta* were found in both FPZs in some basins (Table S3). It is noteworthy that in one replicate of the SSC FPZ of the Maipo River basin, no fish specimens were found. Species richness increased with increasing latitude, independently of the FPZ, from the northern Maipo River basin with a medium of two species in the SSC FPZ, to the southern Toltén River basin with a median of seven species in both FPZ (Fig. 2). NMDS based on the Bray-Curtis dissimilarity matrix on fish abundance at each sampling site did not present any clear similarity pattern for FPZs fish assemblages (Fig. S1). Fish composition and abundance was significantly different among basins and FPZs nested within river basins (Table 4).

3.2. CAP FPZ-Basin

Although PERMANOVA revealed significant differences between the FPZs nested within river basins, the CAP analysis (Fig. 3) indicated poor classification of the Basin-FPZ factor. Only 23 out of 46 sites were classified correctly, resulting in a classification error of 50%. The Maipo-BGDS, Itata-SSC and Itata-BGDS variables achieved 100% correct classification, while the Mataquito-BGDS, Biobío-SSC and Biobío-BGDS variables showed no correct classification (Table S4).

3.3. BASIN IDENTITY

CAP analysis conducted on fish abundance data across the eight study basins revealed a classification accuracy of 78% (Table 5). The Mataquito River basin exhibited the lowest classification percentage, together with a substantial dispersion of its data meaning that sampling sites within the Mataquito River basin present higher similarities with the Maipo, Rapel and Itata river basins (Table 5). However, seven out of the eight study basins showed high percentages of correct classification (>60%). The Maule and Itata river basins reached 100% classification accuracy. Overall, these results revealed a strong basin identity based on fish species presence and abundance. Each basin significantly differed in fish assemblage composition and abundance (Table 4). Based on SIMPER analysis, the dominant species were *T. areolatus* and *P. gillissi* in the Rapel, Mataquito, Itata, Imperial, and Toltén river basins, while in the Biobío River basin *P. irwini* and *Percichthys trucha* were dominant (Fig. 4). *Percichthys trucha* was abundant also in the Itata River basin, and to a lesser extent in the Maipo and Mataquito river basins. Among non-native species *G. holbrooki* was abundant in the Rapel and Maule river basins, whereas *O. mykiss* was abundant in Maipo River basin and southern basins such as Imperial and Toltén (Fig. 4).

Native fish species richness exceeded non-native species richness in all basins (Table S3). The central-southern river basins, Biobío, Imperial and Toltén hosted the highest number of native species, accommodating nine, seven and 10 species, respectively. In contrast, the presence of non-native species appeared relatively uniform across the eight evaluated basins, ranging from one to two introduced species per basin (Table S3). The non-native species found correspond to *Cnesterodon decemmaculatus*, *Cyprinus carpio, G. holbrooki*, *O. mykiss* and *S. trutta.*

3.4. RESILIENCE MECHANISMS

3.4.1. RESOURCES MECHANISM

Fish species richness, total abundance and Shannon diversity index showed significant differences among the eight studied basins (Table 6; Fig. 5; Table S5 and S6). A clear pattern of richness increase with increasing latitude was observed where the Maipo River basin had the lowest richness (median=2) and the Toltén River basins the highest richness (median=7; Fig. 5a). Total abundance also increased with increasing latitude and in the Mataquito River basin exhibited notably high variability in comparison with the rest of the basins (Fig. 5b). Shannon diversity index also increased with increasing latitude (Fig. 5c). In contrast, the Pielou evenness index (J'), trophic guilds and floodplain use did not show significant differences among studied basins (Table 6).

3.4.2. RECRUITMENT MECHANISM

Beta diversity (Sørensen), abundance-weighted average size, rapid sexual maturity, high fecundity, multiple spawning, small egg size and parental care showed significant differences among basins (Table 7). Beta diversity based on presence-absence (Sørensen) was higher in highly fragmented Maipo, Rapel and Biobío river basins (Fig. 6a, Table 1; Table S7). The abundance-weighted average size generally increased with increasing latitude except for the Maipo River basin that exhibited considerable variability (Fig. 6b). No clear pattern of differences among basins was observed for rapid sexual maturity, however, the Rapel, Mataquito, and Maule river basins showed the same fish biomass values for this trait that were higher compared to other basins (Fig.6c). Similarly, high fecundity showed no clear pattern of differences among basins (Fig. 6d), however Biobío and Imperial river basins showed higher variation compared to other studied basins. Maipo and Toltén river basins exhibited the lowest biomass for multiple spawning trait (Fig. 6e; Table S8). Maipo River basin presented the highest variation in small egg size trait, whereas egg size was significantly lower in the Toltén River basin (Fig. 6f; Table S9). Lastly, all river basins were characterised by high variation of the parental care trait, except for the Maipo River basin with zero biomass for this trait (Fig. 6g). Beta diversity based on the Bray-Curtis index and migratory life history did not show significant differences among studied basins (Table 7).

3.4.3. REFUGIA MECHANISM

Richness by taxonomic order, Shannon diversity index by taxonomic order and velocity preference showed significant differences among the eight studied basins (Table 8). Similarly to species richness (resources mechanism), richness by taxonomic order showed a clear pattern of increase with increasing latitude (Fig. 7a; Table S5). Shannon diversity index by taxonomic order also showed a clear increase with increasing latitude (Fig. 7b). Lastly, velocity preference showed a pattern of increase in velocity preference with increasing latitude with Maipo and Itata river being high value outliers indicating higher eurytopic fish biomass (Fig. 7c). Pielou evenness index by taxonomic order and vertical position did not show significant differences among studied basins (Table 8).

3.5. RESILIENCE PER BASIN

Among the eight studied basins, the Maipo and Rapel river basins exhibited the lowest resilience. The Biobío and Toltén river basins were classified as having medium resilience, whereas Mataquito, Maule, Itata and Imperial river basins showed the highest resilience (Fig. 8a). The Maipo River basin showed 10 significant indices, nine of these are of lower resilience, of which six indices correspond to taxonomic and three to functional traits (Fig. 8b; 8c). The Rapel River basin showed seven significant indices, of which four are of lower resilience (two taxonomic and two functional traits). The Mataquito and Maule river basins only exhibited one significant index of low resilience each, a taxonomic index (low richness; Fig. 8b; 8c). For the Itata River basin, the significant index of low resilience corresponds to a functional trait (multiple spawning). The Biobío River basin showed two low resilience indices out of five significant ones, one taxonomic (high beta diversity based on Sørensen index) and one functional trait (multiple spawning). Notably, the Imperial River basin presented all its significant indices of high resilience (Fig. 8b). Lastly, the Toltén River basin was characterised by 10 significant indices, among which four (corresponding to functional traits) represent low resilience (Fig. 8b; 8c).

4. DISCUSSION

Fish assemblages identified in each of the eight river basins allowed assessment of resources, recruitment and refugia resilience mechanisms evaluated through taxonomic and functional trait indices. The most affected resilience mechanism was recruitment (linked to beta diversity indicator), related to the high fragmentation level of rivers such as the Rapel, Biobío and Maipo (Díaz et al., 2019; Habit et al., 2022). Fragmentation in these river basins is caused primarily by hydropower plants, water-diverting structures, and reservoirs for irrigation. Furthermore, functional trait analyses also revealed significant alteration of recruitment mechanism by the invasion of non-native trout in the Toltén River basin. The second most affected mechanism was resources (linked to species richness indicator), mostly due to land use changes and water pollution, evidenced in the Maipo, Rapel, Mataquito and Maule river basins. Lastly, the refugia mechanism was mostly affected in the most disturbed Maipo River basin.

Ecological resilience in river ecosystems, while theoretically well founded, faces substantial challenges in quantification due to the intricate and dynamic nature of these ecosystems (Jaiswal and Pandey, 2021; Quinlan et al., 2016; Standish et al., 2014). Some of the most common difficulties are the presence of multiple environmental stressors, spatial and temporal variability, and scarcity of long-term data (Parsons et al., 2016; Tracy et al., 2022). Despite these difficulties, few empirical approaches that may allow measurement of resilience in river ecosystems have been suggested (Downing and Leibold, 2010; Jaiswal and Pandey, 2019, 2021; Tracy et al., 2022). Downing and Leibold (2010) experimentally assessed resilience in aquatic food webs, evaluating how species richness and composition responded to a disturbance. Tracy et al. (2022) focused on creating a river resilience index for a river basin that includes multiple relevant natural and anthropogenic impact factors, such as landscape features, connectivity, heterogeneity, land use and water extraction, whereas Jaiswal and Pandey (2019, 2021) created a river resilience risk index focused on biochemical processes as resilience feedbacks to characterize tipping points in large disturbed rivers. As such, there are different approaches to understand river ecosystem resilience, some based on the ecological components, while others based on biochemical processes. In the present study we employed an empirical approach based on fish assemblage taxonomic and functional trait indices adapted and expanded from the original proposal of Van Looy et al. (2019). Data availability is a common issue when working with functional traits and there is a growing disconnect between trait-based ecology and the actual availability and interpretability of trait data (Kremer et al., 2017). To address this issue, we combined extensive literature review and expert knowledge to obtain most comprehensive trait database for Chilean river fish species. Despite the conceptual framework provided by Van Looy et al. (2019), identifying and measuring ecologically relevant traits remains a challenge (Kremer et al., 2017). Not all functional traits are equally useful, and their utility depends on their ecological relevance (Streit and Bellwood, 2023). Indeed, in this study functional traits such as trophic guild, floodplain use, migratory life history and vertical position were not significantly different among river basins. Therefore, we suggest further exploration of functional traits that are ecologically meaningful for assessing resilience based on fish assemblages.

Another concern to measure resilience is finding an appropriate spatial scale. RES conceptual framework suggests FPZ as an appropriate scale to assess river functioning processes and resilience (Parsons and Thoms, 2018; Thorp et al., 2008). Our results support a strong identity of fish assemblages at the river basin scale that overarches differences at the hydrogeomorphological FPZ scale for eight studied river basins. However, our results are based on limited samples for each FPZ in each basin and as such we recognize the necessity for further research to elucidate the effects of type, size, and location (both longitudinal and lateral) of FPZs within each basin. Indeed, advance in understanding the critical factors influencing resilience in river ecosystems is often hindered by a limited focus on spatial dimensions (Thorp et al., 2023). Strong fish assemblage river basin identity revealed in the present study is associated with geological isolation of assessed basin for over 10,000 years (Charrier et al., 2015) that resulted in native fish assemblages characterized by multiple early-diverged and highly endemic species (Habit et al., 2006). River basins evaluated in the present study are located in two of the three areas of endemism described for the Chilean ichthyographic province. The Central area, which includes the Maipo and Rapel river basins, with two endemic species: *Diplomystes chilensis* (extinct) and *Cheirodon pisciculus*; and the South-central area, between Maule and Imperial river basins, with six endemic species: *B. maldonadoi, C. galusdae, D. nahuelbutaensis, D. arratie, T. chiltoni* and *P. irwini.* The latter three species are endemic to the Biobío River basin (Arratia and Quezada-Romegialli, 2020; Dyer, 2000; Muñoz-Ramírez et al., 2023; Vila and Habit, 2015).

In this study, recruitment appeared to be the resilience mechanism most affected by anthropogenic disturbance. Beta diversity index was an effective indicator of lower resilience related to recruitment mechanism and strongly associated with high fragmentation of several studied basins. Indeed, beta diversity has been shown to be a good predictor of river fragmentation (Baldan et al., 2023; Edge et al., 2017; Gauthier et al., 2020). Barriers cause fish assemblages to become increasingly different because of the loss of longitudinal connectivity, causing a higher turnover of species or higher beta diversity between the local fish assemblages (Díaz et al., 2021; Xia et al., 2022). Fragmentation is one of the major threats to riverine ecosystems and this is most explicitly expressed by the decline in numbers of migratory fish species (van Puijenbroek et al., 2019). In fact, the most fragmented Maipo, Rapel and Biobío river basins were characterized by the highest beta diversity indices (Díaz et al., 2019). In the case of the Maipo River basin, this is not only due to the presence of barriers, but there also sections of the river that have lost longitudinal connectivity due to water scarcity (Fuster, 2021). Indeed, fragmentation driven loss of resilience linked to recruitment mechanism in the Maipo and Rapel river basins seems to be related to impediment of recolonisation after disturbance and resulting extirpation of migratory species such as *Mordacia lapicida, G. australis* and *Galaxias maculatus* (Díaz et al., 2023).

An interesting finding was that the recruitment mechanism appears to be also affected by lower resilience functional traits, such as large body size, late sexual maturity, single spawning, and large egg size, in less impacted and non-fragmented basins. These functional traits are dominant in non-native trout *O. mykiss* and *S. trutta* (Arismendi et al., 2011; Estay et al., 2021; Gonzalez et al., 2012; Tyler et al., 1996). The Toltén River basin resulted as an example of this effect because the recruitment mechanism is altered by the high abundance of non-native trout. Salmonid invasion is the most important threat to native biodiversity in southern Chilean river basins. Indeed, trout negatively impact native fish assemblages, leading to a decline in their abundances, due to predation and competition (Arismendi et al., 2009; Habit et al., 2015). Furthermore, trout affect the trophic position of native fish changing natural food webs (Belk et al., 2014; Correa et al., 2012; Habit and Victoriano, 2012). Here, these effects of trout and lower resilience traits that trout contribute to fish assemblage are reflected in lower resilience in the recruitment mechanism and specifically in functional trait indicators. Furthermore, in less intervened Toltén river basin the functional traits indices captured the effects of biological disturbances that in other river basins with higher number of physical disturbances did not emerge.

The resources mechanism linked to species richness indicator was the second most affected by anthropogenic disturbances in the studied basins. A major driver of species richness decline worldwide is land use change (Allan et al., 2015; Cardinale et al., 2012; Gossner et al., 2016; Murphy and Romanuk, 2014; Powers and Jetz, 2019; Simkin et al., 2022). Conversion of natural landscape into other productive systems affects integrity of river ecosystems in terms of nutrient cycling, increase surface runoff and reduced water quality (Esse et al., 2021; Fierro et al., 2019; Miserendino et al., 2011). Therefore, land use changes can modify the consumer-resource interactions and reconfigure the flow of energy through the entire river ecosystem food web altering the resources mechanism (Price et al., 2019). Water pollution from domestic and industrial effluents is also a major threat to biodiversity in river ecosystems (Bassem, 2020; Dudgeon et al., 2006; Gomez et al., 2014; Groh et al., 2022), it reduces the abundance and diversity of native fish fauna and other organisms (Magurran and Phillip, 2001; Ngor et al., 2023; Paruch et al., 2019; Sun et al., 2019). Loss of resilience in relation to the resources mechanism due to extensive land use changes in the Maipo, Rapel, Mataquito and Maule river basins was reflected in significantly lower species richness compared to the rest of the studied basins. During the last decades land use has changed from native forest to agriculture and urbanisation, as well as exotic plantations of *P. radiata* and *E. globulus* for pulp production in the Central-southern basins (Mataquito and Maule river basins) (Aguayo et al., 2009; Henríquez-Dole et al., 2018; Hermosilla-Palma et al., 2021; Puertas et al., 2014). For example, in the Rapel River basin, land use changes have caused high loads of organic matter and nutrients in the Rapel reservoir located in the lower basin, causing several algal blooms, hypoxia and anoxia events, and associated fish mortalities (Vila et al., 2000). The Maipo River basin is the most disturbed among studied basins and this is reflected in other resources mechanism's indicators such as low abundance and low Shannon's diversity. It is also the only river basin within the study area with low resilience taxonomic indicators for the refugia mechanism, such as low richness by taxonomic order and low Shannon's diversity by taxonomic order. Indeed, apart from fragmentation, land use changes and pollution, Maipo River basin concentrates 40% of Chilean population (7 million people; INE, 2024) and it has been described as one of the most contaminated river basins in Chile (Habit et al., 2024). Indeed, these anthropogenic disturbances seem to have profound impact on the availability and quality of refuges for fish assemblages. As a consequence, it seems to have reduced ability to facilitate the survival of fish species and possibly other aquatic organisms under these adverse conditions (Keppel et al., 2012; Van Looy et al., 2019).

Relationships between anthropogenic disturbances and river resilience assessed by fish assemblage indicators resulted in non-linear responses across river basins, i.e. a highly disturbed river basin did not always result in lower resilience. Indeed, medium resilience was detected in river basins with different levels of anthropogenic disturbances. These results have different local explanations, such as the unexpected case of the Toltén River basin that is a representation of the significance of biological invasions in physically well-conserved ecosystems (Bernery et al., 2022; Costantini et al., 2023; Hou et al., 2023). Meanwhile, the highly disturbed Biobío River basin still hosts a naturally highly diverse fish assemblage, indicating higher resilience (Habit et al., 2007). Also, the cases of the Itata and Mataquito river basins, with medium levels of disturbances, showed high resilience. These basins possibly exemplify that at medium level of disturbances fish assemblages can adapt to these disturbances and resilience of the river ecosystem could be maintained. This diversity and non-linearity of responses highlights the complexity of river resilience mechanisms, where the influence of disturbances varies across basins, challenging assumptions about disturbance-resilience patterns.

The resilience assessment based on fish assemblages of Andean River basins of Central-southern Chile provided insights into resources, recruitment and refugia resilience mechanisms in river ecosystems. Fish assemblages resulted to be suitable indicators of river ecosystem resilience that could be related to different anthropogenic disturbance levels at basin scale. The use of several resilience indicators revealed different responses of the fish assemblages to anthropogenic disturbances associated with each resilience mechanism. Recruitment indices (beta diversity Sørensen and functional traits) revealed low resilience due to fragmentation and presence of non-native trout. Meanwhile, resources indices (richness, abundance, and Shannon's diversity) revealed the effects of land use changes and water pollution. Thus, these indices emerged as key indicators of river resilience in the studied basins. Integrated strategies, such as the one used here, are necessary in the current environmental scenario since the interplay between climate change, land use intensification, species invasion and human population growth bring new challenges to the global management and conservation of freshwater ecosystems. This highlights the need to continue understanding adaptive management approaches for ecosystem resilience and measures to improve resilience of river ecosystems.

AUTHOR CONTRIBUTIONS

Conceptualisation: PV, KG, EH. Developing methods: PV, KG, EH. Conducting the research: PV, KG, EH. Data analysis: PV. Data interpretation: PV, KG, EH. Preparation figures & tables: PV. Writing: PV, KG, EH.

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DATA AVAILABILITY STATEMENT

Data are available from the authors upon reasonable request.

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ETHICS STATEMENT

Fish study was reviewed and approved by Comité de Ética, Bioética y Bioseguridad de la Vicerrectoría de Investigación y Desarrollo de la Universidad de Concepción.

CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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TABLES

Table 1. Geographic position, catchment area, predominant climate, flow regime, mean, annual precipitation, mean annual discharge at the mouth of the eight river basins and Fragmentation Index (Díaz et al., 2021; Habit et al., 2022). Csa, hot-summer Mediterranean climate; Csb, warm-summer Mediterranean climate; Cfb, Oceanic climate (Marine west coast).

Basin	Latitude (° ')	Longitude (° ')	Area (km²)	Maximum Altitude (m)	Predominant Climate	Flow Regime	PP_{MA} (mm)	Q_{MA} (m³/s)	Fragmentation Index
Maipo	32◦ 55′ –34◦ 18′ S	69◦ 48′ –71◦ 38′ W	15,273	6,546	Csa-Csb	Snowmelt	650	134	0.393
Rapel	33◦ 54′ –35◦ 00′ S	70◦ 01′ –71◦ 51′ W	13,766	5,138	Csa-Csb	Snowmelt-rain	882	169	0.463
Mataquito	34◦ 48′ –35◦ 38′ S	70◦ 24′ –72◦ 11′ W	6,332	4,058	Csb	Snowmelt-rain	1373	113	0.080
Maule	35◦ 06′ –36◦ 35′ S	70◦ 21′ –72◦ 27′ W	21,052	3,931	Csb	Snowmelt-rain	1400	495	0.361
Itata	36◦ 12′ –37◦ 20′ S	71◦ 02′ –72◦ 52′ W	11,326	3,178	Csb	Snowmelt-rain	1764	331	0.044
Biobío	36◦ 52′ –38◦ 54′ S	70◦ 50′ –73◦ 12′ W	24,369	3,487	Csb	Rain	1873	971	0.436
Imperial	37◦ 49′ –38◦ 58′ S	71◦ 27′ –73◦ 30′ W	12,668	3,066	Csb-Cfb	Rain	2056	264	0.002
Toltén	38◦ 36′ –39◦ 38′ S	71◦ 24′ –73◦ 14′ W	8,448	3,710	Cfb	Rain	2062	540	0.016

Table 2. Taxonomic and functional traits indices used for each resilience mechanism. ↑ indicates resilience increase as the value of the index increases; ↓ indicates resilience decrease as the value of the index increases. † indicates indices and traits proposed in this study.

Mechanism	Resources	Recruitment	Refugia
Taxonomic indices	Richness ↑	Beta diversity (Sørensen) ↓	†Richness by taxonomic order ↑
	Total Abundance ↑		†Shannon diversity index by taxonomic order ↑
	Shannon diversity index ↑	Beta diversity (Bray-Curtis) ↓	†Pielou evenness index by taxonomic order ↑
	†Pielou evenness index ↑		
Functional traits	Trophic guilds	Migratory life history	†Vertical position
		†Abundance-Weighted Average Size	
		†Sexual maturity	
		Fecundity	
	†Floodplain use	†Spawning	†Velocity preference
		†Egg size	
		†Parental care	

Table 3. Functional traits used to assess fish assemblages' resilience mechanisms in each basin. These traits were selected based on the available knowledge about fish species captured in the eight basins (Table S1). ↑ indicates resilience increase as biomass of fish in a particular trait category increase. ↓ indicates resilience decrease as the biomass of fish in a particular trait category increase.

Trait type	Trait	Categories	Categorical – Value
Ordinal	Trophic guilds	Detritivore ↓	1
		Invertivore ↓	2
		Inv-Piscivore ↓	3
		Omnivore ↑	4
Ordinal	Floodplain use	Scarcely↓	1
		Frequently ↑	2
Ordinal	Migratory Life History	Non-migratory ↑	1
		Amphidromous facultative ↓	2
		Catadromous facultative ↓	3
		Anadromous ↓	4
Continuous	Maximum length	Species maximum size recorded in literature ↓	-
Ordinal	Sexual Maturity	Rapid (1st year) ↑	1
		Late (after 1st year) ↓	2
Ordinal	Fecundity	Low ↓	1
		High (>1000 oocytes or eggs) ↑	2
Ordinal	Spawning	Single ↓	1
		Multiple ↑	2
Ordinal	Egg size	Small ↑	1
		Large (> 2 mm) ↓	2
Ordinal	Parental care	Absent ↓	1
		Present ↑	2
Ordinal	Vertical position	Benthic ↓	1
		Benthopelagic ↑	2
		Pelagic ↓	3
Ordinal	Velocity preference	Limnophilic ↓	1
		Eurytopic ↑	2
		Reophilic ↓	3

Table 4. Results of PERMANOVA conducted on Bray-Curtis similarity matrix based on fish abundance data. df, degrees of freedom; SS, sums of squares; Pseudo-F, distance-base pseudo-F-statistic; P, probability values (obtained using 9999 permutations of residuals under a reduced model). Significant effects are indicated in bold.

Factor	df	SS	Pseudo-F	P(perm)	Unique perms
Basin	7	55789	2.9212	**0.0001**	9885
FPZ (Basin)	8	21840	2.0736	**0.0003**	9861
Res	30	39496	-	-	-

Table 5. Canonical Principal Coordinate Analysis (CAP) on fish abundance data in the eight basins.

Original Group	Maipo	Rapel	Mataquito	Maule	Itata	Biobío	Imperial	Toltén	Total	% Correct
Maipo	5	0	1	0	0	0	0	0	6	83.3
Rapel	0	4	1	1	0	0	0	0	6	66.7
Mataquito	1	1	2	0	2	0	0	0	6	33.3
Maule	0	0	0	5	0	0	0	0	5	100.0
Itata	0	0	0	0	6	0	0	0	6	100.0
Biobío	1	0	0	0	0	5	0	0	6	83.3
Imperial	0	0	0	0	0	0	5	1	6	83.3
Toltén	0	0	1	0	0	0	0	4	5	80.0

Table 6. Effects of Basin factor on resources mechanisms' variables based on ANOVA and Kruskal-Wallis' analyses (see Table S5 and S6 for details). Significant differences (*P*<0.1) are indicated in bold. F, F value; H, chi-squared.

Resources Mechanism	F/H	p-value
Richness (S)	F=5.284	**0.000282**
Total Abundance (N)	H=16.888	**0.018130**
Shannon Diversity Index (H')	F=2.98	**0.013600**
Pielou Equitability Index (J')	H=3.0509	0.880300
Trophic Guilds	F=1.559	0.178000
Floodplain Use	H=4.2598	0.749400

Table 7. Effects of Basin factor on recruitment mechanisms' variables based on ANOVA and Kruskal-Wallis' analyses. Significant differences (*P*<0.1) are indicated in bold (see Table S5, S6 and S7 for details). F, F value; H, chi-squared.

Recruitment Mechanism	F/H	*P*
Beta Diversity (Sørensen)	F=2.8644	**P(perm)= 0.0819**
Beta Diversity (Bray-Curtis)	F=2.3564	P(perm)= 0.1855
Migratory Life History	F=6.1954	0.5060000
Abundance Weighted Average Size	H=24.641	**0.0008784**
Rapid Sexual Maturity	H=20.374	**0.0048150**
High Fecundity	H=21.502	**0.0030940**
Multiple Spawning	F=6.1770	**0.0000797**
Small Egg Size	H=15.264	**0.0327600**
Parental Care	H=18.024	**0.0118600**

Table 8. Effects of Basin factor on refugia mechanisms' variables based on ANOVA and Kruskal-Wallis' analyses (see Table S5 and S6 for details). Significant differences (*P*<0.1) are indicated in bold. F, F value; H, chi-squared.

Refugia Mechanism	**F/H**	**p-value**
Richness by taxonomic order	F=3.5410	**0.00503**
Shannon Diversity Index by taxonomic order	F=2.3450	**0.04300**
Pielou Evenness Index by taxonomic order	H=2.3511	0.93790
Vertical Position	F=1.5230	0.18900
Velocity Preference	F=2.9840	**0.01350**

FIGURE CAPTIONS

Fig. 1. Geographic location of the eight studied basins and location of sampling sites associated with two Functional Process Zones (FPZs). SSC, Sinuous Single Channel; BGDS, Braided Gentle Downstream Slope.

Fig. 2. Fish species richness in both FPZs in each river basin. SSC, Sinuous Single Channel; BGDS, Braided Gentle Downstream Slope FPZ.

Fig. 3. Canonical Principal Coordinate Analysis (CAP) on fish abundance data in each FPZ of the eight basins. SSC, Sinuous Single Channel; BGDS, Braided Gentle Downstream Slope.

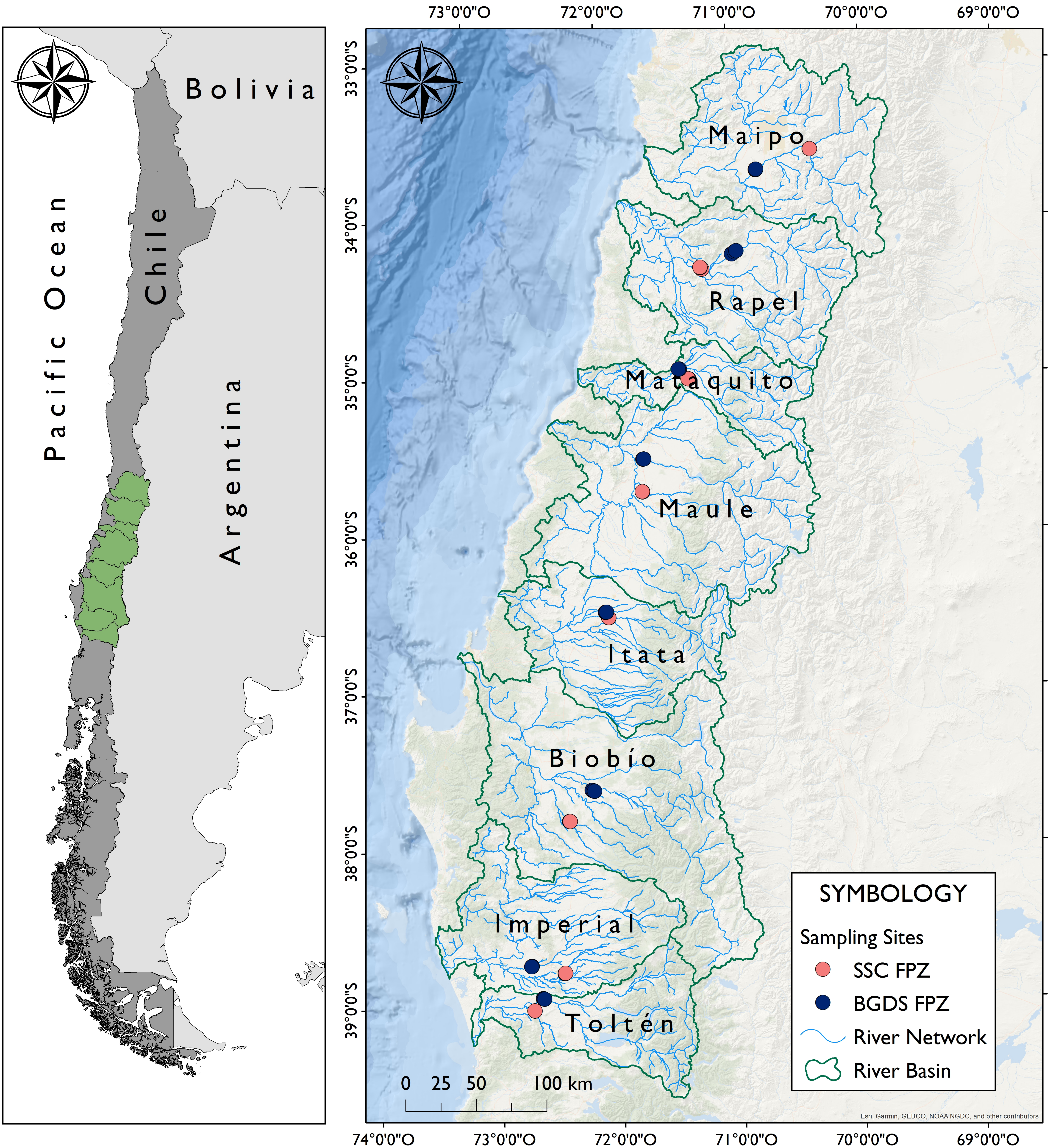
Fig. 4. Fish assemblage composition in eight Andean river basins. The pie chart represents the percentage of contribution of each species to the differences among basins (similarity percentage analysis). Species marked with * are non-native.

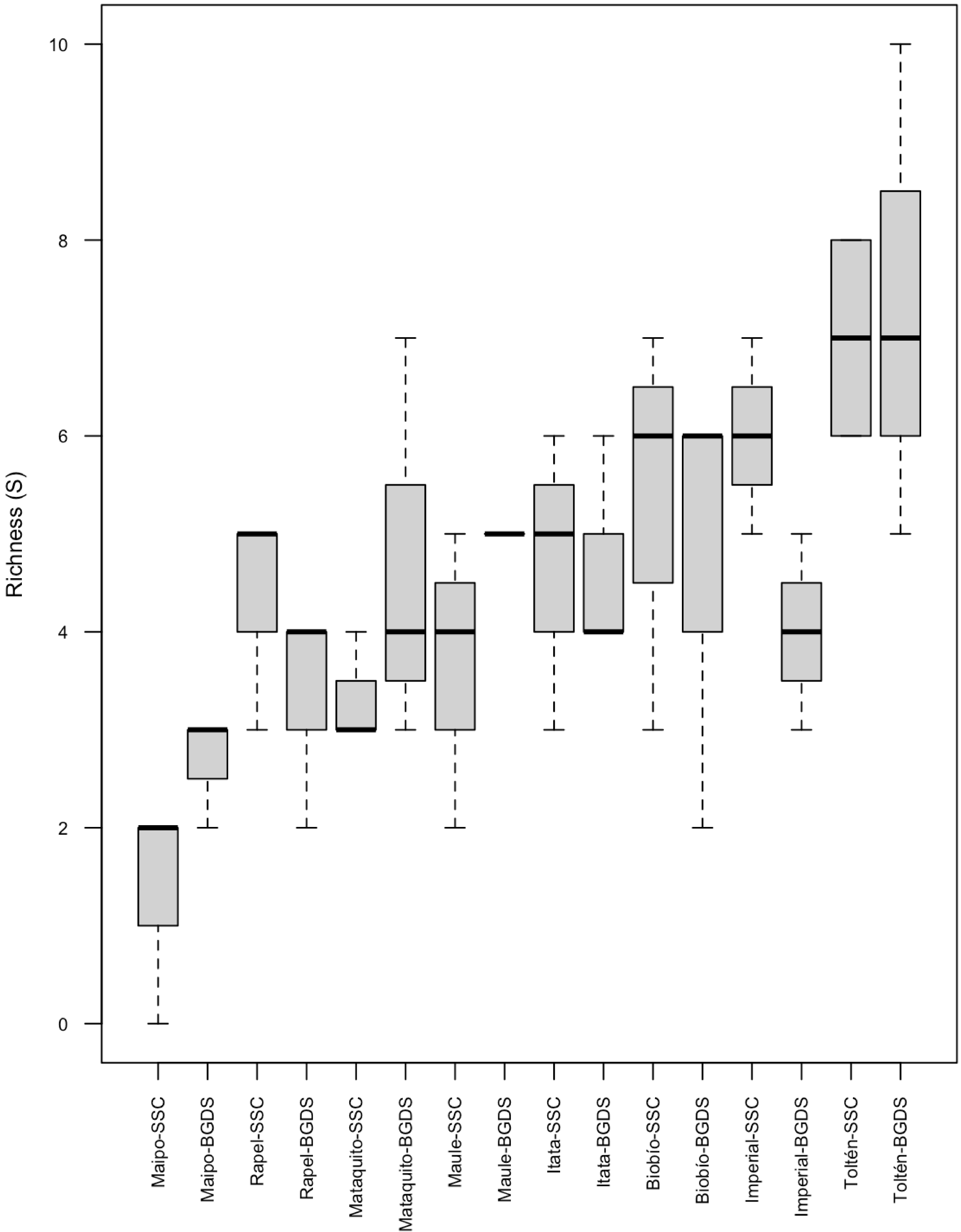
Fig. 5. Boxplot of a) Richness (S), b) Total Abundance, c) Shannon Diversity Index (H'), for eight studied basins. The lower end of the whisker represents the minimum value, the upper end the maximum value, the black line in the boxplot represents the median and the dotted line represents the standard deviation.

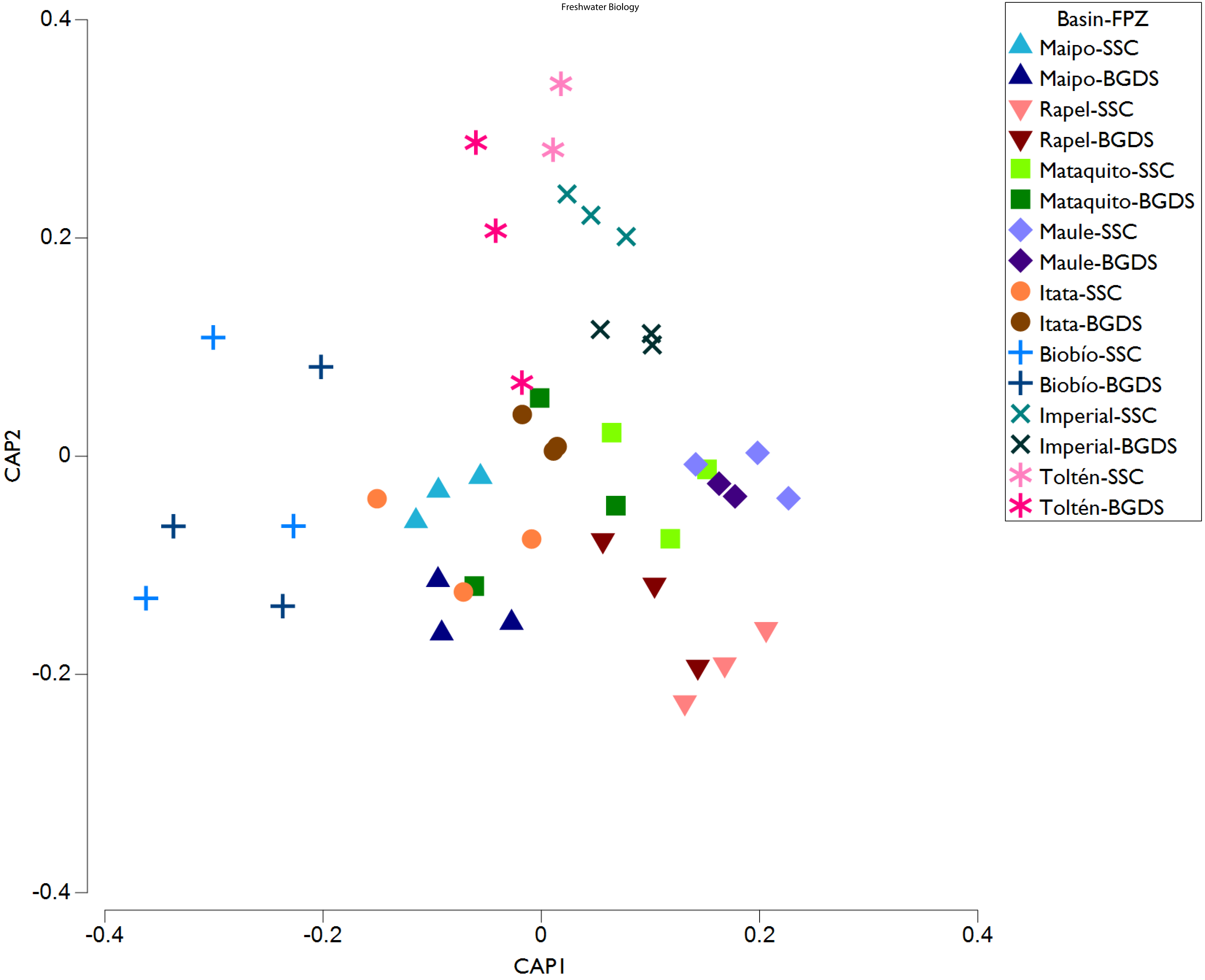
Fig. 6. Boxplot of a) Beta Diversity (Sørensen), b) Abundance Weighted Average Size, c) Rapid Sexual Maturity, d) High Fecundity, e) Multiple Spawning f) Small Egg Size, g) Parental care for eight studied basins. The lower end of the whisker represents the minimum value, the upper end the maximum value, the black line in the boxplot represents the median and the dotted line represents the standard deviation.

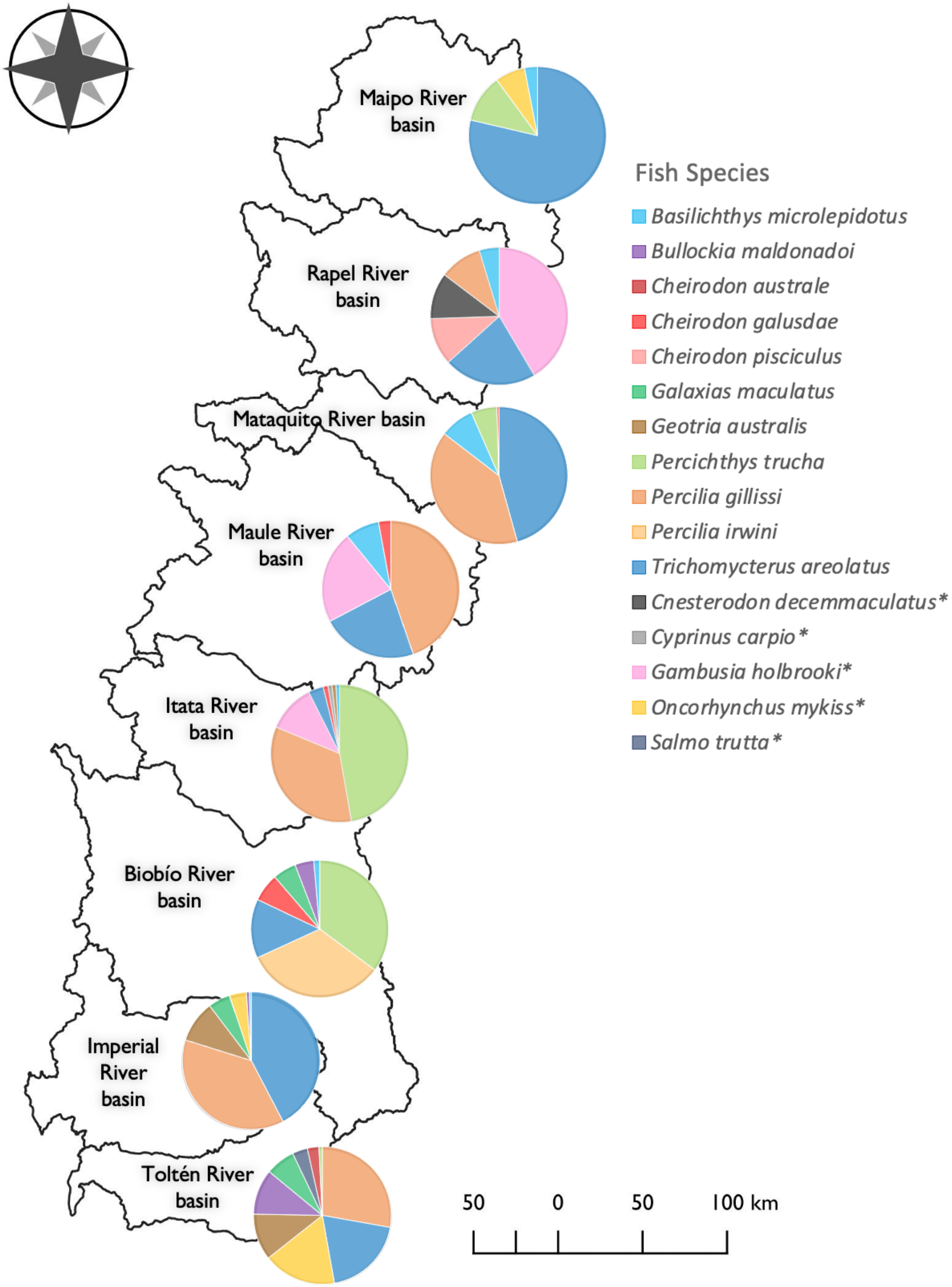
Fig. 7. Boxplot of a) Richness by taxonomic order, b) Diversity Index by taxonomic order, c) Velocity for eight studied basins. The lower end of the whisker represents the minimum value, the upper end the maximum value, the black line in the boxplot represents the median and the dotted line represents the standard deviation.

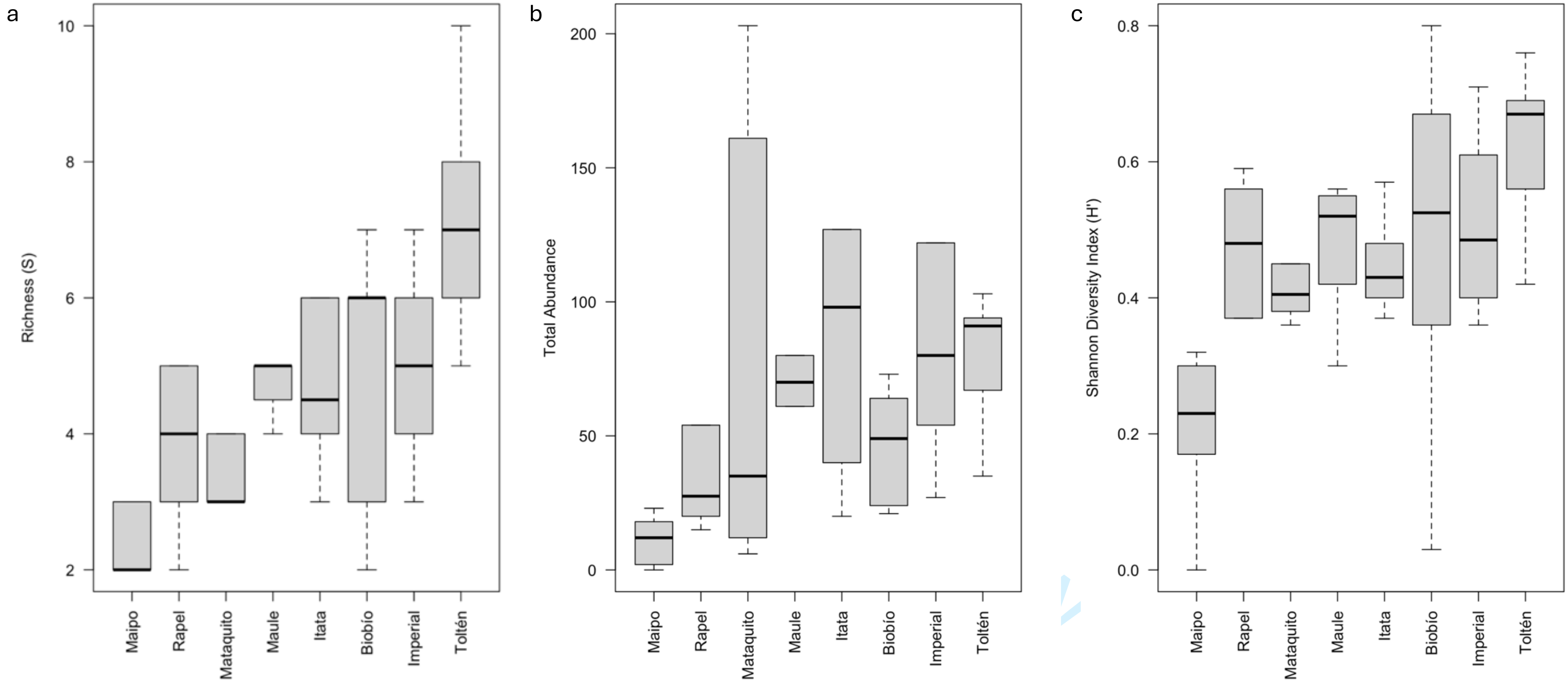
Fig. 8. a) Resilience classification for studied basins based on evaluated indices; b) The number of significant resilience indices per basin; c) The number of significant lower resilience taxonomic and functional trait indices per basin.

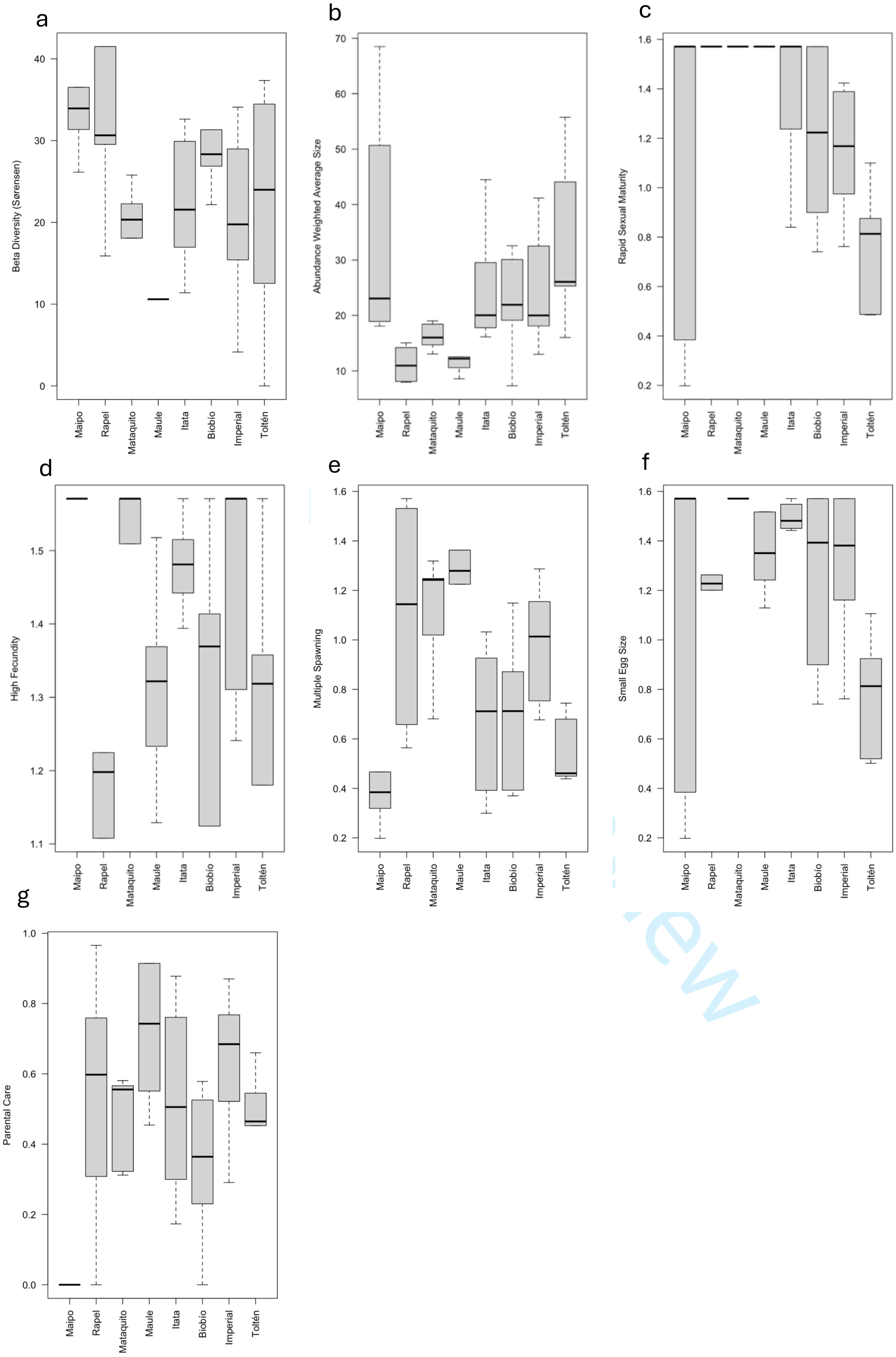

Bolivia
Pacific Ocean
Chile
Argentina
73°0'0"O
72°0'0"O
71°0'0"O
70°0'0"O
69°0'0"O
33°0'0"S
34°0'0"S
35°0'0"S
36°0'0"S
37°0'0"S
38°0'0"S
39°0'0"S
Maipo
Rapel
Mataquito
Maule
Itata
Biobío
Imperial
Toltén
0 25 50 100 km
SYMBOLOGY
Sampling Sites
SSC FPZ
BGDS FPZ
River Network
River Basin
Esri, Garmin, GEBCO, NOAA NGDC, and other contributors
74°0'0"O
73°0'0"O
72°0'0"O
71°0'0"O
70°0'0"O
69°0'0"O

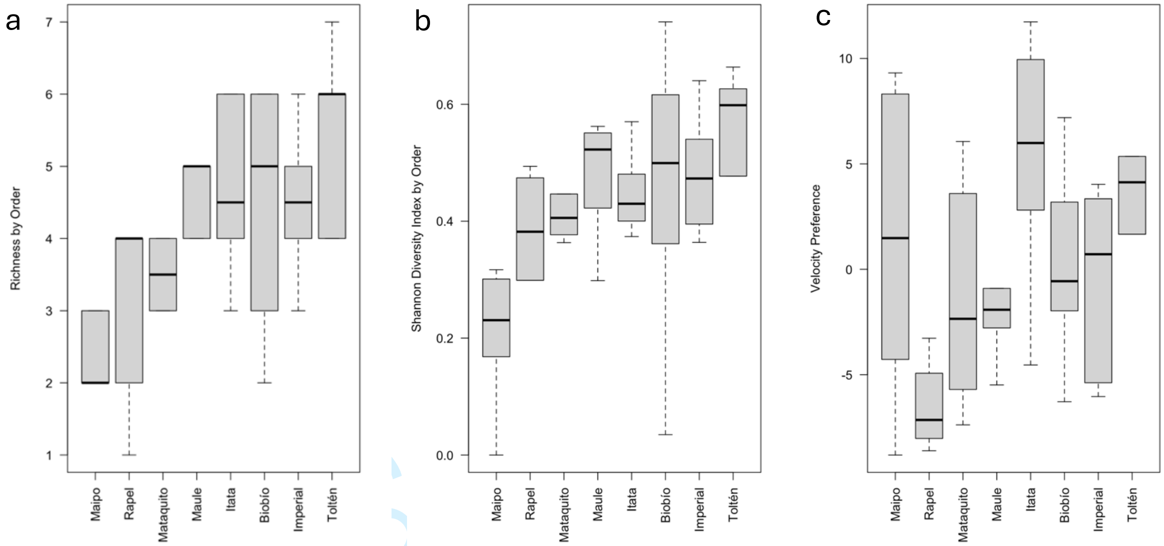

Richness (S)
0
2
4
6
8
10
Maipo-SSC
Maipo-BGDS
Rapel-SSC
Rapel-BGDS
Mataquito-SSC
Mataquito-BGDS
Maule-SSC
Maule-BGDS
Itata-SSC
Itata-BGDS
Biobío-SSC
Biobío-BGDS
Imperial-SSC
Imperial-BGDS
Toltén-SSC
Toltén-BGDS


Basin-FPZ
Maipo-SSC
Maipo-BGDS
Rapel-SSC
Rapel-BGDS
Mataquito-SSC
Mataquito-BGDS
Maule-SSC
Maule-BGDS
Itata-SSC
Itata-BGDS
Biobío-SSC
Biobío-BGDS
Imperial-SSC
Imperial-BGDS
Toltén-SSC
Toltén-BGDS
CAP2
0.4
0.2
0
-0.2
-0.4
CAP1
-0.4
-0.2
0
0.2
0.4


Maipo River basin
Rapel River basin
Mataquito River basin
Maule River basin
Itata River basin
Biobío River basin
Imperial River basin
Toltén River basin
Fish Species
Basilichthys microlepidotus
Bullockia maldonadoi
Cheirodon australe
Cheirodon galusdae
Cheirodon pisciculus
Galaxias maculatus
Geotria australis
Percichthys trucha
Percilia gillissi
Percilia irwini
Trichomycterus areolatus
Cnesterodon decemmaculatus*
Cyprinus carpio*
Gambusia holbrooki*
Oncorhynchus mykiss*
Salmo trutta*
50
0
50
100 km


a
Richness (S)
2
4
6
8
10
b
Total Abundance
0
50
100
150
200
c
Shannon Diversity Index (H')
0.0
0.2
0.4
0.6
0.8
Maipo
Rapel
Mataquito
Maule
Itata
Biobío
Imperial
Toltén


a
Beta Diversity (Sørensen)
0
10
20
30
40
b
Abundance Weighted Average Size
10
20
30
40
50
60
70
c
Rapid Sexual Maturity
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
d
High Fecundity
1.1
1.2
1.3
1.4
1.5
e
Multiple Spawning
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
f
Small Egg Size
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
g
Parental Care
0.0
0.2
0.4
0.6
0.8
1.0
Maipo
Rapel
Mataquito
Maule
Itata
Biobio
Imperial
Toltén


a
Richness by Order
1
2
3
4
5
6
7
Maipo
Rapel
Mataquito
Maule
Itata
Biobío
Imperial
Toltén
b
Shannon Diversity Index by Order
0.0
0.2
0.4
0.6
Maipo
Rapel
Mataquito
Maule
Itata
Biobío
Imperial
Toltén
c
Velocity Preference
-5
0
5
10
Maipo
Rapel
Mataquito
Maule
Itata
Biobío
Imperial
Toltén

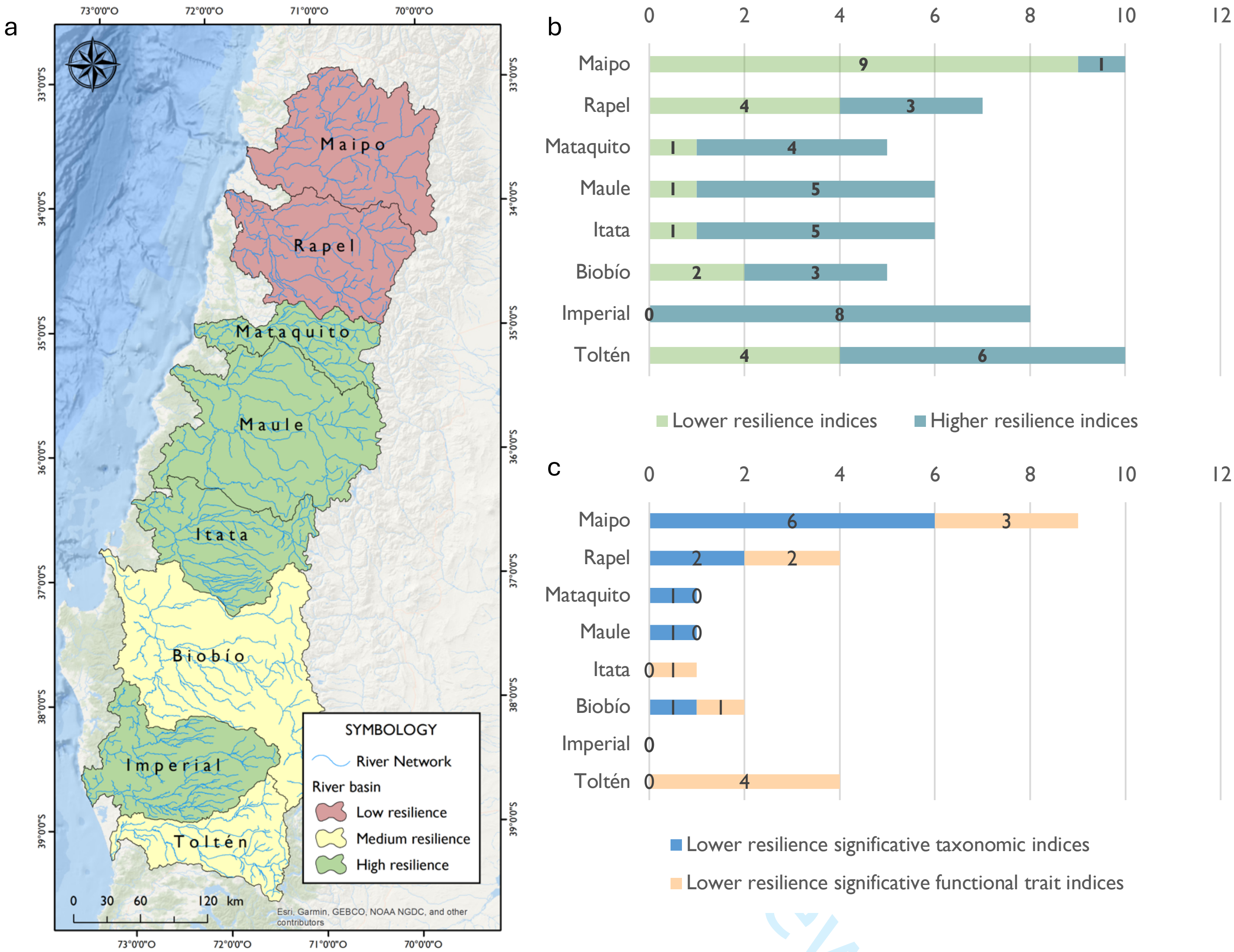

a
73°0'0"O
72°0'0"O
71°0'0"O
70°0'0"O
33°0'0"S
34°0'0"S
35°0'0"S
36°0'0"S
37°0'0"S
38°0'0"S
39°0'0"S
Maipo
Rapel
Mataquito
Maule
Itata
Biobío
Imperial
Toltén
SYMBOLOGY
River Network
River basin
Low resilience
Medium resilience
High resilience
0 30 60 120 km
Esri, Garmin, GEBCO, NOAA NGDC, and other contributors
b
0 2 4 6 8 10 12
Maipo 9 1
Rapel 4 3
Mataquito 1 4
Maule 1 5
Itata 1 5
Biobío 2 3
Imperial 0 8
Toltén 4 6
Lower resilience indices
Higher resilience indices
c
0 2 4 6 8 10 12
Maipo 6 3
Rapel 2 2
Mataquito 1 0
Maule 1 0
Itata 0 1
Biobío 1 1
Imperial 0
Toltén 0 4
Lower resilience significative taxonomic indices
Lower resilience significative functional trait indices

Table S1. Classification of functional traits for each species.
Information was extracted from different sources (Baker et al., 2017; Campos, 1969; Campos, 1970; Chiang et al., 2012; Estay et al., 2021; Ferriz et al., 1999; Golusda, 1927; Habit & Victoriano, 2005; Habit et al., 2009; Manríquez et al., 1998; Montoya et al., 2012; Oyanedel et al., 2018; Patimar, 2010; Prochelle & Campos, 1985; Ruiz, 1993; Ruiz & Marchant, 2004; Serezli et al., 2010) and expert knowledge. *Non-native species.

Species	Trophic guild	Floodplain use	Migratory life history	Maximum size	Sexual maturity	Fecundity	Spawning	Egg size	Parental care	Velocity preference	Vertical position
Aplochiton taeniatus	2	1	3	36,1	1	2	1	1	1	2	3
Bullockia maldonadoi	2	1	1	8,6	1	1	1	1	1	3	1
Basilichthys microlepidotus	3	2	1	40	1	2	1	1	1	1	3
*Cyprinus carpio**	4	2	1	120	2	2	2	1	1	1	2
*Cnesterodon decemmaculatus**	4	2	1	3,8	1	1	2	2	2	1	3
Cheirodon australe	4	1	1	7	1	1	2	1	1	1	3
Cheirodon galusdae	4	1	1	6,7	1	1	2	1	1	1	3
Cheirodon pisciculus	4	1	1	6,8	1	1	2	1	1	1	3
Diplomystes camposensis	2	1	1	24,9	2	1	1	2	1	3	1
Diplomystes incognitus	2	1	1	17,9	2	1	1	2	1	3	1
Diplomystes arratie	2	1	1	35	2	1	1	2	1	3	1
Geotria australis	1	2	4	57	2	2	1	1	2	3	1
*Gambusia holbrooki**	4	1	1	8	1	1	2	2	2	1	2
Galaxias maculatus	2	1	2	12	1	2	1	1	1	1	3
*Oncorhynchus mykiss**	3	1	1	122	2	2	1	2	1	2	3
Percilia gillissi	2	1	1	9	1	2	2	1	2	2	2
Percilia irwini	2	1	1	9,6	1	2	2	1	2	2	2
Percichthys trucha	3	1	1	45	1	2	1	1	1	2	3
*Salmo trutta**	3	1	1	140	2	2	1	2	1	2	3
Trichomycterus areolatus	2	1	1	15	1	2	2	1	1	3	1

Table S2. Scores of Principal Coordinate Analysis (PCA) for Trophic Guilds, Migratory Life History, Vertical Position and Velocity Preference

Trophic Guilds				Migratory Life History				Vertical Position			Velocity Preference		
SCORE1	SCORE2	SCORE3	SCORE4	SCORE1	SCORE2	SCORE3	SCORE4	SCORE1	SCORE2	SCORE3	SCORE1	SCORE2	SCORE3
-7,9018124	-5,0923596	-1,3306215	-0,8751661	-6,0487367	1,13868338	-0,0895643	0,0401241	-4,5731169	-7,3199068	6,0525745	8,3138126	-1,5433542	-2,6351661
-1,6611649	-6,8534163	-1,0370659	-0,4383727	-0,1447563	0,81163657	-0,0579688	0,02684599	0,39076354	-7,0962409	1,85330904	3,0515796	-4,5953739	-0,3290774
9,87612574	-3,8490673	-1,1360313	-0,0200208	11,7665769	0,15181672	0,00577524	5,7274E-05	10,2641082	-1,6995932	-2,1106863	-8,8100502	-5,836686	-0,0446789
-8,5143932	-6,338433	-1,2139925	-0,8298322	-6,7807363	1,17923197	-0,0934816	0,04177037	-5,2182324	-8,4713666	5,60360011	9,31386622	-2,2413335	-1,9596446
-0,4067189	-3,7281993	-1,3346844	-0,5668599	1,48251625	0,72149496	-0,0492604	0,02318623	1,77563841	-4,2817565	3,12078709	-0,0935239	-0,3806692	0,54187811
4,04333835	-1,5111779	-1,4813254	-0,4712817	5,46682431	0,50078704	-0,0279382	0,01422548	5,70162363	-1,3578527	2,23407471	-4,2753177	-1,8881245	-1,956501
3,26443498	-3,7669313	1,39011424	-0,1518832	4,69798455	0,54337637	-0,0320527	0,01595461	3,49879724	-3,6270225	-2,9079216	-6,4574522	-1,6649905	5,16897999
1,83261952	-2,6681475	1,65122646	-0,2621577	3,18220778	0,62734175	-0,0401644	0,01936361	1,96358538	-3,2450665	-3,733287	-4,9298916	-1,1397884	6,02191177
8,21217609	-0,215967	1,94150758	-0,0446801	6,73057414	0,43078251	-0,0211752	0,0113833	7,1785506	2,23326539	-1,4384085	-8,6063918	-0,8025636	0,19224931
-0,1649963	5,98675908	2,63006161	-0,7472972	-2,780708	0,95765324	-0,0720753	0,03277427	0,26434329	5,28773761	5,85561208	-7,8325571	8,3654922	-3,1467171
6,58386478	2,91860471	-1,8893686	-0,6134146	4,19148689	0,57143345	-0,0347632	0,01709373	8,29497505	2,83007931	3,64818352	-8,0235078	-0,1218252	-4,9723272
4,91370752	-0,6469055	1,30963851	-0,2419771	5,38038235	0,50557543	-0,0284008	0,01441989	4,47551218	-0,9070316	-4,7133776	-3,2700874	-4,2208568	2,71356473
-5,5782346	-0,3069217	-1,7790499	-1,0507874	-4,1103875	1,0313099	-0,0791911	0,03576473	-5,5945502	-1,0381565	-1,1486803	6,0608804	-0,2584177	0,72884933
5,22973202	-0,9112429	-1,5213297	-0,4463519	6,24792485	0,45751853	-0,0237581	0,01246878	5,40912647	0,43461614	-0,553669	-5,6992487	-1,268578	0,0281436
3,37076792	2,75795765	-1,9311041	-0,7719517	2,44453764	0,66820447	-0,0441121	0,02102264	3,27265322	3,70045738	0,91073901	-3,269083	1,40522657	-2,0502672
-3,5580418	6,35941998	17,337478	0,27895005	-13,215694	1,53569189	-0,1279186	0,05624266	-11,268955	10,7527878	-4,8153833	-1,4270882	16,0346606	9,6086143
8,01262447	-1,6658287	-1,3935736	-0,2534825	8,87968484	0,31173405	-0,0096741	0,00654992	8,49983365	-0,03252	-0,5396349	-7,3773562	-3,896436	-1,6393004
-2,3762935	8,62196975	-1,5565268	-1,3484185	-5,7445264	1,12183186	-0,0879363	0,03943993	-3,0728613	8,37434434	3,20260134	3,59401968	4,54304187	-6,8262937
8,35248005	-0,6176761	0,13096905	-0,1660502	7,97903188	0,36162508	-0,014494	0,0085755	8,1679407	0,39740699	-4,4768376	-5,4857471	-4,9274998	1,54037294
-1,7861627	1,60513727	0,71175999	-0,7537434	-1,2405423	0,87233686	-0,063833	0,02931042	-1,7440638	1,25827063	1,98380342	-2,7803458	5,55796498	1,83004594
2,77064658	5,30719156	-1,5852781	-0,910676	0,15186615	0,79520538	-0,0563815	0,02617888	2,4996655	6,01200512	1,83452354	-1,9179838	2,75858484	-3,7784089
-1,3245087	7,09558948	1,46831321	-0,9621804	-4,1119572	1,03139685	-0,0791995	0,03576826	-2,8428257	7,05241358	0,01549847	2,02420274	5,79191087	-0,596673
2,97608291	3,63391562	1,46501137	-0,5575639	1,26335025	0,7336355	-0,0504333	0,02367914	1,72920389	4,43935067	-2,4695405	-0,9032049	1,07214091	0,5955614
-7,2340621	-8,9475093	6,07578512	1,18706848	-7,5105754	0,22546205	-0,7713338	0,04564758	-8,1073102	-7,5908146	-2,1777599	8,74656592	-1,1012239	6,4020744

-1,7271819	-5,7647082	0,21372642	-0,3964866	-0,0586587	0,80686725	-0,0575081	0,02665235	-0,6303908	-6,3444559	-2,1824038	2,80774958	-5,4757698	2,22830758
5,56600743	-4,5815368	2,35545349	1,62494195	6,08153041	-0,7979131	-0,8819273	0,01568699	4,46097037	-1,2329571	-2,4510422	-4,5374642	-2,5191987	2,13460687
-7,7068453	7,66712962	-1,4572636	-1,5605234	-9,2782816	1,31758172	-0,1068474	0,04738738	-9,1549872	6,42116424	-1,0097626	9,94847115	3,33164794	-2,9290383
-1,036704	1,76849201	-0,3243856	-0,8102148	-0,5403373	0,8335495	-0,0600858	0,02773565	-1,5353992	0,8404545	-4,6106429	3,23471372	-3,3182407	0,67023022
-11,302514	2,36169803	-2,1562791	-1,5169173	-10,343905	1,37661117	-0,1125501	0,04978398	-11,669584	-0,8611503	-5,0432913	11,7338292	0,82429998	4,85126683
1,70012671	1,4504384	0,71283028	-0,5677342	1,93423263	-0,2528581	1,34922943	0,07990649	1,19271087	1,30367358	0,59858284	-1,9699001	1,36403884	-0,1538029
-2,0866165	-4,8596196	-1,2491411	-0,5846332	-0,2339747	0,81657876	-0,0584463	0,02704664	-1,2586283	-5,0292669	-1,3362076	3,18873964	-5,1768185	0,18687467
-0,0273393	0,1248268	-2,003748	2,91027141	1,15548659	-2,6836659	-1,5979794	0,05270903	0,14316673	1,01812171	1,54862643	0,39738623	-0,5104424	-3,2170981
-6,3886165	-4,1900243	-0,218001	-0,7542738	-4,5189147	1,05393997	-0,0813774	0,03668351	-5,6089264	-5,3062063	-1,0718814	7,19200428	-3,0693695	1,47723141
7,15477947	-4,4214485	5,2808913	0,40395884	4,77099378	0,53933208	-0,031662	0,01579041	4,71490181	-5,772674	-0,8044237	-6,2821811	-1,7725457	5,07221877
1,26149738	-1,0026175	-1,5838444	-0,6488016	2,80153539	-0,399085	1,49825782	0,08392721	2,26969332	-1,0650675	2,20170378	-1,5268457	-0,6089194	-1,6369692
-4,4437048	6,69292153	-3,0441156	6,0477744	-5,1588209	-8,217109	0,29517281	0,24138965	-5,636017	5,41827781	5,18122237	3,34610571	8,27744838	-3,1541939
-3,4794266	0,36850176	-1,8102644	-0,9826952	-2,2071053	-0,1306524	1,48471485	0,09574012	-3,4706376	0,005611	0,33656465	4,03038969	-0,3104899	-1,5021627
1,72290031	3,52475628	-2,1104397	0,02655316	1,05308226	-1,7050956	1,89166001	0,12791816	0,49579292	3,29187548	-0,9002083	0,10531111	0,58550068	-1,079981
-0,8316387	2,32540008	-2,1345193	1,29251672	-0,558728	-1,7089008	-0,3396026	0,07288182	0,6176845	1,71316916	5,01669492	-5,3791413	6,11741365	-0,9548248
8,08425042	-0,2536777	-1,6688786	1,39717009	7,77165139	-1,0642793	-0,9899815	0,01227436	8,00470374	1,75596287	-0,934156	-6,034102	-3,2777458	-2,0881898
2,22446598	5,2566633	-2,3415857	0,77017631	-0,1413943	-0,6449181	-1,0451922	0,03011356	1,11480402	6,01694985	-1,5766487	1,32519997	-0,6984056	-3,8413588
-0,7450635	1,39586346	-0,0683	1,89073583	-0,0527685	-2,1361826	-0,4090156	0,07805374	-1,2265888	1,39940501	-0,2478676	1,66206819	-0,0008082	-1,2225015
-4,4090843	-3,2631186	-1,5742976	0,76570308	-2,3552698	-1,2022876	0,26725489	-1,9726256	-3,7260806	-4,7661753	-2,4118377	5,3563825	-4,3697247	1,49811362
-3,4422289	-0,1823163	0,58729061	-0,7525019	-2,0432947	-0,3741183	1,83028464	0,10962689	-3,6233055	-1,2423398	-0,9878951	4,12780867	-0,699322	0,69646796
-11,492452	-1,5895891	-0,6168803	2,51949117	-9,662528	-2,8377848	-0,5238537	0,12351488	-11,024898	-3,1082396	1,52715846	11,8774231	0,46772071	-0,894917
2,47317714	0,00520362	-1,7101616	-0,0563801	3,40914026	0,12462435	-0,37121	0,0199555	4,58660985	-0,5615388	3,92759533	-4,550038	1,1984292	-1,5774704

Table S3. Fish composition in each FPZ by basin. SSC, Sinuous Single Channel; BGDS, Braided Gentle Downstream Slope.

Order	**Family**	**Species**	**Maipo**		**Rapel**		**Mataquito**		**Maule**		**Itata**		**Biobío**		**Imperial**		**Toltén**	
			SSC	**BGDS**	**SSC**	**BGDS**	**SSC**	**BGDS**	**SSC**	**BGDS**	**SSC**	**BGDS**	**SSC**	**BGDS**	**SSC**	**BGDS**	**SSC**	**BGDS**
Native species																		
Atheriniformes	Atherinopsidae	*Basilichthys microlepidotus*	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1
Centrarchiformes	Perciliidae	*Percilia gillissi*	0	0	1	1	1	1	1	1	1	1	0	0	1	1	0	0
		Percilia irwini	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Characiformes	Characidae	*Cheirodon australe*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
		Cheirodon galusdae	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0
		Cheirodon pisciculus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Osmeriformes	Galaxiidae	*Aplochiton taeniatus*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
		Galaxias maculatus	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
Perciformes	Percichthyidae	*Percichthys trucha*	0	1	0	1	1	1	0	0	1	1	1	1	0	1	0	1
Petromyzontiformes	Geotriidae	*Geotria australis*	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	1
Siluriformes	Diplomystidae	*Diplomystes camposensis*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
		Diplomystes incognitus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
		Diplomystes arratie	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
	Trichomycteridae	*Bullockia maldonadoi*	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1
		Trichomycterus areolatus	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1
Non-native species																		
Cypriniformes	Cyprinidae	*Cyprinus carpio*	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Cyprinodontiformes	Poeciliidae	*Cnesterodon decemmaculatus*	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
		Gambusia holbrooki	0	0	1	1	0	1	1	1	1	1	0	0	0	0	0	0
Salmoniformes	Salmonidae	*Oncorhynchus mykiss*	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1
		Salmo trutta	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1

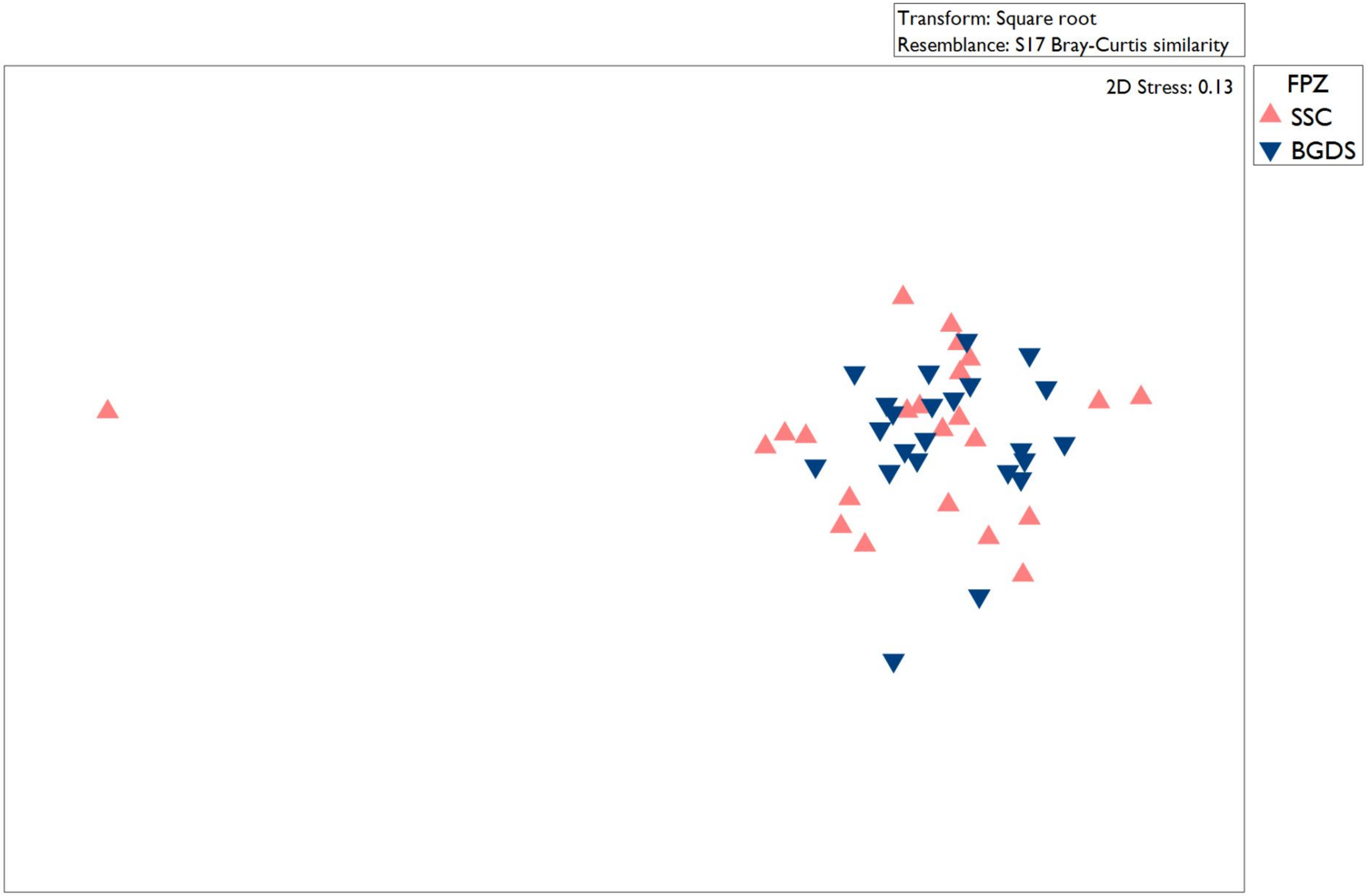


Fig. S1. Non-metric multidimensional scaling (NMDS) based on the Bray-Curtis dissimilarity matrix of fish abundance at each sampling site. SSC, Sinuous Single Channel FPZ; BGDS, Braided Gentle Downstream Slope FPZ.

Table S4. Canonical Principal Coordinate Analysis (CAP) on fish abundance data in Basin-FPZ. SSC, Sinuous Single Channel; BGDS, Braided Gentle Downstream Slope.

Original Group	Maipo		Rapel		Mataquito		Maule		Itata		Biobío		Imperial		Toltén		Total	% Correct
	SSC	BGDS	SSC	BGDS	SSC	BGDS	SSC	BGDS	SSC	BGDS	SSC	BGDS	SSC	BGDS	SSC	BGDS		
Maipo-SSC	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	3	66.67
Maipo-BGDS	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	100.00
Rapel-SSC	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	3	66.67
Rapel-BGDS	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	3	33.33
Mataquito-SSC	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	3	66.67
Mataquito-BGDS	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	3	0.00
Maule-SSC	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	3	0.00
Maule-BGDS	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	2	50.00
Itata-SSC	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	3	100.00
Itata-BGDS	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	3	100.00
Biobío-SSC	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	3	0.00
Biobío-BGDS	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	3	0.00
Imperial-SSC	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	3	66.67
Imperial-BGDS	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	3	66.67
Toltén-SSC	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	2	50.00
Toltén-BGDS	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	3	33.33

Mis-classification error: 50%

Table S5. ANOVA results for Richness, Shannon Diversity Index, Trophic Guilds, Migratory Life History, Multiple Spawning, Richness by Taxonomic order, Shannon Diversity Index by Taxonomic Order, Vertical Position, Velocity Preference.

RESOURCES MECHANISM	**Df**	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
Richness					
Basin	7	81.54	11.648	5.284	0.000282
Residuals	38	83.77	2.204		
Shannon Diversity Index					
Basin	7	0.5297	0.07567	2.98	0.0136
Residuals	38	0.9651	0.02540		
Trophic Guilds					
Basin	7	289	41.29	1.559	0.178
Residuals	38	1006	26.49		
RECRUITMENT MECHANISM	**Df**	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
Migratory Life History					
Basin	7	197.1	28.16	0.915	0.506
Residuals	38	1170.9	30.81		
Multiple Spawning					
Basin	7	3.380	0.4829	6.177	0.0000797
Residuals	37	2.892	0.0782		
REFUGIA MECHANISM	**Df**	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
Richness by taxonomic order					
Basin	7	43.81	6.259	3.541	0.00503
Residuals	38	67.17	1.768		
Shannon by taxonomic order					
Basin	7	0.3980	0.05686	2.345	0.043
Residuals	38	0.9214	0.02425		
Vertical position					
Basin	7	298.8	42.69	1.523	0.189
Residuals	38	1065.1	28.03		
Velocity preference					
Basin	7	531.4	75.91	2.984	0.0135
Residuals	38	966.6	25.44		

Table S6. Kruskal-Wallis results for Abundance, Pielou Evenness Index, Floodplain Use, Abundance Weighted Average Size, Rapid Sexual Maturity, High Fecundity, Small Egg Size, Parental Care and Pielou by Taxonomic Order.

RESOURCES MECHANISM	**chi-squared**	**df**	**p-value**
Abundance	16.888	7	0.01813
Pielou Evenness Index	30.509	7	0.8803
Floodplain Use	42.598	7	0.7494
RECRUITMENT MECHANISM	**chi-squared**	**df**	**p-value**
Abundance Weighted Average Size	24.641	7	0.0008784
Rapid Sexual Maturity	20.374	7	0.004815
High Fecundity	21.502	7	0.003094
Small Egg Size	15.264	7	0.03276
Parental Care	18.024	7	0.01186
REFUGIA MECHANISM	**chi-squared**	**df**	**p-value**
Pielou by taxonomic order	23.511	7	0.9379

Table S7. PERMANOVA results for Beta Diversity (Sørensen) and Beta Diversity (Bray-Curtis).

Beta Diversity (Sørensen)		
DEVIATIONS FROM CENTROID		
F: 2.8644	df1: 7	df2: 38
P(perm): 0.0819		
Number of permutations: 9999		
PAIRWISE	COMPARISONS	
Groups	t	P(perm)
(Maipo,Rapel)	0.37476	0.6751
(Maipo,Mataquito)	2.5285	0.0044
(Maipo,Maule)	2.6819	0.0773
(Maipo,Itata)	2.128	0.0545
(Maipo,Biobío)	1.0476	0.5401
(Maipo,Imperial)	2.1735	0.066
(Maipo,Toltén)	1.7066	0.2495
(Rapel,Mataquito)	2.2304	0.0183
(Rapel,Maule)	2.4438	0.0539
(Rapel,Itata)	1.7935	0.1543
(Rapel,Biobío)	0.63404	0.6263
(Rapel,Imperial)	1.8536	0.1579
(Rapel,Toltén)	1.4143	0.2377
(Mataquito,Maule)	0.69599	0.6262
(Mataquito,Itata)	0.82231	0.4673
(Mataquito,Biobío)	2.4856	0.0229
(Mataquito,Imperial)	0.44421	0.6698
(Mataquito,Toltén)	0.5135	0.6322
(Maule,Itata)	1.4631	0.1749

(Maule,Biobío)	2.8726	0.0483
(Maule,Imperial)	1.0339	0.4737
(Maule,Toltén)	0.94753	0.3865
(Itata,Biobío)	1.8557	0.0668
(Itata,Imperial)	0.27417	0.7579
(Itata,Toltén)	0.0229	0.9912
(Biobío,Imperial)	1.8439	0.1146
(Biobío,Toltén)	1.2341	0.3588
(Imperial,Toltén)	0.16579	0.8718
Beta Diversity (Bray-Curtis)		
DEVIATIONS FROM CENTROID		
F: 2.3564	df1: 7	df2: 38
P(perm): 0.1855		
Number of permutations: 9999		

Table S8. Post-hoc Tukey test results for Richness, Shannon Diversity Index, Multiple Spawning, Richness by Taxonomic Order, Shannon Diversity Index by Taxonomic Order, Velocity Preference.

Richness	diff	lwr	upr	p adj
Rapel-Maipo	1,83333333	-0,914396773	4,58106344	0,409919761
Mataquito-Maipo	2,00000000	-0,747730106	4,747730106	0,302987667
Maule-Maipo	2,20000000	-0,681843648	5,081843648	0,249036036
Itata-Maipo	2,66666667	-0,08106344	5,414396773	0,062592901
Biobío-Maipo	3,00000000	0,252269894	5,747730106	0,023985648
Imperial-Maipo	3,00000000	0,252269894	5,747730106	0,023985648
Toltén-Maipo	5,20000000	2,318156352	8,081843648	2,90288E-05
Mataquito-Rapel	0,16666667	-2,58106344	2,914396773	0,999999349
Maule-Rapel	0,36666667	-2,515176981	3,248510315	0,999895694
Itata-Rapel	0,83333333	-1,914396773	3,58106344	0,975717510
Biobío-Rapel	1,16666667	-1,58106344	3,914396773	0,868746788
Imperial-Rapel	1,16666667	-1,58106344	3,914396773	0,868746788
Toltén-Rapel	3,36666667	0,484823019	6,248510315	0,012558961
Maule-Mataquito	0,20000000	-2,681843648	3,081843648	0,999998345
Itata-Mataquito	0,66666667	-2,08106344	3,414396773	0,993339667
Biobío-Mataquito	1,00000000	-1,747730106	3,747730106	0,936465235
Imperial-Mataquito	1,00000000	-1,747730106	3,747730106	0,936465235
Toltén-Mataquito	3,20000000	0,318156352	6,081843648	0,020548766
Itata-Maule	0,46666667	-2,415176981	3,348510315	0,999482652
Biobío-Maule	0,80000000	-2,081843648	3,681843648	0,985267508
Imperial-Maule	0,80000000	-2,081843648	3,681843648	0,985267508
Toltén-Maule	3,00000000	-0,009987522	6,009987522	0,051294486
Biobío-Itata	0,33333333	-2,414396773	3,08106344	0,999924317
Imperial-Itata	0,33333333	-2,414396773	3,08106344	0,999924317
Toltén-Itata	2,53333333	-0,348510315	5,415176981	0,120537170
Imperial-Biobío	8,88178E-16	-2,747730106	2,747730106	1,000000000
Toltén-Biobío	2,20000000	-0,681843648	5,081843648	0,249036036
Toltén-Imperial	2,20000000	-0,681843648	5,081843648	0,249036036
Shannon Diversity Index	diff	lwr	upr	p adj
Rapel-Maipo	0,211666667	-0,083259539	0,506592872	0,319689553
Itata-Maipo	0,238333333	-0,056592872	0,533259539	0,190985881
Mataquito-Maipo	0,241666667	-0,053259539	0,536592872	0,178037126
Maule-Maipo	0,261666667	-0,047654547	0,57098788	0,150282649
Biobío-Maipo	0,276666667	-0,018259539	0,571592872	0,079543721

Imperial-Maipo	0,3	0,005073795	0,594926205	0,043743191
Toltén-Maipo	0,411666667	0,102345453	0,72098788	0,002915059
Itata-Rapel	0,026666667	-0,268259539	0,321592872	0,99998976
Mataquito-Rapel	0,03	-0,264926205	0,324926205	0,999977086
Maule-Rapel	0,05	-0,259321214	0,359321214	0,999488672
Biobío-Rapel	0,065	-0,229926205	0,359926205	0,99629725
Imperial-Rapel	0,088333333	-0,206592872	0,383259539	0,977347397
Toltén-Rapel	0,2	-0,109321214	0,509321214	0,449866584
Mataquito-Itata	0,003333333	-0,291592872	0,298259539	1
Maule-Itata	0,023333333	-0,28598788	0,332654547	0,999997056
Biobío-Itata	0,038333333	-0,256592872	0,333259539	0,99987964
Imperial-Itata	0,061666667	-0,233259539	0,356592872	0,997332084
Toltén-Itata	0,173333333	-0,13598788	0,482654547	0,626296555
Maule-Mataquito	0,02	-0,289321214	0,329321214	0,999998986
Biobío-Mataquito	0,035	-0,259926205	0,329926205	0,999934755
Imperial-Mataquito	0,058333333	-0,236592872	0,353259539	0,998120302
Toltén-Mataquito	0,17	-0,139321214	0,479321214	0,648373261
Biobío-Maule	0,015	-0,294321214	0,324321214	0,999999862
Imperial-Maule	0,038333333	-0,27098788	0,347654547	0,99991262
Toltén-Maule	0,15	-0,173075471	0,473075471	0,80872879
Imperial-Biobío	0,023333333	-0,271592872	0,318259539	0,99999591
Toltén-Biobío	0,135	-0,174321214	0,444321214	0,852065565
Toltén-Imperial	0,111666667	-0,197654547	0,42098788	0,938984382
Multiple Spawning	diff	lwr	upr	p adj
Toltén-Maipo	0,11356	-0,454125215	0,681245215	0,997952569
Itata-Maipo	0,237833333	-0,30568388	0,781350547	0,849278862
Biobío-Maipo	0,260066667	-0,283450547	0,80358388	0,783208445
Imperial-Maipo	0,5421	-0,001417214	1,085617214	0,051011069
Rapel-Maipo	0,6609	0,117382786	1,204417214	0,008340763
Mataquito-Maipo	0,6843	0,140782786	1,227817214	0,005688748
Maule-Maipo	0,82484	0,257154785	1,392525215	0,00094409
Itata-Toltén	0,124273333	-0,41924388	0,667790547	0,99529495
Biobío-Toltén	0,146506667	-0,397010547	0,69002388	0,98742146
Imperial-Toltén	0,42854	-0,114977214	0,972057214	0,214408899
Rapel-Toltén	0,54734	0,003822786	1,090857214	0,047361088
Mataquito-Toltén	0,57074	0,027222786	1,114257214	0,033754901
Maule-Toltén	0,71128	0,143594785	1,278965215	0,006006806
Biobío-Itata	0,022233333	-0,495989996	0,540456663	0,99999994

Imperial-Itata	0,304266667	-0,213956663	0,822489996	0,56926972
Rapel-Itata	0,423066667	-0,095156663	0,941289996	0,18085593
Mataquito-Itata	0,446466667	-0,071756663	0,964689996	0,135245496
Maule-Itata	0,587006667	0,043489453	1,13052388	0,026502042
Imperial-Biobío	0,282033333	-0,236189996	0,800256663	0,657641652
Rapel-Biobío	0,400833333	-0,117389996	0,919056663	0,234167087
Mataquito-Biobío	0,424233333	-0,093989996	0,942456663	0,178333259
Maule-Biobío	0,564773333	0,02125612	1,108290547	0,036839026
Rapel-Imperial	0,1188	-0,39942333	0,63702333	0,995219085
Mataquito-Imperial	0,1422	-0,37602333	0,66042333	0,986054008
Maule-Imperial	0,28274	-0,260777214	0,826257214	0,705579645
Mataquito-Rapel	0,0234	-0,49482333	0,54162333	0,999999915
Maule-Rapel	0,16394	-0,379577214	0,707457214	0,976174968
Maule-Mataquito	0,14054	-0,402977214	0,684057214	0,990139539
Richness by taxonomic order	diff	lwr	upr	p adj
Rapel-Maipo	1,166666667	-1,293787918	3,627121251	0,792067687
Mataquito-Maipo	2,000000000	-0,460454585	4,460454585	0,185465011
Maule-Maipo	2,200000000	-0,380546539	4,780546539	0,143938516
Biobío-Maipo	2,500000000	0,039545415	4,960454585	0,044132018
Imperial-Maipo	2,500000000	0,039545415	4,960454585	0,044132018
Itata-Maipo	2,666666667	0,206212082	5,127121251	0,025621488
Toltén-Maipo	3,400000000	0,819453461	5,980546539	0,003297153
Mataquito-Rapel	0,833333333	-1,627121251	3,293787918	0,955992432
Maule-Rapel	1,033333333	-1,547213206	3,613879872	0,899308668
Biobío-Rapel	1,333333333	-1,127121251	3,793787918	0,663976589
Imperial-Rapel	1,333333333	-1,127121251	3,793787918	0,663976589
Itata-Rapel	1,500000000	-0,960454585	3,960454585	0,524400793
Toltén-Rapel	2,233333333	-0,347213206	4,813879872	0,132128921
Maule-Mataquito	0,200000000	-2,380546539	2,780546539	0,999996452
Biobío-Mataquito	0,500000000	-1,960454585	2,960454585	0,997769699
Imperial-Mataquito	0,500000000	-1,960454585	2,960454585	0,997769699
Itata-Mataquito	0,666666667	-1,793787918	3,127121251	0,987193457
Toltén-Mataquito	1,400000000	-1,180546539	3,980546539	0,662732142
Biobío-Maule	0,300000000	-2,280546539	2,880546539	0,999943234
Imperial-Maule	0,300000000	-2,280546539	2,880546539	0,999943234
Itata-Maule	0,466666667	-2,113879872	3,047213206	0,998939765
Toltén-Maule	1,200000000	-1,495292955	3,895292955	0,839008148
Imperial-Biobío	0,000000000	-2,460454585	2,460454585	1,000000000

Itata-Biobío	0,166666667	-2,293787918	2,627121251	0,999998600
Toltén-Biobío	0,900000000	-1,680546539	3,480546539	0,948782613
Itata-Imperial	0,166666667	-2,293787918	2,627121251	0,999998600
Toltén-Imperial	0,900000000	-1,680546539	3,480546539	0,948782613
Toltén-Itata	0,733333333	-1,847213206	3,313879872	0,983153376
Shannon diversity index by taxonomic order	diff	lwr	upr	p adj
Rapel-Maipo	0,130546568	-0,157640066	0,418733202	0,826975516
Itata-Maipo	0,239468323	-0,04871831	0,527654957	0,16552013
Mataquito-Maipo	0,242111765	-0,046074869	0,530298399	0,15605976
Biobío-Maipo	0,250799515	-0,037387118	0,538986149	0,127928735
Maule-Maipo	0,263365193	-0,038887498	0,565617884	0,127007821
Imperial-Maipo	0,272988694	-0,01519794	0,561175327	0,074384014
Toltén-Maipo	0,295083119	-0,007169573	0,59733581	0,059925677
Itata-Rapel	0,108921755	-0,179264878	0,397108389	0,923470775
Mataquito-Rapel	0,111565197	-0,176621437	0,399751831	0,914108726
Biobío-Rapel	0,120252947	-0,167933686	0,408439581	0,878500393
Maule-Rapel	0,132818625	-0,169434066	0,435071316	0,847685194
Imperial-Rapel	0,142442126	-0,145744508	0,430628759	0,756327318
Toltén-Rapel	0,164536551	-0,137716141	0,466789242	0,658992335
Mataquito-Itata	0,002643442	-0,285543192	0,290830075	1,000000000
Biobío-Itata	0,011331192	-0,276855442	0,299517826	0,999999968
Maule-Itata	0,02389687	-0,278355822	0,326149561	0,999995929
Imperial-Itata	0,03352037	-0,254666263	0,321707004	0,999943035
Toltén-Itata	0,055614795	-0,246637896	0,357867487	0,998814748
Biobío-Mataquito	0,00868775	-0,279498883	0,296874384	0,999999995
Maule-Mataquito	0,021253428	-0,280999263	0,323506119	0,999998187
Imperial-Mataquito	0,030876929	-0,257309705	0,319063562	0,999967366
Toltén-Mataquito	0,052971354	-0,249281338	0,355224045	0,999134223
Maule-Biobío	0,012565678	-0,289687014	0,314818369	0,999999953
Imperial-Biobío	0,022189178	-0,265997455	0,310375812	0,999996609
Toltén-Biobío	0,044283603	-0,257969088	0,346536295	0,999732489
Imperial-Maule	0,009623501	-0,292629191	0,311876192	0,999999993
Toltén-Maule	0,031717926	-0,283974715	0,347410566	0,999978938
Toltén-Imperial	0,022094425	-0,280158266	0,324347116	0,99999763
Velocity preference	diff	lwr	upr	p adj
Imperial-Biobío	-0,600906677	-9,934544429	8,732731075	0,999999015
Itata-Biobío	5,155777022	-4,177860731	14,48941477	0,642664721
Maipo-Biobío	1,083527224	-8,250110528	10,41716498	0,99994378

Mataquito-Biobío	-1,519513205	-10,85315096	7,814124547	0,999464261
Maule-Biobío	-1,979149636	-11,7683515	7,810052223	0,997840554
Rapel-Biobío	-6,686515209	-16,02015296	2,647122543	0,321868771
Toltén-Biobío	3,528195015	-6,261006845	13,31739687	0,939481999
Itata-Imperial	5,756683699	-3,576954053	15,09032145	0,509798103
Maipo-Imperial	1,684433901	-7,649203851	11,01807165	0,998953704
Mataquito-Imperial	-0,918606528	-10,25224428	8,415031224	0,999981706
Maule-Imperial	-1,378242959	-11,16744482	8,410958901	0,999794669
Rapel-Imperial	-6,085608532	-15,41924628	3,24802922	0,439212514
Toltén-Imperial	4,129101692	-5,660100168	13,91830355	0,872517089
Maipo-Itata	-4,072249798	-13,40588755	5,261387955	0,852270868
Mataquito-Itata	-6,675290227	-16,00892798	2,658347525	0,323885232
Maule-Itata	-7,134926658	-16,92412852	2,654275202	0,301403023
Rapel-Itata	-11,84229223	-21,17592998	-2,508654479	0,005150614
Toltén-Itata	-1,627582007	-11,41678387	8,161619853	0,999385249
Mataquito-Maipo	-2,60304043	-11,93667818	6,730597323	0,98487025
Maule-Maipo	-3,062676861	-12,85187872	6,726524999	0,971190191
Rapel-Maipo	-7,770042433	-17,10368019	1,563595319	0,163913459
Toltén-Maipo	2,444667791	-7,344534069	12,23386965	0,992079943
Maule-Mataquito	-0,459636431	-10,24883829	9,329565429	0,99999989
Rapel-Mataquito	-5,167002004	-14,50063976	4,166635748	0,64020487
Toltén-Mataquito	5,04770822	-4,74149364	14,83691008	0,716013956
Rapel-Maule	-4,707365573	-14,49656743	5,081836287	0,780407368
Toltén-Maule	5,507344651	-4,71714323	15,73183253	0,670557506
Toltén-Rapel	10,21471022	0,425508364	20,00391208	0,035538045

Table S9. Post-hoc Dunn test results for Abundance, Abundance Weighted Average Size, Rapid Sexual Maturity, High Fecundity, Small Egg Size and Parental Care.

Abundance	Z	P.unadj	P.adj
Biobío - Imperial	-1,16175159	0,245336385	1,000000
Biobío - Itata	-1,15099463	0,249734446	1,000000
Imperial - Itata	0,01075696	0,991417354	1,000000
Biobío - Maipo	2,07609311	0,03788534	1,000000
Imperial - Maipo	3,2378447	0,001204364	0,033722
Itata - Maipo	3,22708774	0,001250571	0,035016
Biobío - Mataquito	0,02151392	0,982835701	1,000000
Imperial - Mataquito	1,1832655	0,236703939	1,000000
Itata - Mataquito	1,17250855	0,240992943	1,000000
Maipo - Mataquito	-2,05457919	0,039919667	1,000000
Biobío - Maule	-0,70563744	0,480413636	1,000000
Imperial - Maule	0,40204924	0,68764779	1,000000
Itata - Maule	0,39179288	0,695211256	1,000000
Maipo - Maule	-2,68511455	0,007250495	0,203014
Mataquito - Maule	-0,72615015	0,467746725	1,000000
Biobío - Rapel	0,44103532	0,659187424	1,000000
Imperial - Rapel	1,60278691	0,108981708	1,000000
Itata - Rapel	1,59202995	0,111377975	1,000000
Maipo - Rapel	-1,63505779	0,102036934	1,000000
Mataquito - Rapel	0,41952141	0,674835114	1,000000
Maule - Rapel	1,12614812	0,260102829	1,000000
Biobío - Toltén	-1,0625587	0,287982125	1,000000
Imperial - Toltén	0,04512798	0,964005303	1,000000
Itata - Toltén	0,03487162	0,972182113	1,000000
Maipo - Toltén	-3,04203582	0,002349839	0,065796
Mataquito - Toltén	-1,08307142	0,278776725	1,000000
Maule - Toltén	-0,34172609	0,732557035	1,000000
Rapel - Toltén	-1,48306938	0,138055978	1,000000
Abundance Weighted Average Size	Z	P.unadj	P.adj
Biobío - Imperial	0,00000000	1,00000000	1,00000000
Biobío - Itata	-0,1098967	0,912491264	1,0000000
Imperial - Itata	-0,1098967	0,912491264	1,0000000
Biobío - Maipo	-0,6496511	0,515917617	1,0000000
Imperial - Maipo	-0,6496511	0,515917617	1,0000000
Itata - Maipo	-0,5448687	0,585843849	1,0000000

Biobío - Mataquito	1,3187609	0,187249044	1,0000000
Imperial - Mataquito	1,3187609	0,187249044	1,0000000
Itata - Mataquito	1,4286577	0,153102644	1,0000000
Maipo - Mataquito	1,9070403	0,056515366	1,0000000
Biobío - Maule	2,3932308	0,016700731	0,4676205
Imperial - Maule	2,3932308	0,016700731	0,4676205
Itata - Maule	2,4980133	0,012489152	0,3496963
Maipo - Maule	2,9133376	0,003575877	0,1001246
Mataquito - Maule	1,1358416	0,256022863	1,0000000
Biobío - Rapel	2,7254393	0,006421599	0,1798048
Imperial - Rapel	2,7254393	0,006421599	0,1798048
Itata - Rapel	2,835336	0,004577751	0,1281770
Maipo - Rapel	3,2482555	0,00116115	0,0325122
Mataquito - Rapel	1,4066783	0,15952279	1,0000000
Maule - Rapel	0,2053736	0,837280265	1,0000000
Biobío - Toltén	-0,77539	0,438109229	1,0000000
Imperial - Toltén	-0,77539	0,438109229	1,0000000
Itata - Toltén	-0,6706076	0,502470548	1,0000000
Maipo - Toltén	-0,1203859	0,904177498	1,0000000
Mataquito - Toltén	-2,0327793	0,04207483	1,0000000
Maule - Toltén	-3,0337235	0,002415557	0,0676356
Rapel - Toltén	-3,3739944	0,000740859	0,0207440
Rapid Sexual Maturity	Z	P.unadj	P.adj
Biobío - Imperial	0,7158368	0,474092111	1,00000000
Biobío - Itata	-1,049894	0,293766846	1,00000000
Imperial - Itata	-1,7657308	0,077441017	1,00000000
Biobío - Maipo	-0,1638057	0,869884127	1,00000000
Imperial - Maipo	-0,8463293	0,397369064	1,00000000
Itata - Maipo	0,837229	0,402463865	1,00000000
Biobío - Mataquito	-1,3242981	0,185404053	1,00000000
Imperial - Mataquito	-2,040135	0,041336886	1,00000000
Itata - Mataquito	-0,2744041	0,78377408	1,00000000
Maipo - Mataquito	-1,098863	0,271827806	1,00000000
Biobío - Maule	-1,9110662	0,055996078	1,00000000
Imperial - Maule	-2,5935898	0,009497973	0,26594325
Itata - Maule	-0,9100315	0,362805892	1,00000000
Maipo - Maule	-1,6728746	0,094351992	1,00000000
Mataquito - Maule	-0,6483975	0,516727919	1,00000000

Biobío - Rapel	-1,7060778	0,087993602	1,00000000
Imperial - Rapel	-2,4219146	0,015438979	0,43229140
Itata - Rapel	-0,6561838	0,511705899	1,00000000
Maipo - Rapel	-1,4628757	0,143501407	1,00000000
Mataquito - Rapel	-0,3817796	0,702624822	1,00000000
Maule - Rapel	0,2843848	0,77611547	1,00000000
Biobío - Toltén	1,6244062	0,104289135	1,00000000
Imperial - Toltén	0,9418826	0,346252743	1,00000000
Itata - Toltén	2,6254409	0,008653683	0,24230312
Maipo - Toltén	1,7120826	0,086881454	1,00000000
Mataquito - Toltén	2,887075	0,003888416	0,10887564
Maule - Toltén	3,3849571	0,000711894	0,01993302
Rapel - Toltén	3,2510876	0,001149644	0,03219004
High Fecundity	Z	P.unadj	P.adj
Biobío - Imperial	-1,65292844	0,098345429	1,0000000
Biobío - Itata	-1,25937405	0,207895259	1,0000000
Imperial - Itata	0,39355439	0,693910061	1,0000000
Biobío - Maipo	-2,64811796	0,008094128	0,2266356
Imperial - Maipo	-1,07211253	0,283669489	1,0000000
Itata - Maipo	-1,44735192	0,147798384	1,0000000
Biobío - Mataquito	-2,05772724	0,039616324	1,0000000
Imperial - Mataquito	-0,4047988	0,685625411	1,0000000
Itata - Mataquito	-0,79835319	0,424665559	1,0000000
Maipo - Mataquito	0,68615202	0,492617249	1,0000000
Biobío - Maule	0,14366308	0,885766527	1,0000000
Imperial - Maule	1,71966851	0,085492716	1,0000000
Itata - Maule	1,34442912	0,178809663	1,0000000
Maipo - Maule	2,67292685	0,007519265	0,2105394
Mataquito - Maule	2,10562902	0,03523659	0,9866245
Biobío - Rapel	0,88830848	0,37437484	1,0000000
Imperial - Rapel	2,54123691	0,011046104	0,3092909
Itata - Rapel	2,14768253	0,031738985	0,8886916
Maipo - Rapel	3,49508686	0,000473908	0,0132694
Mataquito - Rapel	2,94603572	0,003218752	0,0901251
Maule - Rapel	0,70330582	0,481865183	1,0000000
Biobío - Toltén	0,13079773	0,895935319	1,0000000
Imperial - Toltén	1,70680316	0,087858646	1,0000000
Itata - Toltén	1,33156377	0,183003578	1,0000000

Maipo - Toltén	2,66060921	0,007799943	0,2183984
Mataquito - Toltén	2,09276367	0,036370257	1,0000000
Maule - Toltén	-0,01231764	0,990172198	1,0000000
Rapel - Toltén	-0,71617117	0,473885661	1,0000000
Small Egg Size	Z	P.unadj	P.adj
Biobío - Imperial	-0,06719131	0,9464294	1,00000000
Biobío - Itata	-0,43674354	0,662297348	1,00000000
Imperial - Itata	-0,36955223	0,711716152	1,00000000
Biobío - Maipo	0,07687729	0,938721168	1,00000000
Imperial - Maipo	0,14094169	0,887916007	1,00000000
Itata - Maipo	0,49329591	0,621803516	1,00000000
Biobío - Mataquito	-1,57899588	0,114337002	1,00000000
Imperial - Mataquito	-1,51180457	0,130583587	1,00000000
Itata - Mataquito	-1,14225234	0,253349146	1,00000000
Maipo - Mataquito	-1,58239079	0,113560387	1,00000000
Biobío - Maule	0,3331349	0,739032454	1,00000000
Imperial - Maule	0,39719931	0,691220494	1,00000000
Itata - Maule	0,74955353	0,453523647	1,00000000
Maipo - Maule	0,24534799	0,806186997	1,00000000
Mataquito - Maule	1,8386484	0,065966917	1,00000000
Biobío - Rapel	0,85108998	0,394719372	1,00000000
Imperial - Rapel	0,91828129	0,358471619	1,00000000
Itata - Rapel	1,28783352	0,197803921	1,00000000
Maipo - Rapel	0,73460517	0,462579989	1,00000000
Mataquito - Rapel	2,43008586	0,015095246	0,42266690
Maule - Rapel	0,47834755	0,632402857	1,00000000
Biobío - Toltén	2,15256398	0,031352962	0,87788293
Imperial - Toltén	2,21662839	0,026648496	0,74615789
Itata - Toltén	2,56898261	0,010199758	0,28559321
Maipo - Toltén	1,98731871	0,046887089	1,00000000
Mataquito - Toltén	3,65807748	0,000254114	0,00711520
Maule - Toltén	1,74197072	0,081513567	1,00000000
Rapel - Toltén	1,34108153	0,179893983	1,00000000
Parental Care	Z	P.unadj	P.adj
Biobío - Imperial	-1,7616003	0,07813686	1,0000000
Biobío - Itata	-1,0569602	0,290529772	1,0000000
Imperial - Itata	0,7046401	0,481034234	1,0000000
Biobío - Maipo	1,6376294	0,101499017	1,0000000

Imperial - Maipo	3,3172494	0,000909084	0,0254544
Itata - Maipo	2,6454014	0,008159406	0,2284634
Biobío - Mataquito	-0,9248401	0,35504907	1,0000000
Imperial - Mataquito	0,8367601	0,402727416	1,0000000
Itata - Mataquito	0,13212	0,894889362	1,0000000
Maipo - Mataquito	-2,5194299	0,011754504	0,3291261
Biobío - Maule	-2,1667097	0,030256994	0,8471958
Imperial - Maule	-0,4870898	0,626194706	1,0000000
Itata - Maule	-1,1589378	0,246481555	1,0000000
Maipo - Maule	-3,6423775	0,000270132	0,0075637
Mataquito - Maule	-1,2849093	0,198823995	1,0000000
Biobío - Rapel	-1,2771602	0,201545699	1,0000000
Imperial - Rapel	0,4844401	0,628073586	1,0000000
Itata - Rapel	-0,2202	0,825715371	1,0000000
Maipo - Rapel	-2,8553539	0,00429889	0,1203689
Mataquito - Rapel	-0,3523201	0,724598252	1,0000000
Maule - Rapel	0,9489853	0,342628104	1,0000000
Biobío - Toltén	-0,5290803	0,596749759	1,0000000
Imperial - Toltén	1,1505397	0,249921668	1,0000000
Itata - Toltén	0,4786917	0,632157983	1,0000000
Maipo - Toltén	-2,0744666	0,038035995	1,0000000
Mataquito - Toltén	0,3527202	0,724298223	1,0000000
Maule - Toltén	1,5679108	0,116901945	1,0000000
Rapel - Toltén	0,6886442	0,491047213	1,0000000

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