Metacommunity organization of tropical and Mediterranean temporary ponds
PhD Thesis Ángel Gálvez Núñez 2022

PhD Thesis

Doctoral Programme in Biodiversity and Evolutionary Biology
January 2022

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Organización de las metacomunidades de charcas temporales tropicales y mediterráneas

Ángel Gálvez Núñez

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Programa de Doctorado en Biodiversidad y Biología Evolutiva

January 2022
Enero de 2022

Tesis titulada **Metacommunity organization of tropical and Mediterranean temporary ponds** presentada por **Ángel Gálvez Núñez** para optar al título de doctor en Biodiversidad y Biología Evolutiva por la Universidad de Valencia.

Ángel Gálvez Núñez

Tesis dirigida por los doctores **Francesc Mesquita Joanes**, profesor titular del departamento de Microbiología y Ecología en la Universidad de Valencia; **Javier Armengol Díaz**, profesor titular del departamento de Microbiología y Ecología en la Universidad de Valencia; y **Andreu Castillo Escrivà**, investigador doctor contratado por la Universidad de Valencia, todos ellos adscritos al Instituto Cavanilles de Biodiversidad y Biología Evolutiva.

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Esta tesis ha sido financiada por un contrato de Formación de Personal Investigador (BES-2017-080022) concedido a Ángel Gálvez Núñez por el Ministerio de Economía, Industria y Competitividad, y por el proyecto de investigación METACOM-SET (CGL2016-78260-P), concedido a los doctores Francesc Mesquita Joanes y Javier Armengol Díaz como investigadores principales, por el Ministerio de Economía y Competitividad

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AGRADECIMIENTOS

Este sinuoso (y a veces tortuoso) camino, que empezó levantando piedras y acabó despedazando plancton, no habría sido posible sin la ayuda directa o indirecta de muchísima gente. Es por ello que agradezco a todas las personas que han contribuido a que esta tesis doctoral fuera completada.

En primer lugar, quisiera agradecer la dedicación, cercanía y confianza de mis tres directores de tesis: a Andreu Castillo, por su mano mágica en R y su aparición salvadora durante el tercer acto; a Javier Armengol, que me ha enseñado donde almorzar y todo lo que he necesitado de ese micromundo ~~infernal~~ espectacular que es el zooplancton; y a Paco Mesquita, por su infinita paciencia, ayudándome, corrigiendo versiones y más versiones de manuscritos, intentando (no sé si con éxito) que fuera menos escueto en mis correos. Sin el apoyo de los tres, todo esto habría sido imposible. Mención especial para Juan Monrós, con quien empecé en el mundillo de los anfibios y me encaminó hacia esta tesis.

En segundo lugar, he de agradecer a toda la gente que ha estado metida en este proyecto, sin cuyo trabajo no se puede entender todo lo que a continuación podrá leerse. Por tanto, muchas gracias a Juan Rueda con sus macroinvertebrados (y sus excepcionales fotos), a Eduardo García con los quironómidos, a Sanda Iepure con los copépodos, a Mati Segura con el fitoplancton y a Xavi Miralles y Antonio Picazo con los procariotas. Agradezco su contribución al resto de participantes en este proyecto, incluyendo a Carmen Rojo, María Sahuquillo, Antonio Camacho, Pedro Peres-Neto y Anne Magurran. Gracias también a la gente de Costa Rica: a Mahmood Sasa, por recibirme en el Clodomiro Picado durante casi dos meses excepcionales, y a Fabián Bonilla, por enseñarme de dónde crecen las piñas. He de agradecer a toda la gente de Valencia que ha participado en el trabajo de campo o de laboratorio, con una implicación más directa o menos, pero importantísima, en cualquier caso. Así que muchas gracias, en especial a Carla Olmo, por días de campo y revisiones, pero también a Álex Mestre, Iván Alambiaga, Berenice de Manuel, María Bisquert, Claudia Rodríguez, Fábio Martins, Maria Marinho y un largo etcétera de gente que ha pasado por el laboratorio de Ecología y Biogeografía de Sistemas Acuáticos, poniendo su granito de arena.

Finalmente, más allá de las colaboraciones puramente laborales, hacer una tesis podría hacerse muy cuesta arriba sin todas las personas que convierten el lugar de trabajo en un sitio donde dé gusto ir cada mañana. Así que gracias otra vez a mis directores de tesis, a todos mis compañeros de laboratorio e instituto, así como a la gente que me ha recibido durante las estancias y muestreos varios. Eso implica, además de los ya arriba mencionados, agradecer a Edgar Bernat (al que le agradezco más que esta tesis), Dani Morant, Eric Puche, Ana María Moreno, Rebeca Genís, Andrés López, Noemí Colinas, Cristina Arenas, Raquel Ortells, José Antonio Gil-Delgado, Javier Montero, Miguel Solano, Marco Reyes y toda la gente de la que me estoy olvidando.

Pero no todo en la vida es la tesis. Debo dar las gracias a todos los amigos que han estado ahí durante estos años, permitiendo que uno no pierda la cabeza entre nubes de nauplios y errores en los códigos de R. Gracias a todos los compañeros del campamento Timon, porque uno nunca debe dejar de levantar piedras. Gracias a Pit-roig, que ha evitado que pierda la poca cordura que me quedaba durante el tramo final del doctorado. Gracias a mis amigos de Alcublas, aunque en realidad la mitad son peroleros, y a mis amigos de Benicalap porque con ellos empezó todo. En especial, gracias a los que más cerca han estado durante este tiempo: a Vicent Gisbert, Ana Martínez, Sergio Orrios, Héctor Izquierdo, Javi Civera y otra vez a Edgar Bernat, Iván Alambiaga, Xavi Miralles, Carla Olmo, Claudia Rodríguez y María Bisquert. Finalmente, y más importante de todo, porque lo mejor se guarda para el final, muchas gracias a mi familia, por todo su cariño durante tantos años. A mi hermana, Laura y a mis padres, Aquilina y Ángel, porque sin su apoyo y esfuerzo durante todos estos años poco habría conseguido.

RESUMEN

El concepto de metacomunidad ofrece un marco teórico que permite explicar la distribución de los organismos, englobando procesos que actúan a diferentes escalas espaciales y temporales. La selección ambiental y la dispersión son procesos clave estructurando las metacomunidades, actuando con diferentes intensidades según los ecosistemas u organismos estudiados. Sin embargo, pocos son los patrones generales que parecen emerger en las diversas revisiones y meta-análisis que se han llevado a cabo al respecto.

En esta tesis estudiamos las similitudes y diferencias respecto a cómo los efectos ambientales, espaciales y temporales estructuran las metacomunidades de charcas temporales tropicales y mediterráneas. Nuestros resultados muestran que, a pesar de las diferencias ambientales entre charcas situadas en regiones distintas, la heterogeneidad ambiental puede ser similar. No obstante, las charcas mediterráneas presentaban una mayor heterogeneidad en las variables limnológicas, más locales, mientras que las charcas tropicales presentaban una mayor heterogeneidad climática, más regional y espacialmente estructurada.

Encontramos efectos ambientales puros más intensos en la metacomunidad mediterránea, mientras que la metacomunidad tropical se ve más influenciada por el ambiente espacialmente estructurado. Estas diferencias en la intensidad de los efectos ambientales podrían estar relacionadas con la magnitud de la heterogeneidad limnológica y climática, mayores en la metacomunidad mediterránea y tropical, respectivamente. Los efectos espaciales puros son más relevantes en la metacomunidad tropical, sugiriendo una mayor limitación dispersiva derivada de barreras orográficas (ecológicas) más intensas en los trópicos. Estos patrones se repiten en el tiempo a lo largo de un mismo año hidrológico.

No existen patrones en estos efectos de acuerdo a la capacidad dispersiva de los organismos. De hecho, las metacomunidades de organismos con dispersión activa y pasiva están estructuradas de forma similar por efectos ambientales y espaciales. Sin embargo, las diferencias entre regiones son más marcadas en los dispersores activos.

Los efectos temporales puros son importantes, tanto incluso como los efectos ambientales, y especialmente en organismos de tamaño corporal intermedio. Estos efectos temporales puros son mayores en la metacomunidad mediterránea, posiblemente relacionados con sucesiones más variables a lo largo del tiempo.

Por otro lado, la diversidad regional en la metacomunidad tropical, mayor que en la mediterránea, no se debe a una mayor variación temporal de la diversidad, ni a una mayor heterogeneidad espacial de las comunidades, sino que está relacionada con una mayor diversidad local.

RESUM

El concepte de metacomunitat ofereix un marc teòric que permet explicar la distribució dels organismes, englobant processos que actuen a diferents escales espacials i temporals. La selecció ambiental i la dispersió són processos clau estructurant les metacomunitats, actuant amb diferents intensitats segons els ecosistemes o organismes estudiats. No obstant això, pocs són els patrons generals que pareixen emergir en les diverses revisions i meta-anàlisis que s'han dut a terme sobre aquest tema.

En aquesta tesi estudiem les similituds i diferències respecte a com els efectes ambientals, espacials i temporals estructuren les metacomunitats de basses temporals tropicals i mediterrànies. Els nostres resultats mostren que, a pesar de les diferències ambientals entre basses situades en regions distintes, l'heterogeneïtat ambiental pot ser semblant. No obstant això, les basses mediterrànies presentaven una major heterogeneïtat en les variables limnològiques, més locals, mentre que les basses tropicals presentaven una major heterogeneïtat climàtica, més regional i espacialment estructurada.

Trobem efectes ambientals purs més intensos en la metacomunitat mediterrània, mentre que la metacomunitat tropical està més influenciada per l'ambient espacialment estructurat. Aquestes diferències en la intensitat dels efectes ambientals podrien estar relacionades amb la magnitud de l'heterogeneïtat limnològica i climàtica, majors en la metacomunitat mediterrània i tropical, respectivament. Els efectes espacials purs són més rellevants en la metacomunitat tropical, suggerint una major limitació dispersiva derivada de barreres orogràfiques (ecològiques) més intenses en els tròpics. Aquests patrons es repeteixen en el temps al llarg d'un mateix any hidrològic.

No existeixen patrons en aquests efectes d'acord amb la capacitat dispersiva dels organismes. De fet, les metacomunitats d'organismes amb dispersió activa i passiva estan estructurades de manera similar per efectes ambientals i espacials. No obstant això, les diferències entre regions són més marcades en els dispersors actius.

Els efectes temporals purs són importants, fins i tot com els efectes ambientals, i especialment en organismes de grandària corporal intermèdia. Aquests efectes temporals purs són majors en la metacomunitat mediterrània, possiblement relacionat amb successions més variables al llarg del temps.

D'altra banda, la diversitat regional en la metacomunitat tropical, major que en la mediterrània, no es deu a una major variació temporal de la diversitat, ni a una major heterogeneïtat espacial de les comunitats, sinó que està relacionada amb una major diversitat local.

ABSTRACT

The metacommunity concept provides a theoretical framework to explain the distribution of organisms, encompassing processes acting at different spatial and temporal scales. Environmental selection and dispersal are key processes structuring metacommunities, acting with different intensities depending on the ecosystems or organisms studied. However, few general patterns seem to emerge in the various reviews and meta-analyses that have been carried out in this regard.

In this thesis, we study the similarities and differences in how environmental, spatial and temporal effects structure metacommunities in tropical and mediterranean temporary ponds. Our results show that, despite environmental differences between ponds located in different regions, environmental heterogeneity may be similar. However, mediterranean ponds showed greater heterogeneity in limnological variables, which are considered more local, whereas tropical ponds showed higher climate heterogeneity, considered more regional, and spatially structured.

We found more intense pure environmental effects in the mediterranean metacommunity, whereas the tropical metacommunity was more influenced by the spatially structured environment. These differences in the intensity of pure and spatially structured environmental effects could be related to differences in limnological and climate heterogeneity, higher in the mediterranean and tropical metacommunity, respectively. Pure spatial effects are more relevant in the tropical metacommunity, suggesting a greater dispersal limitation derived from more intense orographic (ecological) barriers in the tropics. These patterns are repeated in time throughout the same hydrological year.

There are no patterns in these effects according to the dispersal ability of the organisms. Metacommunities of actively and passively dispersing organisms are structured similarly by environmental and spatial effects. However, differences between regions are more marked in active dispersers.

Pure temporal effects are important, even as much as environmental effects, and especially in organisms with intermediate body size. These pure temporal effects are higher in the mediterranean metacommunity, possibly related to more variable successions over time.

In addition, regional diversity in the tropical metacommunity was higher than in the mediterranean one. This was not caused by greater temporal variation in diversity, nor by a greater spatial heterogeneity of communities, but rather related to higher local diversity.

RESUMEN AMPLIADO

La teoría de metacomunidades permite estudiar la distribución heterogénea de las especies englobando procesos que actúan a diferentes escalas espaciales y temporales. Entre estos procesos, los más frecuentemente considerados han sido la selección ambiental, entendida como el filtrado llevado a cabo por la disponibilidad de recursos o la severidad del medio; la dispersión, entendida como el flujo de propágulos (incluyéndose la limitación o el exceso de estos) entre parches de hábitat; y los procesos neutros, englobando parámetros de muy difícil estimación o incluso aleatorios. Aunque la teoría de metacomunidades ha cambiado mucho a lo largo de las últimas décadas, la mayoría de los estudios empíricos actuales presentan un enfoque mecanicista, tratando de buscar los procesos responsables de la organización de las metacomunidades. Es por ello que existe un gran volumen de bibliografía sobre estudios de metacomunidades de diferentes grupos taxonómicos habitando diversos ecosistemas de distintas regiones biogeográficas. Sin embargo, los resultados obtenidos, generalmente fruto de metodologías variadas, no aportan patrones generales claros en la estructuración de las metacomunidades. Además, son escasos los trabajos que comparan la organización de las metacomunidades entre varios grupos de organismos y entre distintas regiones del planeta, o que incorporen la variabilidad temporal en el análisis de estos sistemas tan dinámicos.

Las diferencias ambientales, principalmente climáticas, asociadas a la latitud pueden tener efectos sobre la organización de las metacomunidades. En el caso de los ecosistemas de agua dulce tropicales, la relativamente menor variabilidad ambiental (al menos en términos de temperatura) respecto a las zonas templadas y la fuerte estacionalidad de las precipitaciones (resultando en eventos periódicos de inundación), pueden generar importantes diferencias en la intensidad con la que actúan los procesos estructuradores de las metacomunidades.

El objetivo principal de esta tesis es estudiar cómo los efectos ambientales, espaciales y temporales estructuran las metacomunidades de charcas temporales tropicales y mediterráneas, estudiando una amplia gama de grupos de organismos y empleando la misma metodología. Así mismo, bajo el marco teórico que ofrece la teoría de metacomunidades, se estudia y compara la diversidad biológica y su variabilidad en el espacio y en el tiempo en charcas temporales tropicales y mediterráneas.

En el **Capítulo 1** se revisa el conocimiento actual sobre la teoría de metacomunidades y su estudio, con especial énfasis en los estudios llevados a cabo en humedales tropicales. Las comunidades de aguas continenta-

les no están espacialmente distribuidas en parches aislados sobre una matriz terrestre, sino que están potencialmente conectadas a través de procesos de dispersión y, por lo tanto, pueden estudiarse como un conjunto interconectado de comunidades, que constituyen una metacomunidad. En este capítulo, exploramos los diferentes procesos que dan forma a la estructura de la metacomunidad y su relación con los patrones de diversidad. Nos centramos en tres importantes procesos ecológicos que estructuran las metacomunidades: el control ambiental, la dispersión y la deriva ecológica. El control ambiental se refiere al efecto de filtrado del medio a través de la selección de especies adaptadas a unas condiciones ambientales determinadas, trabajando a escala local y regional. Otro proceso clave, integrando las comunidades locales en la metacomunidad, es la dispersión, un proceso fuertemente dependiente de la escala espacial con una gran influencia en la biodiversidad. La intensidad con la que actúa la dispersión, dando lugar a limitación dispersiva o a efectos de masa, determinará en gran medida la organización de la metacomunidad. Finalmente, la deriva ecológica y otros procesos estocásticos pueden conducir a cambios impredecibles pero importantes en la estructura de la comunidad. Centrándonos en la influencia de estos mecanismos a través de diferentes organismos y escalas, se muestra cómo los roles relativos de la selección ambiental, la dispersión y la deriva ecológica son cruciales en la organización de las metacomunidades de humedales tropicales (en sentido amplio) en todo el mundo, incluyendo marjales, llanuras de inundación, meandros abandonados y charcas. También se ilustra cómo el análisis de partición de la varianza, uno de los métodos más utilizados para el estudio de las metacomunidades empíricas, proporciona información sobre el papel principal de los efectos ambientales, espaciales y neutros en la organización de las metacomunidades de humedales tropicales. Finalmente, se presentan algunos comentarios sobre la biología de la conservación bajo el prisma de la teoría de metacomunidades, que asume que no solo las condiciones locales, sino también el ambiente regional y la conectividad son elementos esenciales a considerar para una planificación y manejo exitoso de los ecosistemas acuáticos.

Las metacomunidades son sistemas muy dinámicos, pero la influencia del tiempo, independientemente de la variación temporal del ambiente, rara vez se ha considerado en el estudio de la organización de las metacomunidades. De hecho, en las charcas temporales, unos ecosistemas con unos límites temporales muy marcados, podríamos esperar que fuertes efectos temporales influyan en el ensamblado de la metacomunidad, incluso en ambientes relativamente poco variables como los ecosistemas tropicales. En el **Capítulo 2** exploramos cómo el tiempo, como factor independiente, además del ambiente y el espacio, pueden modular la estructura de una metacomunidad de charcas temporales tropicales. Además, esperamos que los organismos con elevadas capacidades dispersivas estuvieran más ambientalmente estructurados que aquellos con bajas capacidades dispersivas, que estarían más controlados por efectos espaciales. Finalmente, esperamos que la relevancia de los efectos temporales variara entre organismos en función de sus diferentes tiempos de generación. Para probar estas hipótesis, muestreamos 30 charcas temporales localizadas en un clima tropical seco, a lo largo de la costa Pacífica de Costa Rica y Nicaragua, en tres periodos diferentes del mismo año hidrológico: poco después del llenado de los cuerpos de agua, a mitad del hidroperiodo y justo antes de la desecación. Obtuvimos datos sobre 56 variables ambientales, y las coordenadas geográficas de cada laguna fueron utilizadas para construir variables espaciales (Moran Eigenvector Maps, MEMs). Recolectamos muestras biológicas y estimamos la abundancia específica de fitoplancton, zooplancton e invertebrados bentónicos. Para evaluar el papel relativo de los efectos ambientales, espaciales y temporales en la organización de la metacomunidad, utilizamos análisis de partición de varianza mediante análisis de redundancia (RDA) para cada grupo de organismos. La inclusión del tiempo destacó que los efectos temporales puros explicaban parte de la variación de la metacomunidad en casi todos los taxones, siendo tan importante como los efectos espaciales o incluso ambientales para algunos grupos de organismos. A pesar de los teóricamente reducidos gradientes ambientales en las regiones tropicales (debido a temperaturas altas y estables), encontramos fuertes efectos ambientales. Los dispersores pasivos estaban más influenciados por los factores ambientales que los activos, sugiriendo menor limitación dispersiva. También encontramos una relación positiva entre el tamaño corporal de los diferentes grupos de organismos y la magnitud de los efectos temporales, relacionado probablemente con mayores tiempos de generación. Finalmente, al analizar cada periodo de muestreo por separado, encontramos grandes oscilaciones en el papel relativo del ambiente y el espacio en los diferentes periodos de muestreo, lo que demuestra que los estudios de foto fija pueden no ser representativos en sistemas tan dinámicos como las metacomunidades de lagunas temporales.

Esta tesis tiene como uno de los objetivos principales esclarecer la contribución de los efectos ambientales, espaciales y temporales en la estructuración de la metacomunidades de diferentes organismos acuáticos mediterráneos y tropicales. Para ello, es fundamental una caracterización ambiental lo más exhaustiva posible. En el **Capítulo 3** caracterizamos el ambiente de charcas temporales de tres regiones biogeográficas distintas en busca de similitudes y diferencias entre cada grupo de lagunas. Las características ambientales de estos ecosistemas están influenciadas por un conjunto de factores regionales (principalmente climáticos) y locales (naturales o antropogénicos). Para evaluar las diferencias en el funcionamiento ecológico entre regiones geográficas distantes, evaluamos las características principales de 90 charcas temporales ubicadas en tres áreas distintas: dos regiones de clima mediterráneo (este de la península ibérica y Chile central) y un entorno tropical en Costa Rica. El ambiente de cada charca fue caracterizado tres veces durante el ciclo hidrológico de 2017-2018, obteniéndose cinco conjuntos de parámetros: limnológicos, hidrogeomorfológicos, bióticos, paisajísticos y macroclimáticos. Mediante análisis multivariados, determinamos la heterogeneidad ambiental de cada región y las principales diferencias ambientales entre ellas. Como era de esperar, los factores hidrogeomorfológicos no difirieron entre las regiones, pero las variables climáticas mostraron marcadas diferencias entre la región tropical y las regiones mediterráneas. También detectamos claras diferencias entre las charcas mediterráneas y tropicales en términos de sus patrones de mineralización (principalmente conductividad y alcalinidad), coberturas de vegetación acuática y uso del suelo alrededor de la charca. A pesar de las similitudes entre las regiones mediterráneas, se encontraron fuertes diferencias en cuanto a cobertura vegetal, concentración de nutrientes y estado trófico, probablemente asociadas a actividades humanas (agricultura y ganadería extensiva).

Gracias al desarrollo de herramientas estadísticas que permiten estimar y aislar parcialmente el papel de cada uno de los procesos que estructuran la metacomunidad, los estudios empíricos sobre metacomunidades se han multiplicado a nivel mundial. Sin embargo, pocos trabajos se centran en múltiples taxones al mismo tiempo, y aún menos comparan dos regiones biogeográficas distantes utilizando la misma metodología. En el **Capítulo 4**, comprobamos la hipótesis de que las metacomunidades de charcas temporales templadas (clima mediterráneo) estarían más influenciadas por procesos ambientales y espaciales que las tropicales, debido a gradientes ambientales más intensos y un mayor aislamiento de los cuerpos de agua en la matriz terrestre. Muestreamos 30 charcas temporales tropicales y 32 charcas temporales mediterráneas de Costa Rica y España, respectivamente. Para cada charca, obtuvimos datos sobre 49 variables ambientales (incluidas variables limnológicas, hidrogeomorfológicas, bióticas, climáticas y paisajísticas). Además, caracterizamos las comunidades biológicas de bacterias y arqueas (tanto de la columna de agua como del sedimento), fitoplancton, zooplancton, invertebrados bentónicos, anfibios y aves. Finalmente, estimamos el papel relativo del espacio y del ambiente en la organización de la metacomunidad para cada grupo y región. En lugar de emplear particiones de varianza basadas en análisis de redundancia (RDA) o de correspondencias canónicas (CCA), que asumen una relación lineal o unimodal entre las variables predictoras y las variables respuesta, desarrollamos un nuevo método de partición de la varianza basado en modelos aditivos generalizados (GAMs). La selección ambiental fue importante tanto en las charcas tropicales como en las mediterráneas, pero notablemente más intensa en las últimas, probablemente debido a su mayor heterogeneidad limnológica (más local). El ambiente correlacionado con el espacio y los efectos espaciales puros fueron mayores en la metacomunidad tropical, relacionados con una mayor heterogeneidad climática y posibles procesos de dispersión (limitación dispersiva o efectos de masa) que actúan a diferentes escalas. La variabilidad entre grupos taxonómicos en las contribuciones espaciales y ambientales fue muy amplia. Los efectos sobre los dispersores activos y pasivos fueron similares dentro de cada región, pero diferentes entre las regiones, con mayores efectos ambientales en los dispersores pasivos mediterráneos. La variación residual (no explicada) fue mayor en la metacomunidad tropical, lo que sugiere un papel más importante de los procesos estocásticos o de elementos ambientales no medidos (como interacciones bióticas) en los trópicos. En general, estos resultados en charcas temporales apoyan, para una amplia variedad de organismos acuáticos, la visión clásica de unas constricciones abióticas más intensas en las zonas templadas que en los trópicos, al menos al inicio del hidroperiodo.

La literatura existente acerca de trabajos empíricos sobre metacomunidades coincide en que estos sistemas son muy dinámicos, y que los estudios basados en muestreos puntuales pueden dar lugar a conclusiones sesgadas o erróneas. Sin embargo, la mayoría de estudios que incorporan el tiempo en el estudio de las metacomunidades lo han hecho bajo un enfoque espacial, comparando varios muestreos puntuales consecutivos y buscando variación temporal en los efectos ambientales y espaciales. Sin embargo, rara vez se ha llevado a cabo un enfoque espacio-temporal, analizando toda la variación de la metacomunidad, incluyendo el tiempo como una variable de interés. En el **Capítulo 5** comparamos el papel del ambiente, el espacio y el tiempo, bajo un enfoque espacial y espacio-temporal, en la organización de dos metacomunidades de 30 charcas temporales tropicales (en Costa Rica) y 32 mediterráneas (en el este de la Península Ibérica). Comparamos múltiples grupos de organismos de agua dulce (desde bacterias a anfibios), muestreados usando la misma metodología, en tres ocasiones a lo largo del mismo año hidrológico. Para ello, llevamos a cabo análisis de partición de la varianza, utilizando modelos aditivos generalizados (GAMs). En el enfoque espacial, nuestros resultados muestran una disminución en los efectos ambientales puros con el tiempo, probablemente no relacionada con cambios en la heterogeneidad o conectividad ambiental. Hipotetizamos que las interacciones bióticas, no medidas, pueden ganar relevancia con el tiempo. Los efectos ambientales puros son más fuertes en la metacomunidad mediterránea, quizás debido a una mayor heterogeneidad limnológica. Por el contrario, los efectos del espacio puro y el ambiente espacialmente estructurado son mayores en la metacomunidad tropical, quizás relacionados con una mayor heterogeneidad climática, una mayor limitación de la dispersión y distribuciones más restringidas o parcheadas de especies y ambientes. En el enfoque espacio-temporal, el tiempo puro es tan importante como los efectos ambientales puros, por lo que la sucesión podría jugar un papel clave en la organización de la metacomunidad, siendo más relevante en la metacomunidad mediterránea y en organismos con tamaño corporal y tiempos de generación intermedios (macroinvertebrados). Sin embargo, los efectos espaciales puros se convierten en el componente puro más importante en ambas metacomunidades, lo que sugiere que este enfoque espacio-temporal puede detectar nuevos patrones espaciales, no percibidos en el enfoque espacial. Por otro lado, el ambiente temporalmente estructurado y el espacio-temporalmente estructurado son más importantes, respectivamente, en la metacomunidades mediterránea y tropical, lo que sugiere un papel importante de la variabilidad estacional del ambiente y del ambiente espacialmente estructurado. Estos resultados vuelven a constatar la idea de que sistemas tan dinámicos como pueden ser las metacomunidades acuáticas deben ser estudiados con un enfoque temporal, afianzando así también los resultados y patrones obtenidos en los Capítulos 2 y 4.

Por último, la teoría de metacomunidades propone un marco teórico adecuado para el estudio de la diversidad biológica, integrando diferentes escalas espaciales. Con unos límites espaciales y temporales marcados, las metacomunidades de charcas temporales constituyen un ecosistema ideal para investigar cómo cambia la diversidad en el espacio y en el tiempo. El gradiente latitudinal de biodiversidad, uno de los patrones mejor descritos en ecología, predice que las regiones tropicales deberían tener una mayor diversidad local, una mayor diferencia de composición entre las comunidades locales y una mayor diversidad regional (es decir, mayor diversidad alfa, beta y gamma) que las regiones templadas. Sin embargo, solo unos pocos estudios utilizan un enfoque temporal para evaluar dónde es más variable la diversidad a lo largo del tiempo. En el **Capítulo 6** comparamos, utilizando un enfoque espacial y temporal, la diversidad de múltiples taxones (desde bacterias hasta anfibios) que habitan charcas temporales tropicales (Costa Rica) y mediterráneas (este de la Península Ibérica), muestreadas en tres ocasiones durante el mismo año hidrológico y con la misma metodología. Bajo el enfoque espacial, analizamos las diversidades gamma (índice de Chao), alfa (orden 0: riqueza de especies; orden 1: diversidad transformada de Shannon y orden 2: Simpson; y equidad de Pielou) y beta espacial (índices de disimilitud de Bray-Curtis o Sørensen). Con un enfoque temporal, comparamos los coeficientes de variación en la diversidad alfa para cada comunidad local y la diversidad beta temporal. Las diferencias entre regiones y periodos de muestreo se comprobaron utilizando modelos lineales generalizados (GLMs). Encontramos una mayor diversidad gamma en las charcas tropicales, tal y como se esperaba, correlacionada con una también mayor diversidad alfa, que en las charcas mediterráneas. Sin embargo, esta mayor diversidad gamma en la metacomunidad tropical no vino acompañada de una mayor diversidad beta espacial, que no difirió consistentemente entre regiones. Además, el fitoplancton y especialmente los microinvertebrados, igualaron o incluso excedieron la diversidad alfa tropical en la última etapa del hidroperiodo. La diversidad beta espacial decreció a lo largo del tiempo en bacterias, micro y macroinvertebrados y anfibios. En consecuencia, los procesos de homogeneización (por ejemplo, la dispersión ligada a inundaciones periódicas) y heterogeneización (limitación dispersiva o heterogeneidad ambiental) deben de estar equilibrados en ambas regiones. La observación de que la variación temporal en la diversidad alfa y beta fue similar para las charcas de ambas regiones sugiere que las diferencias en la heterogeneidad ambiental de cada charca a lo largo del hidroperiodo no generan diferencias temporales importantes en la composición de la comunidad. Las excepciones a este patrón incluyen macroinvertebrados, con mayor variación en la diversidad alfa en las charcas mediterráneas, y anfibios, con mayor diversidad beta temporal en la metacomunidad tropical.

En conjunto, parece claro que los efectos ambientales son los principales procesos (entre los medidos) que estructuran las metacomunidades de charcas temporales. Sin embargo, los efectos ambientales puros son más intensos (y de forma sostenida en el tiempo) en la metacomunidad mediterránea, mientras que los efectos ambientales están más correlacionados con el espacio en la metacomunidad tropical. Estos resultados podrían estar relacionados con una mayor heterogeneidad limnológica en la metacomunidad mediterránea, mientras que la heterogeneidad climática, actuando a un nivel más regional, es mayor en la metacomunidad tropical. Por otro lado, los efectos espaciales puros son mayores en la metacomunidad tropical, lo que sugiere procesos dispersivos más marcados (ya sea por limitación dispersiva o por efectos de masa) en la metacomunidad tropical. No encontramos patrones claros en los efectos ambientales y espaciales sobre organismos con diferentes habilidades dispersivas, teniendo mayor impacto las diferencias entre regiones biogeográficas. Sin embargo, estas diferencias son más marcadas en los organismos con dispersión activa. No obstante, en ambas metacomunidades se ha infravalorado el papel de las interacciones bióticas (presumiblemente más importantes en los trópicos que en las regiones templadas), lo que podría dar lugar a subestimaciones de la selección ambiental y sobreestimación de la importancia de los procesos dispersivos. La incorporación del tiempo en el estudio de las metacomunidades de charcas temporales nos ha permitido descubrir que los efectos temporales independientes del ambiente son muy importantes en la organización de las metacomunidades, tanto como el ambiente, llegando a ser los más importantes en algunos grupos de organismos. Además, estos efectos son más intensos en los organismos de tamaño intermedio (con longevidades y tiempos de generación intermedios, tales como los macroinvertebrados). Estos efectos temporales son mayores en la metacomunidad mediterránea, sugiriendo sucesiones más cambiantes por efecto del paso del tiempo que en los ambientes tropicales. Finalmente, los patrones en efectos ambientales y espaciales entre las metacomunidades de las dos regiones se mantienen más o menos constantes a lo largo del tiempo. Sin embargo, a lo largo del año hidrológico, hay un decaimiento en la variación total explicada y en los efectos ambientales puros. Esto podría deberse a que, conforme avanza el hidroperiodo, la organización de la metacomunidad pasa de estar más controlada por el ambiente abiótico, a más controlada por el ambiente biótico no medido.

Esta tesis enfatiza cuán dinámicos son realmente los sistemas naturales, y la importancia de tener en cuenta la variabilidad temporal en su estudio. Dilucidar el grado de control ambiental y espacial al que se ven sometidas las distribuciones de los organismos es crucial para la elaboración de planes de conservación y manejo. Por ello, el desarrollo de técnicas estadísticas intuitivas y flexibles que permitan incorporar las interacciones bióticas supondrá un nuevo salto hacia adelante en el estudio de las metacomunidades. Sin embargo, parece claro que la organización de las metacomunidades de charcas temporales es muy variable y dependiente de la idiosincrasia de cada grupo de organismos y de la región que habitan. Aunque hemos encontrado ciertos patrones que parecen mantenerse en el tiempo, aún parece difícil establecer reglas generales que expliquen cómo se distribuyen las especies en el espacio y el tiempo. Por un lado, la inclusión de escalas temporales mayores, y, por otro lado, el desarrollo de nuevas técnicas estadísticas, que incorporen las interacciones bióticas (competencia, depredación, facilitación, etc.) de forma más intuitiva permitirá dar un paso hacia adelante en el estudio de las metacomunidades.

A partir de esta tesis, se desprenden varias conclusiones generales. En primer lugar, como se desarrolla en el Capítulo 1, a pesar del mayor esfuerzo de investigación sobre metacomunidades en regiones templadas que en tropicales, existe una creciente bibliografía al respecto. Los trabajos llevados a cabo en sistemas tropicales demuestran un fuerte control ambiental. Por otro lado, las inundaciones periódicas durante la estación lluviosa tienen una fuerte relación con los efectos espaciales y la disminución de la diversidad beta.

Por otro lado, en el Capítulo 3 encontramos que la heterogeneidad ambiental en las regiones estudiadas, ya sea en la tropical, en Costa rica, o en las mediterráneas, en España y Chile, es similar. Sin embargo, los dos conjuntos de charcas mediterráneas muestran más heterogeneidad en los parámetros físico-químicos del agua, mientras que el conjunto de lagunas tropicales es más climáticamente heterogéneo. Aún así, el conjunto de charcas tropicales, en Costa Rica, difería respecto a ambos conjuntos de charcas mediterráneas, situadas en España y Chile, en algunas variables ambientales como la conductividad, la cobertura de vegetación acuática o los usos del suelo entorno a las charcas. Además, a pesar de sus similitudes, los conjuntos de charcas mediterráneas se diferenciaban entre ellos en función de las coberturas vegetales o las concentraciones de nutrientes, al estar las charcas chilenas más impactadas que las españolas por actividades humanas como la agricultura o la ganadería.

Al analizar los procesos que organizan las metacomunidades en los Capítulos 2 y 5, encontramos que la estructura de las metacomunidades de charcas temporales estudiadas, tanto las tropicales (en Costa Rica-Nicaragua, y en Costa Rica) como la mediterránea (en España), depende de efectos tanto ambientales como espaciales, pero también temporales, pudiendo estos ser tan importantes como los efectos ambientales. Los efectos espaciales y ambientales son muy variables a lo largo del hidroperiodo. Además, también en el capítulo 4, encontramos que los efectos ambientales, puros o espacialmente estructurados, son generalmente los más importantes en la estructura de las metacomunidades estudiadas, aunque existe una elevada proporción de varianza que permanece sin explicar.

Al comparar metacomunidades situadas en regiones biogeográficas distintas, en los capítulos 4 y 5, observamos que los efectos ambientales puros son más importantes en la estructura de la metacomunidad mediterránea, situada en España, que en la tropical, en Costa Rica. Sin embargo, los efectos espaciales puros y el ambiente espacialmente estructurado son más importantes en la metacomunidad tropical. Este patrón se sostiene a lo largo del año hidrológico. El efecto del tiempo puro es ligeramente superior en la metacomunidad mediterránea.

No encontramos patrones claros en los Capítulos 2 y 4 en el papel de los efectos ambientales y espaciales en cuanto al tamaño corporal y habilidad dispersiva de los diferentes organismos estudiados. De hecho, dentro de cada metacomunidad, tropical (Costa Rica-Nicaragua y Costa Rica) o mediterránea (España), los efectos ambientales y espaciales son similares entre dispersores activos y pasivos (con efectos ambientales algo mayores en dispersores pasivos que en los activos en el sistema tropical). Las diferencias entre regiones señaladas anteriormente son más exacerbadas en los dispersores activos.

Al incorporar el tiempo en el análisis de la estructura de la metacomunidades bajo una perspectiva espacial (Capítulo 2), encontramos que el papel de los efectos ambientales puros decae con el tiempo, a lo largo del hidroperiodo, tanto en la metacomunidad tropical de Costa Rica como la mediterránea de España.

Al analizar la estructura de las metacomunidades incorporando el tiempo en una perspectiva espacio-temporal, en los Capítulos 2 y 5, encontramos que los organismos con tamaños corporales intermedios (macroinvertebrados) presentan, en general, efectos temporales mayores. De esta forma, los efectos temporales puros siguen una distribución unimodal respecto al tamaño corporal. Este patrón es más claro en los organismos tropicales (tanto de la metacomunidad de Costa Rica-Nicaragua como la de Costa Rica) que en los mediterráneos de la metacomunidad española.

Finalmente, en el Capítulo 6, encontramos que la diversidad alfa es generalmente mayor en el conjunto de charcas tropicales de Costa Rica que en las charcas estudiadas en España. Este patrón se cumple en todos los grupos taxonómicos salvo en los microinvertebrados al final del hidroperiodo. Además, la diversidad gamma es generalmente mayor en la metacomunidad tropical de Costa Rica que en la mediterránea de España. Esta mayor diversidad gamma está correlacionada con una mayor diversidad local (diversidad alfa), pero no con una mayor disimilitud entre parches (diversidad beta). Además, la variabilidad temporal de las diversidades alfa y beta de cada parche no difiere entre las metacomunidades de Costa Rica y de España, por lo que cada charca es similarmente variable con el tiempo en ambas regiones.

Laguna de Peje, Costa Rica. Fotografiado por Juan Rueda

INTRODUCCIÓN GENERAL

LA TEORÍA DE METACOMUNIDADES

La distribución de las especies en el espacio y en el tiempo es una cuestión que siempre ha despertado un amplio interés en ecología. En este sentido, la ecología de poblaciones y, por extensión, la ecología de comunidades, han centrado tradicionalmente su atención en factores locales, especialmente ambientales (como en Elton 1927; Fauth et al. 1996). Sin embargo, trascendiendo la consideración de las poblaciones y comunidades como entidades cerradas, y con la intención de añadir una mayor perspectiva espacial y temporal, incorporando procesos que actúan a diferentes escalas más allá de la local, nace el concepto de metacomunidad (Hanski y Gilpin 1991; Wilson 1992), como extensión de la metapoblación de Levins (1969).

Procesos estructuradores de las metacomunidades

Una metacomunidad es un conjunto de comunidades locales, unidas por potenciales procesos de dispersión de especies que interactúan entre sí (Leibold et al. 2004). Son tres los principales procesos que, en mayor o menor medida, estructuran las metacomunidades: la selección ambiental, la dispersión y la deriva ecológica (Vellend 2010). Estos, además, pueden funcionar a diferentes escalas espaciales y temporales (Leibold y Chase 2018), aunque a escalas temporales grandes tomarán también mayor relevancia los procesos evolutivos.

La selección ambiental ha sido considerada tradicionalmente el principal proceso estructurador de las metacomunidades (Chase y Leibold 2003). A escala local, el estrés ambiental o la disponibilidad de recursos filtran la presencia y eficacia de las especies (Chesson 2000; Lozada-Gobilard et al. 2019). A escalas temporales o espaciales mayores, la heterogeneidad ambiental genera un amplio gradiente de condiciones y recursos con gran diversidad de nichos que permite la coexistencia de más especies (MacArthur y MacArthur 1961; Leibold y Chase 2018).

La dispersión es el elemento clave integrando las comunidades locales (usualmente habitando parches o parcelas de hábitat) en el marco de la teoría de metacomunidades (Wilson 1992). Las habilidades dispersivas de las especies y la conectividad entre los parches condicionan la intensidad con la que la dispersión estructura las metacomunidades (Leibold y Chase 2018). Incorporando una escala temporal, estas habilidades dispersivas de las especies pueden cambiar con el tiempo, por ejemplo, estacionalmente. Este es el caso de las migraciones de las aves, vectores de dispersión de multitud de organismos terrestres y acuáticos (Green y Figuerola 2005; Green et al. 2016).

La fuerza con la que actúa la selección ambiental depende en gran medida de la intensidad de los procesos dispersivos. Cuando el grado de dispersión es bajo, bien porque la conectividad es pequeña, o bien porque la escala espacial de trabajo es grande, la distribución de las especies está fuertemente condicionada por su capacidad dispersiva (Heino et al. 2015). De esta forma, los patrones generados por la limitación dispersiva enmascaran el efecto de la selección ambiental. Con conectividades o escalas espaciales intermedias, al aumentar el grado de dispersión, desaparecen en gran medida las limitaciones dispersivas, maximizándose la intensidad con la que actúan los filtros ambientales (Heino et al. 2015). Finalmente, a escalas espaciales reducidas, o conectividades muy altas, los organismos son capaces de dispersarse a todos los parches de la metacomunidad, con un flujo de propágulos o individuos que permite la supervivencia de los organismos incluso en condiciones subóptimas (Shmida y Wilson 1985). Este exceso de dispersión da lugar a efectos de masa (Holt 1985) que eclipsan el filtro ambiental (Heino et al. 2015), llegando incluso a homogeneizar la metacomunidad (Leibold y Chase 2018).

Por último, los procesos neutros tales como la deriva ecológica incluyen fenómenos no deterministas o de muy difícil predicción o estimación. Estos pueden ser englobados bajo la estocasticidad demográfica, así como eventos históricos, o relacionados con el ensamblado y sucesión de las comunidades locales (Hubbell 2001; Orrock y Watling 2010; Vellend et al. 2014).

Recientemente se están desarrollando nuevos enfoques en la teoría de metacomunidades. Esta nueva perspectiva asumiría que los principales procesos que estructurarían las metacomunidades son la respuesta denso-independiente a condiciones abióticas, las interacciones bióticas denso-dependientes y la dispersión, incorporando la estocasticidad de forma implícita a cada uno de estos procesos (Thompson et al. 2020). Sin embargo, este enfoque aún se encuentra poco desarrollado, especialmente desde el punto de vista empírico.

METACOMUNIDADES DE AGUA DULCE: EL CASO DE LAS CHARCAS TEMPORALES

Los ecosistemas de aguas continentales, tanto lóticos como lénticos, han sido tradicionalmente muy utilizados como modelos para el estudio de metacomunidades (Soininen 2014, 2016). Una de las principales razones para ello es la existencia de unos límites espaciales (y en ocasiones temporales) muy marcados entre el ecosistema acuático y la matriz terrestre (Heino et al. 2015; Cañedo-Argüelles et al. 2020), siendo más sencillo delimitar comunidades locales. En el caso de los estudios de metacomunidades en ríos, estos han sido particularmente fructíferos al poder estudiar parches locales en un contexto regional bien delimitado (la cuenca hidrográfica; Heino et al 2017a). Además, la gran diversidad de grupos de organismos diferentes con distintas estrategias dispersivas proporciona multitud de posibilidades para estudiar los efectos de la selección ambiental y la limitación dispersiva en la estructuración de las metacomunidades (De Bie et al. 2012; Heino et al. 2015).

Sin embargo, los ecosistemas acuáticos continentales son muy diversos, incluyendo también lagos, humedales, embalses, aguas subterráneas, etc. Estos ecosistemas se encuentran heterogéneamente distribuidos por el mundo, y son muy diferentes tanto en cuanto a sus características ambientales, como a su funcionamiento ecológico o la composición de especies que los habitan. A lo largo de esta tesis, usaremos lagunas y charcas (*ponds* en inglés) de agua dulce (o levemente salada, con salinidades generalmente inferiores a 5 $g \cdot L^{-1}$) como ecosistemas modelo para el estudio de las metacomunidades, por la relativa simplicidad de su estudio y la ubicuidad de estos sistemas. A partir de ahora, definiremos como charcas a aquellos ecosistemas acuáticos de pequeño tamaño, tanto en términos de profundidad (menor de tres metros) y superficie (menor de ocho hectáreas; Ramsar Convention Secretariat 2013). Estas charcas, por tanto, van a ser sistemas relativamente pequeños, generalmente más aislados en la matriz terrestre que otros cuerpos de agua, como los ríos. Frecuentemente también se denomina lagunas a aquellos cuerpos de agua de mayor entidad, y algunas de las charcas pueden formar parte de sistemas mayores como ocurre en los humedales.

Además, el hidroperiodo, o tiempo de permanencia del agua, es un factor fundamental en el funcionamiento ecológico de las charcas. Estos sistemas, en función de si son permanentes o temporales, influirán profundamente en las especies presentes, con estrategias vitales, adaptaciones y capacidades dispersivas particulares (e.g., Serrano y Fahd 2005; Medley y Havel 2007; Schriever y Williams 2013; Kulkarni et al. 2018). En el caso de las charcas temporales, se caracterizan por alternar fases con agua y fases secas, cuyas duraciones pueden ser variables, desde semanas a años (Williams 2006). De esta forma, las charcas temporales, además de tener unos límites espaciales bien definidos, también tendrán unos marcados límites temporales, lo que las convierte en ecosistemas modelo ideales para estudiar también dinámicas temporales.

El ambiente en las charcas temporales

En general, parece claro que la selección ambiental es un proceso clave en el ensamblado de las metacomunidades de sistemas acuáticos (e.g. Beisner et al. 2006; Vanschoenwinkel et al. 2007; De Campos et al. 2016; Loewen et al. 2020). Sin embargo, la intensidad con la que actúa parece ser muy variable, desde estudios que apuntan a un control principalmente ambiental en ostrácodos (Castillo-Escrivà et al. 2017a), hasta un rol prácticamente nulo en peces (De Bie et al. 2012).

Por la importancia de la selección ambiental en la estructura de las metacomunidades, es crucial realizar una rigurosa caracterización ambiental de los sistemas de estudio, intentando abarcar la mayor parte de su variabilidad ambiental. La variabilidad del ambiente en el espacio y en el tiempo genera una heterogeneidad espacial y temporal que puede influir enormemente en la intensidad con la que la selección ambiental estructura las metacomunidades (Ai et al. 2013). Como consecuencia de amplios gradientes ambientales, son más especies las que pueden responder a ellos y generar patrones ambientales detectables (Leibold y Chase 2018).

En charcas temporales, existe una enorme variedad de factores que pueden influir en los organismos que habitan o hacen uso de las mismas. Algunas de las principales variables ambientales locales que influyen sobre las comunidades biológicas de ecosistemas acuáticos están relacionadas con las características físico-química del agua (categorizadas como variables limnológicas a lo largo de esta tesis; e.g. Cottenie et al. 2003; Benito et al. 2018). Por ejemplo, la concentración de sales disueltas (a menudo estimada como conductividad eléctrica), puede ser un factor clave estructurando las comunidades acuáticas, afectando al equilibrio osmótico de los organismos (Antón-Pardo y Armengol 2012; Nursuhayati et al. 2013). Los factores locales relativos a la hidrología, la geología y la morfología de las charcas, aquí categorizados como variables hidrogeomorfológicas, también son esenciales. Se incluyen aquí variables como la superficie o la profundidad de cada punto de agua, los cuales pueden ser importantes a la hora de generar microhábitats (Strayer et al. 1997; Werner et al. 2007; Heino et al. 2017b) o incluso influir en el hidroperiodo. Finalmente, las variables bióticas son factores muy importantes en el establecimiento y supervivencia de las especies en un ecosistema, y por tanto en la estructuración de las metacomunidades (Wisz et al. 2013) y, de hecho, existe bastante literatura acerca del efecto depredador de la presencia de peces o la arquitectura de la vegetación acuática sobre las comunidades biológicas (Lemma et al. 2001; Tessier et al., 2004; Barker et al. 2014).

Sin embargo, aunque los sistemas acuáticos se encuentren más o menos aislados entre ellos, embebidos en una matriz terrestre, esto no significa que estos no se vean influenciados por los terrestres y viceversa (Likens y Bormann 1974; Sardans et al. 2012; Kayler et al. 2019). El ambiente terrestre es relevante en las dinñamicas de los organismos acuáticos, ya sea de forma directa, actuando como hábitat o fuente de recursos para animales anfibios o con fases adultas terrestres, o de forma indirecta, limitando la dispersión o aportando nutrientes al agua. Tener en cuenta el ambiente terrestre es, por lo tanto, necesario para entender el funcionamiento de las metacomunidades acuáticas. Es por ello que las variables paisajísticas relativas al uso del suelo y a la heterogeneidad del paisaje que rodea a los sistemas acuáticos deben tenerse en cuenta en los estudios de metacomunidades.

Por otro lado, el clima tiene un efecto muy relevante en la composición de especies (MacArthur 1972). Las diferencias climáticas entre parches, además, influenciadas por la disposición latitudinal y longitudinal de los parches, pueden generar heterogeneidad ambiental en el espacio y con ello influir en la intensidad de la selección ambiental. Además, las fuertes diferencias ambientales (en términos de temperaturas y precipitaciones) derivadas de la variación latitudinal del clima y su estacionalidad dan lugar a marcados límites en la distribución de muchas especies (Olson et al. 2001). Por tanto, la respuesta de los organismos a diferentes condiciones macroclimáticas puede dar lugar también a una distinta organización de las metacomunidades. Es por ello que los resultados o patrones encontrados en la mayoría de estudios, llevados a cabo en regiones con unas características climáticas concretas, podrían no ser extrapolables a metacomunidades de todo el mundo.

La dispersión entre las charcas temporales

El grado de conectividad entre parches es esencial para la dispersión de los organismos. Algunas especies, como los peces, necesitan una conectividad total entre parches para moverse de unos sistemas a otros (Hartz et al. 2019). La conectividad, además, puede ser variable entre épocas del año y puede ser heterogénea entre los parches de una misma metacomunidad. Cuando la conectividad es baja o intermedia, la limitación dispersiva de los organismos da lugar a patrones espaciales cuantificables (Heino et al. 2015). Sin embargo, conforme la conectividad aumenta, las limitaciones dispersivas desaparecen de modo que la distribución de las especies ya no es el resultado de sus habilidades dispersivas sino de filtros ambientales locales. Cuando la conectividad es máxima, los efectos de masa contrarrestan los filtros ambientales y todas las especies ocupan todos los parches, llegando a producirse una homogeneización de la metacomunidad (Heino et al. 2015). En ecosistemas acuáticos totalmente conectados, como aquellos situados en llanuras de inundación de ríos, la conectividad entre cuerpos de agua puede dar lugar también a una homogeneización ambiental (Thomaz et al. 2007; Brasil et al. 2020).

La adaptación al secado de los sistemas acuáticos temporales implica la existencia de estrategias que permitan a las poblaciones sobrevivir a la inhabitabilidad del sistema (Griffiths 1998; Strachan et al. 2015). La diversidad de estrategias implica, en última instancia, diversidad de métodos de dispersión y colonización de nuevos hábitats (Brendonck y Riddoch 2008; Incagnone et al. 2014; De Morais-Junior et al. 2019). Esta dispersión de los organismos acuáticos puede darse de forma activa o de forma pasiva. Para los dispersores activos (por ejemplo, anfibios o insectos), la principal estrategia, que permite la supervivencia de los individuos durante el secado de las charcas, es el abandono del parche y o la colonización de sistemas acuáticos cercanos, o del medio terrestre en el caso de organismos con etapas adultas no acuáticas. La capacidad dispersiva de estos va a depender del método de dispersión y el tamaño corporal, siendo mucho menor la limitación dispersiva en organismos voladores grandes (De Bie et al. 2012; Padial et al. 2014).

En los organismos de dispersión pasiva, la desecación implica generalmente la muerte de los individuos, así que la supervivencia de la población depende de la generación de formas de resistencia capaces de sobrevivir a la sequía (Cáceres 1997). Estas formas de resistencia permanecen en el sedimento, desde donde colonizan el nuevo hábitat resultante del llenado de las charcas en el siguiente ciclo hidrológico (e.g. Frisch y Green, 2207). Además, las formas de resistencia son los principales propágulos en una dispersión que puede ser hidrocórica, anemocórica o zoocórica (Frisch 2002; Incagnone et al. 2014; Brendonck et al. 2016). Se ha descrito que los organismos con dispersión pasiva de pequeño tamaño están menos limitados dispersivamente que los que tienen propágulos mayores, pudiendo alcanzar áreas de distribución muy grandes (De Bie et al. 2012; Padial et al. 2014). De hecho, tradicionalmente se ha considerado que muchos microorganismos son cosmopolitas y no presentarían biogeografía (Finlay 2002; Finlay y Fenchel 2004; Meyer et al. 2018).

Estos procesos dispersivos suelen tener menor importancia que la selección ambiental, aunque algunos autores sugieren que son más importantes en charcas que en otros sistemas acuáticos, al estar más aislados (Heino et al. 2015). Sin embargo, varios estudios encuentran efectos de la dispersión nulos o casi nulos en distintos grupos de organismos (bacterias en De Bie et al. 2012; fitoplancton en Brasil et al. 2020; macrófitos en Padial et al. 2014; zooplancton en Beisner et al. 2006 o macroinvertebrados, peces y anfibios en De Bie et al. 2012). Por otro lado, pocos son los estudios en los que los procesos dispersivos dominen la estructuración de la comunidad (por ejemplo, macroinvertebrados en Li et al. 2020 o peces en Fernandes et al. 2014).

Metacomunidades tropicales y mediterráneas

Aunque existe un sesgo geográfico en el número de estudios sobre metacomunidades de agua dulce, con más trabajos en zonas templadas que en tropicales, la cantidad de literatura disponible con resultados de casi todo el mundo está creciendo en los últimos años. Estas investigaciones, además de ser difícilmente comparables, por el uso de metodologías diferentes entre grupos de trabajo, aportan resultados en ocasiones contradictorios. Por ello es difícil encontrar patrones generales que expliquen la estructura de las metacomunidades, aunque existen algunas revisiones que han tratado de sintetizar la literatura al respecto (e.g. Soininen 2014; Heino et al. 2015; Soininen 2016).

Sin embargo, el hecho que las diferencias latitudinales entre regiones generan diferencias ambientales y bióticas es algo documentado desde hace siglos (Humboldt 1805), y estas vienen marcadas prioritariamente por el clima. En zonas templadas existe una fuerte estacionalidad térmica y lumínica que da lugar a cuatro estaciones (primavera, verano, otoño e invierno). En cambio, en zonas tropicales no desérticas, la estacionalidad viene marcada principalmente por oscilaciones en las precipitaciones, dando lugar a dos estaciones (estación lluviosa y estación seca), mientras que el régimen de temperaturas es más o menos homogéneo a lo largo del año (MacArthur 1972, Fick and Hijmans 2017). Estas estacionalidades podrían tener consecuencias en la intensidad con la que la selección ambiental y los procesos dispersivos estructuran las metacomunidades. Sin embargo, existen argumentos a favor y en contra de mayores intensidades de los procesos de selección ambiental y de dispersión tanto en regiones tropicales como en regiones templadas o mediterráneas, que son un caso particular de regiones de clima templado, distribuidas por varios continentes y que tienen como particularidad una marcada estación seca que coincide con la época más cálida (Blondel et al. 2010).

La temperatura, entre otros factores que cambian estacionalmente, puede suponer un importante filtro ambiental para muchas especies (Kreyling et al. 2019). Por tanto, es esperable que, por tener más variabilidad (i.e. heterogeneidad) e impredecibilidad ambiental (Blondel et al. 2010), y por tener filtros ambientales (al menos abióticos) más severos (Francis y Currie 2003), las metacomunidades de sistemas templados (p.e. mediterráneos) estén más estructuradas por la selección ambiental que las metacomunidades de sistemas tropicales (Myers et al. 2013; Souffreau et al. 2015). Sin embargo, las fuertes precipitaciones en los trópicos también podrían tener como consecuencia oscilaciones estacionales en los parámetros físico-químicos del agua (e.g., la turbidez; Alcântara et al. 2009). Esto podría generar una heterogeneidad ambiental que intensificara el rol de los efectos ambientales en las metacomunidades tropicales, aunque los ambientes mediterráneos también tienen grandes variaciones estacionales en el régimen de precipitaciones (Blondel et al. 2010).

Por otro lado, los sistemas acuáticos pueden sufrir importantes variaciones en la conectividad de los parches debido a intensas precipitaciones

(Brasil et al. 2020). Esta conectividad puede aumentar con el llenado de las charcas, que en ocasiones pueden sufrir desbordamientos llegando incluso a conectar completamente sistemas cercanos. Este efecto es mucho más marcado en los trópicos, donde las inundaciones derivadas de las precipitaciones pueden llegar a inundar grandes zonas de la cuenca hidrográfica de los ríos (Junk et al. 1989). Como consecuencia, se produciría, por un lado, cierta homogeneización del ambiente y, con ello, un relajamiento en la intensidad de la selección ambiental (Rojo et al. 2016; Brasil et al. 2020). Por otro lado, al aumentar la conectividad también aumenta la importancia de los procesos de dispersión, pudiéndose llegar a producir efectos de masa que homogeneizaran la metacomunidad (Thomaz et al. 2007). Como consecuencia de las inundaciones periódicas, las metacomunidades de charcas tropicales podrían estar menos aisladas y más homogeneizadas ambientalmente que las mediterráneas, al menos regionalmente, dando lugar a efectos ambientales más discretos (Heino et al. 2015). En sistemas tropicales muy conectados, el papel de los procesos dispersivos podría ser variable en función de la intensidad con la que actuaran los efectos de masa (Oikonomou 2021). Por el contrario, en las charcas mediterráneas, más aisladas, podrían esperarse efectos espaciales intensos relacionados con la limitación dispersiva.

Sin embargo, la existencia de barreras orográficas entre los parches de la metacomunidad puede dar lugar también a limitaciones dispersivas teóricamente más intensas en los trópicos. Los organismos tropicales están adaptados a temperaturas localmente más o menos constantes a lo largo del año, mucho menos variables que en zonas templadas, donde los organismos están adaptados a una variabilidad de temperaturas mayor, lo que les permite sobrevivir al verano y al invierno. La orografía, además de una barrera física, también es una barrera climática, con temperaturas menores que en zonas bajas. Al estar adaptados a temperaturas más homogéneas, los organismos tropicales de zonas bajas encuentran más dificultades para traspasar el filtro ambiental de las barreras orográficas que los organismos de zonas templadas. Es por ello que se considera que las montañas son “más altas” en los trópicos que en las zonas templadas (Janzen 1967).

En cuanto al papel del tiempo, son también pocos los estudios que han abordado este proceso, con resultados variables, desde efectos significativos pero débiles (Anderson y Cribble 1998; Padial et al. 2014), hasta efectos temporales que dominan la metacomunidad (Castillo-Escrivà et al. 2017b; Wu et al. 2017). Sin embargo, ningún trabajo previo ha comparado el papel relativo del tiempo en la organización de metacomunidades en diferentes regiones biogeográficas. No obstante, sería esperable encontrar efectos temporales más intensos en metacomunidades mediterráneas que en tropicales. Los cambios ambientales derivados de la estacionalidad (MacArthur 1972; Richter

2016), y la elevada impredecibilidad ambiental de los sistemas mediterráneos (Blondel et al. 2010) podría dar lugar a cambios temporales más rápidos en la estructura de la metacomunidad.

OBJETIVOS

En resumen, el objetivo general de esta tesis es estudiar la relevancia de los diferentes procesos que estructuran las metacomunidades de charcas temporales situadas en regiones biogeográficas distantes, usando una aproximación espacial y temporal. Se revisaron aspectos generales de las metacomunidades en los trópicos y en primer lugar, se estudió la organización de una metacomunidad tropical formada por charcas temporales del Pacífico centroamericano (en Costa Rica y Nicaragua). Posteriormente, se estudiaron y compararon las características ambientales de tres conjuntos de charcas temporales , dos en clima mediterráneo (de España y Chile) y uno tropical, en Costa Rica. Finalmente se compararon dos metacomunidades de charcas temporales situadas en dos regiones con marcadas diferencias climáticas, una tropical (Costa Rica) y una mediterránea (este de España), usando escalas espaciales similares y una metodología común. Los objetivos específicos de esta tesis son:

1. Revisar el conocimiento existente actualmente sobre metacomunidades de humedales tropicales.
2. Evaluar el rol de la selección ambiental, los procesos dispersivos y los efectos temporales en una metacomunidad tropical, estudiando múltiples taxones, a lo largo de un año hidrológico
3. Explorar las diferencias y similitudes en cuanto a características ambientales y heterogeneidad ambiental existente en charcas temporales situadas en una región tropical y dos regiones mediterráneas.
4. Comparar la contribución relativa del ambiente y el espacio a la estructura de metacomunidades de charcas temporales de una zona tropical y una zona mediterránea en el inicio del hidroperiodo, estudiando múltiples taxones
5. Cuantificar la importancia relativa de los efectos ambientales, espaciales y temporales durante un año hidrológico completo en metacomunidades de charcas temporales tropicales y mediterráneas, estudiando múltiples taxones
6. Estimar y comparar las diversidades alfa, beta y gamma en metacomunidades de charcas temporales de dos zonas con diferencias latitudinales, una en un clima tropical y otra en un clima mediterráneo, estudiando múltiples taxones durante un año hidrológico, desde una perspectiva espacial y temporal

ESTRUCTURA DE LA TESIS

La presente tesis presenta una **Introducción general**, seguida de seis capítulos originales, que se describirán brevemente a continuación, y, finalmente, una **Discusión general**.

En el **Capítulo 1**, *Metacommunity structure and dynamics*, se hizo una revisión sobre la teoría de metacomunidades, aunando el conocimiento sobre los diferentes procesos que estructuran las metacomunidades de humedales tropicales y su diversidad biológica. Este capítulo ha sido recientemente publicado como capítulo de un libro de revisión sobre humedales tropicales (Gálvez et al. 2021). En el **Capítulo 2**, *Environment and space rule, but time also matters for the organization of tropical pond metacommunities*, estudiamos una metacomunidad de charcas temporales tropicales, ubicada en la vertiente del Pacífico del norte de Costa Rica y sur de Nicaragua. El objetivo de este capítulo fue estudiar el papel de los efectos ambientales, espaciales y temporales en varios grupos de organismos acuáticos, a lo largo del mismo año hidrológico. Este capítulo ha sido publicado en forma de artículo en un volumen temático dedicado a ecología de metacomunidades (Gálvez et al. 2020a). En el **Capítulo 3**, *The environmental framework of temporary ponds: A tropical-mediterranean comparison*, hicimos una extensa caracterización ambiental de tres conjuntos de charcas temporales ubicadas en regiones biogeográficas distintas: una tropical (Costa Rica) y dos mediterráneas (España y Chile). El objetivo de este capítulo fue identificar las principales similitudes y diferencias ambientales, incluyendo variables locales (fundamentalmente limnológicas), macroclimáticas y paisajísticas, entre las tres regiones. Este capítulo fue publicado en formato de artículo (Olmo et al. 2021). La primera autora, C. Olmo, y el autor de la presente tesis, Á. Gálvez, contribuyeron igualmente en este trabajo. C. Olmo aportó los datos obtenidos en Chile, mientras que Á. Gálvez aportó los obtenidos en Costa Rica y España. Ambos co-autores participaron en el análisis de los datos y la redacción del manuscrito. En el **Capítulo 4**, *Pond metacommunities from bacteria to birds: heterogeneous response among taxa but with overall stronger environmental effects in a mediterranean than in a tropical setting*, comparamos la intensidad con la que actúan los efectos ambientales y espaciales en la estructura de dos metacomunidades de charcas temporales situadas en regiones biogeográficas diferentes, una tropical en Costa Rica y una mediterránea en España (anteriormente caracterizadas en el Capítulo 3). Además de comparar entre regiones, también tenemos en cuenta la capacidad dispersiva de los diferentes grupos de organismos estudiados (desde bacterias hasta aves). En el **Capítulo 5**, *Temporal dynamics in mediterranean and tropical temporary pond metacommunities: a multi-taxon approach*, incorporamos la variable temporal al estudio de las metacomunidades de las charcas temporales trabajadas en el Capítulo 4, incluyendo datos obtenidos en tres ocasiones a lo largo de un mismo año hidrológico. En este capítulo pretendemos, comparando entre regiones y grupos de organismos, comprobar como varía el rol de los efectos ambientales y espaciales con el tiempo. Finalmente, en el **Capítulo 6**, *Higher alpha and gamma, but not beta diversity in tropical than in mediterranean temporary ponds: a spatial and temporal analysis*, comparamos la diversidad biológica en las dos metacomunidades trabajadas en los dos capítulos anteriores. En este capítulo pretendemos comprobar si la diversidad taxonómica en las charcas temporales estudiadas cumple los patrones latitudinales globales descritos en la literatura. Además de esta perspectiva espacial, pretendemos comprobar si la diversidad biológica es más variable con el tiempo en una región u otra. En la discusión general tratamos de englobar los diferentes resultados obtenidos y comprobar si encontramos algún patrón general en la estructura de las metacomunidades temporales estudiadas.

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Laguna de Peje, Costa Rica. Fotografiado por Juan Rueda

CAPÍTULO 1

Metacommunity structure and dynamics.

THE METACOMMUNITY APPROACH

Biological populations are not isolated systems, as they are linked by interspecific interactions such as competition, mutualism, and/or predation. All these populations of different species living together at the same time and in the same area make up an ecological community (Elton, 1927; Fauth et al., 1996). Community ecology can therefore be defined as the study of patterns and processes in the structure and behavior of these multispecies assemblages (Morin, 2011; Mittelbach and McGill, 2019). One of the main goals of community ecology is understanding species distribution according to their biotic and abiotic environments. But ecological communities are not static elements occupying discrete localities. In fact, local communities are regionally related, so that the habitat patches where they live are embedded in a landscape matrix and interconnected through dispersal events **(*Figure 1*;** see Brendonck et al., 2022a,b; Dalu et al., 2022; Piedade et al., 2022; Reichard, 2022; Moraes et al., 2022; Dube et al., 2022). The niche-assembly perspective in Ecology (Hubbell 2001) considers that species distributions are mostly the result of the range of environmental conditions and resources that organisms can tolerate and their function in the ecosystem (the niche concept; Hutchinson, 1957; Chase and Leibold, 2003).

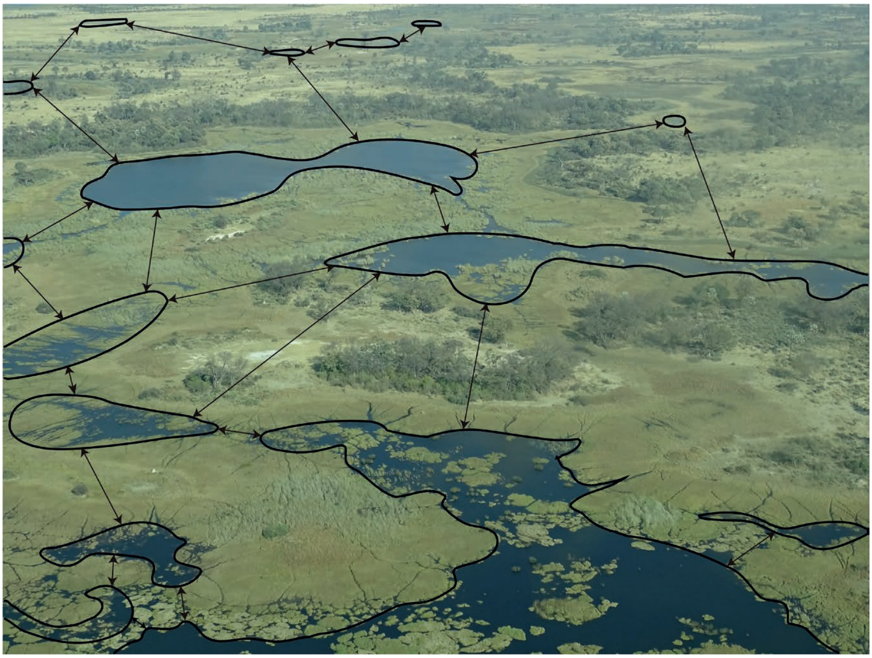

***Figure 1**:* Metacommunity system in Okavango delta, Botswana. Aquatic habitats (patches) are surrounded by terrestrial habitat (matrix), but potentially connected between them (bidirectional arrows). Aerial picture taken from a plane in the vicinity of Maun (Southern delta).

However, this mainstream view usually underestimates other important factors also affecting species distributions. Consequently, modern community ecology considers that species composition in a given locality is the result not only of niche processes but also, and importantly, of dispersal constraints, that is, through spatial filtering of a larger-scale species pool, and of internal dynamics (Belyea and Lancaster, 1999). However, defining the spatial and temporal boundaries of a community may not always be straightforward, and ecological community studies come upon very variable and scale-dependent results (Chave, 2013), so that some authors have even challenged the use of the community concept itself as too artificial (Ricklefs, 2008).

The metacommunity concept was born under the need for a theoretical framework that considered multiple processes at different scales (Leibold and Chase, 2018). A metacommunity consists of a set of communities distributed in ecosystem patches, embedded in a landscape matrix, and potentially connected by dispersal of multiple interacting species (Hanski and Gilpin, 1991; Wilson, 1992). In this way, the metacommunity view stresses the potential connections among communities and highlights the influence of regional-scale processes on diversity and composition at the local scale.

Metacommunity theory shifts the focus from the local to a combination of local and regional processes (***Figure 2***). Species richness and composition are therefore the result of not only environmental filtering (or species sorting; Leibold et al., 2004) but also of dispersal between patches (Wilson, 1992; Bell, 2000; Hubbell, 2001). In addition, dispersal strategies widely differ among species (Leibold, 2011), and dispersal processes are also affected by the landscape matrix characteristics (Castillo-Escrivà et al., 2017a). The emergence of metacommunity neutral models (Bell, 2000; Hubbell, 2001) demonstrated how empirical patterns of biodiversity (e.g., species-area relationships, rank-abundance diagrams) could be replicated in silico relying on stochastic demographic dynamics and neutral migration processes (considering all species equal regarding their niche and dispersal abilities, hence in the absence of selection and adaptation). Therefore, ever since these theories were published, ecological drift and spatial autocorrelation through neutral dispersal had to be considered in null hypotheses when explaining the organization of metacommunities. However, subsequent tests with empirical data suggested that niche-related deterministic processes might dominate over neutral processes, indicating that the niche also needed to be considered in such analyses (Cottenie, 2005).

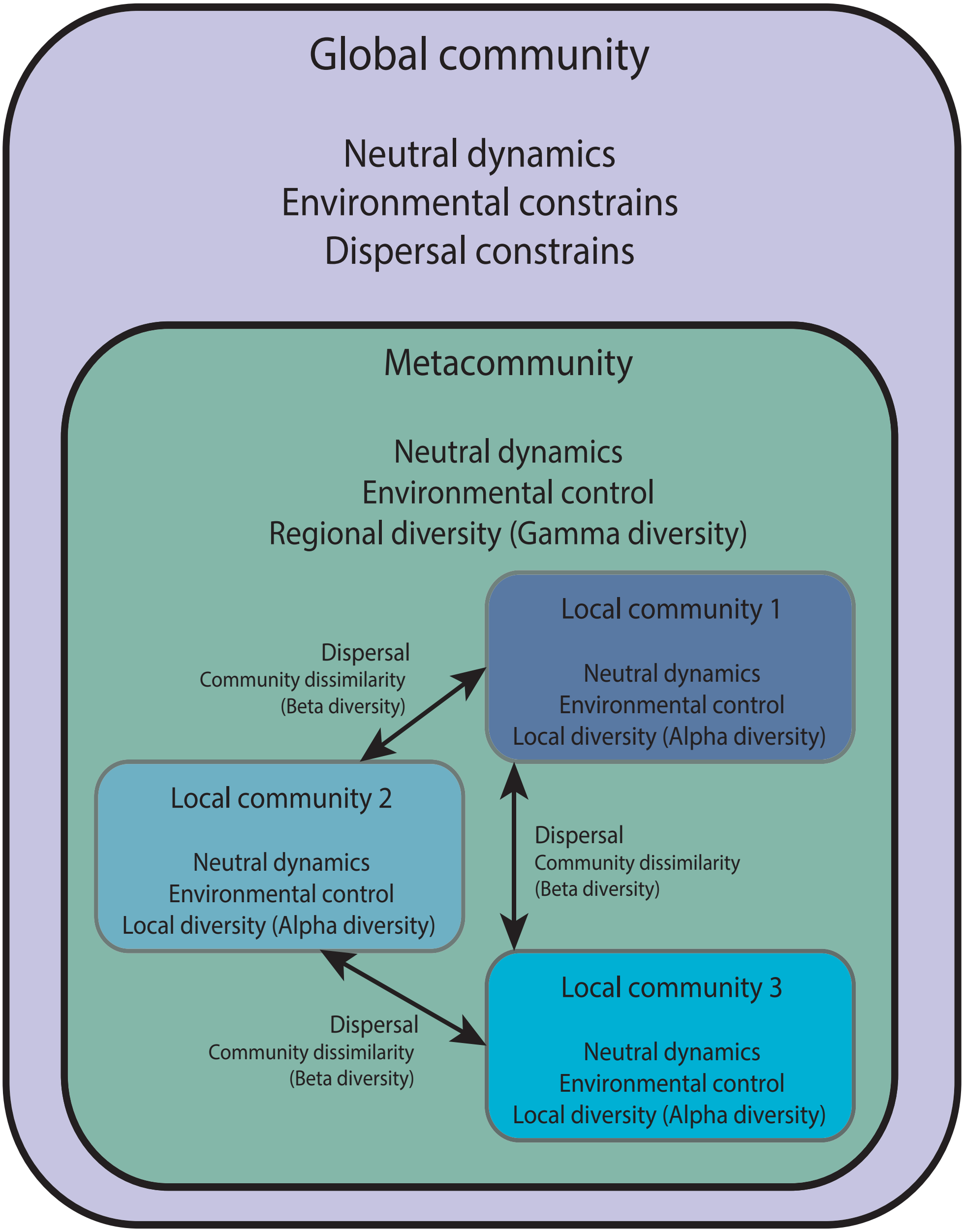

***Figure 2**:* Schematic diagram of the main ecological processes acting at different scales on metacommunity organization, so as indication of the scale focus of diversity components. Neutral dynamics (ecological drift), environmental control (selection), and dispersal are the main ecological processes structuring metacommunities at different spatial scales. Alpha, beta, and gamma diversities describe different dimensions of metacommunity diversity at the local, between localities and regional scales, respectively. Based on Vellend, M., 2010. Conceptual synthesis in community ecology. Quarterly Review of Biology 85, 183-206.

Under this framework of local communities linked by dispersal processes within a regional metacommunity, both local diversity and regional species pools play a role in understanding small-scale biodiversity patterns. As such, metacommunity theory links the multiscale components of biological diversity (Whittaker, 1972; Magurran and McGill, 2011): alpha diversity, corresponding to local diversity, beta diversity, which quantifies the dissimilarity between local communities, and gamma diversity, with focus on the largerscale regional diversity (***Figure 2***).

Along this chapter, we will consider how the three main processes, environmental control, dispersal, and neutral dynamics, structure metacommunities of tropical freshwater wetlands. In addition, we will compare the effects and importance of each of these processes in tropical water bodies, to the more intensely studied temperate wetlands, in relation to their influence on biological diversity. For that purpose, we will provide examples of different groups of organisms and habitat types, as shown by variation partitioning analysis. This analysis allows to disentangle the relative effects on species distribution played by environmental and spatial factors (environmental control and dispersal processes) and the remaining undetermined (partly stochastic or neutral) effects. Finally, we will discuss the implications of metacommunity theory for tropical wetland conservation.

PROCESSES SHAPING AQUATIC METACOMMUNITIES

There is a considerable body of literature discussing the relative fit of different metacommunity paradigms or archetypes, especially on the role of species sorting against neutral theory (Cottenie, 2005); Gravel et al., 2006; Logue et al., 2011; Brown et al., 2017). This has led to general agreement about the main processes structuring metacommunities, both at small and large spatial, and even temporal scales. Among these processes, those assumed to have a marked influence on metacommunity dynamics in the short term are selection (niche or environmental effects, also known as species sorting), dispersal (spatial effects), and neutral processes, epitomized by ecological drift (demographic stochasticity) (see Vellend, 2010). These are general drivers of metacommunities, including those in aquatic environments. Indeed, the study of freshwater metacommunities, because of their relative isolation in a landscape matrix, has been instrumental for the evaluation and understanding of processes of metacommunity organization in the natural context (Heino et al., 2015; Leibold and Chase, 2018).

Environmental control

The concepts of environmental control, niche-control, species sorting, and habitat filtering, all have very similar meaning and refer to biotic and abiotic factors controlling species establishment and fitness (Lozada-Gobilard et al., 2019). This idea is encapsulated by the more traditional term in the biological (evolutionary) literature of "selection" (Vellend, 2010). In this context, selection infers that environmental tolerance and resource utilization varies among species (Chase and Leibold, 2003). At the local scale, abiotic and biotic factors, such as environmental stress, resource availability, or biological interactions (competition, predation, mutualism) can strongly influence species presence, performance, coexistence, and distribution, and therefore metacommunity structure (see Dalu et al., 2022; Deemy et al., 2022). At larger scales, habitat heterogeneity and consequently resource and interaction heterogeneity, allow for the coexistence of more species, increasing regional pools (MacArthur and MacArthur, 1961). This heterogeneity leads to environmental gradients where several species survive with different adaptations.

Important environmental factors

Local environmental biotic and abiotic pressures can deterministically filter the species composition within a patch, what is known as species sorting (Leibold et al., 2004). Unlike the major influence of temperature on temperate wetland metacommunities, where seasonal variation exert a strong control, tropical wetland metacommunities seem to be mostly influenced by hydrological cycles (such as the flood pulse), playing a key role on metacommunity assembly (Wantzen et al., 2016). Tropical wetlands can be highly variable, ranging from large river floodplains to small temporary shallow ponds, and including oxbow lakes and coastal freshwater marshes. The hydrological cycle *per se* can strongly influence other environmental variables, for example, light penetration, salinity, nutrient concentration, pH, or organisms dilution, which work as direct environmental filters (Nursuhayati et al., 2013; Sasa et al., 2015). Other relevant drivers are wide variation in oxygen concentration due to high temperatures, high organic matter decomposition rates, and shading by helophytic and floating vegetation (Roldán and Ramírez, 2008). In addition, there are peculiar microhabitats in tropical wetlands that affect ecosystem functioning but are rare in other climates. For example, vegetation architecture is an important influence on aquatic invertebrate community assembly. Some organisms, especially benthic invertebrates, depend on the root systems of floating vegetation such as *Eichornia* spp. and *Polygonum* spp. (Heckman, 1997; Barker et al., 2014; Ohtaka et al., 2014). In contrast, in temperate wetlands, it is mostly the submerged vegetation (such as *Myriophyllum* spp., macroalgae of the family Characeae) which support a high diversity and biomass of invertebrates, from ostracods to insects (Tessier et al., 2004). Nevertheless, De Klerk and Wepener (2011) highlight the high species richness of aquatic macroinvertebrates inhabiting also marginal and emergent vegetation, which are common in either temperate or tropical wetlands. In addition to facilitation, other positive (mutualism) and negative (predation, competition) biotic interactions also affect metacommunity structure, and some studies suggest that they can be even more intense in tropical compared to temperate areas (Andresen et al., 2018).

The role of scale and patch variability

The strength and direction of the environmental control on species composition in a metacommunity can vary through space and time. Habitat heterogeneity is expected to positively correlate with the increase in area (Rosenzweig, 1995). Furthermore, environmental fluctuations and cycles can be produced by various time-dependent processes such as climatic seasonality, disturbances, or biotic interactions, including shifts related to phenological and demographic changes. In tropical wetland metacommunities, many local environmental factors that deterministically filter the regional pool of species include salinity, oxygen concentration, light intensity, nutrient availability, or the presence of fish and other predators. These environmental conditions can differ between wetlands in the same region, generating spatial heterogeneity. Even within the same waterbody, the presence of different microhabitats (shallow shorelines, water column, aquatic vegetation, etc.) can lead to increased habitat heterogeneity and ultimately to higher species richness (Gleason et al., 2018). Furthermore, water and nutrient inputs during the rainy season, bird migrations, fires, or seasonal desiccation give rise to temporal changes in environmental conditions, that is, temporal heterogeneity. Therefore, temporal changes in niche-control also originate differences in metacommunity structure. As a consequence, one can expect the role of environmental factors and species sorting intensity to vary across time (Rojo et al., 2016; Csercsa et al., 2019; Gálvez et al., 2020). Thus, the length of spatial and temporal environmental gradients can lead to intrapatch and interpatch heterogeneity (Questad and Foster, 2008). As a result of intrapatch heterogeneity, alpha diversity may increase, and interpatch heterogeneity leads to higher beta and gamma (regional) diversity (Larkin, 2018). Such patterns have also been observed in tropical wetlands. In a study of sediment bacteria communities from an Indian mangrove forest, Behera et al. (2018) found that interpatch and seasonal heterogeneity, related to changes in environmental conditions (such as monsoon precipitations), drove differences in bacterial species composition. Crossetti et al. (2018) showed how intrapatch heterogeneity did not correlate with phytoplankton community structure in a Brazilian coastal wetland, but seasonal changes lead to strong differences in community composition. Ronchi-Virgolini et al. (2013) also found no intrawetland differences in a bird community of the Paraná River, although it significantly differed between seasons and years. However, Ferreira et al. (2019), working in the Amazon River floodplain, observed a strong influence of intrapatch heterogeneity on species richness and abundance of ardeid birds, suggesting that this heterogeneity provided suitable microhabitats for a variety of species.

The influence of environmental stress on biological diversity

Variation in the intensity of local environmental (abiotic) control has implications for the biological diversity of a metacommunity. When species sorting by the abiotic environment is weak, but competition is strong, diversity can be reduced through exclusion due to the influence of dominant species, as observed in vegetation studies of temperate environments using productivity as a surrogate of severity (Yang et al., 2015; ***Figure 3***). When the intensity of niche-control increases (in a heterogenous way between patches), so do alpha, beta, and gamma diversities, because each patch diverges in environmental conditions, and can therefore support different species. Finally, under severe species sorting effects, only few species are adapted to survive in such harsh environmental conditions, provoking a decay in biological diversity, revealing a unimodal pattern in the diversity-severity relationship. However, this pattern does not seem to hold in tropical vegetation (Pärtel et al., 2007), with a monotonic decrease of species richness with increasing severity (***Figure 3***). It is still unclear whether or not these relationships of environmental stress with diversity hold in tropical and temperate freshwater ecosystems. Considering the more isolated character of water bodies compared to the terrestrial landscape, the pattern might depend more strongly on connectivity and patch size, influencing, respectively, the arrival of strong competitors and the possibilities of finding refugia by weak ones, and therefore affecting competitive exclusion (Lomolino, 2000).

Extreme environments are also strong environmental filters in tropical aquatic ecosystems. For example, Chakraborty et al. (2011) found that salinity drove important changes in phytoplankton community composition in an Indian estuarine system. Sosa-López et al. (2007) found a negative relationship between fish species richness and salinity in Mexican coastal lagoons. Pinder et al. (2005) showed the same relationship when studying aquatic invertebrates in Australian wetlands. Verschuren et al. (2000) also found this negative relationship in the invertebrate community of a Kenyan shallow lake, but they concluded that this relationship was an indirect effect of changes in microhabitat and resource availability. It is not so clear, however, whether or not reduced environmental stress could produce a reduction in local species richness due to competitive exclusion (Yang et al., 2015), not only in tropical but neither in temperate aquatic communities. For instance, if we consider drought as a stress for aquatic communities, when comparing between permanent and temporary water bodies at a global scale, Antón-Pardo et al. (2019) found reduced species richness in temporary waters, independent of climate and other factors, suggesting a monotonic negative relationship between local diversity and drought stress in fresh waters, not a unimodal one as suggested by Yang et al. (2015).

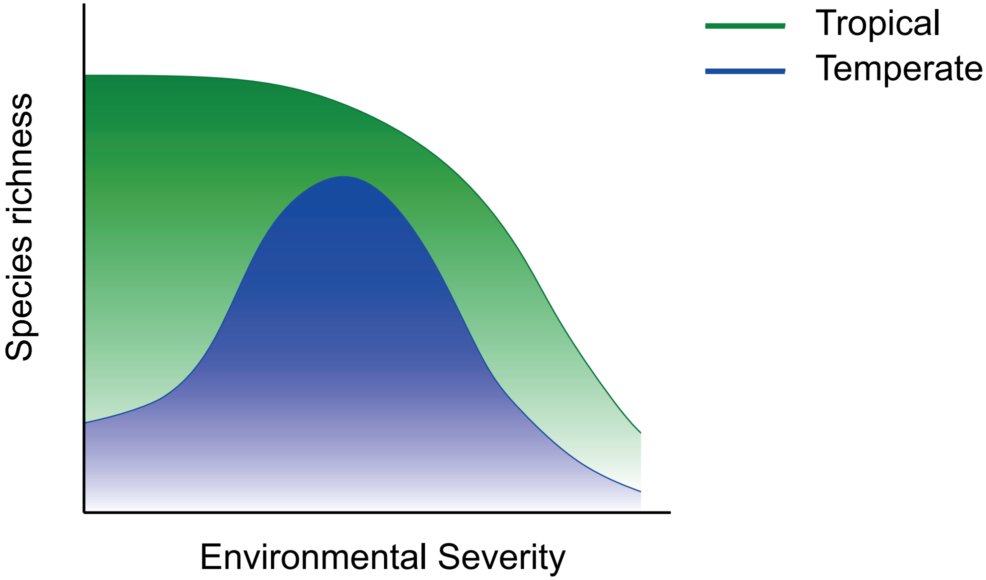

Figure 3: Expected relationship between environmental severity and species richness, based on terrestrial vegetation studies from P*ä*rtel et al. (2007) and Yang et al. (2015), assuming strong competitive exclusion processes and relatively high dispersal in the temperate setting.

Dispersal

Dispersal is the key element integrating local communities in a metacommunity framework. Not only does it allow genetic flow between populations from different patches, but it also enables colonization of patches by species. This process is especially important in colonization-competition dynamics, where good colonizers but bad competitors (fugitive species) compete with bad colonizers but good competitors. Fugitive species are able to successfully colonize empty patches but they become locally extinct when a better competitor arrives (Mittelbach and McGill, 2019). Nevertheless, fugitive species can persist at regional scale (Levins and Culver, 1971), and good competitors may not be able to colonize an already occupied patch because of priority effects (discussed in the next section).

Dispersal limitation, connectivity, and dispersal surplus

Species distribution can be strongly influenced by dispersal ability, not only by niche-control. As a consequence, species distributions are the result of local environment and regional dispersal limitation. Dispersal limitation depends on organism dispersal ability (e.g., flying vs walking dispersal). For example, some organisms will be more dispersal limited between drainage systems than within the same hydrological basin (Heino et al., 2017). In these riverine ecosystems, dispersal can be influenced by water flow (i.e., downstream passive drift vs upstream active movement; Tonkin et al., 2017). Sometimes it is the own ecosystem traits which limit dispersal. For instance, organisms inhabiting small isolated temporary ponds are expected to be more dispersal limited than those inhabiting well-connected marshlands (Heino et al., 2015).

Once again, this process can be time dependent. For example, seasonal bird migration events can become key dispersal mechanisms at a particular time for many organisms (Green and Figuerola, 2005; Green et al., 2016; Viana et al., 2016). Waterways are obviously essential for the dispersal of many aquatic organisms, but these can also be temporary. No matter the taxon or the ecosystem, dispersal is strongly influenced by seasonal hydrology. For example, Thomaz et al. (2007) showed that metacommunities in tropical river-floodplain systems are homogenized by patch connections established in rainy seasons. During the flood phase, connectivity between isolated water bodies increases (***Figure 4***). By the same token, connectivity between tropical water bodies decreases during the dry season (Brasil et al., 2020). Patches become progressively isolated and even wide wetlands can be split into several small ponds, with their communities becoming more environmentally and spatially independent.

With the increased connectivity during the rainy season, and the resulting decrease in dispersal limitation, one might assume that dispersal limitation is not as relevant in tropical wetlands as it is in temperate regions. However, organism dispersal may be limited by strong barriers such as those derived from regional orography. As Janzen (1967) stated, “mountain passes are higher in the tropics”. Strong altitudinal climate gradients, in addition to narrow climatic niches, can restrict species dispersal. Myers et al. (2012), when studying plant beta diversity, found support for stronger dispersal limitation in tropical forests than in temperate ones, although the authors suggest this might be related to the rarity of many species in such rich metacommunities.

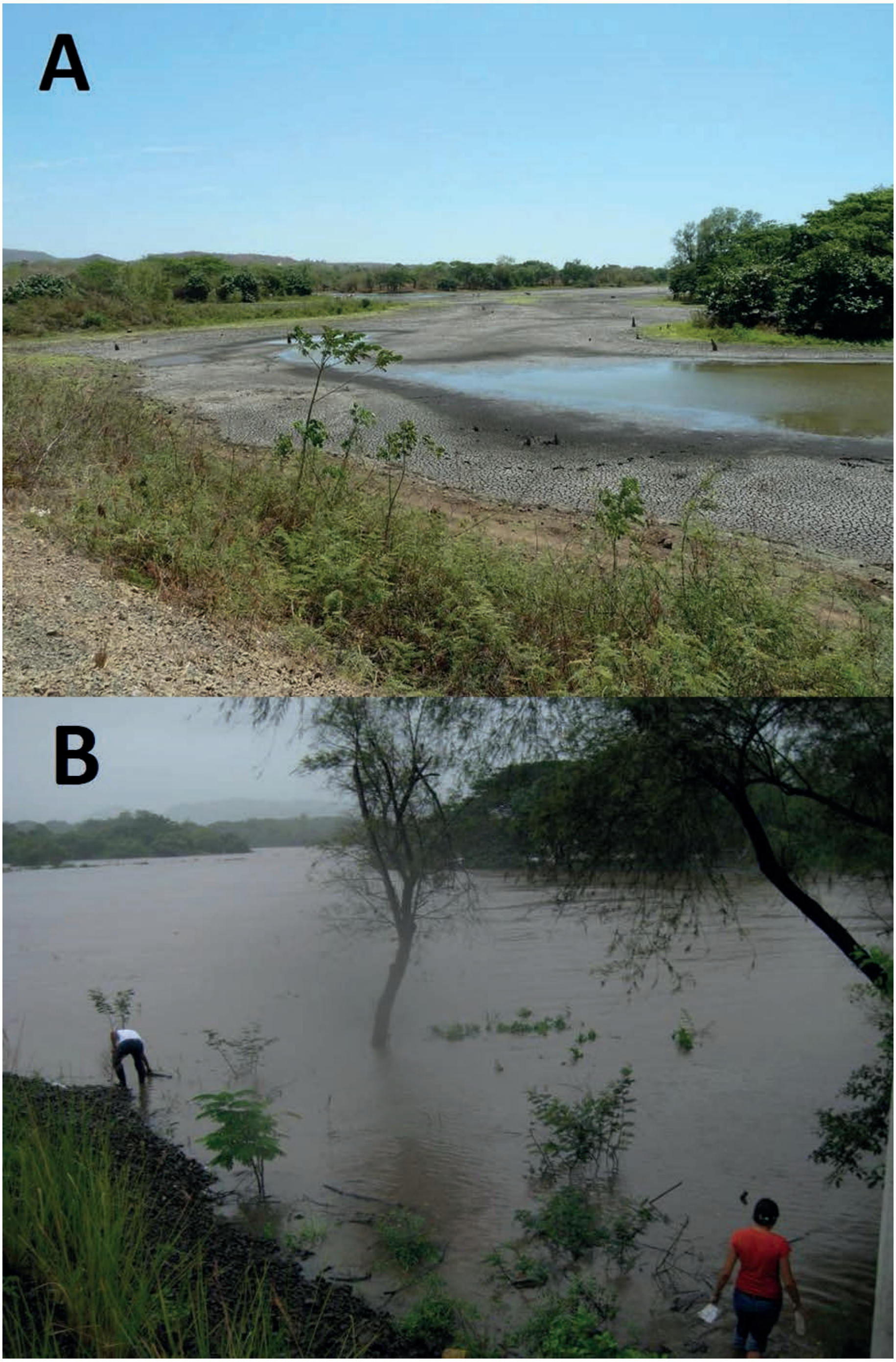

Figure 4: Connectivity between wetlands is highly influenced by seasonal hydrology. Palermo wetland in Nicaragua during the dry (A) and the rainy (B) seasons.

Dispersal surplus is an opposing process to dispersal limitation. Populations of an organism inhabiting a suboptimal patch can be maintained by migration from a near patch, what is known as source-sink dynamics, or mass effects (Loreau and Mouquet, 1999). These mass effects can lead to increasing species richness, but eventually this overdispersal can produce a metacommunity homogenization. However, disentangling unsuccessful dispersal events related to sink habitats from successful colonization needs from monitoring of populations to acknowledge absence of reproduction of the dispersed individuals in those habitats, a type of study seldom performed in natural aquatic environments. In support of the mass-effects expectations, Brasil et al. (2020) found that during rainy seasons in tropical wetlands, patch connectivity lead to metacommunity homogenization in the phytoplankton from Brazilian riparian lakes. Other instances of mass-effects in aquatic metacommunities may include the migration of amphibians to breeding sites (Sinsch, 1990), floating plants drifting downstream (Gay, 1960), or insect oviposition after massive synchronized emergences such as those produced by mayflies (Sartori and Brittain, 2015).

Variation among organisms

Dispersal limitation is considered to differ among organisms and life-cycle strategies (Nathan et al., 2008; Incagnone et al., 2014; Tesson et al., 2015). For instance, plankton dispersal through resting forms must be different from that of active dispersal by amphibians, while birds, with flying abilities, are generally less dispersal limited than fish. In aquatic ecosystems, propagule size and type of dispersal are considered to be key factors for dispersal limitation and therefore metacommunity organization. Some studies in both temperate and tropical regions (De Bie et al., 2012; Padial et al., 2014) found that active dispersers are less influenced by spatial effects than passive dispersers. These works also concluded that propagule size is negatively correlated with dispersal ability in passive dispersers (small propagules can be transported further by wind, water, or animals; Vanschoenwinkel et al., 2008, 2009) and positively in flying active dispersers (bigger animals can fly further). In contrast, fish and amphibians were strongly dispersal limited (De Bie et al., 2012; Padial et al., 2014).

However, such an established pattern between propagule size and type of dispersal has been challenged because of some contradictory results (Astorga et al., 2012; Gálvez et al., 2020). A study in tropical freshwater metacommunities found that the distribution of passively dispersing cladocerans was affected by spatial constraints, even within the same hydrographic basin (Rocha et al., 2017). In addition, Langenheder et al. (2016) found a strong spatial effect in a highly connected bacterial metacommunity. Dias et al. (2016) detected high variability in the role of spatial processes in a zooplankton metacommunity, as did Benito et al. (2018) working on diatoms, whereas Verleyen et al. (2009) found a low influence of dispersal processes on the structure of another diatom metacommunity. In South African rock pools, Vanschoenwinkel et al. (2007) found spatial effects in invertebrates with passive dispersal, but not in active dispersers. Flying active dispersers, such as birds, are important dispersal vectors for microorganisms (Green and Figuerola, 2005; Tesson, 2015; Viana et al., 2016), so that we may expect passive dispersers not to be more strongly limited by spatial barriers compared to birds (although birds could be more efficient, due to their oriented movement toward suitable habitats). It is probable that snapshot surveys, which do not take into account the highly temporal variability of dispersal related with seasonal hydrological cycles, may give rise to misleading results (Rojo et al., 2016; Gálvez et al., 2020). Despite the large variability and apparent disagreement between some studies, all of them remark the importance of dispersal in all taxa, showing how it differs between groups of organisms. This wide variability is summarized in ***Table 1***, which will be discussed below.

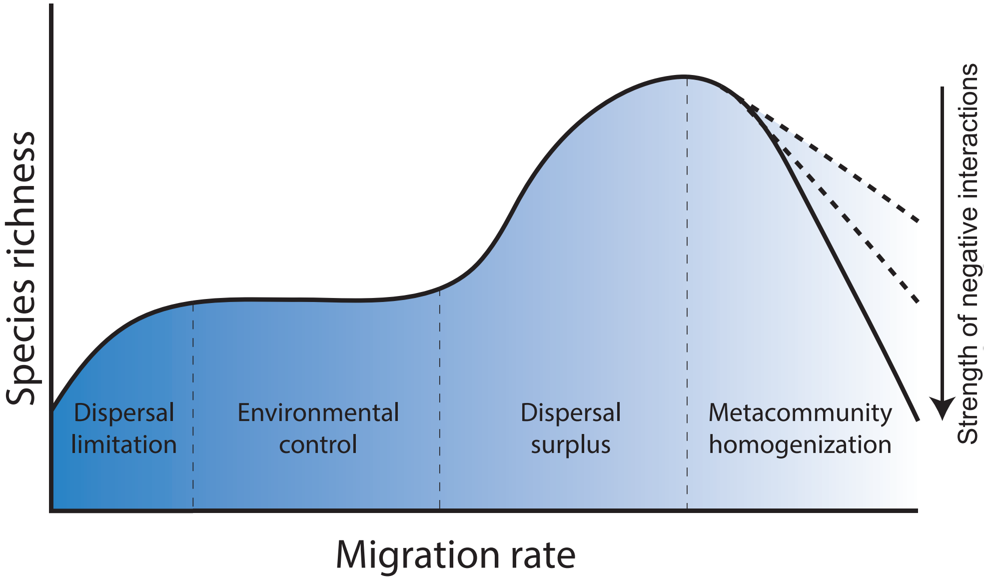

Figure 5: Theoretical relationship between species richness and migration rate. The rate of biodiversity decay due to metacommunity homogenization might be positively related with the strength of negative interactions and negatively with ecological redundancy (dashed lines). Based on Leibold, M.A., Chase, J.M., 2018. Metacommunity Ecology. Princeton University Press, Princeton.

Table 1: Results of variation partitioning analyses for metacommunities of temperate and tropical wetlands, obtained by different authors for various taxonomic groups.

Region	**Taxon**	**$E \mid S$**	**$S \mid E$**	**$E \cap S$**	**R**	**Reference**
Tropical	Bacteria	0-19	0-19	0-16	70-99	Nabout et al., 2009
Temperate	Bacteria	11-14	2-6	4-6	76-81	Beisner et al., 2006
Temperate	Bacteria	8-15	1	0	85-90	De Bie et al., 2012
Temperate	Bacteria	13	10	2	75-77	Langenheder and Ragnarsson, 2007
Temperate	Bacteria	7-16	8-16	1	76	Langenheder et al. 2016
Tropical	Diatomea	0-13	0-38	0-21	37-97	Benito et al., 2018
Tropical	Diatomea	17-18	6-9	2-4	69-75	Verleyen et al., 2009
Temperate	Diatomea	7-8	2-3	2-5	84-89	De Bie et al., 2012
Tropical	Phytoplankton	3-10	0-7	0-2	84-92	Brasil et al., 2020
Tropical	Phytoplankton	20-27	0-7	1-7	66-72	Padial et al., 2014
Tropical	Phytoplankton	0-13	0-9	n.a.	85-94	Rojo et al., 2016*
Temperate	Phytoplankton	2-7	0-3	1-6	92-94	Beisner et al., 2006
Temperate	Phytoplankton	7-8	2-3	0-1	90	De Bie et al., 2012

Table 1: Continued

Region	Taxon	E|S	S|E	E∩S	R	Reference
Temperate	Phytoplankton	27-9	0-6	0-3	73-91	Loewen et al., 2020
Temperate	Phytoplankton	12	12	2	74	Soininen et al. 2007**
Tropical	Macrophytes	1-4	7-28	0-1	68-90	Padial et al., 2014
Temperate	Macrophytes	1-16	0-9	2-14	73-93	Alahuhta et al., 2018
Temperate	Macrophytes	4	6	2	88	De Bie et al., 2012
Tropical	Cladocera	31	1	2	68	Rocha et al., 2017
Temperate	Cladocera	2-6	4	3	87-95	De Bie et al., 2012
Tropical	Zooplankton	3-11	0-8	0-6	75-95	Brasil et al., 2020
Tropical	Zooplankton	0-30	0-25	0-15	55-100	Dias et al., 2016**
Tropical	Zooplankton	4-5	1-3	0-1	88-93	Padial et al., 2014
Temperate	Zooplankton	4-22	0-20	0-6	56-92	Beisner et al., 2006
Temperate	Zooplankton	4	16	4	76	Soininen et al., 2007**
Tropical	Ostracoda	0-25	1-19	2-11	64-89	De Campos et al., 2016
Temperate	Ostracoda	22-59	0-17	0-3	41-77	Castillo-Escrivà et al., 2017
Temperate	Microcrustaceans	4-44	0-30	7-20	38-56	Gascón et al., 2016
Tropical	Macroinvertebrates	12-23	0-17	29-54	27-59	Li et al., 2020

Table 1: Continued

Region	Taxon	E|S	S|E	E∩S	R	Reference
Tropical	Macroinvertebrates	5-41	0-12	0-10	49-90	Li et al., in press.
Tropical	Macroinvertebrates	6-7	4-12	0-1	79-88	Padial et al., 2014
Tropical	Macroinvertebrates	5-20	2-15	3-10	60-90	Petsch et al., 2017**
Temperate	Macroinvertebrates	14-22	13-27	9	42-62	Bertin et al., 2014
Temperate	Macroinvertebrates	2-9	1-8	0-3	86-95	De Bie et al., 2012
Tropical	Fish	9-14	7-19	4-19	53-75	Fernandes et al., 2014
Tropical	Fish	2-7	8-23	1-10	67-76	Padial et al., 2014
Temperate	Fish	4-8	0-11	0-6	81-83	Beisner et al., 2006
Temperate	Fish	1	10-11	2	85-87	De Bie et al., 2012
Temperate	Amphibians	3	11	2	84	De Bie et al., 2012

We include percentages of variance explained by pure environmental component (E|S), pure spatial component (S|E), and the environment-space overlap (E∩S), so as the residuals (R).

*E∩S not indicated in original work.

**Approximated values from graphs due to numeric results not shown in the original work.

Influence on biological diversity

Dispersal is a key process structuring metacommunities, having a strong influence on their biological diversity. According to metacommunity theory (***Figure 5***), for a fixed regional species pool, low migration rates imply low local species richness due to dispersal limitation. As migration rates increase, species richness slightly increases, limited by environmental filtering (species sorting). When mass effects overtake the limiting capacity of species sorting, local species richness reaches its peak. Finally, if migration rates are too high, metacommunity is homogenized. Then, dominant species exclude less competitive ones, and species richness declines (Leibold and Chase, 2018). However, we hypothesize that under a relaxation of the competitive exclusion strength or/and allowing certain degree of ecological redundancy in local communities, the reduction in species richness at high dispersal rates ought not to be as sharp as expected from initial simulations (Mouquet and Loreau, 2002). These models, on which Leibold and Chase (2018) figure is based (see ***Figure 5***), assume strong competition and high probability of local extinction when the number of occupied locations is low (Mouquet and Loreau, 2002). So, we suggest that a certain intermediate diversity level above that attained under pure species sorting effects could be maintained with high intensity of dispersal (dashed lines in ***Figure 5***), notwithstanding priority effects, which could also help avoiding or delaying competitive exclusion of less adapted species.

However, not only local species richness, but all diversity components, either alpha, beta, or gamma, are dispersal-dependent in different ways. Mouquet and Loreau (2003; ***Figure 6***), using metacommunity simulations (20 communities with restricted capacity and 20 competing species), concluded that, with no dispersal, every patch is occupied by a different species, so that alpha diversity is minimal and gamma and beta diversities are maximal. At intermediate dispersal rates, alpha diversity increases, reaching a peak when the local species composition of each patch includes all components from the regional pool, while beta diversity falls to near zero values. When dispersal increases to maximum values in the models (every individual of every species can go everywhere), alpha diversity is reduced due to negative biotic interactions (competition), and so does gamma diversity due to regional extinctions. Beta diversity continues to be low with small variations, because the same species becomes dominant in every patch. However, as previously suggested in ***Figure 5***, we also consider that if the competitive exclusion effects would be relaxed, we might expect a less sharp decline of local and regional diversity at high dispersal scenarios, although this needs to be tested with further models and empirical data.

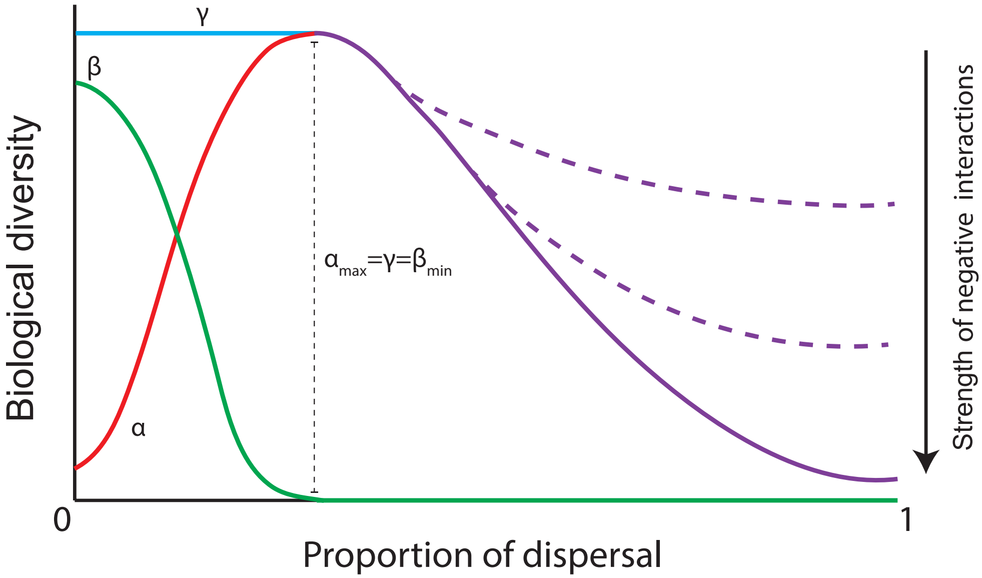

Figure 6: Theoretical relationship between proportion of dispersal between communities and different components of diversity: Local alpha diversity (red line, *α*), regional dissimilarity, or beta diversity (green line, *β*), and regional pool of species, or gamma diversity (blue line, *γ*). Beta diversity decreases with dispersal. Alpha diversity reaches its peak at intermediate dispersal levels, when *α*=*γ*. At increased dispersal, alpha diversity decreases at the same rate as gamma diversity (purple lines). However, we would expect that at high proportion of dispersal, the decay rate in alpha and gamma diversities might be positively related with the intensity of negative interactions (competitive exclusion) and negatively with ecological redundancy (purple-dashed lines). Based on Mouquet, N., Loreau, M., 2003. Community patterns in source-sink metacommunities. The American Naturalist 162, 544-557.

The negative relationship between connectivity (i.e., dispersal) and beta diversity is a well-described phenomenon in the literature, also in tropical ecosystems. This correlation has been found in multiple studies and taxonomic groups, including planktonic organisms (Lopes et al., 2014; Brasil et al., 2020) and wetland vegetation (Deane et al., 2017). Regarding alpha diversity, Hartz et al. (2019) showed that well-connected small lakes support higher alpha diversity (species richness) of fish than larger lakes in a set of Brazilian coastal wetlands. Bao et al. (2017) also found that vegetation diversity was related to the distance among sampled wetlands: closer wetlands showed higher similarities (lower beta diversities) and higher species richness than more isolated ones, suggesting that dispersal limitation plays a key role in wetland diversity. Similar results were obtained by Bortolini et al. (2014), working on phytoplankton of the Paraná River floodplain. These patterns in alpha and beta diversity were also found by Vanschoenwinkel et al. (2007) in invertebrate communities of South African rock pools.

All these results may be representative of the theoretical trends in biological diversities in the first half of ***Figure 5***. However, we found no studies carried out in tropical freshwater ecosystems showing a decay in alpha or gamma diversity at very high dispersal rates (or connectivity). Assuming that connectivity and dispersal rates can be maximal in some ecosystems during the flooding seasons, more effort should be done in order to disentangle if this theoretical expectation proposed by Mouquet and Loreau (2003) is observed from natural patterns, and in tropical wetlands in particular.

Neutral dynamics

The consideration of neutral processes in community ecology has been of paramount importance ever since the early work of Connor and Simberloff (1984), and it has later been also incorporated to metacommunity theory (Bell, 2000; Hubbell, 2001; Leibold et al., 2004; Leibold and Chase, 2018). Although dispersal-related processes are sometimes included in the neutral perspective (Hubbell, 2001), we have discussed these effects separately in the previous subsection. We separated them not only because of the fundamental influence of dispersal on metacommunity organization, but also because of clear nonneutral effects that can be derived from different adaptations of species to movement, and therefore dispersal (Clobert et al., 2012). In any case, the distribution and coexistence of species, or its lack thereof, can be related to processes other than environmental filtering or dispersal limitation and surplus, including demographic stochasticity and derived ecological drift. In this context, stochasticity does not refer to total randomness but probabilistic and hardly predictable processes, such as birth/death, migration, and speciation/extinction rates (Vellend et al., 2014). Demographic stochasticity can drive changes in metacommunity composition through ecological drift. This ecological drift can be especially important in early stages of ecosystem assembly and through priority effects, leading eventually to differences in the more mature communities (Orrock and Watling, 2010).

Historical processes structuring metacommunities

Stochasticity can mask several environmental, spatial, or temporal deterministic processes (Vellend et al., 2014). For example, zooplankton from temporary wetlands will be strongly influenced by apparently stochastic environmental or demographic events. As a consequence, we may wrongly assign to neutral processes some deterministic but difficult to measure environmental effects (Boyce et al., 2006). So, for instance, precipitation intensity could be considered to be stochastic, but it will determine water column depth or organic matter inputs. Also, some organisms will be incorporated from upstream wetlands or displaced downstream from the community during floods, and egg-bank hatching can depend on community structure before desiccation, time-dependent egg-bank deterioration, hatching clues, etc. Colonization rate can also be thought of being stochastic, but it may strongly depend on propagule density or species composition of the potentially colonized patches, so that a colonizing species can be excluded due to priority effects (Vellend et al., 2014).

Nevertheless, demographic stochasticity, especially in small populations or under weak selection, can lead to ecological drift and changes in species richness and composition within and between patches, depending on the spatial scale of this stochasticity (Fukami 2004; Chase, 2007). As a consequence, we can observe species whose distributions or abundances do not respond to niche or dispersal differences, or even find random species coexistence patterns. For example, Castillo-Escrivà et al. (2017b), while comparing living communities with their corresponding past remains, found that an ostracod metacommunity was highly related to environmental and spatial processes, but its past history (estimated through the paleoassemblage) played a key role too, suggesting that contingent, neutral processes had also structured the recent metacommunity.

Colonization is sometimes considered stochastic. In early stages of the assembly of a community, this stochasticity can have a great influence on future species composition (Fukami, 2015; Rojo, 2020). For example, two similar species of Branchiopoda may play the same ecological function, so that they may compete until one species excludes the other. Thus the colonization by one of these species will fail if the other species is already established in the waterbody. This phenomenon is known as the priority effect, and it can be an essential process when a species colonizes a new patch (Drake, 1991). In early stages of the community (or even in early stages of the hydroperiod in temporary waters), there are also important colonization events of the water column from the egg bank in the sediment (Castillo-Escrivà et al., 2017c). Succession can then progressively lead to differences in interpatch assemblages just because of ecological drift (Segre et al., 2014), sometimes related to stochastic demographic dynamics at the onset, then leading to changes in priority effects and followed by further drift or deterministic processes (selection).

ASSESSMENT OF MAIN PROCESSES THROUGH VARIATION PARTITIONING

The methodological approach

The relevance of these three processes, that is, environmental control (selection), dispersal, and neutral dynamics (ecological drift), in metacommunity organization has received much attention in the scientific literature, but their relative role can be difficult to quantify from empirical data. One of the most used and accepted statistical methods for this purpose is known as variation partitioning analysis (Peres-Neto et al., 2006). Using constrained multivariate ordination methods, this analysis decomposes the variance of observed metacommunity data into different components related to several sets of explanatory variables. As a result, the relative contribution of environmental and spatial variables to the observed variance can be quantified. In this way, variation partitioning analysis can give information about the percentage of species variance explained by pure environmental variables (independent from spatial variables, E|S), purely by spatial variables (independent from environmental variables, S|E), the overlap between environmental and spatial variables (related for instance to spatially structured environmental variables such as climate, E∩S), and the remaining unexplained variance or residuals (***Figure** 7*).

The results of variation partitioning analysis provide information about the role of different processes in metacommunity assembly. The pure environmental component is often associated to species sorting (Cottenie 2005), that is, selection or environmental control. The pure spatial component is related to dispersal processes (Cottenie 2005). The overlap between these two components is sometimes assigned to spatialized environment (such as climate, or other environmental variables following a spatial pattern), but cannot readily be disentangled from dispersal processes statistically associated to environmental gradients. Finally, the residuals, or unexplained variance, are usually related to unmeasured environmental variables (both abiotic and biotic factors), temporal dynamics (short and long-term unknown history of the assemblages), or stochasticity (ecological drift), so that neutral processes are probably essential elements in this component of the variance (Legendre et al., 2009).

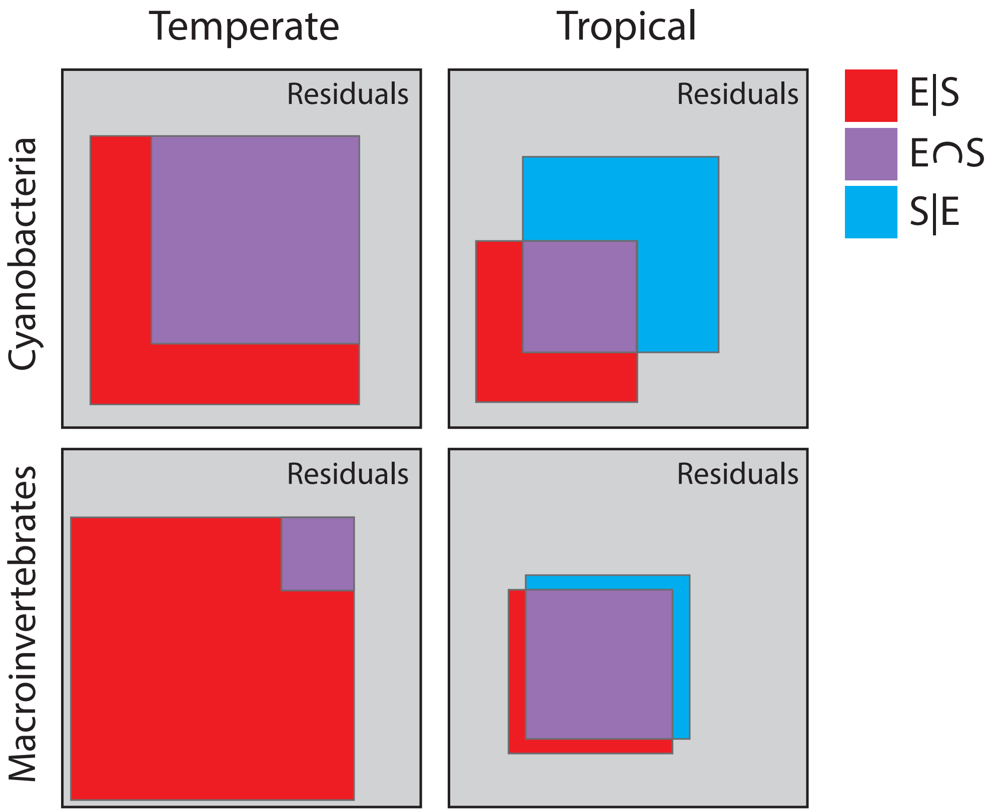

Figure 7: Diagrams depicting the results of variation partitioning analysis for each of the four metacommunity datasets (2 groups of organisms x 2 geographic settings). For each analysis, the bottom left square (E|S+E∩S) is sized to a surface area corresponding to the proportion of metacommunity variance explained by the environmental component (E). The upper right square (S|E+E∩S) represents the proportion of metacommunity variance explained by the spatial component (S). Both squares together (E+S) account for the total explained variance of the metacommunity by the explanatory variables. E|S = pure environmental component, independent from space. S|E = pure spatial component, independent from environment. E∩S = overlap between environmental and spatial components. Residuals (gray) = unexplained metacommunity variance. The larger square represents the metacommunity total observed variance (both explained or not; E|S, S|E, E∩S, and Residuals). See text for further explanations. Based on unpublished data for variation partitioning of Cyanobacteria and macroinvertebrates from temperate and tropical ponds from Gálvez, Á., Peres-Neto, P.R. Castillo-Escrivà, A., Bonilla, F., Camacho, A., García-Roger, E-M., et al., 2021. Pond metacommunities from bacteria to birds: overall stronger environmental than spatial effects on most taxa and in Mediterranean than in tropical habitats. BioRxiv 2021.03.24.436596

Historical effects, due to the difficulty of measuring them, have been set aside in many metacommunity studies, unless repeated samples in time are available. However, Castillo-Escrivà et al. (2017b), using remains of individuals previously occupying an ostracod metacommunity, found strong pure temporal (historical) effects when explaining variation in an ostracod metacommunity; this may be related in part to priority effects. More recently, Oliveira et al. (2020) showed that the best predictor of a tropical fish metacommunity was not space or environment but information on its composition in the previous year. Pure temporal effects can also be significant in tropical metacommunities, although environmental and spatial effects are usually stronger (Gálvez et al., 2020).

Environmental versus spatial effects

Influence of the spatial scale and the regional species pool

The relative importance of environmental (E) and spatial (S) components provide information about which processes are dominant in shaping metacommunities, from environmental control (i.e., selection, accounted for by E| S) to dispersal (S|E) (Cottenie, 2005). Residuals can be assigned to neutral processes, but also to unknown dispersal effects, or to unmeasured environmental factors. Nevertheless, these three components (S, E, and residuals) are not totally independent from one another. The relationship between dispersal and environmental control (as species sorting) is particularly well studied (***Figure 8***). In the context of high dispersal (or small spatial extent), we expect a strong influence of the spatial component and a low percentage of explained variation by the environmental component, due to intense mass effects. At an intermediate range of dispersal ability (or an intermediate spatial scale), species sorting is expected to be dominant, as the environmental component dominates over the spatial one because mass effects are no longer relevant, but there is enough dispersal for organisms to arrive to those habitats with the best conditions to which they are fitted. Finally, at large spatial extents, or with low dispersal ability, dispersal limitation has a strong influence shaping metacommunities, and the spatial component dominates again over the environmental effects (Heino et al., 2015).

Environmental and spatial effects, together with the residuals, must account for the total percentage of metacommunity variance observed. For this reason, increased environmental or spatial effects must necessarily imply a decrease in the residual proportion (and vice versa). The size of the regional pool of species (gamma diversity) is relevant in these analyses: when it increases (increasing variation in community composition), then the unexplained variance (residuals) also increases and, as a consequence, the proportions of spatial and environmental explanation decrease (Leibold and Chase, 2018). Thus the regional pool of species should also be taken into account when comparing variation partitioning among different metacommunities.

Tropical versus temperate metacommunities

All the patterns in metacommunity ecology, although gathered from studies mostly carried out at intermediate latitudes, are also relevant to metacommunities in tropical wetlands (see Wasserman and Dalu, 2022). However, there is a scarcity of information regarding the relative role of space and environment in structuring aquatic tropical metacommunities, although some differences have been observed (or can be predicted) between tropical and temperate wetlands. Before disentangling the relevance of these processes, we would like to note some important differences between these two types of aquatic ecosystems. Climatic seasonality is an important dynamic factor driving major environmental changes of water bodies. In temperate regions, it implies changes in precipitation through time but also wide fluctuations in temperature and light intensity, whereas the climatic seasonality in tropical areas produces changes mostly in precipitations rather than insolation or temperature (Coen, 1983). As a consequence, the hydroregime and the amount of water inflow, rather than temperature variation, will strongly shape tropical aquatic ecosystems, and this temporal dynamic becomes crucial when analyzing tropical metacommunities (Rojo et al., 2016; Brasil et al., 2020).

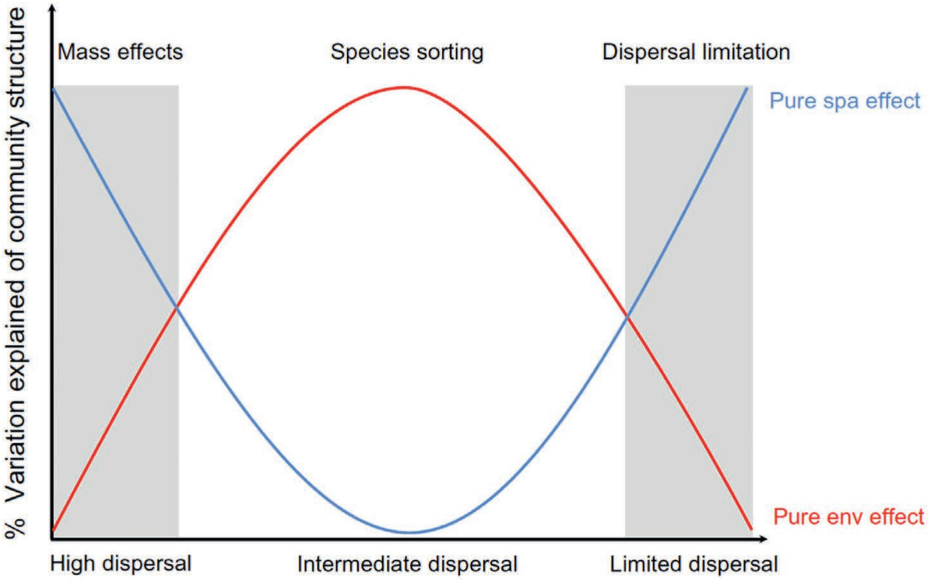

Figure 8: Hypothetical relationship between spatial extent (and consequently dispersal capabilities) and the percentage of variance explained by pure environmental and spatial effects. The dominance of one or another, according to spatial extent and dispersal limitation, gives information about primary processes structuring metacommunities (dispersal limitation, species sorting, and dispersal surplus or mass effects). From Heino, J., Melo, A.S., Siqueira, R., Soininen, J., Valanko, S., Bini, L.M., 2015. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. Freshwater Biology 60, 845-869.

Considering the large temperature variations in temperate wetlands, we might expect a higher temporal variability of the relative role of environmental versus spatial factors than in tropical ones, but the large hydrological effects of the flood pulse in tropical wetlands might strongly affect connectivity and therefore counteract the reduced temperature variation effects. The direct comparison between temperate and tropical ponds (Gálvez et al., 2021; ***Figure 7***) shows the expected prevalence of environmental control in temperate water bodies, and slightly higher dominance of spatial control in tropical ones, for several groups of organisms, but the differences are minimal.

The large environmental gradients (at least regarding temperature fluctuations) present in temperate regions are expected to produce stronger species filtering effects than in tropical wetlands. However, other influential environmental factors can also widely affect tropical water bodies, including dissolved oxygen concentration, water transparency, pH, or salt and nutrient concentrations (Roldán and Ramírez, 2008; Bleich et al., 2009). One remarkable element that gives rise to large differences between tropical and temperate wetlands is the abundance and species richness of floating vegetation in the former, so that many organisms are adapted to microhabitats associated with these macrophytes or use them as basic substrate or refuge (Wantzen et al., 2016). Environmental control is therefore common also in tropical wetlands (***Table 1***). For example, Rojo et al. (2016) found a significant influence of electric conductivity (a surrogate for salt content), dissolved oxygen concentration, macrophyte cover, and water transparency shaping phytoplankton metacommunities. Similarly, De Campos et al. (2018) found ostracod species distribution in a tropical floodplain metacommunity to be significantly affected by dissolved oxygen concentration, salt content, macrophyte species richness, pH, and water temperature. Additionally, Brasil et al. (2020) found a significant influence of salt content, water transparency, pH, and water temperature on plankton assemblages, but not of dissolved oxygen concentration. Also Rocha et al. (2017) observed significant effects of dissolved oxygen concentration, pH, water temperature, electrical conductivity, and water transparency, among others, on macrophyte-associated cladocerans. Therefore important limnological variables, such as dissolved oxygen and salt content, seem to strongly influence metacommunity structure in tropical water bodies.

Despite the importance of temporal dynamics (Magurran and Henderson, 2010; Castillo-Escrivà et al., 2020), snapshot surveys dominate the literature on variation partitioning in aquatic metacommunities. Studies including temporal changes and focused on tropical wetlands are even scarcer. However, whenever seasonal variability is considered, the importance of connectivity during rainy seasons due to flood pulses is often highlighted (Wantzen et al., 2016), although some contradictory results have also been obtained. Thomaz et al. (2007) found an increased similarity between communities of floodplain systems during rainy seasons, and Brasil et al. (2020), studying multiple wetlands from close river basins, found pure spatial effects to have less influence during the rainy season in a floodplain phytoplankton metacommunity. In contrast, Rojo et al. (2016), studying phytoplankton metacommunities from Mesoamerican wetlands, found just the opposite, a dominant spatial effect on phytoplankton from temporary tropical wetlands during the rainy season. They suggested a lag between sampling and homogenization, so that spatial patterning would have been produced earlier due to isolated hatching. Nonetheless, all of these contributions (Thomaz et al., 2007; Rojo et al., 2016; Brasil et al., 2020) agreed on the heterogenization of local communities after isolation during the dry season, quantified as an increase of pure environmental effects (stronger selection and consequently species sorting) in variation partitioning analyses.

Differences according to dispersal ability

As previously discussed, De Bie et al. (2012), according to results on variation partitioning analyses of temperate ponds, proposed the idea that good dispersers are more environmentally controlled than bad dispersers, which are more spatially controlled. They assumed that propagule size and dispersal type (active or passive) are key traits for dispersal, so that active dispersers with larger propagules should disperse better than those with small propagules, while in passive dispersers, those with small propagules would have higher dispersal capabilities. However, few works besides Padial et al. (2014) have found similar results in tropical wetland metacommunities. When Dias et al. (2016) studied zooplankton during rainy and dry seasons for two consecutive hydrological years, they obtained dissimilar results between years. Nevertheless, they clearly found species sorting controlling zooplankton metacommunities of small organisms (amoebae and rotifers), and a significant spatial influence in crustaceans (cladocerans and copepods). This is somehow expected assuming the (controversial) idea of increased dispersal ability of smaller organisms with passive dispersal (De Bie et al., 2012). However, Brasil et al. (2020) found significant spatial effects even in small-bodied zooplankton during the dry season, in agreement with Thomaz et al. (2007), but no pure spatial effects in larger-bodied zooplankton, contrary to the findings of Dias et al. (2016). The idea that spatial processes may affect the structure of metacommunities of all taxonomic groups, no matter their body size (and their supposedly related dispersal ability), was supported by De Campos et al. (2018), who found no differences between crawling and swimming tropical ostracods, and even lower pure spatial effects in larger-bodied species.

As for nonflying active dispersers, all authors agree on the important role of the spatial component, due to dispersal limitation. When studying amphibian beta diversity in the Pantanal, Moreira et al. (2017) found spatial variables significantly driving differences between communities (during the rainy season), suggesting dispersal processes such as mass effects may play an important role in amphibian metacommunity structure. In addition, interwetland landscape can also influence amphibian metacommunity (Gray et al., 2004). As observed by Rojo et al. (2016) for phytoplankton, Fernandes et al. (2013) found stronger spatial effects during the rainy season and higher environmental effects during the dry season for fish metacommunities from tropical floodplains.

All these studies agree on the key role of hydrology and dispersal processes on tropical wetland metacommunity structure, increasing connectivity and dispersal rates during rainy seasons. However, there is no clear pattern for the relative role of space and environment in structuring wetland metacommunities (other than spatial scale effects), but both processes, species sorting and dispersal, seem to be essential (Soininen et al., 2007; Declerck et al., 2011; Gascón et al., 2016; Alahuhta et al., 2018).

Unexplained variation and further limitations

Due to the larger regional pool of species in the tropics, we may expect a higher percentage of unexplained variation when analyzing tropical wetland metacommunities (Leibold and Chase, 2018). Therefore a higher relative influence of neutral, stochastic processes (so as probably also unmeasured biotic interactions) can be predicted for tropical systems. Indeed, residuals usually represent high percentages of the total variation, with wide differences among organisms, in tropical metacommunities: 70%-99% (mostly around 90%) for bacteria (Nabout et al., 2009), 85%-94% for phytoplankton (Rojo et al., 2016), 75%-95% for zooplankton (Brasil et al., 2020), c.70% for cladocerans (Rocha et al., 2017), 70%-90% for ostracods (De Campos et al., 2018), 30%-90% for macroinvertebrates (Li et al., 2020a), or 50%-75% for fish (Fernandes et al., 2014). In a multitaxon approach, Padial et al. (2014) found residuals ranging from approximately 60% in phytoplankton, to more than 90% in zooplankton. Gálvez et al. (2020), in another multitaxon study including temporal dynamics in neotropical ponds, found 67%-91% of residuals. In temperate aquatic metacommunities, which have been studied more intensely and for a longer period of time, nonconcordant results have been recorded. For example, a multitaxon study by Beisner et al. (2006) showed residuals ranging from 60% in zooplankton to 90% in phytoplankton, while residuals in De Bie et al. (2012) were always higher than 83%. There is a lack of comparative studies using the same methodology in similar spatial scales across biogeographic regions, so it is difficult to find a pattern in the residuals. Nevertheless, some studies show lower percentages of residuals in temperate metacommunities compared to those found in tropical metacommunities: 75% in bacteria (Langenheder and Ragnarsson, 2007), 73%-91% in phytoplankton (Loewen et al., 2020), 38%-56% in microcrustaceans (Gascón et al., 2016), or 42%-54% in macroinvertebrates (Bertin et al., 2014). More examples of variation partitioning analyses from temperate andtropical regions are compared in ***Table 1***.

It is difficult to establish general patterns on how relevant are environmental, spatial, and neutral processes, due to disparate results between studies in similar ecosystems, even working within unique biogeographic regions and taking into account ecological traits such as dispersal mode. However, in spite of the big fluctuations in results observed in metacommunities of even the same organism group and biogeographic region, it seems that environmental processes dominate over spatial processes (see ***Table 1***). Can we then expect that all species in the same ecological guild are equally affected by niche, dispersal, and neutral processes? Not all species appear in the same frequencies and abundances. Actually, some species, known as core species, appear in high abundances and frequencies, and this commonness is related to their permanence in time. Satellite or rare species are more prone to extinction and their persistence over time is more dependent on dispersal and drift (Gaston, 1994; Magurran and Henderson, 2003). These rare satellite or transient species are not always detected in snapshot surveys. As a consequence, they will probably inflate the residual proportion in variation partitioning analyses. In tropical ecosystems, we could expect a higher number of satellite species and, in addition to the above-mentioned higher species richness, residuals would then represent a higher proportion than in temperate ecosystems.

In conclusion, environmental control, dispersal, and drift together contribute to metacommunity organization. Even though there are no defined general patterns related to the influence of these processes among organisms, it seems clear that local habitat characteristics and hydrology play a key role in structuring metacommunities in tropical wetlands. Hydrology has an important influence on dispersal and environmental processes, inducing deep changes in interwetland connectivity and regional environmental heterogeneity. As a consequence, not only dispersal rate but also local environmental variables experience wide temporal changes, producing marked differences between rainy and dry seasons.

CONSERVATION IMPLICATIONS

One of the outcomes of metacommunity ecology most relevant to conservation biology is the remarkable role of dispersal on metacommunity structure (see Bredin et al., 2022). However, despite this relevance of dispersal and connectivity, we must not forget that local and regional environments are also essential elements for metacommunity conservation practice. Thus once local environments are properly preserved or restored, a successful management of protected areas must consider connectivity between patches at larger scales through regional environment management (Amezaga et al., 2002). In a wetland context, this connectivity needs to be more or less explicit according to the organism group. Some organisms, such as plankton, with high dispersal ability, will probably not suffer much dispersal limitation from human impacts. Birds, except for large geographical barriers, are not expected to be highly spatially limited. However, for many freshwater fish species, connectivity loss is a worldwide major threat (Gido et al., 2015); but also connectivity gained through artificial corridors or human transport may allow invasive predators or competitors to colonize new basins and reduce native populations (Clavero and García-Berthou, 2005; see Pegg et al., 2021). In organisms with amphibian lifestyles, such as amphibians and many aquatic insects, they will not need such an explicit connection as fish do, but their dispersal capabilities will strongly depend on interpatch terrestrial habitat conditions (Ribeiro et al., 2019).

There is a trade-off between increasing and reducing connectivity for conservation. *A priori*, some degree of connectivity is necessary to prevent local stochastic extinctions, allowing patch colonization. However, despite maintaining connectivity between patches is an important element in metacommunity management, we should not forget the potential for habitat homogenization driven by too high dispersal rates (Mouquet and Loreau, 2003). In addition, high connectivity can be a concerning issue when effective competitors, predators, and pathogens, either native or invasive, could be a threat to some species of conservation concern. When an invasive species is established, increasing connectivity between patches can lead to higher migration and colonization of connected patches, producing a short-term increase in alpha diversity, but a long-term biodiversity loss (Crooks and Suarez, 2006). As shown by Harding et al. (2012), increased migration in host-pathogen metapopulations can produce regional host extinction due to the spread of the pathogen. Finally, connectivity is necessary to properly preserve metapopulations of several species, but we must not forget that habitat fragmentation and isolation is also a source of speciation (e.g., in freshwater fish, Dias et al., 2013), and isolation is necessary for effective conservation of these species. Indeed, fragmentation *per se* does not seem to be as detrimental to biodiversity as formerly thought; habitat destruction and the reduction of undisturbed habitat area is the most negative outcome of the ongoing fragmentation of natural environments (Fahrig, 2017).

In the current and future humanized world, where habitat loss is one of the major threats to biodiversity, artificial wetlands, such as rice fields, could be important elements in maintaining wetland area (even if disturbed), connecting more natural wetlands of high conservation value, and as transition or buffer ecosystems between terrestrial and aquatic habitats. Rice fields can therefore host species that are at risk due to human development and urbanization. For example, Holzer et al. (2017) found that Vietnamese rice paddies are refugia for many amphibians, which were being displaced by rapid human urbanization and habitat alteration. Nevertheless, although rice fields can be an interesting option in metacommunity management of tropical wetlands in an anthropized landscape, we must take into account that rice fields can also facilitate naturalization of exotic species, in temperate regions and elsewhere (Valls et al., 2014; Smith et al., 2018). Conservation science has traditionally focused on preserving patches with high species richness or unique organisms, as opposed to patches with high similarity (in other words, protecting those patches with the highest alpha and beta diversity). However, under the metacommunity framework, Economo (2011) highlighted that the persistence of species at large spatial scales is an important element for regional biodiversity conservation. When removing a low-dissimilar patch, cascade effects could drive to extinctions at the remaining metacommunity. Consequently, Economo (2011) suggests that increasing the number of protected (and connected) areas is more important in the long term than protecting a small number of patches with high diversity representation.

In certain cases, especially regarding conservation of species with particular ecological needs, a metapopulation rather than a metacommunity approach might also be effective. For example, conservation of large mammals suffering from habitat fragmentation needs a large-scale management that is not necessary in conservation of organisms such as micromammals or insects (Elmhagen and Angerbjörn, 2001). In this metapopulation framework, patch size, dispersal, and connectivity are essential (as they are in metacommunity ecology), giving rise to different metapopulation models with direct implications on management and conservation (Hanski and Gyllenberg, 1993). However, provided that knowledge on interacting species with the species of interest is available, we believe that a metacommunity approach to conservation of such key species is more integrative and can better deal with interactions that might become unexpected when not included in single-species metapopulation models.

In conclusion, the conservation implications of metacommunity theory can be summarized in five statements proposed by Bengtsson (2009): (1) Control local environment via management; (2) landscape management and not only local management; (3) keep regional environmental heterogeneity; (4) increase regional connectivity avoiding landscape homogenization; and (5) keep disturbance regimes close to natural. However, there is a lack of general knowledge about direct and explicit implications of metacommunity ecology in conservation biology, and most of its proposals are purely theoretical. Nevertheless, metacommunity theory offers an excellent framework to forthcoming applied studies which integrate local and regional processes, hopefully also including temporal processes, and giving rise to new approaches in environmental management and conservation.

CONCLUSIONS

Even though metacommunity ecology is still in its infancy, its theoretical assumptions and predictions are highly relevant to the study of aquatic ecosystems. An increasing number of studies on tropical wetlands show that environmental control has a strong influence on metacommunity structure. In addition, dispersal limitation and dispersal surplus, which can be readily studied in tropical freshwater bodies such as river floodplains during rainy and dry seasons, also have a crucial effect on metacommunity homogenization and heterogenization and therefore on beta diversity. Different studies using variation partitioning analysis suggest a major role for neutral processes, even higher than in temperate regions, suggesting that stochasticity is fundamental for tropical metacommunity assembly. Finally, metacommunity theory can have interesting implications for wetland conservation; by confirming the importance of local environmental management and also by proving the significance of regional management and the essential role of dispersal for metacommunity conservation.

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Laguna de Peje, Costa Rica. Fotografiado por Juan Rueda

CAPÍTULO 2

Environment and space rule, but time also matters for the organization of tropical pond metacommunities.

ABSTRACT

Metacommunities are dynamic systems, but the influence of time independently of environmental change in their configuration has been rarely considered. In temporary ponds, strong temporal effects are expected to influence their metacommunity structure, even in relatively constant environments such as tropical habitats. We therefore expect that time as an independent factor could modulate tropical pond metacommunities, which would be also less affected by niche-related processes than by dispersal-related processes. In addition, good dispersers should be more environmentally structured than bad dispersers, which should be more spatially structured. Finally, the relevance of temporal effects should vary among organisms with different generation times. To test these hypotheses, we surveyed 30 temporary ponds along the dry tropical region of western Costa Rica and Nicaragua at three different moments of their hydroperiod: shortly after the infilling of the water bodies, at the middle of the hydroperiod and just before desiccation. We obtained data on 56 environmental variables and used geographic coordinates to build spatial variables (Moran Eigenvector Maps). We collected biological samples and estimated the specific abundance of phytoplankton, zooplankton and benthic invertebrates. To evaluate the relative role of environmental, spatial and temporal (sequential sampling season) effects for metacommunity organization, we used variation partitioning with distance-based redundancy analyses for each group of organisms. The inclusion of time in the analysis highlighted that pure temporal effects explained part of metacommunity variance in almost every group, being as important as spatial or even environmental effects for some groups of organisms. In contrast to the assumed low environmental constraints in tropical areas (i.e., high and stable temperatures), we found strong environmental effects. Passive dispersers were more influenced by environmental factors than active ones. We also found a positive relationship between the body size of the different groups of organisms and the magnitude of the temporal effects, interpreted as related to generation time. Finally, when analyzing each sampling period separately, we found differences in the relative role of environment and space at different sampling periods, showing that snapshot surveys may not be representative of highly dynamic metacommunities.

Key words: multi-taxon study, dbRDA, MEM analysis, dispersal limitation, species sorting, temporal effects, tropical limnology

INTRODUCTION

The establishment of the metacommunity concept as referring to a group of communities linked by dispersal of their interacting species (Hanski and Gilpin, 1991; Wilson, 1992) prompted a turning point in understanding species distributions and abundances. Not only environmental filtering (the species sorting paradigm; Leibold et al., 2004), but other mechanisms related to spatial effects and dispersal rates, play a key role structuring metacommunities. Patch-dynamics (Levins and Culver, 1971), sink-source dynamics (or mass-effects; Holt, 1993) and neutral (Hubbell, 2001) paradigms are complementary to the species sorting approach when studying metacommunity assembly. In this framework, there is however a temporal component that has seldom been considered when testing theoretical expectations with empirical data. The common snapshot-survey studies neglect not only temporal changes in environmental conditions and in the influence of the spatial context, but also direct temporal effects on metacommunity structure due to processes such as life cycles, population growth or priority effects (Brendonck and De Meester, 2003; Fukami, 2015; Leibold and Chase, 2018).

Under the metacommunity framework, freshwater ecosystems are particularly interesting due to their isolation in relation to the terrestrial landscape. Rivers, lakes and ponds have largely been studied in order to understand the role of dispersal limitation and species sorting in such isolated communities (e.g., Soininen et al., 2007; Escrivà et al., 2015; López-Delgado et al., 2019). Pond metacommunities show a high degree of randomness (Chase, 2007), although strong environmental effects are also frequently observed (Leibold and Chase, 2018). Mass and priority effects at small scales (Heino et al., 2015; Castillo-Escrivà et al., 2017b) and dispersal limitation at large (Soininen et al., 2011; Heino et al., 2015) or even small spatial scales (Castillo-Escrivà et al., 2017a) seem also to be important processes affecting pond metacommunity structure. Temporary ponds, as intermittent ecosystems, strongly depend on seasonal dynamics related to their hydroperiod, egg-bank hatching and colonization processes (Williams, 2005; Chase, 2007; Castillo-Escrivà et al., 2017c). Desiccation is a major evolutionary pressure in temporary water bodies, where habitat availability changes cyclically, sometimes unpredictably, and organisms are adapted to this desiccation by means of different life-cycle strategies: while some organisms resist drought in the sediment (resting eggs, anhydrobiosis, seeds, etc.), some others need to abandon the habitat and recolonize from neighboring waterbodies (Brendonck and De Meester, 2003; Richter-Boix et al., 2011; Olmo et al., 2012; Brendonck et al., 2017; Wisnoski et al., 2019). As a consequence, some traits such as generation time, type of dispersal or survival strategy toward desiccation may influence temporal dynamics, which in turn may strongly regulate metacommunity composition (Boix et al., 2004; Holt et al., 2005; Fernandes et al., 2014; Castillo-Escrivà et al., 2017c).

Freshwater metacommunity studies are biased toward temperate regions with strong temperature seasonality, this possibly driving major changes in metacommunity structure. In contrast, tropical regions show a reduced thermal variability, while precipitations, especially in areas with a dry tropical climate, have large annual fluctuations. These fluctuations, consequence of the alternation of rainy and dry seasons, may lead to a high connectivity between ponds through extensive floods, producing a regional environmental homogenization (Thomaz et al., 2007) that locally diverges when the waterbodies become isolated during the dry season (Rojo et al., 2016). Thus, results on spatial and environmental effects on pond metacommunities sampled in temperate regions are expected to notably differ from those of tropical areas, not only because of differences in temperature regimes but also because of heavy rain effects on connectivity.

Previous studies on freshwater metacommunities point toward dispersal mode as an important trait driving metacommunity structure. It is expected that better dispersers will show weaker spatial patterns than those with lower dispersal ability. As a consequence, flying active dispersers and small-size passive dispersers will be more affected by species sorting than non-flying active dispersers or large-bodied passive dispersers (De Bie et al., 2012; Padial et al., 2014). However, this pattern has not been supported by all metacommunity studies (Heino et al., 2012; Schulz et al., 2012; Grönroos et al., 2013; Leibold and Chase, 2018). Perhaps, differences among studies in spatial scales, connectivity or groups of organisms being analyzed may hinder the observation of consistent patterns or, alternatively, dispersal abilities might be more idiosyncratic that one may expect from body size and moving capabilities. For these reasons, a multi-taxon approach in metacommunity research, including groups of different body sizes and dispersal strategies could help to disentangle how metacommunities are actually structured.

In this study, we test the influence of environmental, spatial and temporal factors on metacommunity structure of a wide range of organisms inhabiting tropical temporary ponds, including algae, rotifers, microcrustaceans, and macroinvertebrates (mainly mollusks and insects). Thus, we encompass multiple life-cycle strategies against desiccation (including resting eggs or spores in algae, rotifers and crustaceans, anhydrobiosis in some rotifers and copepods, terrestrial adult stages in insects, etc.) and distinct reproductive strategies (binary fission in cyanobacteria, strict parthenogenesis in some rotifers, cyclic parthenogenesis in rotifers or cladocerans, sexual reproduction in insects, etc.) which are strongly related with dispersal ability (active and passive dispersal) and colonization. In addition, the wide variability of taxa also includes a wide variability in body size, from a few microns in cyanobacteria to several centimeters in adult insects, which is correlated with generation time (Sammarco and Strychar, 2009; Brown et al., 2018). Empirical metacommunity analyses have seldom been carried out surveying multiple taxonomic groups from the same waterbodies, on repeated occasions, and over a wide spatial extent (e.g., Beisner et al., 2006), and even fewer of these at low latitudes (Domis et al., 2013; Padial et al., 2014; Rojo et al., 2016). This work aims at filling these gaps. Considering the standing issues on temporary pond metacommunity dynamics and the differences between groups of organisms and climatic settings we hypothesize that (i) not only spatial and environmental components drive metacommunity structure but also independent temporal factors; (ii) niche-related processes should be relatively less important than dispersal-related processes in structuring tropical pond metacommunities, as compared to published data on more seasonally variable temperate pond metacommunities; (iii) metacommunities of small passive dispersers should be strongly environmentally structured thanks to a high connectivity in tropical ponds through flooding, while metacommunities of larger-bodied organisms with reduced dispersal abilities might still show strong patterns of spatial structure; (iv) the influence of the temporal component should vary between organisms with different generation times, showing a positive relationship between these two variables, and (v) metacommunity patterns observed in snapshot surveys may provide a biased view of the major ecological processes structuring metacommunities because of considerable variation through time.

MATERIALS AND METHODS

Study area and environmental characterization

We surveyed 30 temporary stagnant freshwater bodies from a dry tropical region on the Pacific watersheds of Costa Rica and Nicaragua. These 30 ponds were selected in order to include a wide range of environmental conditions regarding salt content, nutrient concentration or land use, covering a large spatial extent. Selected waterbodies were grouped in four main clusters over a maximum distance among them of 370 km: Palo Verde National Park (Tempisque River lower basin) and the slopes of Miravalles and Tenorio volcanoes (Tempisque River middle basin), both in Costa Rica, and the delta of Estero Real and the Western region of Nicaragua, both in Nicaragua (*Figure 1*). Sasa et al. (2015) provide further details on the location, geographical setting and environmental characterization of sampling sites. Due to the temporality of these water bodies, we surveyed them thrice during their hydroperiod: 2

weeks after infilling (June 2010); once again in the middle of the hydroperiod, during the flooding peak (September 2010) and the last time immediately after the end of the rainy season, before the desiccation of the ponds (January 2011).

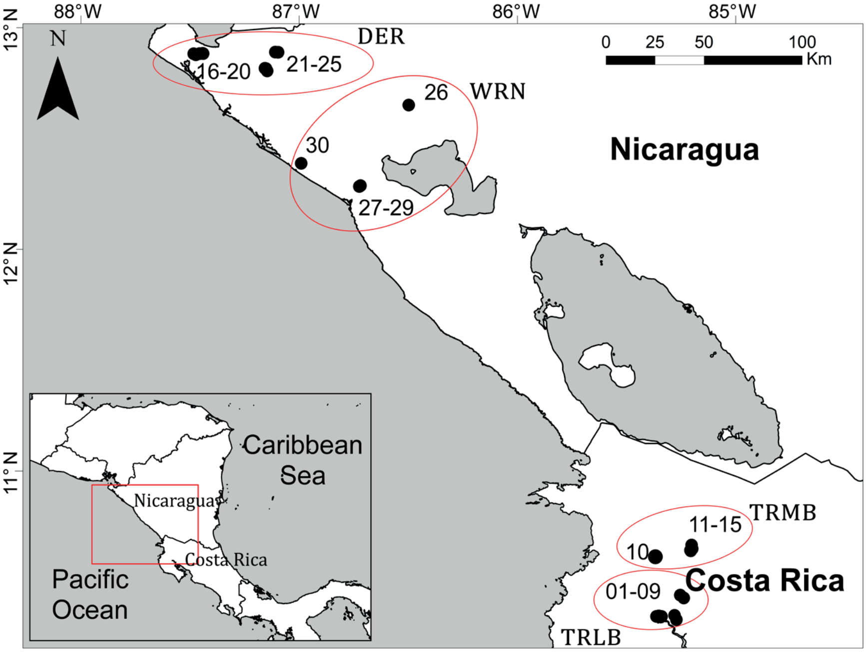

Figure 1: Map of the study area with the location of the studied ponds, grouped in four main clusters: DER (Delta of Estero Real), WRN (Western Region of Nicaragua), TRMB (Tempisque River Medium Basin), and TRLB (Tempisque River Low Basin). Based on Figure 1 in Sasa et al. (2015).

We assessed a set of 56 environmental variables for each pond, including limnological, hydrogeomorphological, biotic, climatic, landscape, and conservation status. In every survey, we measured in situ water temperature, total dissolved solids (TDS), electric conductivity (EC) and pH using a Hanna pH/EC meter HI 98130; oxygen concentration was measured with the Winkler method and transparency with a Snell tube. In addition, we took water samples in order to analyze nutrient and ion concentrations in the lab: 250 ml of unfiltered water for anion analyses (bicarbonate and carbonate alkalinity (Alk), chloride and sulfate), 100 ml of unfiltered water, fixed with nitric acid, for cation analysis (Na^+, K^+, Mg^{+2}, Ca^{+2}), and 100 ml of filtered water (through GF/F Whatman filters) for nutrient (PO_4^{3-}, NO_3^-, NO_2^-, NH_4^+) concentration analysis (Rice et al., 1992). The used GF/F filters were analyzed for chlorophyll-a concentration following Jeffrey and Humphrey (1975). Further details on sampling and analytical methods and limnological results are described in Sasa et al. (2015). We calculated some ratios between nutrient or ionic concentrations to be used as possible explanatory variables (Alk/Ca^{+2}, Alk/(Cl^- + SO_4^{2-}), (Ca^{+2} + Mg^{+2})/(Na^- + K^-), Ca^{+2}/Mg^{+2}, NO_3^-/NO_2^-, NO_3^-/NH_4^+). As for hydrogeomorphological variables, we measured the maximum and average depth of each water body, using a graduated stick, and gathered information from field data on the origin of the water (rain, streams, phreatic) and hydroperiod length (seasonal or semipermanent). Furthermore, we measured the area, perimeter, morphology {shoreline development: $DL = L/[2\sqrt{(\pi A)}]$; Aronow, 1982} and altitude. Regarding biotic variables (besides chlorophyll-a concentration), we visually estimated the percentage of water surface and shoreline covered by macrophytes and helophytes, respectively, and recorded the presence of livestock. We downloaded climatic variables, including maximum annual temperature, minimum annual temperature, average annual temperature, temperature range, annual average precipitation, and precipitation seasonality from the online server worldclim.org (using historical climate data from 1970 to 2000; Fick and Hijmans, 2017) and extracted these data by means of ArcGis 10.0 (ESRI, 2006). As for the landscape and land use of the watershed surrounding each pond, we estimated the percentage of land surface occupied by agriculture, buildings, forest, scrub, low grass and high grass, and landscape heterogeneity. For this purpose, we manually measured the percentage cover of these categories in a buffer area of 100 m of diameter around the sampling point using Google Earth (Google Inc.) satellite images. The landscape heterogeneity was calculated with a Shannon index of the proportions of the above-mentioned landscape categories. Finally, we determined the conservation status of each wetland through the ECELS (ECELS1-5 and total ECELS) index (Boix et al., 2010; Sasa et al., 2015). Instead of using latitude and longitude as spatial variables, we calculated Moran's Eigenvector Maps (MEMs) (Dray et al., 2006), consisting of a matrix of positively autocorrelated orthogonal variables of different spatial scales. The environmental characterization is summarized in ***Supplementary Table S1***.

We built three different matrices with the data gathered: (i) a spatial matrix, including MEMs, presence or absence of connectivity with other neighboring waterbodies and a categorical factor corresponding to the region (Costa Rica or Nicaragua), (ii) a temporal matrix, with the sampling period, as a dummy variable, and (iii) an environmental matrix, with all the variables explained above. These matrices were further used in statistical analyses together with the biological communities data (see below).

Biological communities

We collected biological samples of phytoplankton, zooplankton, and benthic invertebrates at each site and sampling period. Phytoplankton samples were collected in 100-ml amber-colored glass bottles, directly from the water column, and fixed with Lugol's iodine solution. Zooplankton quantitative samples were taken by filtering a volume of water (2–20 L measured with a graded jar, until filter got plugged) through a 35-µm mesh filter in order to ensure the capture of the smallest rotifers and microcrustaceans, and fixed with 4% formaldehyde. These samples were collected from the different microhabitats observed, including different depths, substrate or vegetation types and coverages. Benthic invertebrates were collected using a 250 µm pore-size hand net, taking samples from every distinct microhabitat. These samples where fixed with ethanol 96%. In the lab, all the collected groups of organisms were identified and counted using a Leica Leitz Biomed microscope, a Leica DMIL Led inverted microscope and a Leica M205C stereomicroscope, up to the maximum taxonomic resolution possible using a variety of taxonomic works, mostly the following: Huber-Pestalozzi (1976–1982) and Wołowski and Hindák (2005) for phytoplankton; Koste (1978) and Segers (1995) for rotifers in the zooplankton samples; Elías-Gutiérrez et al. (2008) and references therein for cladocerans and copepods (Cyclopoida and Calanoida); Meisch (2000) and Karanovic (2012) and references therein for ostracods; and Domínguez and Fernández (2009), Springer et al. (2010), and Thorp and Covich (2010), and references therein, for benthic invertebrates other than ostracods.

With these data, we built species abundance matrices of all three sampling periods for a series of (nested) groups of organisms: the whole phytoplankton dataset, and separately for Cyanobacteria, Chlorophyceae, mixotrophic phytoplankton (Chrysophyceae, Cryptophyceae, Euglenophyta, and Dinoflagellata) and Diatomea; Rotifera; non-Decapoda nor Isopoda crustaceans (from now on, Crustacea), and separately for Branchiopoda, Copepoda, and Ostracoda; all benthic macroinvertebrates (excluding Ostracoda) and separately for Mollusca, Insecta, Paleoptera (Ephemeroptera and Odonata), Heteroptera, Coleoptera, and Diptera.

Statistical Analysis

In order to determine the role of environmental, temporal and spatial factors over the structure of the metacommunity, we carried out variation partitioning analyses (Peres-Neto et al., 2006). The relative abundance matrices were Hellinger-transformed in order to reduce the influence of rare and ubiquitous species (Legendre and Gallagher, 2001). Environmental variables were transformed depending on their initial frequency distribution, using either logarithms, the arcsine of the square root, or the square-root, in order to reduce the leverage effect of outliers and to approach them to a normal distribution.

We implemented 17 partial distance-based redundancy analyses (dbRDA) with the purpose of explaining the variation of each species matrix in relation to the environmental [E], spatial [S], and temporal [T] matrices. Variation partitioning allows quantifying the percentage of variation explained purely by the environmental component [E|(S+T)], purely by the spatial component [S|(E+T)] and purely by the temporal component [T|(E+S)]. Furthermore, part of the metacommunity variation can also be explained by an overlap between two or more components: environmental and spatial overlap [(E∩S)|T], environmental and temporal overlap [(E∩T)|S], spatial and temporal overlap [(S∩T)|E] and environmental, spatial and temporal overlap [E∩S∩T]. Variables from environmental, spatial and temporal data matrices went through a forward selection process prior to each variation partitioning analysis, with a double stopping criterion (Blanchet et al., 2008). To further study the relative effects of the temporal component on metacommunity organization across organisms, we compared three groups of taxa with varying generation times, which are highly correlated with body size (Sammarco and Strychar, 2009; Brown et al., 2018): phytoplankton, microinvertebrates (rotifers, branchiopods, copepods and ostracods) and macroinvertebrates (remaining groups of analyzed benthic invertebrates).

In order to check if snapshot survey results are representative of the whole metacommunity dynamics through time, we performed a variation partitioning analysis for selected groups, following the same method as explained above but now performing a test separately for each sampling period and group of organisms, and therefore excluding temporal variables from analyses.

To test for significant differences in the pure temporal component between groups with different generation times (phytoplankton, micro-, and macroinvertebrates), and in pure components between groups of organisms with different dispersal strategies (passive/active), we performed Kruskal-Wallis tests (Kruskal and Wallis, 1952). All analyses were performed with R (v3.6.0; R Core Team, 2019) and R packages vegan (Oksanen et al., 2019), ade4 (Bougeard and Dray, 2018) and adespatial (Dray et al., 2019).

RESULTS

Altogether, we found 295 phytoplankton taxa, most of them identified to species level (Cyanobacteria: 44 taxa; Chlorophyceae: 114 taxa; mixotrophic phytoplankton: 56 taxa; Diatomea: 77 taxa), 102 rotifer taxa, most of them identified to species level, so as the 80 crustacean taxa (Branchiopoda: 34 taxa, Copepoda: 15 taxa, including 13 Cyclopoida and 2 Calanoida, Ostracoda: 31 taxa) and 169 macroinvertebrate taxa, including 19 mollusks, 34 paleopterans, 19 heteropterans, 28 coleopterans, and 32 dipterans (121 insect taxa). The list of identified species can be found in ***Supplementary Table S2***.

Selected variables in dbRDA are shown in the ***Supplementary Table S3***. The proportion of metacommunity variation explained by the selected significant variables, considering all three components (E + S + T) together, varied between 0.09 in Insecta and 0.33 in Ostracoda (average 0.20 ± 0.06). The results of the variance partitioning analyses show a significant effect of environmental, spatial and temporal components for most taxonomic groups (***Figure 2*** and ***Table 1***), with a predominance of pure environmental over pure spatial and temporal effects. Especially remarkable are the mixotrophic phytoplankton, with a stronger pure temporal component than any other phytoplankton group; Heteroptera, with a large pure spatial component; and Diptera, with the highest pure temporal component. We did not find significant pure environmental effects only in Heteroptera and Insecta (probably influenced by Heteroptera). Part of the variation of all phytoplankton groups was significantly explained by pure spatial factors, but none in the case of Rotifera, Branchiopoda and Paleoptera. Finally, we found non-significant pure temporal effects only in small body size taxa (Chlorophyceae, Diatomea, Branchiopoda and Ostracoda), but these effects were always significant in macroinvertebrates.

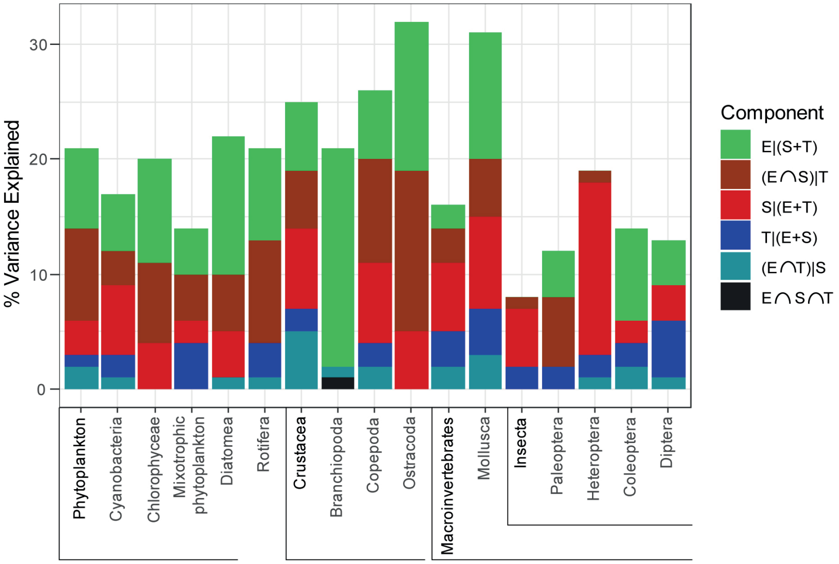

Figure 2: Results of variation partitioning analysis for each group of organisms. The percentage of variation explained by each component is represented with a different color (green: pure environment; brown: environment-space overlap; red: pure space; dark blue: pure time; cyan: environment-time overlap; black: environment-space-time overlap). Only significant components ($P < 0.05$) are shown. Taxa in bold type include species from the following underlined groups.

Table 1: Results of variation partitioning analysis for each group, where E, environmental component; S, spatial component; T, temporal component.

Taxonomic group	**E|(S+T)**	**S|(E+T)**	**T|(E+S)**	**(E∩S)|T**	**(E∩T)|S**	**(S∩T)|E**	**E∩S∩T**	**E+S+T**
Phytoplankton	0.07**	0.03**	0.01**	0.08	0.02	0	0	0.21**
Cyanobacteria	0.05**	0.06**	0.02**	0.03	0.01	0	0	0.17**
Chlorophyceae	0.09**	0.04**	$0^{n.s.}$	0.07	0	0	0	0.20**
Mixotrophic phytoplankton	0.04**	0.02*	0.04**	0.04	0	0	0	0.14**
Diatomea	0.12**	0.04**	$0.01^{n.s.}$	0.05	0.01	0	0	0.23**
Rotifera	0.08**	$0.01^{n.s.}$	0.03**	0.09	0.01	0	0	0.22**
Crustacea	0.06**	0.07**	0.02**	0.05	0.05	0	0	0.25**
Branchiopoda	0.19**	$0^{n.s.}$	$0.02^{n.s.}$	0	0.01	0	0.01	0.23**
Copepoda	0.06**	0.07**	0.02*	0.09	0.02	0	0	0.26**
Ostracoda	0.13**	0.05*	$0.01^{n.s.}$	0.14	0	0	0	0.33**
Macroinvertebrates	0.02*	0.06**	0.03**	0.03	0.02	0	0	0.16**
Mollusca	0.11**	0.08**	0.04**	0.05	0.03	0	0	0.31**
Insecta	$0.01^{n.s.}$	0.05**	0.02**	0.01	0	0	0	0.09**
Paleoptera	0.04*	$0.02^{n.s.}$	0.02*	0.06	0	0	0	0.14**
Heteroptera	$0.02^{n.s.}$	0.15**	0.02*	0.01	0.01	0	0	0.21**
Coleoptera	0.08**	0.02*	0.02*	0	0.02	0	0	0.14**
Diptera	0.04**	0.03**	0.05**	0	0.01	0	0	0.13**

The table shows the proportion of variation (R^2_{adj}) explained by each pure component and the overlaps between components. Significance codes: **(P<0.001), (P<0.05), n.s. (non-significant).

When comparing passive and active dispersers, the pure environmental component was significantly higher in the former group (***Figure 3***, Kruskal-Wallis: P = 0.037). On the other hand, there were no differences neither in pure spatial nor temporal effects between these groups. Therefore, although the spatial structure and temporal dynamics seem to have the same influence for both types of dispersal strategies, passive dispersers seem to be more environmentally structured than active dispersers

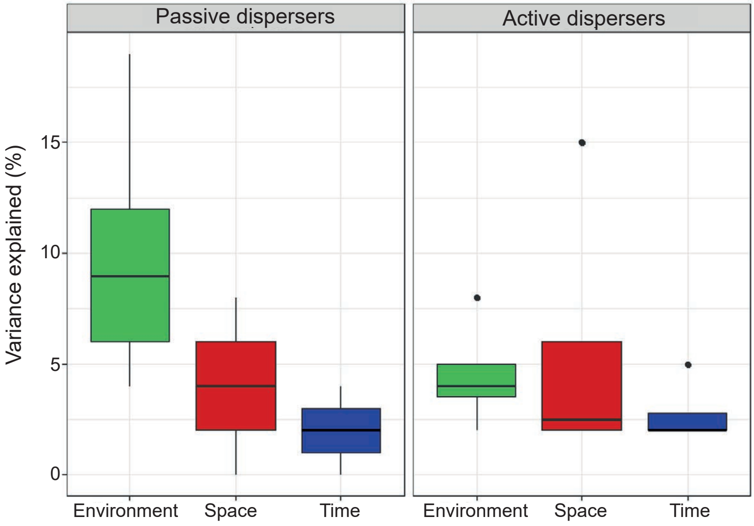

Figure 3: Percentage of metacommunity variance explained by pure environmental, spatial and temporal components, according to the type of dispersal of the studied groups of organisms.

Table 2: Number and type of environmental variables selected in the variation partitioning analyses for each group of organisms.

Taxonomic group	Limnological variables	Climatic variables	Landscape variables	Hydrogeomorphological variables	Biotic variables	Conservation variables
Phytoplankton	7	2	1	2	2	0
Cyanobacteria	3	1	0	1	0	0
Chlorophyceae	5	1	0	3	0	2
Mixotrophic phytoplankton	2	1	1	1	0	2
Diatomea	4	1	1	3	1	1
Rotifera	5	2	1	1	1	2
Crustacea	6	1	2	2	2	1
Branchiopoda	7	0	0	2	0	0
Copepoda	2	1	1	1	1	0
Ostracoda	3	4	2	2	0	0
Macroinvertebrates	0	2	0	1	2	1
Mollusca	2	1	1	1	1	0
Insecta	0	1	1	0	0	1
Paleoptera	1	1	2	0	0	1
Heteroptera	1	1	0	0	0	0
Coleoptera	1	1	1	0	1	0
Diptera	1	0	1	0	1	0

In ***Table 2***, we show the number and type of significant environmental variables explaining the variance of each group. In organisms with small body size and passive dispersal (from Phytoplankton to Crustacea), species sorting is dominated by limnological variables. In Mollusca and active dispersers, limnological, climatic, and landscape variables seem to play a similar role, but no hydrogeomorphological variables were selected for insects.

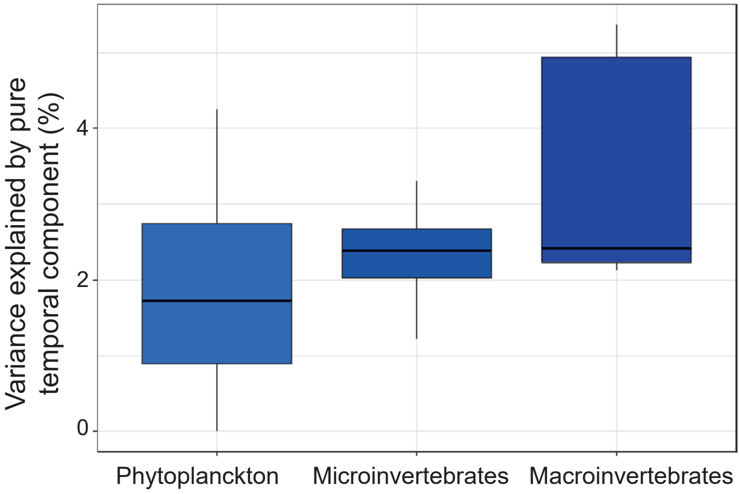

Figure 4: Percentage of variance explained by pure temporal effects for three groups with different generation times: Phytoplankton (Cyanobacteria, Chlorophyceae, mixotrophic phytoplankton, and Diatomea), Microinvertebrates (Rotifera, Branchiopoda, Copepoda, and Ostracoda) and Macroinvertebrates (Mollusca, Paleoptera, Heteroptera, Coleoptera, and Diptera).

The influence of the temporal component seems to follow an increasing trend that might be related to increasing length of the life-cycle, from phytoplankton groups to microscopic metazoans to macroinvertebrate groups (***Figure 4***). However, we did not find significant differences among these three groups (K-W test, P = 0.354).

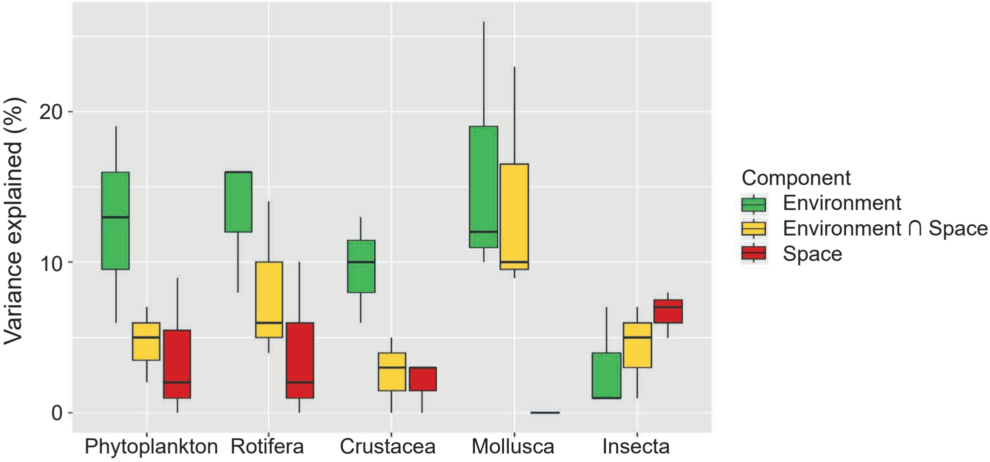

Figure 5: Results of variation partitioning analyses of Phytoplankton, Rotifera, Crustacea, Mollusca, and Insecta studied for each sampling season separately. The variability among seasons is represented in a boxplot graph. The percentage of explained variation for each component is represented with a different color.

Finally, separated variation partitioning analyses for each of the three sampling seasons were carried out for five different groups of organisms (Phytoplankton, Rotifera, Crustacea, Mollusca, and Insecta) (***Figure 5*** and ***Table 3***) to check for variability of spatial and environmental effects through time. Selected variables are shown in the ***Supplementary Table S4***. We observed a temporal variation in the percentage of variance explained by the pure environmental component, even though this component appears to be significant in every group through time. The pure spatial component decreases with time in every group except for Mollusca, which do not present a significant pure spatial component in any sampling period, and for Insecta, whose pure spatial component remains almost constant.

DISCUSSION

Our results show that species distributions of most of the studied taxa are environmentally, spatially and temporally structured, notwithstanding the relatively low percentage of variances explained by the set of selected variables. Such low values are not uncommon, according to previous studies of freshwater metacommunities (Soininen et al., 2007; De Bie et al., 2012; Padial et al., 2014; Rojo et al., 2016) and, because we made an intensive effort of environmental and spatial characterization, the unexplained variation might be largely attributable to other unmeasured processes. For example, biotic interactions such as predation, competition, facilitation, etc. seem to play an important role structuring metacommunities, increasing the influence of environment (both abiotic and biotic) on metacommunity assembly (Leibold and Chase, 2018; García-Girón et al., 2020). Furthermore, ecological drift, or random variation of species abundances, generating differences between sites, is also a strong process influencing metacommunity structure and dynamics (Jeffries, 1988; Chase, 2007).

Table 3: Results of variation partitioning analysis for Phytoplankton, Rotifera, Crustacea, Mollusca and Insecta, each sampling campaign analyzed separately, where E, environmental component; S, spatial component.

Taxonomic group	**E|S**	**S|E**	**E ∩ S**	**E + S**
Phytoplankton				
Season 1	0.13**	0.09**	0.07	0.29**
Season 2	0.19**	0.02$^{\text{n.s.}}$	0.02	0.23**
Season 3	0.06**	0$^{\text{n.s.}}$	0.05	0.11**
Rotifera				
Season 1	0.08**	0.02$^{\text{n.s.}}$	0.06	0.16**
Season 2	0.16**	0.1**	0.04	0.30**
Season 3	0.16**	0$^{\text{n.s.}}$	0.14	0.30**
Crustacea				
Season 1	0.06*	0.03$^{\text{n.s.}}$	0.05	0.14**
Season 2	0.13**	0.03$^{\text{n.s.}}$	0	0.16**
Season 3	0.1**	0$^{\text{n.s.}}$	0.03	0.13**
Mollusca				
Season 1	0.12*	0$^{\text{n.s.}}$	0.1	0.22**
Season 2	0.26**	0$^{\text{n.s.}}$	0.09	0.35**
Season 3	0.1$^{\text{n.s.}}$	0$^{\text{n.s.}}$	0.23	0.33*
Insecta				
Season 1	0.01$^{\text{n.s.}}$	0.07**	0.05	0.13**
Season 2	0.01$^{\text{n.s.}}$	0.05**	0.01	0.07**
Season 3	0.07**	0.08**	0.07	0.22**

Temporal effects were found to be relevant in our analysis of metacommunity dynamics. On the one hand, there is an overlap between temporal and environmental components that suggests that part of the significant environmental variables undergo temporal changes throughout the hydroperiod (Bellier et al., 2013). In this sense, species sorting snapshot studies are not fully representative of the whole metacommunity (Rojo et al., 2016). Actually, in highly dynamic ecosystems such as ponds, temporal changes drive fast variations in community structure through turnover processes. On the other hand, we found significant pure temporal effects on most organisms, which even had a stronger influence than pure spatial or pure environmental components in some cases: the temporal component was higher or equal than environmental or spatial effects in 9 out of 17 taxa, being the most important component in Diptera (5% of variance explained, maybe influenced by seasonal dynamics in some families such as Chironomidae or Culicidae; Yunjun and Xiaoyu, 2007). Most previous studies focused on the temporal change of species sorting and neutral effects by comparing between sampling periods (e.g., Fernandes et al., 2014; Rojo et al., 2016), not checking the proportion of variation explained by time itself and, when they did, they usually found a very weak or non-significant influence of temporal effects on the metacommunity (Anderson and Gribble, 1998; Padial et al., 2014). However, our results show that time per se, can indeed be an important element in metacommunity structure, even more important than space and environment in some cases, as also found by Bortolini et al. (2019) in a study of subtropical phytoplankton.

Species sorting appears to be an important process for most groups, evidenced by the significant percentage of variance explained by the pure environmental component in all the groups except Heteroptera and Insecta. In addition, this component showed the highest explanatory power in 9 out of 17 metacommunity groups being analyzed. These results highlight the idea that pond communities, even in tropical regions with high species richness and relatively low environmental variability, can be structured by the environment. As a consequence of the relatively small overall niche space in relation to the high number of coexisting species responding to this reduced environmental variability, we might expect narrow realized niches due to niche packing (Lamanna et al., 2014). In addition, we found high percentages of overlap between the environmental and spatial components, perhaps attributable to spatially structured environmental gradients (Clappe et al., 2018), such as climate or landscape variables.

The observed niche-related processes seem to be modulated by dispersal capability. According to the selected environmental variables, passive dispersers were strongly influenced primarily by limnological variables. Many phytoplankton and zooplankton species have wide distributions (Vyverman, 1996; Finlay, 2002; Forró et al., 2008; Segers, 2008) (but see Fontaneto, 2011), and their resting forms are highly resistant to environmental stress (Alekseev et al., 2007; Holzinger and Karsten, 2013; Radzikowski, 2013). The distribution of these organisms is therefore unlikely to be controlled by regional environmental variables, such as climate or landscape, so that local environment might play a stronger influence in their colonization success and population dynamics. On the other hand, we found that active dispersers were influenced at a similar intensity by both local (limnological) and regional (landscape, geographic) variables, being sensitive to aquatic and terrestrial environmental conditions, as also found by other authors (Nnoli et al., 2019). Passive dispersers showed higher pure environmental effects compared to active dispersers, in agreement with previous works that found that the distribution of organisms with high dispersal ability, such as phytoplankton, was more influenced by local environmental conditions (Padial et al., 2014), although other authors consider that actively moving organisms should show a stronger relationship with environmental factors than passively dispersing ones (De Bie et al., 2012; Soininen, 2014). Maybe insects, despite being able to fly, are not so easily dispersed at long distances as are passive dispersers such as algae, rotifers or microcrustaceans. These differences may even be stronger in tropical areas due to the expected increase in dispersal limitations (mountains are "higher" in the tropics; Janzen, 1967). The relative influence of space and environment on metacommunity organization depends on the extent of spatial and environmental gradients and on connectivity, not only on organisms' dispersal traits (Heino et al., 2015; Castillo-Escrivà et al., 2020). One may expect that if we would include semi-permanent ponds and seasonally connected ponds, or other types of water bodies, in the study, the observed influence of species sorting on the structure of aquatic metacommunities would probably increase (Wellborn et al., 1996; Cottenie et al., 2003). We need not to forget that other factors may influence the relative influence of these components, such as the number of measured environmental variables, the way that space is considered in the analyses, the sampling resolution, habitat heterogeneity or species pool size (Leibold and Chase, 2018). In any case, our expectation that small body sized, passively dispersing organisms are proportionally less affected by spatial factors than environmental ones, seem to be supported, although perhaps not so much because of the influence of flood connectivity but rather by regionally related aspects of reduced dispersal in larger bodied organisms such as the abovementioned Janzen's effect.

Neutral processes seem to have high importance in these isolated systems, as suggested by the residuals and the significant pure spatial component in most of the analyzed groups, in agreement with previous studies (De Bie et al., 2012; Baguette et al., 2013). This component was especially strong for the flying Heteroptera, with about 70% of their total variation explained by pure spatial effects. This was unexpected, given the high dispersal ability and colonization efficiency of many heteropterans (Williams, 2005), so this perhaps reflects high small-scale dispersal among nearby ponds, together with larger-scale dispersal limitation. In this sense, the distribution of some groups with low dispersal ability, such as Mollusca, is expected to be more affected by dispersal limitation than by mass effects dynamics, although this depends on sampling extent and connectivity. On the other hand, groups with high dispersal ability, sometimes with cosmopolitan distributions, also showed a significant pure spatial component, which cannot be directly attributable to dispersal limitation but perhaps to mass effects instead (Leibold et al., 2004; Ng et al., 2009; Winegardner et al., 2012). Due to the similar percentage of variance explained by the pure spatial component in groups with very different dispersal strategies and abilities (e.g., Chlorophyceae: 4%; Cyanobacteria: 6%; Copepoda: 7%; Mollusca: 8%; Diptera: 3%) we interpret that both dispersal limitation and mass effects may contribute to spatially structuring the studied metacommunity (Declerck et al., 2011). However, the relative importance of spatial factors compared to species sorting was not as high as we initially expected from the reduced environmental fluctuations in tropical environments, so we must reject our hypothesis that environmental processes should have a lower influence than spatial processes in tropical metacommunity organization.

Even though the temporal effects were found to widely vary among taxonomic groups with similar generation times, the influence of the temporal component related positively (although this relationship was not significant) to organism generation time (or its surrogate of body size). Many biological processes that strongly affect individuals and populations of (aquatic) organisms, such as maturation, reproduction, senescence, or population growth depend on time spanned (Lahr et al., 1999; Cayrou and Céréghino, 2005; Williams, 2005). In addition, egg-bank hatching and immigrant colonization are also time-dependent (Frisch and Green, 2007; Vanschoenwinkel et al., 2010). We found no significant differences in the temporal component between active and dispersal colonizers, so we cannot state that any of these groups is more strongly structured by time-related processes. We could not provide a strong support for our expectation of higher temporal effects in longer-lived organisms, but the observed (non-significant) trend calls for further research on this possibility, maybe increasing the time extent to be able to detect temporal effects (Castillo-Escrivà et al., 2020). The taxonomic groups with non-significant temporal effects were all passive dispersers, which usually leave diapausing propagules in the sediment and have fast life-cycles. These temporal effects or their lack thereof might therefore be related to colonization processes (faster from the sediment, with certain lag from other ponds), increased turbidity and dilution of planktonic populations during the rainy season, overlapping generations, biotic interactions or metamorphosis and flee from the waterbody by juvenile insects when molting to flying adult instars (Anderson et al., 1999; Williams, 2005; Nursuhayati et al., 2013).

Snapshot surveys are common in metacommunity studies, and high variability of results are observed between them regarding the most influential factors, with even contradictory conclusions (e.g., De Bie et al., 2012; Farjalla et al., 2012). When analyzing our temporal series as three separate snapshots, we found clear differences not only between periods but also compared to our overall results when analyzing the three sampling campaigns altogether. These inconsistencies evidence that single-survey metacommunity studies may drive to misleading or uncomplete conclusions. Our results show an unexpectedly high neutral-based structuring during the seasons corresponding to infilling and maximum flooding, that eventually decreases during the dry season (the desiccation phase), in relation to the relative importance of environmental filtering for all groups (except Mollusca). The observation of relatively high neutral structure at the onset of the hydroperiod was previously observed by Castillo-Escrivà et al. (2017c) in ostracods from temporary lakes, suggesting an initial hatching bloom of opportunistic species from the egg bank (Olmo et al., 2012) provoking more random associations that would later become structured by species filtering, i.e., niche-related processes. As previous studies suggest, seasonal floods produce spatial deconstruction, increasing connectivity and dispersal of many organisms, so as dilution effects and environmental homogenization (Thomaz et al., 2007; Rojo et al., 2016). Thus, in early phases of the hydroperiod, community structure might highly depend on egg-bank hatching and, soon after, also on spatial processes, such as hydrochory via flooding or colonization by immigrants. Conversely, pond isolation and consequent environmental heterogenization as the pond succession proceeds toward the end of the rainy season produce an increment of species sorting effects (Fernandes et al., 2014). However, in organisms without an egg bank, such as most aquatic insects, we observe a constant strong influence of pure spatial components. Insects must leave ponds before desiccation and recolonize other water bodies after infilling, so that colonization events can happen repeatedly all along the hydroperiod (Tronstad et al., 2007), but constrained by life-cycles and distance between sites. Anyway, when comparing snapshot and periodic sampling analyses considering time as a set of variables to partial out different structuring effects, remarkable differences can arise; for instance, in the whole hydroperiod analyses of the mollusk metacommunity, the pure spatial component explained an important percentage of variance, while it appeared to be non-significant in single-period analyses, where there is a higher overlap between spatial and environmental effects. This overlap could then be disentangled when considering three sampling periods together.

We may conclude that time is a relevant factor organizing metacommunities of tropical temporary ponds, becoming almost as important as environment and space (Langenheder et al., 2012), as expected from ecological theories of community assembly and succession (Pickett et al., 2011; Fukami, 2015). Many temporal processes are difficult to study, especially long-term ones, but short-term temporal dynamics seems to modulate tropical (pond) metacommunities on a par with niche and dispersal related processes. In addition, species with larger body sizes (and longer generation times) seem to be more influenced by environment-independent temporal effects than smaller, faster developing, organisms. However, despite the importance of spatio-temporal factors influencing metacommunity structure, environment seems to be the main process in metacommunity assembly, supporting the relevance of the species sorting paradigm. Moreover, this environmental component is higher in passive dispersers, mainly influenced by local environment, than in active dispersers, influenced by local and regional environment. Finally, our results show that in many organisms, environmental and spatial components are highly variable between periods, so snapshot surveys provide only partial information about metacommunity organization.

AUTHOR CONTRIBUTIONS

FM-J, JM, RR, CR, and MS equally contributed to project design and logistics. FB, JM, RR, MS, FM-J, and CR carried out field work. Phytoplankton identification was supervised by CR. ÁG, CO, and XA identified Rotifera, Branchiopoda, and Calanoida. SI identified Cyclopoida. FM-J and JA-A identified Ostracoda. JR identified macroinvertebrates. ÁG did data analysis and manuscript writing. FM-J supervised and reviewed the manuscript with comments from XA, JR, SI, CR, and CO. All authors contributed to the article and approved the submitted version.

FUNDING

This research was supported by AECID Grants A1024073/09 and A/031019/10 of the Spanish Ministry of Foreign Affairs to the University of Valencia and by Vicerrectoría de Investigación Universidad de Costa Rica Grant 741-B1-517. This study was also sustained by the Spanish Ministry of Economy, Industry and Competitivity–AEI, and FEDER (EU), through project METACOM-SET (CGL2016-78260-P). The Spanish Ministry of Economy and Competitiveness partially supported this study through project CGL2014-54502-C2-1-ÁG was also supported by an FPI fellowship BES-2017-080022 from the Spanish Ministry of Economy, Industry and Competitiveness.

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.

ACKNOWLEDGMENTS

We want to thank Matilde Segura for phytoplankton identification. We are also grateful to Sergio Padilla, Arelly Reyes, and Davinia Beneyto for field assistance, Ulises Chavarría and the Palo Verde National Park personnel, Darío Hernández (Vicerrectoría de Investigación, UCR), Julieta Carranza, WalterMarín, Odeth Esquivel, and Yorleny Aguilar (Oficina Asuntos Internacionales, UCR) for logistic support at different stages of the project. We are also very grateful for the comments and suggestions of Jani M. Heino, Man K. Cheung, and Fábio A. Lansac Toha, which improved the present paper.

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Laguna de Peje, Costa Rica. Fotografiado por Juan Rueda

CAPÍTULO 3

The environmental framework of temporary ponds: A tropical-mediterranean comparison.

ABSTRACT

Temporary ponds are distributed worldwide, providing significant ecological services. Their limnological features are influenced by a set of regional (mainly climate) and local (natural or anthropogenic) factors. To evaluate the differences in their ecological functioning in distant geographic regions, we analysed the main features of 90 temporary ponds located in three distinct areas: two mediterranean-climate regions (Eastern Iberian Peninsula and Central Chile) and a tropical setting in Costa Rica. Each pond was surveyed thrice during the hydrological cycle of 2017–2018, and five sets of parameters were obtained: limnological, geomorphological, biotic, landscape and climatic variables. Through multivariate analyses, we determined the environmental heterogeneity of each region and the main environmental differences among them. As expected, hydrogeomorphological factors did not differ between regions, but climate variables showed marked differences between the tropical and the two mediterranean regions. We also detected clear differences between mediterranean and tropical ponds in terms of their mineralization patterns (mainly conductivity and alkalinity), natural vegetation cover and land use. Despite the regional similarities between mediterranean regions, some strong differences were found concerning vegetation cover, nutrient concentration and trophic state, probably related to human activities (agriculture and extensive stockbreeding).

Key words: Small freshwater bodies, Central America, South America, Iberian Peninsula, Land use, Eutrophication

INTRODUCTION

Small water bodies account for a larger amount of the Earth's surface than lakes (Downing et al., 2006), and they also differ in their ecological functioning (Søndergaard et al., 2005; Cole et al., 2007) and the biotic communities they host (Scheffer et al., 2006; Downing, 2010). The term "pond" is the common name used to refer to small water bodies which are shallow (<8 m depth, but frequently shallower) with surfaces between 1 m^2 and 10 ha (Grillas et al., 2004). They provide numerous ecosystem services, such as nutrient sinks, water sources for livestock and wildlife, reservoirs of biodiversity, or cultural elements of landscapes (Williams, 2006). Moreover, their particular hydrology and rapid responses to disturbances make them quick sentinel ecosystems in environmental monitoring facing habitat degradation caused by pollution or climate change (Céréghino et al., 2008). However, the rate of degradation and disappearance of ponds is drastically increasing worldwide (Rhazi et al., 2012). This situation may be more dramatic in mediterranean and tropical areas, where information about the conservation and ecological functioning of water bodies is still scarce (Junk, 2002; Boix et al., 2016). In karstic, arid and semiarid regions with a mediterranean climate, temporary ponds are well represented (Ramsar Convention, 2002), being there more important than permanent ponds or lakes, which are scarce (Parra et al., 2021). Nevertheless, ponds are widely distributed across all climatic zones and continents, although they present regional differences (Williams, 2006). Wherever they are located, all temporary ponds share the alternative wet and dry phases that normally depend on rainfall events (Williams, 2006). Beyond this common characteristic, other environmental factors, operating at different scales, also influence the ecological processes and functioning of these long neglected water bodies (Bagella et al., 2016; Gálvez et al., 2020).

At the regional scale, climatic factors are expected to exert strong influences on water bodies (Moss, 2010). Precipitation (and direct runoff) is the main input of water to temporary ponds and, consequently, the rainfall regime should influence their water chemistry dynamics (Sasa et al., 2015). Rainfall seasonality is considered to be the major factor regulating ecological processes of these water bodies in the tropics (Mukhopadhyay et al., 2004). Most tropical regions are warm with highly seasonal rainfall events (Allaby, 2006; Roth, 2007; Tonkin et al., 2017). This feature allows the maintenance of seasonal dry forests, widely distributed in all tropical regions, including Western Central America, and which are among the world's most threatened terrestrial ecosystems (Janzen, 1988). Mediterranean-climate zones, restricted to a few areas within temperate regions, present a marked dry summer season, that coincides with the maximum temperature, but are also characterised by wet autumn and spring seasons (Blondel et al., 2010). The influence of these special features results in xerophytic vegetation dominated by shrubs and low-growing species (Esler et al., 2018). As ponds are mostly shallow water bodies, they are strongly influenced by direct sunlight and the air temperature of each region (Williams, 2006). Solar radiation is stronger in the tropics than in temperate regions, facilitating photodecomposition and increasing the degradation rate of chemical compounds (Magallona, 1989). In addition, higher air (and water) temperature strongly influence other related limnological features of water bodies (Williams, 2006). Increasing water temperature reduces the concentration of dissolved oxygen in the water and accelerates chemical and biological processes such as the microbial reposition of organic matter (Wetzel, 2001). When decomposition rate increases, pH and oxygen concentration decline (Brönmark and Hansson, 2017), and these may affect the limnological traits and processes of temperate compared to tropical ponds. It should be noted that diel temperature changes in tropical water bodies can be wider than average annual variations (Barbosa and Tundisi, 1989). Such high homogeneity in temperature and photoperiod through the year allows maintaining a fairly constant biological production in tropical ponds during the wet season (Mukhopadhyay et al., 2004). On the contrary, temperate regions, where seasonal changes of light and temperature are wider, may show higher annual environmental variability of pond limnological parameters (Brönmark and Hansson, 2017).

Besides climate features, other natural or anthropogenic factors at the local scale may also influence the ecological dynamics of temporary ponds. Within the same region, these factors can be highly variable, and they may determine differences among ponds and therefore can either emphasise or attenuate the limnological dissimilarities between climatic regions. Among natural factors, morphometry, so as the characteristics of the drainage area and its own biota, influence pond limnological parameters in different ways, including the duration of the hydroperiod, the dilution or concentration of chemical compounds in the water, or the amount of organic matter inputs from the vegetation to the water column (Williams, 2006). The hydroperiod length of ponds, which is a critical determinant of pond dynamics, depends on the regional climate and the hydrological conditions of the area, but also on the geomorphometrical characteristics of each basin, chiefly shape, depth and surface (Williams, 2006). Moreover, the dominant geological substrate of the drainage area and the basin itself, highly determines the mineralization and pH of the water. Evaporation can increase the proportion of dissolved ions in the water, this being particularly important in semi-arid and arid regions and those with seasonally hot dry seasons (Cañedo-Argüelles et al., 2013; Parra et al., 2021). In calcareous regions, pH is mostly regulated by the carbonate buffer system (Wetzel, 2001), the pH of those water bodies being generally alkaline with values around 8–9. The high connectivity between inland waters and the terrestrial environment makes anthropogenic activities in the landscape surrounding the ponds to potentially alter the water bodies embedded in the area of human influence. Different land uses affect freshwater ecosystems in diverse ways (Stendera et al., 2012). Among other effects, anthropogenic activities usually degrade the natural vegetation of aquatic habitats and their surrounding areas. Thus, the presence of this vegetation is considered as a bioindicator of habitat state and water quality (Flor-Arnau, 2014; Moss et al., 2003; Rodrigo et al., 2010).

The five mediterranean regions of the planet are densely populated and, consequently, the anthropogenic activities disturbing the ecological functioning of water bodies are intense (Blondel et al., 2010). Along the homonymous Mediterranean basin, many freshwater bodies have been studied regarding impacts, functioning, biodiversity or ecosystem services during the last few decades. However, aquatic systems from other mediterranean regions are poorly studied, including Chilean ones (De los Ríos-Escalante and Kotov, 2015). A similar situation occurs with temporary ponds in dry tropical areas, where there is a general lack of knowledge on the limnological characteristics and seasonal dynamics of these systems (Sasa et al., 2015). In this framework, our study aims at disentangling the main ecological differences and similarities between three sets of temporary ponds, two located in mediterranean regions (Central Chile and Eastern Spain) and one in a region with tropical climate (Costa Rica). We anticipate that climate would play the main role in explaining ecological divergences, especially between tropical and mediterranean ponds. However, the type and intensity of some local factors in each region are also expected to exert significant effects on local biotic and abiotic features of these water bodies. By using the same methodology and sampling design across the 90 ponds studied, we aim at developing a framework for understanding limnological disparity of temporary ponds under different geographical settings.

METHODS

Study area, pond selection and sampling period

We surveyed 90 temporary ponds from three different biogeographic regions (30 ponds each): a tropical region in Costa Rica and two areas with mediterranean climate: Central Chile and the Eastern Iberian Peninsula in Spain (hereafter CR, CH and SP, respectively; ***Figure 1***). We sampled an area of similar extension for each of the three regions in order to get a comparable range of habitat variability and maximum distances among sites. For each region, we also tried to select ponds within a similar range of variability in terms of size, hydroregime, altitude, salt content (avoiding brackish waters), nutrient concentration and land use. Ponds were sampled thrice in each region during the hydrological cycle of 2017–2018; the first time a few weeks after the infilling of the ponds, once again in the middle of the hydroperiod and finally before the desiccation of most of the ponds. In CR, the first sampling campaign took place in May-June 2017, the second one in October 2017 and the last in January-February 2018, coinciding with the first sampling period in SP. The second and third sampling campaigns in Spain were in April-May and June-July of 2018, respectively. In CH, the sampling campaigns were in July-August, then October and finally in December of 2018. The number of ponds sampled during each campaign was reduced in the second, and particularly the third sampling seasons because some ponds dried out earlier than expected (eventually, a total of 30, 29 and 23 ponds were sampled in CR during the three sampling periods; 30, 21 and 12 in CH, and 30, 29 and 29 in SP). The ratio of ponds that were strictly temporary (annual dry phase) against those with semipermanent hydroregime (with dry phases but not necessarily annual) were 21/9, 25/5 and 21/9 for CR, CH and SP, respectively. For each region we selected three (four in CR) weather stations distributed along the study area to obtain meteorological information for the study period. In CR, these stations belonged to the National Weather Institute (Instituto Meteorológico Nacional de Costa Rica, 2021) and were located in Liberia Airport, Santa Rosa National Park, Limon Airport and Juan Viñas town. In CH, they belonged to the Center for Climate and Resilience Research of the Universidad de Chile (Centro de Ciencias del Clima y la Resiliencia, 2021), and were located in the towns of Quilimari, Colliguay and Melipilla. In SP, we selected the weather stations located in the towns of Morella, Caudete de las Fuentes/Carcaixent and Bocairent/Alcoi, belonging to the National Climatological Agency (Agencia Estatal de Meteorología, 2021).

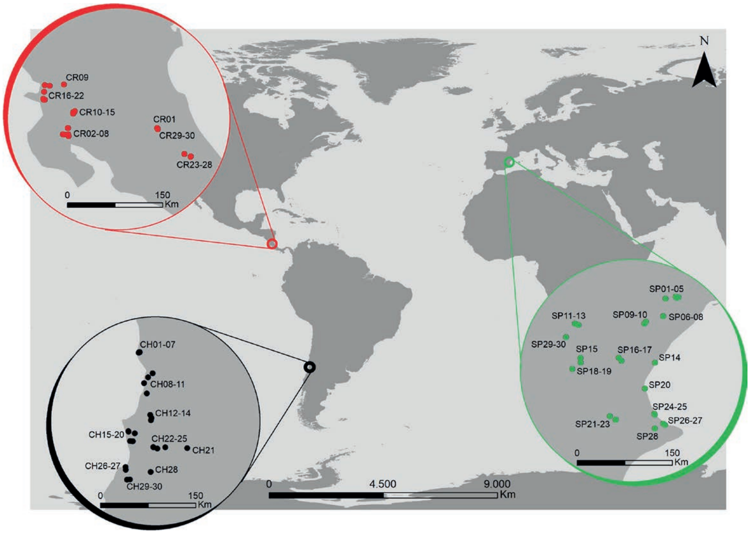

Figure 1*:* Ponds location. Location of ponds in each study region.

Pond sampling and lab analysis

A total of 41 variables were measured and recorded for each pond. These variables were split into five different types: 16 limnological, 4 biotic, related to pond primary producers, 7 hydrogeomorphological, 8 landscape and 6 climate variables (***Supplementary Material I***).

Regarding limnological variables, we measured water temperature, dissolved oxygen, electric conductivity and pH in situ using the multi-parametric probe WTW® Multi 3430 (with WTW® SenTix 940 for pH, TetraCon 925 for conductivity and FDO 925 for oxygen), and water transparency with a Snell tube (Van de Meutter et al., 2006). Moreover, water samples were collected to analyse other parameters in the laboratory, including anions (alkalinity [Alk], chloride and sulphate, using Aquamerck 1.11109 and 1.11106 and Spectroquant 1.73014 Merck ® kits, respectively) and nutrients (ammonium, nitrite, nitrate and reactive soluble phosphorus with Spectroquant 1.14752, 1.14776, 1.14773 and 1.14848 Merck® kits, respectively) following APHA (2005). Anion and nutrient concentrations were transformed to meq L^{-1} units and some ratios were calculated (Alk/Cl^{-}, Alk/SO_4^{2-}, NO_3^{-}/ NH_4^{+} and NO_3^{-}/ NO_2^{-}).

As biotic variables, we visually estimated the cover percentages of three types of vegetation: submerged macrophytes, helophytes and floating vegetation. Moreover, chlorophyll a (as a surrogate of planktonic primary producers) was measured from filtered water samples (through Whatmann® GFF) following the method developed by Jeffrey and Humphrey (1975).

As hydrogeomorphological variables, we measured the maximum and mean depth and the length and width (diameters) of the ponds; moreover, we calculated the surface of ponds using the ellipse area formula. For each of these five variables we calculated the average for the three samplings campaigns. Within this group of variables, we also included the organic matter and carbonate content of the pond sediment, sampled just once during the dry season, and estimated following Heiri et al. (2001).

Regarding landscape variables, we obtained pond altitude and estimated the percentage of land cover around the site, grouped in six categories (agricultural, low grass, high grass, scrub, forest and human infrastructures). For this purpose, we measured the proportion of each type in a buffer of 100 m of diameter around the pond sampling point, using satellite images from Google Earth (Google Inc.) The heterogeneity of land cover was estimated for each pond using the Shannon index of the proportions of the above-mentioned categories (Baudry and Burel, 1982).

Finally, historical climate variables (based on the period 1970–2000) were obtained from the online server worldclim.org (Fick and Hijmans, 2017). Mean maximum annual temperature, mean minimum annual temperature, mean annual temperature, annual temperature range, annual accumulated precipitation and precipitation seasonality (as the precipitation coefficient of variation) were extracted with ArcGis 10.0 (ESRI, 2006) for each pond location.

It must be noticed that 21 variables (hydrogeomorphological, landscape and climate variables) were held constant for each site for all sampling campaigns (hereafter called “fixed variables”) while 20 variables (limnological and biotic variables) changed between sampling campaigns (hereafter called “changing variables”). This distinction is important for further data analysis. Further qualitative variables were visually estimated or gathered from local informants, including type of hydroregime (temporary or semi-permanent), presence of livestock, water origin (rain, streams, phreatic) and connectivity with other water bodies.

Data analysis

Prior to data analyses, for each sampling region we built four different matrices in order to compare their effects separated or combined and depending on data variation between seasons or their lack thereof. Three matrices included one or two groups of variable types: 1) climate, 2) limnological with biotic and 3) hydrogeomorphological with landscape. Another matrix 4) was built with all the variables together.

In order to analyse the data variability for each region and their pairwise differences, we used Multivariate Homogeneity of Groups Dispersions (Variances) tests with Euclidean distance (Anderson, 2006). This analysis was performed four times, one for each of the four matrices described above.

A two-way PERMANOVA test (Anderson, 2017) with Euclidean distances, was used to test for differences between the three regions, between sampling campaigns and their interaction on the whole environmental datasets.

We used Discriminant Analyses (DA) to check which variables accounted for main differences among the three regions during the whole hydroperiod. We checked the differences of both fixed and changing variables among the three regions (CR vs CH vs SP) and between pairs of regions (CR vs CH, CR vs SP and CH vs SP).

Finally, to explore environmental variation among regions and sampling seasons, we performed three Principal Component Analyses (PCA) for three of the matrices mentioned above: climate variables (PCA-I), limnological and biotic variables (PCA-II) and hydrogeomorphological and landscape variables (PCA-III).

To reduce large deviations from normality, some data were log- transformed, or with the arcsine of the square root in the case of proportions. Multivariate Homogeneity of Groups Dispersions analyses were carried out with the software R version 3.2.2 (R Core Team, 2021), using the *betadisper* function in *vegan* (Oksanen et al., 2019). The software PAST 3.18 (Hammer et al., 2001) was used for the two-way PERMANOVA test and the Principal Component Analyses. Discriminant Analyses were implemented in the program SPSS Statistics 26 (IBM Corp., 2019).

RESULTS

Environmental framework

Since some ponds dried earlier than expected due to variations in the amount and distribution of rainfall events, the number of flooded ponds diminished through time. This was particularly noticeable in CH. The hydrological year in CH was very xeric, with a median accumulated rainfall of 148 mm in 2018 (range 14–420 mm), whereas the median for the period 1970–2000 was 436 mm according to the obtained climate data (***Supplementary Material I***).

When analysing limnological variables, conductivity was higher in CH, followed by SP and CR (***Figure 2*** and ***Supplementary Material I***). In CR, conductivity showed lower variation between ponds and sampling campaigns than in CH or SP, but its variability was not related to a clear seasonal pattern in these mediterranean regions. The anionic composition, both in terms of proportions and absolute concentrations, varied between regions. The chloride fraction reached higher values in CH and SP and this anion was responsible for the highest conductivity values. In general, carbonates (alkalinity) were the anionic dominating fraction in SP and CR, and the highest absolute values corresponded to SP and CH (***Figures 2 and 3*** and ***Supplementary Material I***). In agreement with the proportions shown in ***Figure 2***, the obtained mean Alk/Cl^- ratios were similar among regions, but the Alk/SO_4^{2-} ratio was particularly high and variable in CR. Sulphates were actually dominant (>50%, ***Figure 2***) only in a few samples, mostly from SP. Other limnological variables also differed between regions, particularly water temperature, which was highest in CR, and water transparency, with highest values in SP. Only those variables that presented a higher number of significant differences between regions, according to discriminant analysis (see below) are represented in ***Figure 3*** (“changing variables”) and ***Figure 4*** (“fixed variables”). Regarding pH, oxygen and nitrate, CR always presented the lowest values, while CH and SP shared similar records (***Figure 3*** and ***Supplementary Material I***). The other nutrients analysed, i.e. ammonium, nitrite and soluble reactive phosphorus, generally had very low concentration values. The ratios NO_3^-/NH_4^+ and NO_3^-/NO_2^- were always highest in CH and lowest in CR. Biotic variables also presented differences between regions; chlorophyll a attained the highest concentrations in CH, reaching hypertrophic status in some ponds and sampling seasons (***Figure 3*** and ***Supplementary Material I***). Submerged vegetation cover was generally higher in SP, and helophytic vegetation was very low in CH, contrary to CR and SP, where the helophytic coverage was similar (***Figure 3*** and ***Supplementary Material I***). On the other hand, floating vegetation cover was slightly higher in CR and similar between both mediterranean regions.

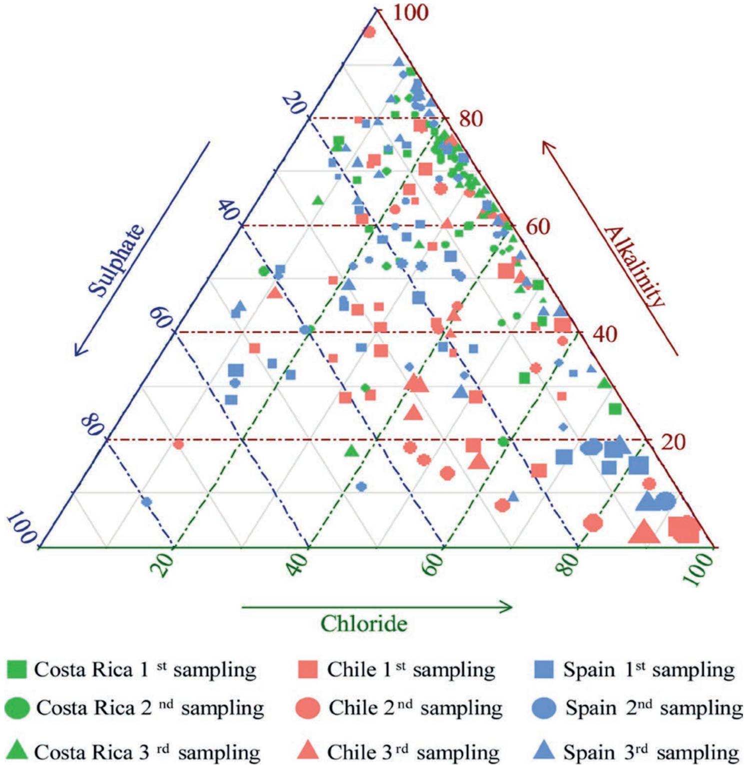

Figure 2: Mineralization. Ternary mineralization diagram for the three regions. Symbol size is proportional to conductivity levels, ranging from 8 to 14,050 µS cm^{-1}.

Regarding hydrogeomorphological variables, the largest ponds were found in CH and CR. The deepest ponds were also located in the tropical region. Altitude was higher in SP, followed by CR and CH (***Figure 4*** and ***Supplementary Material I***). Organic matter content in the sediments showed the highest values in CR, followed by SP and CH, while carbonates were highest in SP and lowest in CH (***Figure 4*** and ***Supplementary Material I***). Land cover heterogeneity was lower in CR than in the mediterranean regions, where the typologies were more evenly distributed. The proportion of short grass vegetation, scrubs and human infrastructures (mostly paved roads) were higher in CH ponds. In SP, the agricultural use was more conspicuous, while in CR it was not relevant, and neither was the scrub vegetation; forest was the dominant cover surrounding the ponds in the tropical region (***Figure 4*** and ***Supplementary Material I***). Minimum and maximum air temperatures, as well as precipitation were higher in CR, followed by CH and SP (***Figure***

3 and ***Supplementary Material I***). On the other hand, the temperature range was wider in both mediterranean areas than in the tropics, whereas precipitation seasonality was higher in CH.

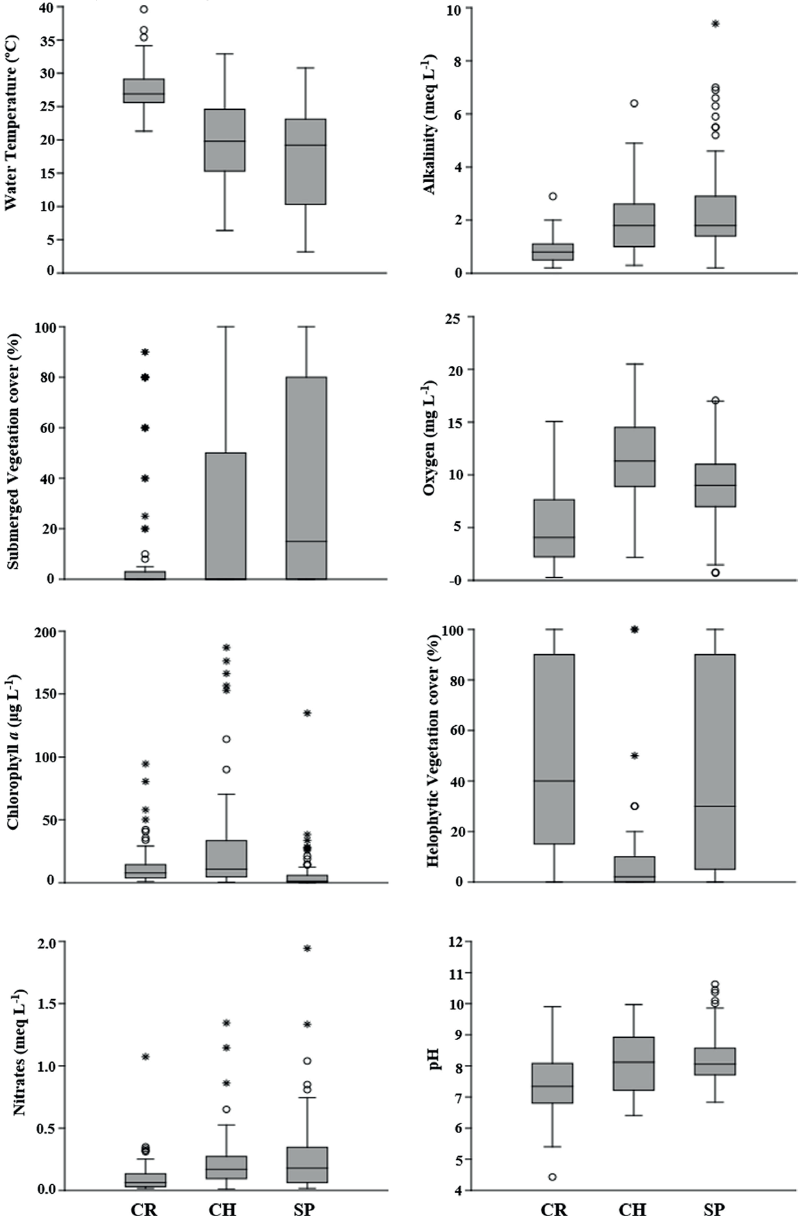

Figure 3: Changing variables. Boxplots of the "changing variables" that presented the highest significant differences in the Discriminant Analysis (see text and *Table 2*) between regions. Three sampling campaigns were included (Costa Rica, n =82; Chile, n =63 and Spain, n =88). The boundaries of the boxes indicate the 25th and the 75th percentiles; lines within the boxes mark the median. Whiskers (error bars) indicate the 90th and 10th percentiles. Dots are outliers.

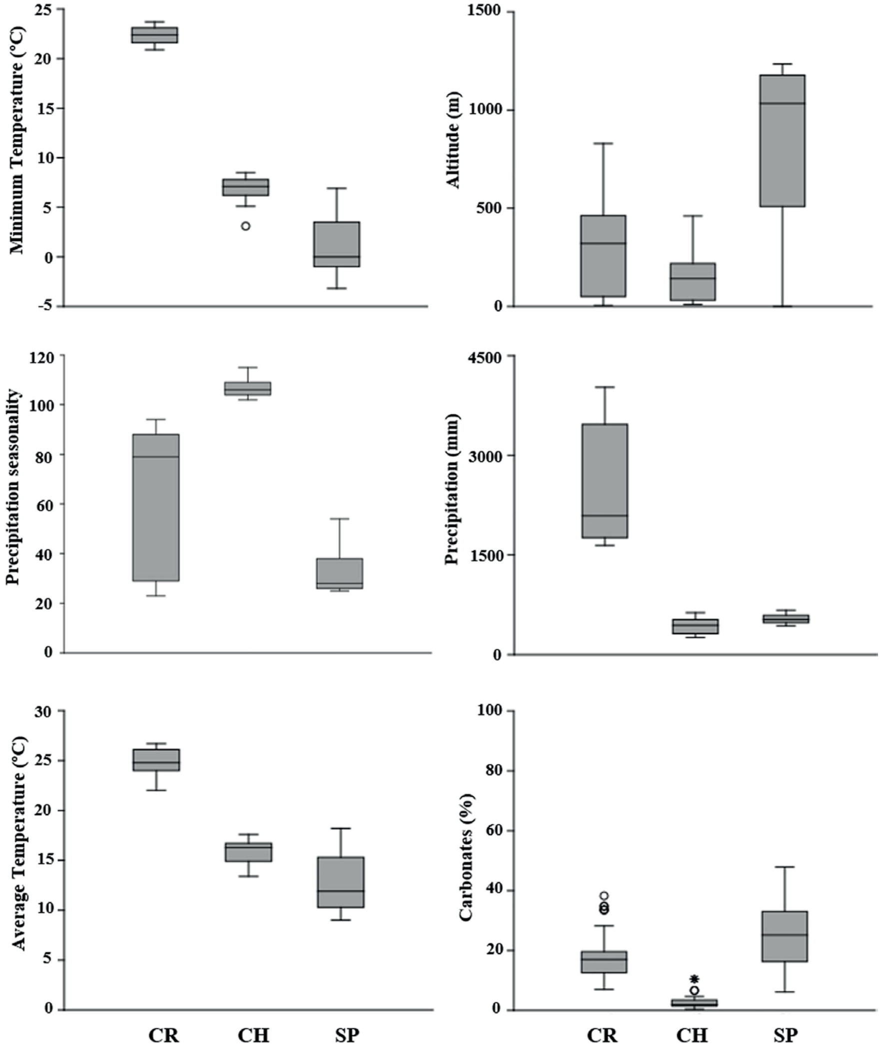

Figure 4: Fixed variables. Boxplots of the "fixed variables" that presented the highest significant differences in the Discriminant Analysis (see text and ***Table 2***). The boundaries of the boxes indicate the 25th and the 75th percentiles; lines within the boxes mark the median. Whiskers (error bars) indicate the 90th and 10th percentiles. Dots are outliers.

Environmental heterogeneity and differences between regions

The PCA-I obtained with the six climate variables clearly divided the samples of different regions along the first two extracted components (***Figure 5a***). The first one (71% of total variance) separated mediterranean sites (CH and SP) with negative values, from CR with positive values, this first axis was strongly and positively correlated with temperature (except its range) and precipitation.

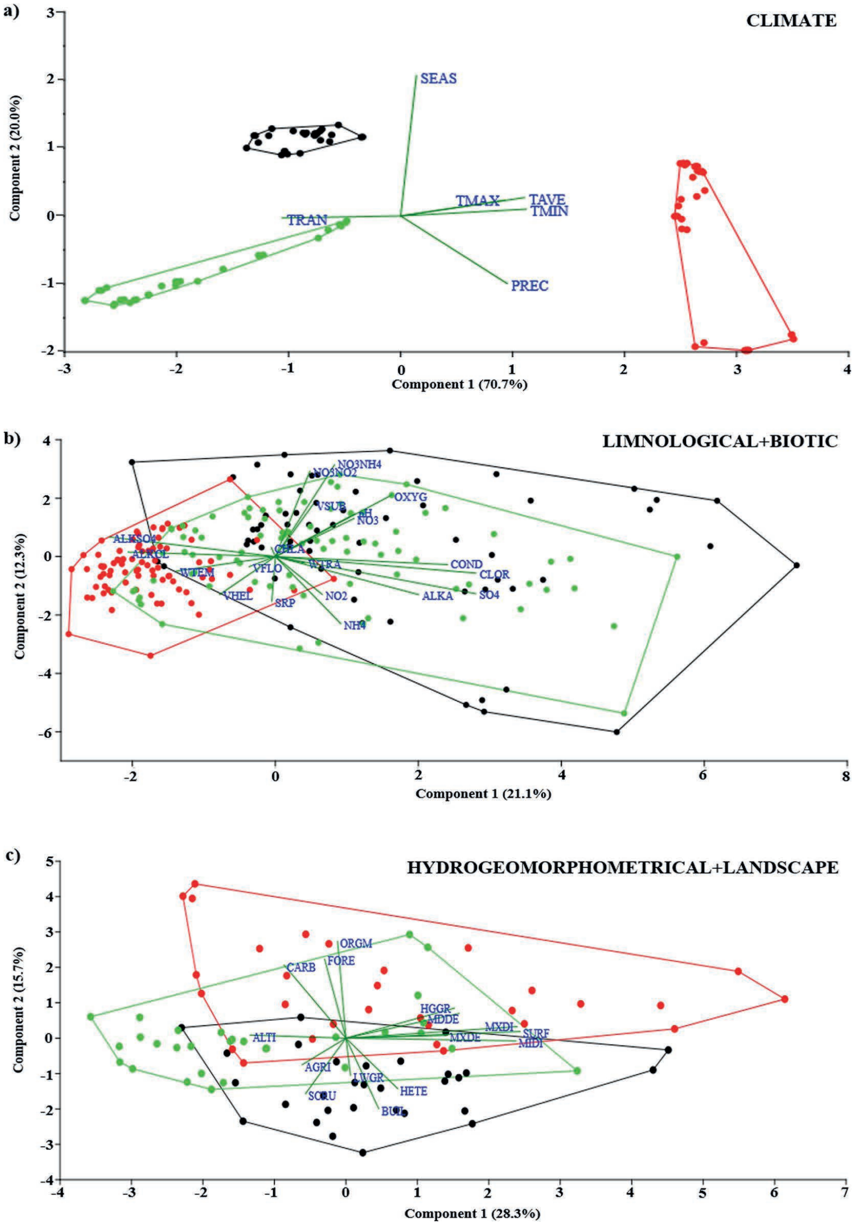

Figure 5: Multivariate analyses of the three regions. Principal Components Analyses for the three regions, a) PCA-I, climate variables, b) PCA-II, limnlogical and biotic variables and c) PCA-III, hydrogeomorphological and landscape variables. Symbols and lines in red, black and green correspond to samples from CR, CH and SP, respectively. Abbreviations: TRAN (air temperature range), TMIN (minimum air temperature), TMAX (maximum air temperature), TAVE (average air temperature), PREC (annual accumulated precipitation) and SEAS (annual precipitation seasonality),WTEM (water temperature), COND (Conductivity), OXYG (oxygen concentration), WTRA (water transparency), ALKA (alkalinity),

CLOR (chloride), NH4 (ammonium), NO2 (nitrite), NO3 (nitrate), SRP (soluble reactive phosphorus), SO4 (sulphate), ALKCL (alkalinity-chloride ratio), ALKSO4 (alkalinity-sulphate ratio), NO3NH4 (nitrates-ammonium ratio), NO3NO2 (nitrate-nitrite ratio), VSUB (submerged vegetation), VFLO (floating vegetation), VHEL (helophytic vegetation), CHLA (chlorophyll a), MXDE (maximum depth), MDDE (mean depth), MXDI (maximum diameter), MIDI (minimum diameter), SURF (surface area), ORGM (sediment organic matter content), CARB (sediment carbonate content), ALTI (altitude), AGRI (land cover, agriculture), SHGR (land cover, short grass), TAGR (land cover, tall grass), SCRU (land cover, scrubs), FORE (land cover, forest), BUIL (land cover, buildings), HETE (land cover heterogeneity).

The second component (20%) separated the two mediterranean regions, with CH on its positive part and SP along the negative one, whereas CR sites were scattered over both the positive and negative part of the axis; precipitation seasonality was strongly and positively correlated with this second axis while annual precipitation appeared negatively correlated. In the PCA-II on limnological (including biotic) variables (***Figure 5b***) and PCA-III on hydrogeomorphological plus landscape variables (***Figure 5c***), samples were more widely spread, and the separation between regions was therefore not so clear as in PCA-I. In PCA-II, summarising the 20 limnological and biotic variables (***Figure 5b***), CR samples were placed closely grouped over the negative part of the first axis (21%), unlike CH and SP samples which were more widespread, probably related to the lower ionic concentration in CR ponds in comparison to the mediterranean samples. This axis was highly and positively correlated with all the mineralization variables, and less strongly with oxygen, pH and the three forms of nitrogen. It was also negatively correlated with both mineralization ratios (Alk/Cl^- and Alk/ SO_4^{2-}), water temperature and two types of vegetation, floating and helophytic. CH and SP samples were the more spread along the second axis (12%), and most CR samples were distributed on the negative side of this axis, which was positively correlated with nutrient ratios ($NO_3^-/NH_4^+$and NO_3^-/NO_2^-), oxygen and submerged vegetation, and negatively correlated with ammonium and soluble reactive phosphorus.

In PCA-III, involving the 15 hydrogeomorphological and landscape variables (***Figure 5c***), the samples from the three regions spread similarly over the first axis (28 % of explained variance), with large overlap among them, but SP samples were mostly located in the negative part of this axis, because of their higher altitude, smaller size and reduced depth. Regarding the second axis (16%), CR ponds were mostly spread over its positive part, related to sediment variables (higher carbonate and organic matter contents) and to forest land cover. On the other hand, most CH samples were placed opposite to CR samples along this axis, which was also strongly and negatively correlated with four types of land cover (agricultural, short grass, scrubs and buildings), and with landscape heterogeneity.

Data dispersion presented significant differences among the three regions so as between some pairs (***Table 1*** and ***Supplementary Material II***). Comparing the three regions, all groups of variables, except for hydrogeomorphological plus landscape variables, showed significant differences. When comparing pairs of regions, and regarding all variables together, CH and SP presented higher data dispersion than CR. But the differences in heterogeneity between both mediterranean areas were not significant. The set of six climate variables presented more heterogeneity in CR and SP than in CH. Finally, comparing the 20 limnological (including biological) variables, CH was significantly more heterogeneous than SP and CR, and SP more than CR.

Table 1*:* Values of the Multivariate Homogeneity of Groups Dispersions (Variances) for each group of variables. Significant differences in bold: * $p < 0.05$ and ** $p < 0.01$. Non-significant p results are shown within parentheses. Coefficients for pairwise comparisons indicate that the first member of the pair has higher (+) or lower (-) multivariate variance than the second member of the pair. See ***Supplementary material II***.

	CHvsCRvsSP	**CRvsCH**	**SPvsCH**	**SPvsCR**
All	**	-1.006 **	-0.405 (0.246)	0.600 *
Climate	**	0.565 **	0.335 **	-0.230**
Limnological + Biotic	**	-1.666 **	-0.629 *	1.036 **
Hydrogeomorphological + Landscape	(0.698)	0.138 (0.691)	0.107 (0.795)	-0.031 (0.978)

Results of a two-way PERMANOVA test showed significant differences between regions (F =63.103, p <0.001) and an interaction effect between region and sampling campaign (F =3.031, p =0.013), but not significant differences among sampling campaigns (F =0.345, p =0.831).

According to these results, we performed eight DAs, comparing between regions, but not between sampling campaigns. Figs. 3 and 4 show only those variables that exhibited large differences between regions according to DAs. Regarding the 20 seasonally changing variables, 11 of them were significantly different among the three studied regions (***Table 2***). Nevertheless, when comparing between pairs, only three variables (water temperature, alkalinity and submerged vegetation) were different at every pairwise comparison. Important differences were also detected for oxygen, chlorophyll a, helophytic vegetation, nitrate concentration and pH. Oxygen was significantly lower in CR than CH and SP, but it did not differ between the two mediterranean regions. Chlorophyll a was the lowest in SP, with no differences between CH and CR. The same pairwise differences as in chlorophyll a appeared for pH, but in this case higher for SP. Samples from CH ponds had significantly lower helophytic vegetation cover than those from CR and SP. Nitrate content was highest in CH compared to CR and SP. Conductivity, ammonium and NO_3^-/NH_4^+ were significantly different between both mediterranean regions, while floating vegetation and the Alk/SO_4^{2-} ratio differed only between CH and CR. Summarising differences by pairs of regions, CH and CR differed in eight variables, CH and SP in 10 and CR and SP in six.

Table 2**:** Values of Wilk's λ and F from Discriminant Analysis for changing and fixed variables. Analyses were performed separately for each group of variables. Obtained p values were < 0.001 in all cases. Abbreviations are shown in the caption of ***Figure 5***.

	CR vs CH vs SP		**CH vs CR**		**CH vs SP**		**CR vs SP**	
	Wilk's λ	F	Wilk's λ	F	Wilk's λ	F	Wilk's λ	F
TMIN (ºC)	0.049	850.5	0.017	3394.9	0.010	1823.7	0.047	1185.2
ALTI (m)	0.001	746.0	0.012	1566.4	0.014	1938.0	0.023	1216.4
WTEM (ºC)	0.639	65.0	0.294	112.7	0.379	22.9	0.554	135.0
ALKA (meq L^{-1})	0.323	57.8	0.382	114.9	0.494	29.6	0.329	113.1
VSUB (%)	0.233	48.5	0.222	59.5	0.390	24.5	0.423	113.8
SEAS	0.012	352.5	0.005	2539.9	0.038	1474.4		
PREC (mm)	0.002	541.3	0.003	3582.5	0.007	1515.4		
TAVE (ºC)	0.0003	922.4	0.007	1870.0			0.006	2944.7
CARB (%)	0.0002	942.5			0.008	1640.1	0.004	3651.6
OXYG (mg L^{-1})	0.457	54.8	0.599	95.6			0.296	98.2
CHLA (µg L^{-1})	0.259	54.7			0.727	55.8	0.280	84.5
VHEL (%)	0.209	44.6	0.253	82.0	0.602	49.0		
NO3 (meq L^{-1})	0.158	33.5	0.266	96.8	0.404	26.2		
pH	0.152	31.3			0.534	31.8	0.272	72.7
TMAX (ºC)	0.0002	865.0	0.014	1970.6				
TAGR (%)	0.0002	864.4	0.003	3473.7				
COND (µS cm^{-1})	0.192	41.1			0.564	37.9		
NH4 (meq L^{-1})	0.183	37.3			0.470	27.1		
NO3NH4	0.170	35.2			0.433	26.8		
AGRI (%)							0.004	4254.8
ORGM (%)							0.003	3194.6
SCRU (%)							0.003	2860.0
VFLO (%)			0.241	72.3				
ALKSO4			0.232	64.7				

Regarding the 21 fixed variables (climatic, hydrogeomophological and landscape), eight of them were significantly different among the three studied regions (***Table 2***). Only two variables (minimum temperature and altitude) were different in all pairwise comparisons. Also precipitation seasonality and annual precipitation presented high differences, except comparing CR and SP. Average temperature significantly differed between CR and both mediterranean regions and sediment carbonates between SP and the other two regions. Maximum temperature was highest in CR, but significantly different only from CH. Three further variables, i.e. agriculture cover, scrubs cover and sediment organic matter, only differed between CR and SP. Considering pairwise comparisons, CR differed in seven variables with the mediterranean regions, while these two regions differed in five variables.

DISCUSSION

Climate determines both the timing for infilling and the hydroperiod length of temporary ponds, which strongly influences their local ecological features in different ways (Williams, 2006). As expected, climate variables presented wide differences between the tropical and the mediterranean regions, but also differed between both mediterranean areas. Furthermore, the climate heterogeneity was higher in SP than CH, probably due to the wider altitudinal range of the ponds in the first region. Notwithstanding potential biases in prior pond selection, this was enforced by the idiosyncrasy of each region that imposes the distribution of ponds. Lowlands in the Mediterranean basin are densely occupied by human activities, such as intensive agriculture and urbanization, and this fact has historically promoted the degradation and disappearance of natural aquatic habitats, which were considered unhealthy (Blondel et al., 2010). Due to this scarcity of ponds between 10 and 500 m a.s.l. in the study area of SP, we focused our effort on water bodies associated with protected coastal wetlands or on ponds located at higher altitude, where land cover was more heterogeneous and agriculture appeared combined with natural vegetation. Conversely, the distribution of ponds in CH was restricted to lowlands, as there was a lack of suitable ponds in the mountain ranges (Costa and Los Andes) in our Chilean study area. Our selection of ponds in CR agree with the findings of Umaña-Villalobos and Paaby-Hansen (1991), who reported that more than 85% of aquatic systems in CR are located below 500 m of elevation and in sparsely populated areas, although many lowland lakes have been drained for agriculture and livestock (Umaña-Villalobos et al., 1999). On the other hand, certain homogeneity and the lack of major differences in morphometrical features between regions was an achievement that we pursued when ponds were selected and allowed us to discard the possible influences of these parameters on the limnological differences between regions. Nevertheless, Ballón et al. (2016) determined that local features and typology (e.g. mountain or lowland) of Mediterranean temporary ponds may have more influence on their ecological function than their size or even the region, although this may not apply to tropical ponds.

Besides dissimilarities due to climate, there are other local diffences in geology, land use, vegetation, etc. large enough to create habitat-specific characteristics within each region. These local features of temporary ponds are especially exposed to a high degree of environmental variability in mediterranean areas, through seasonal variation (Florencio et al., 2009), a pattern that was evident in our results with the higher local environmental heterogeneity in CH and SP ponds. Among local factors, water mineralization, mainly as conductivity and ionic composition, presented important differences between regions, probably related to climatic and geological factors. In dryer climates, with high evaporation/precipitation ratios, water evaporates through the hydroperiod in temporary ponds, and consequently ions become more concentrated with time (Williams, 2006). Studies that measured the mineralization of water bodies in CR (mainly lakes and wetlands) (Haberyan et al., 2003; Sasa et al., 2015) coincided with the low levels of ionic concentrations found in our survey, a common pattern also find in Asian tropical ponds (Sreenivasan, 1976; Mukhopadhyay et al., 2004). These low values seem to be due to the higher precipitation in tropical areas that increase the connectivity of the ponds with the hydrological network (Larsen et al., 2019), enabling the dilution of salts during the wet season. In addition, due to the similar geological (igneous) origin of the different regions in CR, most water bodies have similar water chemistry despite their different location within the country (Haberyan et al., 2003). In this way, ionic content was lower and ionic composition more homogenous in CR compared to SP and CH, coinciding with previous information for CR and SP temporary ponds (Sahuquillo et al., 2012; Sahuquillo and Miracle, 2013; Sasa et al., 2015; Rojo et al., 2016; Olmo et al., 2019). In agreement with our results, Haberyan et al. (2003) classified almost all Costa Rican water bodies as freshwaters. The higher, although not significant, chloride concentration in the studied mediterranean regions could be related to the marine influence, as some of the SP ponds are relatively closer to the sea than CR ponds. This effect is also noticeable in CH ponds, whose conductivity is higher and significantly differ from the SP ponds.

Organic matter input to freshwaters is one of the factors that can modify several limnological features. This input comes usually from the vegetation inhabiting ponds (submerged, floating and emergent) or growing in their vicinity. The CR ponds probably received high amounts of organic matter from their surrounding areas, frequently covered by tropical forest which, together with the high temperature, increase the decomposition rate in these water bodies. The higher decomposition activity in tropical areas also explain the lower levels of oxygen (Por, 1995; Sasa et al., 2015) and pH in CR ponds, as compared to the mediterranean areas, because the balance between decomposition and primary production is tilted towards the first process. Vegetation architecture can also contribute to lower oxygen concentrations, reducing the amount of light available to aquatic primary producers (phytoplankton and submerged macrophytes). Oxygen concentration can be lower in tropical than in mediterranean ponds due to the shading effects of higher forest coverage or helophytic and floating vegetation density (Gálvez et al., 2022). In addition, lower pH values may be also attributed to the effects of typically acidic soils in tropical areas (Sanchez, 1987; Motavalli et al., 1995). Thus, Costa Rican water bodies are classified as circumneutral (Haberyan et al., 2003) while mediterranean ponds in karstic areas are widely considered as alkaline (Sahuquillo et al., 2012).

Local land uses have a narrow bond with their nearby ponds, exerting a strong influence on water parameters. Anthropogenic activities such as agriculture, logging, livestock grazing and urbanization modify the natural vegetation associated to ponds (Siqueira et al., 2015; Simião-Ferreira et al., 2018; Dala-Corte et al., 2020). Vegetation plays a key structuring role in ecological and biochemical processes of aquatic ecosystems by stabilizing the sediment, incorporating nutrients, oxygenating the water, limiting phytoplankton proliferation and maintaining a clear-water state (Tripathi et al., 1991; Van den Berg et al., 2002; Scheffer and Jeppesen, 2007; Barko and James, 2012). Agriculture, which was not detected around the ponds sampled in CR, was the dominant land cover around ponds in both mediterranean regions, where the landscape was a mixture of land uses and, therefore, the heterogeneity of the land cover measured around the ponds was higher than in tropical areas. This recurrent human activity promotes the overexploitation of surface and ground waters, the use of fertilisers and biocides, the discharge of industrial and urban effluents and the removal of the natural vegetation (directly by clearing or indirectly with herbicides). Consequently, intensive land uses could result in the salinization of water bodies and increase the nutrient input, promoting eutrophication of surface waters (Moss, 2008; Cañedo-Argüelles et al., 2013, Onandia et al., 2021). This trophic state fits the idiosyncrasy of CH ponds, where the intensive and extensive crops promote the reduction of native vegetation around them (in CH the presence of submerged and helophytic vegetation was significantly lower than in CR and SP). Moreover, the rise of nutrients (mainly nitrates) and chlorophyll a, were significantly higher in CH than in the other two regions. Besides the intensive agriculture practices in the Chilean area, the presence of livestock around these ponds seems to have a strong impact on native vegetation, either via stepping on them or via direct consumption. Focusing on bovine cattle, and according to the last national census of this livestock in CH by provinces (Instituto Nacional de Estadísticas, 2021), the number of individuals reached 108366 and 107704 in the Metropolitana and Valparaíso regions (where the majority of ponds were located), respectively. In CR there is also a large livestock pressure and, in fact, the numbers in CH are smaller than those for Guanacaste and Limón regions in CR (where the ponds were located), with 281500 and 120587 individuals, respectively (Instituto Nacional de Estadística y censos, 2021). However, at a local scale, the occurrence of cattle detected in CH ponds (directly or via footprints or faeces) was higher (28 over 30 ponds) than in CR (20 over 30), as in the latter case most of the ponds were included in protected areas. Bovine cattle were detected in the same number of ponds in Spain than in CR, although the number of registered individuals in 2018 was considerably lower for the provinces of Castellón and València (where the majority of ponds were located) with 21094 and 26693, respectively (Ministerio de Agricultura, Pesca y Alimentación, 2021). Although measuring agricultural and stockbreeding impact on ponds was not our goal, degradation and reduction of pond vegetation due to these practices may be indicative of certain ecological processes which can trigger a cascade of effects through increased nutrient accumulation, algal blooms (sometimes harmful) and severe eutrophication. In order to clarify these effects, it appears necessary to conduct further studies to quantify the direct and indirect impacts of human activities over such fragile water bodies in these regions where pond ecosystems are still overlooked.

Our study highlights that not only climate, but many local drivers such as ionic composition, nutrient concentration and vegetation structure, influence the characteristics of ponds within a region. Deeper research at the local scale of these neglected habitats is therefore necessary in order to develop desirable management strategies to avoid the loss of these habitats which are sentinels of environmental changes and worldwide reservoirs of native biodiversity.

CONCLUSIONS

Here we report the similarities and differences in the environmental framework of temporary ponds between three distant regions during a hydrological year, contributing to the global understanding of temporary ponds in two climate types, tropical and mediterranean.

We have clarified the divergence of pond characteristics (regional and local) between the two climatic regions, but also between both mediterranean sets of ponds. The main tropical-mediterranean differences can be attributed to regional factors related to climate variables which have a strong impact over local, mainly limnological and biotic, pond traits. The local factors of substrate and land use, clearly different between regions, also generated other deep tropical-mediterranean differences among pond features, mainly regarding mineralization and other limnological factors such as pH or dissolved oxygen content. Despite sharing climatic features, both mediterranean regions also showed large environmental divergences between their sets of ponds. These differences between the Chilean and the Spanish ponds could be attributed to local factors such as the type and intensity of local land uses (e.g. agriculture) and other anthropogenic activities surrounding the ponds, chiefly stockbreeding. Ponds from mediterranean Chile presented the highest levels of trophic status measured via chlorophyll a, so as the highest concentrations of nutrients, mainly nitrates. In addition, the Chilean ponds showed a reduced cover of native aquatic vegetation, which could be also favouring the observed eutrophication processes.

DECLARATION OF COMPETING INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

ACKNOWLEDGEMENTS

We thank stakeholders, CONAF and Universidad de Chile for the permissions for sampling some ponds in Chile. We appreciate the field assistance of Antonio Camacho, Mariela Guajardo, Gerardo De La Motte, María Sahuquillo, Claudia M. Rodríguez, Sanda Iepure, Iván Alambiaga, Fabio Martins, Maria Marinho and Davinia Beneyto.

FUNDING

C. Olmo has an ANID/FONDECYT Postdoctorado 2020 funding [Project number 3200340]. This study was sustained by the Spanish Ministry of Economy, Industry and Competitivity–AEI, and FEDER (EU), through project METACOM-SET (CGL2016-78260-P). Á. Gálvez was also supported by an FPI fellowship BES-2017-080022 from the Spanish Ministry of Economy, Industry and Competiveness. R. Ramos-Jiliberto received partial support from grant ANID/FONDECYT 1190173.

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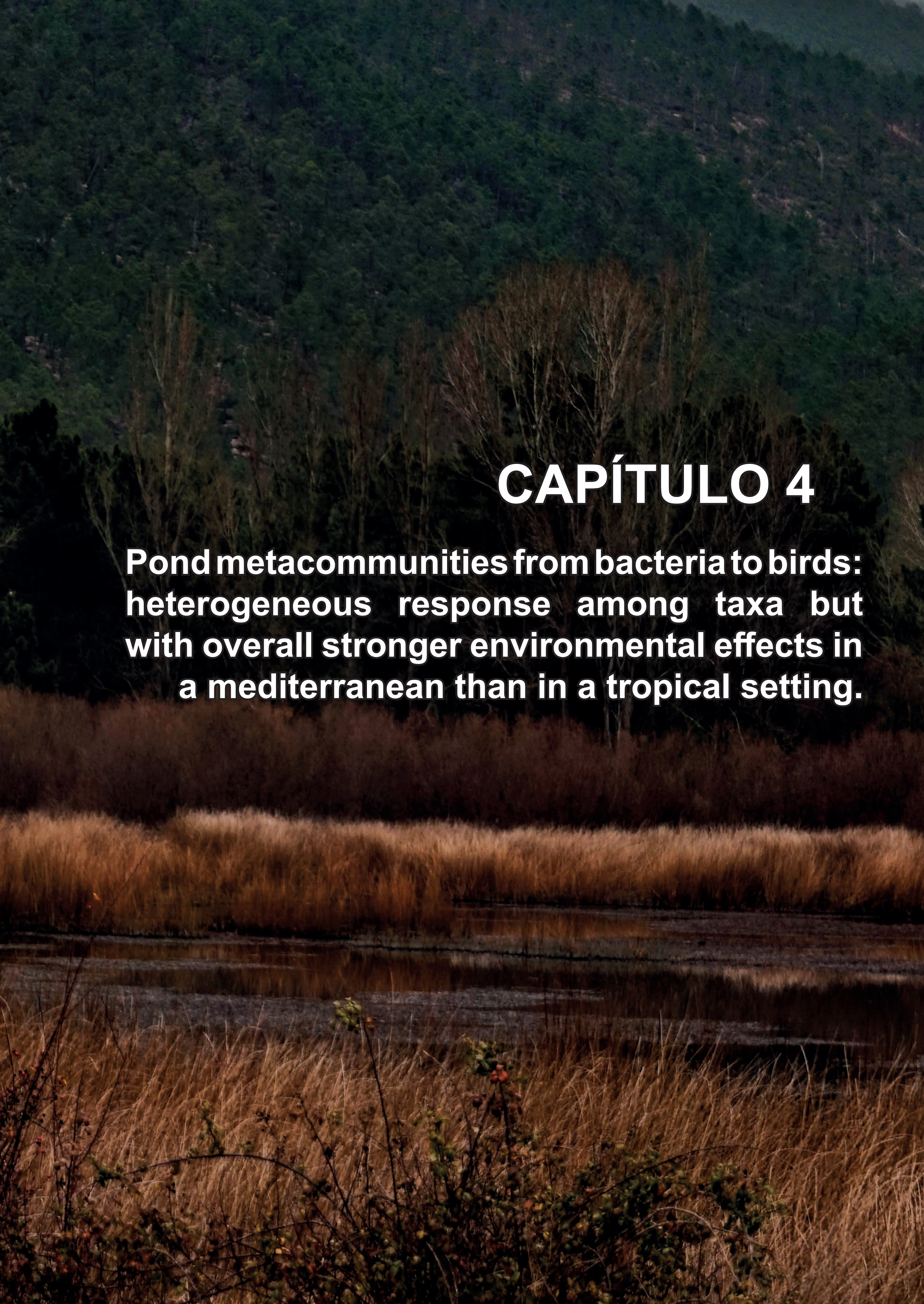

CAPÍTULO 4

Pond metacommunities from bacteria to birds: heterogeneous response among taxa but with overall stronger environmental effects in a mediterranean than in a tropical setting.

ABSTRACT

The metacommunity concept provides a theoretical framework that aims at explaining organism distributions by a combination of environmental filtering, dispersal and drift. With the development of statistical tools to quantify and partially isolate the role of each of these processes, empirical metacommunity studies have multiplied worldwide. However, few works attempt a multi-taxon approach and even fewer compare two distant biogeographical regions using the same methodology. Under this framework, we tested the expectation that temperate (mediterranean-climate) pond metacommunities would be more influenced by environmental and spatial processes than tropical ones, because of stronger environmental gradients and greater isolation of waterbodies. However, the pattern should be different among groups of organisms depending on their dispersal abilities.

We surveyed 30 tropical and 32 mediterranean temporary ponds from Costa Rica and Spain, respectively, and obtained data on 49 environmental variables (including limnological, hydrogeomorphological, biotic, climatic, and landscape variables). We characterized the biological communities of Bacteria and Archaea (from both the water column and the sediments), phytoplankton, zooplankton, benthic invertebrates, amphibians and birds, and estimated the relative role of space and environment on metacommunity organization for each group and region, by means of variation partitioning using Generalized Additive Models (GAMs).

Purely environmental effects were important in both tropical and mediterranean ponds, but markedly stronger in the latter, probably due to their higher limnological heterogeneity. Spatially-correlated environment and pure spatial effects were greater in the tropics, related to higher climatic heterogeneity and dispersal processes (e.g. limitation, surplus) acting at different scales. The variability between taxonomic groups in the contribution of spatial and environmental factors to metacommunity variation was very wide, but higher in active compared to passive dispersers. Higher environmental effects were observed in mediterranean passive dispersers, and higher spatial effects in tropical passive dispersers. The residual (unexplained) variation was larger in tropical pond metacommunities, suggesting a higher role for stochastic processes, unmeasured abiotic environmental factors or biotic interactions in the tropics, although this difference affected some actively dispersing groups (insects and birds) more than passive dispersers. These results, despite our limitations in comparing only two regions, provide support, for a wide variety of aquatic organisms, for the classical view of stronger abiotic niche constraints in temperate areas compared to the tropics. The heterogeneous response of taxonomic groups between regions also points to a stronger influence of regional context than organism adaptations on metacommunity organization.

Key words: multi-taxon analysis, dispersal limitation, environmental selection, tropical and temperate ecology, freshwater metacommunity.

INTRODUCTION

Ecological communities are not isolated systems, as they were often considered in the past, but are instead components of large spatial networks connected by dispersal, known as metacommunities (Hanski and Gilpin 1991; Wilson 1992). The development of metacommunity theory was fostered by the establishment of four main archetypes (i.e. species sorting, mass effects, patch dynamics, neutral theory) by Leibold et al. (2004), based on previous ecological theories. This allowed new research avenues, soon testing whether empirical data fitted these archetypes. These tests mostly showed a higher enforcement of niche-related versus spatial effects (these attributed to dispersal limitation), although the latter could also be important, especially at large spatial scales (Cottenie, 2005; Soininen et al. 2007). The use of the paradigmatic archetypes, however, has been criticized on the basis of their restricted, exclusive views as extreme patterns, so that ecologists should better focus on the underlying mechanisms structuring metacommunities (Winegardner et al. 2012). These mechanisms can be classified into four broad sets, involving selection, dispersal, speciation and drift (Vellend 2010; Leibold and Chase 2018). Recently, Thompson et al. (2020) slightly modified Vellend’s (2010) list of main processes; besides ignoring speciation for tractability, these authors suggested to split selection-based processes in two types: those depending on density, related to biotic interactions, and those being density-independent, affected by abiotic conditions. In addition, these authors suggest to apply the stochasticity involved in ecological drift to all density independent or dependent processes, so as to dispersal, therefore embedding demographic changes affected by different mechanisms.

Research in the past two decades has established that the processes driving metacommunity organization depend on complex interactions between local patch attributes (and their landscape settings) and species attributes. In this framework, higher connectivity among patches may increase dispersal, homogenizing the metacommunity and allowing habitat matching for low dispersers, while environmental heterogeneity among sites may be essential for species selection and increased beta diversity (Grönroos et al. 2013; Erös et al. 2017; Castillo-Escrivà et al. 2017a). Focusing on the organisms traits, it has been suggested that body size, dispersal mode or trophic level may influence the outcome of metacommunity organization, so that large active dispersers or those with small propagules may be less affected by spatial barriers than passive dispersers or than those with larger propagules (Vanschoenwinkel et al. 2010; De Bie et al. 2012; Astorga et al. 2012), although these relationships can be strongly dependent on the environmental context (Soininen et al. 2014).

Our ability to detect, differentiate and understand the roles of different processes on (meta-)community assembly have been particularly challenging because of the complex ways that landscape and species characteristics may affect local patches and dispersal between them. Despite the complexity in which assembly processes may proceed, these are often conceptualized as taking place continuously at different spatial scales (Peres-Neto et al. 2012; Viana and Chase 2019): large-scale processes (including biogeography; Leibold et al. 2010) that regulate the movement of organisms among local communities (e.g., landscape heterogeneity, connectivity, dispersal limitation); and fine-scale processes that regulate the success of species following either their own arrival or the arrival of other species (e.g., niche differentiation, local environment, microhabitat heterogeneity). Consequently, our understanding of metacommunities is, more often than not, scale dependent (e.g., stream, basin and ecoregion; Heino et al. 2015; Leibold and Chase 2018). For instance, small spatial scales, with dispersal surplus and/or homogeneous environmental conditions, favour metacommunity homogeneity, whereas at large spatial scales, dispersal rates decrease, generating metacommunity variation consistent with dispersal limitation and wider environmental gradients. Notwithstanding the potential increase in environmental gradients with spatial extent, both small and large spatial scales may however reduce the strength of environmental selection and/or environmental tracking, which should be more relevant at intermediate scales. This is because intermediate scales may be large enough to encompass heterogenous environments, yet allowing moderate dispersal rates to track suitable localities (Heino et al. 2015). As such, keeping spatial extent constant is somewhat essential for contrasting metacommunity structure across different landscapes and/or taxonomic groups (as spatial effects also depend on the dispersal abilities of each organism; Wiens 1989). Few studies, however, have explored metacommunity structure contrasting distinct biogeographical regions (with large differences in their abiotic settings and biota) while controlling for spatial extent (Myers et al. 2013), or have used a multitude of taxonomic groups (e.g. Beisner et al. 2006; Heino et al. 2017). None of them however, as far as we know, combined in the same empirical test a large taxonomic gradient with distant biogeographical regions to check if context dependency effects may overlay taxon-specific responses.

The expectation of more uniform environmental conditions in tropical regions (at least through time) should lead to reduced species sorting compared to the more heterogeneous environment in temperate areas (Leibold and Chase 2018). Indeed, some studies found that temperate communities were more environmentally controlled than tropical ones for a given group of organisms (Myers et al. 2013; Souffreau et al. 2015). In the case of aquatic habitats, massive floods during the rainy season increase aquatic connectivity in tropical areas (Junk et al. 1989; Bunn et al. 2006; Larsen et al. 2019), reducing dispersal limitation and homogenizing local communities (Thomaz et al. 2007; Brasil et al. 2020), in contrast with the more intense isolation of water bodies in the mediterranean-climate regions. In both tropical and mediterranean systems, we may then expect that metacommunity structure is a result of dynamic switches between dispersal limitation and environmental filtering through time (Jacobson and Peres-Neto. 2010; Fernandes et al. 2014), which could exert stronger effects on aquatic ecosystems of dry temperate areas than in the wetter tropical regions.

Metacommunity studies focusing on distinct organisms within the same landscape and localities revealed strong differences among taxa regarding spatial versus environmental effects (Beisner et al. 2006; Padial et al. 2014; Brasil et al. 2020; Gálvez et al. 2020), largely interpreted as affected by mechanisms of dispersal limitation versus selection, respectively, sensu Vellend (2010). Variation in dispersal mode and body size are important features associated with dispersal capacity and, consequently, modulating the strength of environmental filtering and dispersal limitation (De Bie et al. 2012). For active dispersers, dispersal ability increases with body size, being easier for large organisms to spread among suitable sites (favoring species sorting), thus avoiding dispersal limitation (Grönroos et al. 2013; Csercsa et al. 2019). Passive transport, on the other hand, may limit dispersal capacity of large-sized organisms in contrast to small ones (which also produce more propagules; Finlay 2002). As a result, environmental selection should in principle be stronger for small organisms (Van der Gucht et al. 2007) although the evidence about this association is mixed (e.g., Heino et al. 2012; Schulz et al. 2012; Soininen 2014). Despite the large differences between several published studies, it seems that environmental selection is a proportionally stronger process than dispersal for the organization of freshwater metacommunities, especially in smaller organisms. However, some groups such as diatoms, ostracods or macroinvertebrates show high variability in the role of these processes (Gálvez et al. 2022). Altogether, dispersal capacity, species traits, geographic variation in environmental features and biogeographic context should interact in structuring metacommunities (see Leibold et al. 2010 for a discussion).

One way to address the complexity in which local communities assemble and metacommunity dynamics proceed is by determining whether: 1) Different taxa (including completely different life cycle strategies, e.g., bacteria versus birds) assemble differently within the same landscape; or 2) different environmental settings (landscapes) structure different taxa in similar ways. To answer these questions, one needs to study the metacommunity structure of multiple taxa across different landscapes. While this approach can provide strong inferences about the generality (or lack thereof) of assembly mechanisms and whether contingencies are due to landscapes or species attribute differences, there are obvious logistic challenges. In this study, we set out an ambitious empirical study to contrast the relative importance of environmental versus spatial factors on structuring metacommunities. We sampled temporary pond metacommunities in an extremely wide range of taxonomic groups (across 24 groups of organisms in total, varying from bacteria to vertebrates) across two very distinct biogeographic regions (Neotropical and Mediterranean) within the same temporal span and encompassing the same spatial extent within regions, and based on the same sampling design, protocols and data measurements. We tried to encompass as much information on environmental variability as possible, including data from both aquatic and surrounding terrestrial habitats (Likens y Bormann 1974; Sardans et al. 2012). For that purpose, we carried out and intense effort on (mainly abiotic) environmental characterization, including macroclimate, landscape and local water body variables. In both study regions, Costa Rica and Spain, precipitations are distributed seasonally, with a marked dry season that promotes the formation of temporary ponds. These are valuable ecosystems for metacommunity studies due to their well delimited spatial and temporal boundaries, and their isolation within a terrestrial matrix (at least for aquatic organisms). We framed our study around three predictions: 1) both environmental and spatial effects should have lower influences on metacommunity structure of tropical in contrast to mediterranean ponds; 2) different taxa should respond differently within regions but similarly between regions, and in particular 3) metacommunity structure should be related to the variation of dispersal abilities among taxa, in which higher environmental filtering should occur for small passive dispersers and large-bodied active dispersers in contrast to smaller active dispersers.

METHODS

Study area

We looked for well-preserved temporary freshwater bodies from sea level up to 1,500 m a.s.l. within a similar spatial extent in two distant biogeographic regions (Neotropical and Mediterranean) with dry tropical and mediterranean climates respectively. We selected 30 tropical and 32 mediterranean (seasonal or semipermanent) temporary ponds in a study area of 13,000 km^2 in Eastern Spain and 10,000 km^2 in Northern Costa Rica. The maximum distances between ponds were 209 and 252 km in Spain and Costa Rica, respectively (***Figure 1***). The selected ponds encompass different typologies including peripheral areas of coastal wetlands, inland shallow lakes, interdunal slacks and small naturalized farmland ponds. All ponds are shallow (< 2 meters), fresh to oligohaline waters (< 7000 µS/cm) and vary in their hydroperiod lengths, from six months to some years. The tropical ponds experience almost constant warm temperatures during the whole year (24.9 ± 1.3 ºC) and high but variable precipitation (2486 ± 934.7 mm). The mediterranean ponds are in a region with warm annual mean temperature (12.9 ± 3.0 ºC) and reduced annual precipitation (537 ± 68.3 mm) (Fick and Hijmans 2017). We sampled the ponds at the beginning of the hydroperiod (two weeks after infilling, during the rainy season), in May 2017 for the selected tropical ponds and January 2018 for the mediterranean ponds.

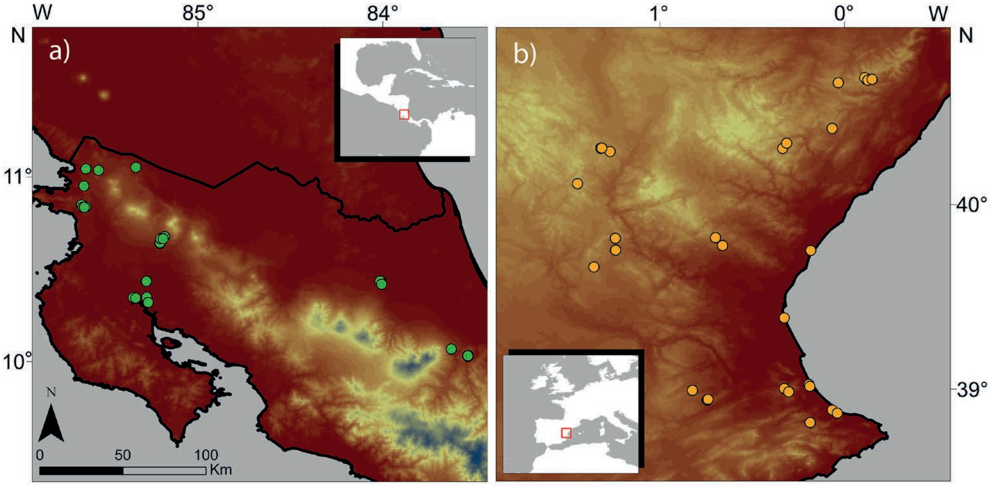

Figure 1: Map of the study area with the location of the ponds sampled in each region: Costa Rica (a) and eastern Spain (b).

Environmental characterization

We measured limnological variables in situ including water transparency, which was measured with a Snell tube (Van de Meutter et al. 2006), as well as water temperature, pH, electrical conductivity and dissolved oxygen concentration, determined using a WTW® Multi 3430 Multiparameter Meter (with WTW® SenTix 940 for pH, TetraCon 925 for conductivity and FDO 925 for oxygen concentration). Unfiltered water samples were taken for further volumetric analyses of chloride and alkalinity, and filtered water for photometric determination of ammonium, nitrite, nitrate, sulphate and phosphate (SpectroquantMerk® and AquaMerk® test kits and T90+UV/VIS Spectrophotometer) in the lab. The water used for nutrient content analyses was filtered in situ through Whatmann® GF/F filters. We extracted chlorophyll-a from these GF/F filters with acetone 90% and analyzed the extract by spectrophotometry (Jeffrey and Humphrey 1975). Hydrogeomorphological variables included maximum and average depth, measured with a graduated stick, so as maximum and minimum diameter, surface area and shoreline development, as $DL=L/(2\sqrt{\pi A})$, where L=perimeter and A=area (Aronow 1984), using Google Earth Pro 7.3.2.5776 (Google Inc.). We took six random sediment samples at different depths to analyze its granulometry (following De Vaasma 2010), and organic and carbonate content (according to Heiri et al. 2001); we estimated the proportion of dry weight represented by different grain sizes (>2 mm, 2-1 mm, 1-0.5 mm, 0.5-0.25 mm, 0.25-0.063 mm, 0.063-0.036 mm, <0.036 mm), and by organic matter and mineral carbonates. We estimated the hydrological regime (seasonal or semipermanent) and the main water origin (rain, streams or phreatic inputs) from information by local experts, direct observation and maps. Biotic variables (in addition to chlorophyll-a) included the percentage of surface area of the pond covered by submerged, floating and emergent vegetation (visually estimated), the presence of fish and the presence of livestock. Landscape metrics were estimated using Google Earth (resolution ~1 m^2), including elevation above sea level and the percentage of different types of land cover (agricultural fields, low grass, high grass, scrub, forest or buildings) in a circular buffer of 100 m in diameter around the sampling point (Pedersen et al. 2006; Gálvez et al. 2020). Land cover diversity was measured using the Shannon index of the different land cover types. Finally, macroclimatic variables were extracted from WorldClim (resolution 30 arcseconds; Fick and Hijmans 2017) to obtain mean annual, maximum and minimum temperatures, temperature range, mean annual precipitation, and precipitation seasonality for each pond, using the software ArcGIS 10.3 (ESRI 2014).

Biological communities

For each pond, we characterized prokaryotic (Bacteria and Archaea), phytoplankton, zooplankton, benthic invertebrate, amphibian, and bird communities. For prokaryotic organisms, two samples were obtained: a 1-L sterilized bottle with pond water and a microtube with 2 mL of pond wet sediment. Afterwards, in the laboratory, we filtered the water through 3 µm pore polycarbonate filters (Nucleopore, Whatman) to remove larger particles. The remaining water was filtered again through 0.2 µm pore polycarbonate filters (Nucleopore, Whatman) to concentrate samples for subsequent DNA analysis. Filters and sediment samples were cold-stored in microtubes filled with

RNAlater™ reagent, until further processing. DNA extractions, PCR and bioinformatics for taxonomic assignments were done following Picazo et al. (2019).

Phytoplankton samples were obtained directly from the water column at the center of the pond (100 mL stored in amber colored glass bottles) and fixed with 3 mL of Lugol's solution. Phytoplankton taxa were identified to species level whenever possible using mainly Huber-Pestalozzi (1976-1982) and Wolowski and Hindák (2005). Zooplankton samples were taken dragging a hand net (63 µm mesh-size) through 10-20 m of water column, whenever possible, integrating all different microhabitats and depths. Samples were fixed in formaldehyde 4% (final concentration, v/v) and identified at the species level, whenever possible, following Koste (1978) and Segers (1995) for rotifers, Alonso (1996), Elías Gutiérrez et al. (2008), and references therein for branchiopods, Dussart (1967; 1969) and Elías Gutiérrez et al. (2008) for copepods, and Błędzki and Rybak (2016) for both branchiopods and copepods.

Benthic invertebrate communities were sampled using a hand net (20 x 20 cm, 250 µm mesh-size). About 10 m in total (if ponds were large enough) were sampled across all microhabitats. Samples were fixed in ethanol 96% and invertebrates identified to the lowest taxonomic rank possible mostly following Wiederholm (1983), Tachet et al. (2010), Thorp and Covich (2010) and Springer et al. (2010), and references therein, for macroinvertebrates, and Meisch (2000), Karanovic (2012) and references therein for Ostracoda.

The occurrence of amphibian species in the ponds was registered in situ by noting the presence of eggs, tadpoles, adults and calls. Due to the low species richness and the easy detectability of species in the mediterranean ponds, we surveyed each pond with a hand net (800 cm^2, 2 mm mesh pore) with a constant effort of ten minutes, and we examined the surroundings of the pond for ten more minutes (Wilkinson 2015). When in situ identification of larvae was not possible, we identified them in the laboratory by their oral disk. In tropical ponds, with higher species richness and lower detectability, we performed night surveys looking for individuals in the surroundings of each pond with an effective effort of up to 2 hours per pond (the sum of the total effort by all the surveyors; Heyer et al. 1994), avoiding full moon nights. Adults specimens were identified visually or by calls. Bird surveys were performed by single 15-minute point-counts per pond with one surveyor, in which we recorded species presences identified either visually (up to a maximum distance of c. 100 m) or by their calls (Ralph et al. 1995).

Statistical analyses

We quantified the role of environmental and spatial effects, by partitioning metacommunity variation (Peres-Neto et al. 2006) of each taxon and region between environmental variables and spatial functions. The groups considered were Archaea from the sediment, Archaea from the water, Bacteria from the sediment, Bacteria from the water, phytoplankton, Rotifera, microcrustaceans, macroinvertebrates, Amphibia and Aves. We also analyzed subgroups of these organisms separately due to major taxonomic and trophic differences among them. Phytoplankton was therefore split as Cyanobacteria, Chlorophyceae, Bacillariophyceae (diatoms) and mixotrophic flagellate phytoplankton (including Chrysophyceae, Cryptophyta, Euglenophyta and Dinoflagellata). Microcrustaceans were split in Branchiopoda, Copepoda and Ostracoda, and macroinvertebrates in Mollusca and Insecta. Moreover, insects were divided in Palaeoptera (including Odonata and Ephemeroptera), Heteroptera, Coleoptera and Diptera (considering also Chironomidae separately as another subgroup). Separately, groups and subgroups accounted for 24 species matrices based on presence-absence data for each region.

For each group (and subgroup) and region, we performed variation partitioning via Generalized Additive Models (GAMs; Wood 2011), recently used to explore metacommunity variation (Viana et al. 2021). Despite its popularity in community analyses, the performance of Redundancy Analyses (RDA) is weak when species respond non-linearly to environmental variation (e.g., Makarenkov and Legendre 2002). To tackle its limitations, we used GAMs as a non-linear modeling framework considering both environmental and spatial variables, allowing a better fit to the data.

Response matrices in GAMs were composed of predicted values of the presence/absence data, obtained from Generalized Linear Latent Variable Models (GLLVM with binomial distribution) with the lowest AIC (Niku et al. 2017). This allowed us to concentrate on the common sources of variation among species and reduce computational time from extracting GAMs for a large number of taxa. Prior to these analyses, environmental variables were inspected and transformed either logarithmically or with the arcsine of the square root, depending on the distribution of the raw data, in order to reduce skewness and leverage of extreme values (McDonald 2014). When applying GAMs, due to the small sampling size (30 tropical and 32 mediterranean ponds), we were limited to a maximum number of three variables, to allow GAMs generate nine splines per variable (3 variables x 9 splines = 27), maximizing the response of the selected variables. As a consequence, before executing GAMs (using a quasi-binomial distribution), we reduced the number of environmental predictors by using the first three principal components

(PCs) in a PCA of all variables. This three PCs accounted for 47.17% and 49.19% of the measured environmental variation of the mediterranean and tropical ponds respectively. As spatial predictors, we used spatial functions (the default splines in the mgcv R package) calculated from longitude and latitude coordinates.

We reduced the number of environmental and spatial predictors (three PCs, longitude and latitude) introduced in GAMs by means of forward selection, with a double-stopping criterion (Blanchet et al. 2008). First, we selected only significant variables ($p\text{-value}<0.05$). Second, the adjusted R^2 of the selected variables had to be lower than the adjusted R^2 of the model with the whole set of variables. This procedure was repeated for the environmental variables (three PCs) and spatial variables (latitude and longitude) separately. We included at least one environmental or spatial variable in rare cases that the double-stopping criterion was not satisfied, as long as the selected variable was significant. If more than three variables were selected, we manually reduced the number of variables (either spatial or environmental) by removing the selected variables which less contributed to explaining the observed variation, until reaching the maximum number of three selected variables. As a result, GAMs provide information on the total proportion of metacommunity variation explained by environmental (E) and spatial (S) factors together (E+S) and separately, estimating the pure environmental fraction (E|S; often associated with environmental selection), the pure spatial fraction (S|E; that most authors interpret as variation due to dispersal, but see Gilbert and Bennet 2010; Smith and Lundholm 2010; Livingston et al. 2017) and the overlap of environment and space ($E \cap S$; which represents environmental variation that is spatially structured). The unexplained proportion or residuals represent common and uncommon sources of variation not explained by (measured) environmental and spatial variation, usually interpreted as sampling issues, stochasticity driving to ecological drift, unmeasured biotic or abiotic factors or interactions among factors (Leibold and Chase 2018).

The contribution (R^2) of environmental variation to species distributions (i.e., species sorting via environmental selection) can be inflated when residuals and response variables (i.e., species distributions here) are both autocorrelated. Traditionally, ecologists remove the spatialized component of the environment via variation partitioning, focusing then solely on the E|S fraction. This procedure, however, may reduce estimates of the importance of environmental selection because even the spatialized component of the environment that may not bias estimates of variation partitioning is eliminated from the E|S fraction (see Clappe et al. 2018 for a discussion). To assess the importance of environmental drivers (spatialized and non-spatialized) we used the correction method for the environmental component as described in Clappe et al. (2018). This method produces unbiased estimates of the environmental contribution even under spatial autocorrelation of residuals. In order to make results comparable among taxa and region, we transformed the fractions of explained variation into the relative proportion of purely environmental effects (E|S/(E+S)), purely spatial effects (S|E/(E+S)) and spatially-correlated environment (E∩S/(E+S)).

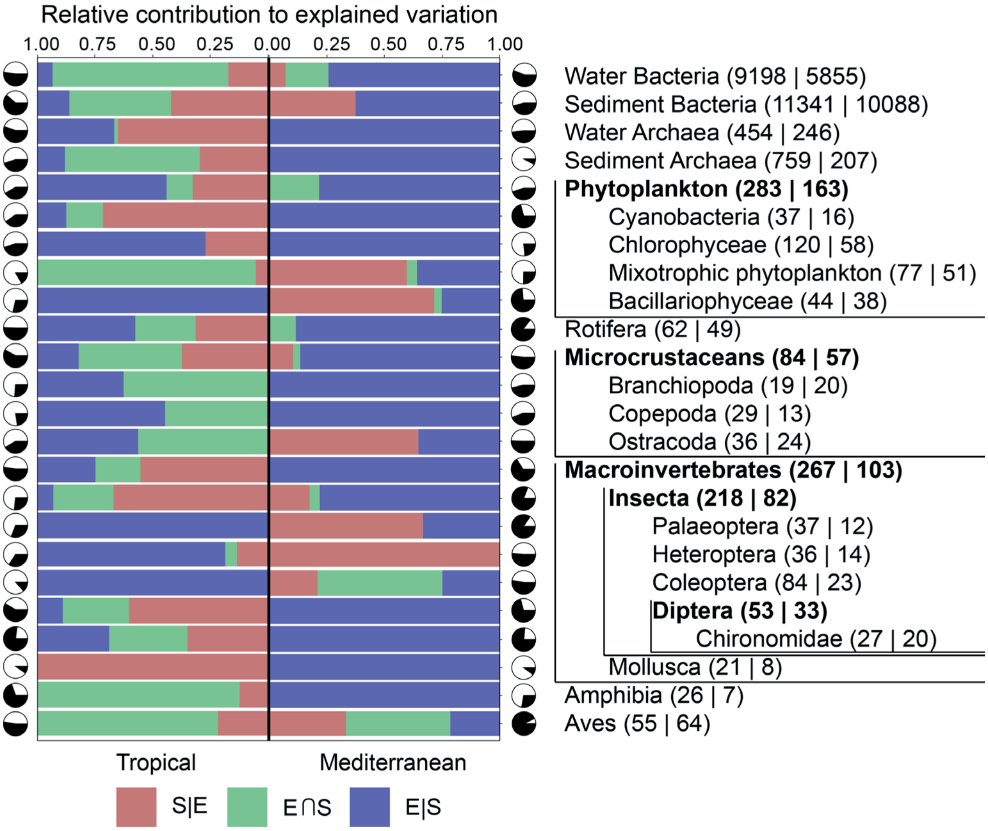

Figure 2: Results of variation partitioning analysis for each group of organisms in tropical and mediterranean metacommunities. The relative contribution of pure environment (E|S/(E+S)), spatialized environment (E∩S/(E+S)) and space (S|E/(E+S)) are represented with a different color. Black portions in pie charts represent the total proportions of explained variation, and white portions the residual variation. Groups in bold type include species from the groups enclosed in the corresponding following indented line(s). Number of identified taxonomic units, i.e. species in most groups, are shown between brackets (tropical | mediterranean) next to each group label.

Finally, we carried out a test of homogeneity of multivariate dispersion (PERMDISP; Anderson 2006) to contrast the environmental heterogeneity of both regions (tropical versus mediterranean) using the whole set of measured environmental variables, as well as a matrix of just limnological variables (which are expected to be more local) and a matrix of just macroclimatic variables (which are expected to vary at regional scale, and to be more spatially-correlated). All analyses were performed with R (v4.0.2; R Core Team 2021) and R packages vegan (Oksanen et al. 2019), ade4 (Bougeard and Dray 2018), adespatial (Dray et al. 2021), gllvm (Niku et al. 2020) and mgcv (Wood 2017). Environmental characterization and community matrices can be found in Figshare (doi.org/10.6084/m9.figshare.14644608.v4). Codes for variation partitioning analyses can be found here: github.com/Angel-Galvez/Bacteria-to-birds. More details about the environmental framework of each set of ponds are provided in Olmo et al. (2022).

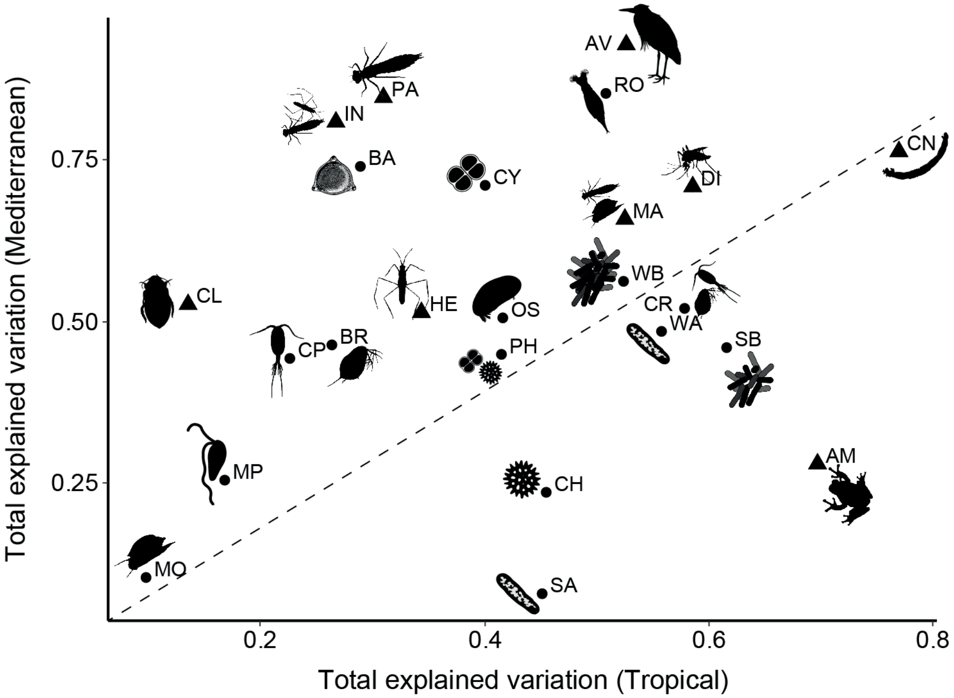

Figure 3: Relationship between the total explained variation (E+S) in the tropical and the mediterranean metacommunities. Dashed line represents the 1:1 theoretical correspondence of the total explained variation in both regions. Passive dispersers are represented with circles, while active dispersers are represented with triangles. WB: water Bacteria, SB: sediment Bacteria, WA: water Archaea, SA: sediment Archaea, PH: phytoplankton, CY: Cyanobacteria, CH: Chlorophyceae, MP: mixotrophic flagellate phytoplankton, BA: Bacillariophyceae, RO: Rotifera, CR: microcrustaceans, BR: Branchiopoda, CP: Copepoda, OS: Ostracoda, MA: macroinvertebrates, IN: Insecta, PA: Palaeoptera, HE: Heteroptera, CL: Coleoptera, DI: Diptera, CN: Chironomidae, MO: Mollusca, AM: Amphibia, AV: Aves. Silhouettes obtained from PhyloPic.org.

RESULTS

The total proportion of explained variation by environmental and spatial components (E+S) ranged from 0.10 for mollusks to 0.77 for chironomids in the tropical ponds (average 0.42 ± 0.18). In the mediterranean ponds, the explained variation varied from 0.08 for sediment Archaea to 0.93 for birds (average 0.54 ± 0.23). Results of these variation partitioning analyses are shown graphically in ***Figure 2*** and detailed in ***Appendix S1: Table S1*** and ***Figure S1***. The E+S proportion for each taxonomic group was usually very different when comparing tropical with mediterranean ponds (***Figure 3***). Only a few groups, including water archaea and bacteria, phytoplankton, cyanobacteria, mixotrophic phytoplankton, microcrustaceans and ostracods had similar proportion of explained variance for both regions, but there were a larger number of groups, particularly insects and birds, with much higher explained variance in mediterranean than in tropical ponds. Only prokaryotes from the sediment, chlorophycean algae and amphibians had markedly higher E+S proportion in the tropical ponds. Overall, E+S proportions were higher in the mediterranean metacommunities compared to the tropical ones, but this difference was mostly due to differences between some groups of active dispersers (insects and birds), while passively dispersing metacommunities seem to have a similar E+S proportion both in tropical and mediterranean ponds (***Figure 4***). The only group of active dispersers that had lower E+S in the mediterranean ponds were the amphibians (***Figure 5***).

The groups with very low E+S values in one region usually showed relationship to only one pure fraction (either E|S or S|E) (***Figure 2***) in that region, which accounted for 100% of the total explained variance (see e.g. molluscs in both regions or beetles in the tropical region; ***Figure 2***). This might be related to the analytical methods used so that no more summarizing variables would be selected at low values of explained variance. Therefore, to avoid biases for further graphical explorations of the data regarding E|S/(E+S) or S|E/(E+S) we indicated which groups had low E+S values (i.e. in the fourth quartile) (***Figure 5***) or excluded them from the calculations (***Figure 4***). We found overall higher pure environmental effects (E|S) in mediterranean than in tropical metacommunities (***Figures 2-5***). In contrast, the pure spatial fraction (S|E) was generally higher in the tropical metacommunities, despite some mediterranean groups exhibited an important spatial control (Ostracoda, Heteroptera, Palaeoptera, diatoms and the mixotrophic flagellate phytoplankton), and surprisingly some of these (Heteroptera, Paleoptera) where apparently more influenced by environment in the tropical setting (***Figure 5***). The response of most groups was very different comparing tropical and mediterranean settings; only ostracods showed a similar E|S fraction between both regions, and bacteria and birds in the case of S|E (besides a few groups with values of zero for these fractions) (***Figure 5***). The overlap of environment and space (E∩S) was greater in tropical ponds, and usually very low in the mediterranean metacommunities (***Figure 4***). The total environmental fraction (E) was higher in the mediterranean-climate region, while total spatial fraction (S) was higher in the tropical region (***Figure 4***). Pure environment (E|S) explained a higher proportion of variance than purely spatial component (S|E) in mediterranean ponds, while pure spatial and pure environmental effects were similar in tropical ponds.

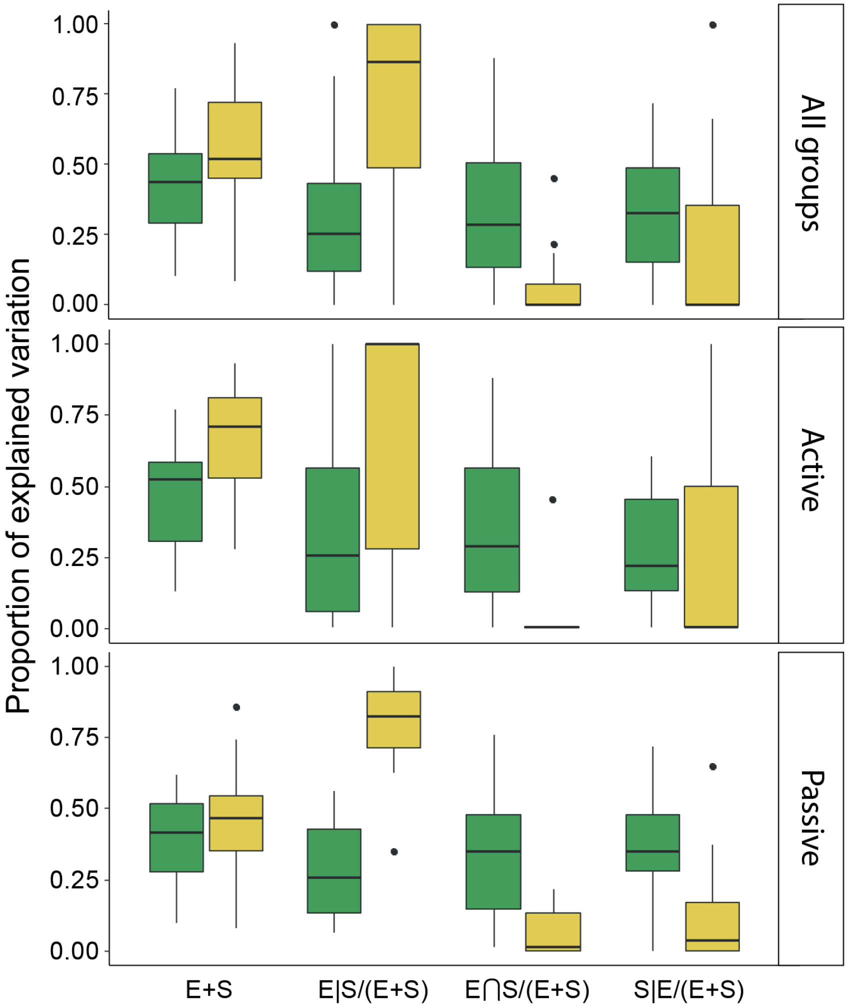

Figure 4: Total explained variation (E+S) for all groups or separately for passively and actively dispersing organisms. Relative contribution to total explained variation of the pure environmental component (E|S/(E+S)), the spatialized environmental component (E∩S/(E+S)), and the pure spatial component (S|E/(E+S)), omitting those groups with E+S in the fourth quartile. Green and yellow colors represent tropical and mediterranean ponds, respectively.

Pairwise comparisons for each taxonomic group between regions showed that the pure environmental fraction generally played a greater role in mediterranean groups than in their tropical counterparts (***Figure 5***), and this pattern was especially strong in the case of passive dispersers, but not so clear in active ones. Pure spatial effects were important in structuring metacommunities of even small organisms such as algae, bacteria or archaea. Regarding the spatially-correlated environment and the pure spatial fraction, we found tropical groups to be more influenced by these effects than their mediterranean homologous groups, with most exceptions to this pattern occurring in active dispersers (***Figure 5***), such as insects and birds. The relative contributions of these components did not follow any clear trend on body (or propagule) size neither for active nor passive dispersers. When we compared the relative contributions of space and environment between merged groups of passive and active dispersers (***Figure 4***), we found similar fractions explained by purely environmental, spatially-correlated environmental and spatial effects in passive and active tropical dispersers, although the latter showed higher variability. Despite large differences in environmental and spatial contributions in the mediterranean ponds, both passive and active dispersers behave similarly, although mediterranean passive dispersers were more affected by pure environmental factors, and more distant in that matter from the tropical groups, than active ones. Environmental effects were therefore generally higher in mediterranean than in tropical ponds, while the spatial component was higher in the tropical than in the mediterranean-climate region. This pattern is most clearly seen in passive than in active dispersers (***Figure 4***), whose wider variability in explained variance for the different components makes the comparison less straightforward.

Results of PERMDISP showed non-significant differences in environmental heterogeneity between regions for the whole environmental dataset (p-value=0.303, 6.159 average distance to centroid in mediterranean ponds, 5.613 in tropical ponds). However, mediterranean ponds showed significantly higher limnological heterogeneity (p-value=0.002, 3.113 average distance to centroid in mediterranean ponds, 1.752 in tropical ponds), while tropical ponds exhibited significantly higher climatic heterogeneity (p-value=0.005, 1.311 average distance to centroid in tropical ponds, 0.921 in mediterranean ponds).

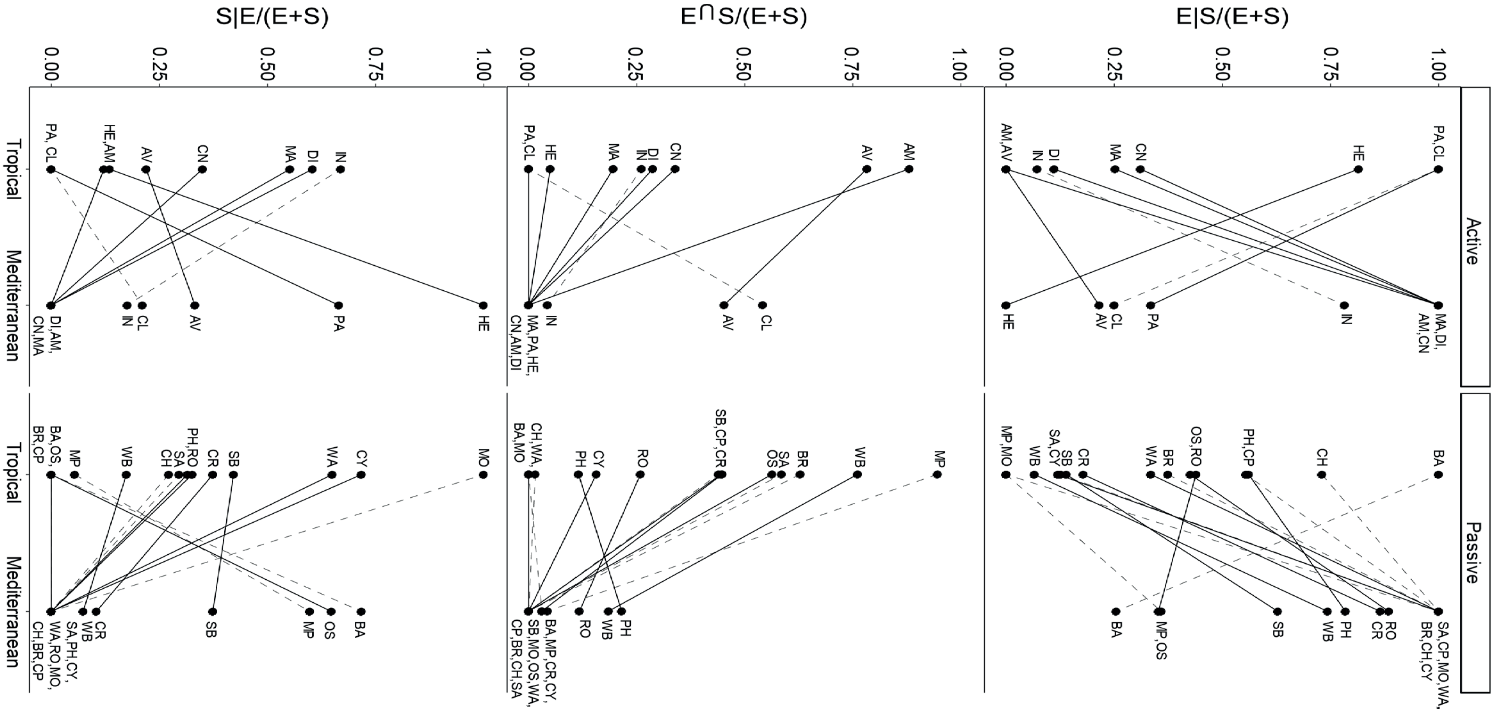

Figure 5: Relative contributions to total explained variation by the pure environmental component (E|S/(E+S), spatialized environment (E∩S/(E+S)) and pure spatial effects (S|E/(E+S)), for each group of organisms, and according to geographic region and dispersal mode. WB: water Bacteria, SB: sediment Bacteria, WA: water Archaea, SA: sediment Archaea, PH: phytoplankton, CY: Cyanobacteria, CH: Chlorophyceae, MP: mixotrophic flagellate phytoplankton, BA: Bacillariophyceae, RO: Rotifera, CR: microcrustaceans, BR: Branchiopoda, CP: Copepoda, OS: Ostracoda, MA: macroinvertebrates, IN: Insecta, PA: Palaeoptera, HE: Heteroptera, CL: Coleoptera, DI: Diptera, CN: Chironomidae, MO: Mollusca, AM: Amphibia, AV: Aves. Black lines connect the same groups from different regions. Dashed lines for the groups with total explained variation (E+S) in the fourth quartile.

DISCUSSION

In this study, we set out to contrast the environmental and spatial contributions on metacommunity structure among a wide range of taxa inhabiting temporary ponds in two distant biogeographic regions, Neotropical and Mediterranean, with large differences in climate and biodiversity. Overall, we found a lower proportion of explained variation in tropical than in mediterranean pond metacommunities, considering both environmental and spatial effects across the diverse array of studied organisms. Notwithstanding the limitation of our study comparing only two areas, these results are consistent with the expectation that more productive environments in the tropics, with less variable and higher temperatures, might display more stochasticity in community assembly than less productive ones (Gomes-Mello et al. 2021), and with higher temperature fluctuations, such as ponds in mediterranean areas, where metacommunities might be modulated more tightly by environmental determinism (Chase 2010). The higher explanation of metacommunity variance in mediterranean ponds seem to be mostly related to active dispersers (e.g. insects, birds), with the exception of amphibians. Possibly, larger demographic stochasticity (not linked to environmental changes), together with the higher diversity of the tropical fauna (and hence higher number of uncommon species), hampered the match of environmental and/or spatial patterns to species distributions in these habitats (Leibold and Chase 2018).

Our results show that both environmental and spatial effects, usually interpreted mainly as environmental selection and dispersal processes respectively (but see Gilbert and Bennet 2010; Smith and Lundholm 2010; Livingston et al. 2017), played an important role in the assembly of pond metacommunities in both regions for most groups. However, pure environmental effects were stronger in mediterranean compared to tropical pond metacommunities, as previously found for vegetation and bacterioplankton metacommunities (Myers et al. 2013; Souffreau et al. 2015). Given the higher limnological heterogeneity across the studied mediterranean water bodies, these results were therefore not unexpected (Ai et al. 2013), as larger gradients can generate more environmental space for divergently specialized organisms. So, even if there are more species in the tropical ponds, given their shorter environmental gradient and reduced species sorting, we expect to find a higher degree of ecological redundancy and stochasticity in these ponds. However, we cannot discard unmeasured important environmental factors or intense biotic interactions, which could play important roles in aquatic metacommunities (García-Girón et al. 2020) and can be particularly strong in tropical environments (Roslin et al. 2017; Leibold and Chase 2018).

We hypothesized spatial effects to be lower in the tropical metacommunity, due to a shift in connectivity during the rainy season, which should lead to community homogenization (Thomaz et al. 2007; Rojo et al. 2016; Brasil et al. 2020), in comparison to the reduced precipitation in the mediterranean region, which is expected to make ponds more isolated from one another. Unexpectedly, we found the opposite pattern. Low spatial effects in mediterranean ponds might reflect historical connectivity due to transhumance (Incagnone et al. 2014) or intense movements of potential vectors including birds and mammals among ponds (Frisch et al. 2007; Vanschoenwinkel et al. 2008; Valls et al. 2016, 2017). The strong spatial effects in the tropical metacommunity might also be partly explained by the sampling period, given that at early stages of the hydroperiod, connectivity is not yet at maximum. It is possible that during early stages of the hydroperiod, dispersal constraints might be equally strong for aquatic organisms in both regions. Additionally, annual floods during the wet season drive connectivity changes, homogenizing both environmental conditions and biological communities (Thomaz et al. 2007; Brasil et al. 2020). Thus, early-hydroperiod spatial patterns in small tropical organisms can be the result of historical contingencies (Castillo-Escrivà et al. 2017b), such as sequential flooding events (or heavy rain periods) that shifted connectivity at regional scale. These events may increase the spatial structure of passively dispersed organisms in more connected areas compared to other distant and more isolated regions.

In addition to hydrology, orography could be a stronger dispersal barrier in the tropical than in the mediterranean metacommunity. Dispersal of tropical species, adapted to homogeneous temperature regimes, could be more limited by sharp altitudinal climate shifts than temperate species, adapted to a wider range of temperatures (Janzen 1967). The tropical ponds in our study are distributed across two watersheds separated by the Continental Divide, with wide differences in rainfall amount and seasonality, which can have varying impacts on the distributions of some species (Chandler and King 2011). This orographic barrier and the associated abrupt climatic transition are probably characterized by the shared components between environmental and spatial components (E∩S), which was found to be higher for the tropical ponds, where climatic heterogeneity was also higher. Thus, reduced limnological gradients and orographic barriers can lead to dispersal limitation (Janzen 1967) at larger scales, and higher regional connectivity can lead to dispersal surpluses (Thomaz et al. 2007; Heino et al. 2015; Brasil et al. 2020) at smaller scales in the tropical area. These two processes could explain the proportionally greater role of space in tropical than in mediterranean metacommunities.

Some studies have found that the degree of variation of spatial versus environmental effects on metacommunity structure strongly depends on propagule size and the dispersal mode of organisms (Beisner et al. 2006; De Bie et al. 2012; Heino et al. 2015). However, we found it to be very variable for the same group between geographical settings (i.e., mediterranean versus tropical). A significant spatial effect was found even in the smallest studied organisms, including prokaryotes, planktonic protists and small metazoans. Organisms smaller than 1 mm have traditionally been considered ubiquitous, lacking biogeographical effects (Finlay 2002), although more recent analyses suggest there is no strong support for or against this statement (Fenchel et al. 2019). In this sense, we found significant spatial effects in both active and small passive dispersers, including Bacteria and Archaea, supporting the view that microorganisms are subjected to basically the same processes as those affecting macroorganims (Hortal 2011). For instance, the effects of extreme isolation unveil dispersal limitation allowing allopatric differentiation even in bacterial subspecies, as it was shown for Maritime Antarctic lakes (Hahn et al, 2015). Contrarily, some groups that should exhibit strong spatial control, such as coleopterans or molluscs (e.g. De Bie et al. 2012), were apparently mostly controlled by the environment in some of our studied metacommunities (but their total explained variance was frequently very low). Indeed, we did not find the expected differences in spatial and environmental effects between different body-sized, active or passive dispersers from the same region (De Bie et al. 2012; Padial et al. 2014), as neither did Heino et al. (2012) nor Schulz et al. (2012). Only few groups showed similar proportions of pure spatial and (purely plus spatially-correlated) environmental effects in both regions, including Bacteria from the water column and the sediment, branchiopods and copepods. Both Bacteria from the water column and the sediment, which are supposed to have higher dispersal ability than branchiopods and copepods, showed higher spatial effects in both metacommunities. Considering only pure environmental factors, there is only on group, the Ostracoda, that had a similar response between regions. These unalike results across regions, also different from those found in other multi-taxon studies (Beisner et al. 2006; De Bie et al. 2012; Padial et al. 2014; Gálvez et al. 2020), suggest the impossibility to extract general patterns on environmental and spatial influence on metacommunity structure according to organism dispersal ability. Nevertheless, the results obtained for the mediterranean metacommunity are somehow in tune with those found in the abovementioned similar studies (e.g. stronger role of purely environmental effects in bacteria, phytoplankton, rotifers, microcrustaceans or macroinvertebrates than purely spatial effects), among others (Gálvez et al., 2022). Contrarily, these patterns were much more diffuse in the tropical metacommunity, or even inverted.

Passive and active dispersers within the same region barely differed between them in their spatial and environmental effects, suggesting that spatial and environmental constraints are similar for organisms with different dispersal abilities (Schulz et al. 2012), and rather depend strongly on context. Large fractions of community variation remain, however, unexplained. This suggests an important role for the elements of chance or randomness (Jeffries 1989), but also unmeasured (biotic or abiotic) environmental effects, or interactions between effects (Leibold and Chase 2018). On the one hand, stochastic demographic processes and priority effects are expected to be strong at the beginning of the hydroperiod due to egg-bank hatching, before abiotic and biotic sorting of species can effectively act as filters in structuring local communities (Antón-Pardo et al. 2016; Castillo-Escrivà et al. 2017c; Mahaut et al. 2018). This may result in increased unexplained variation, with model residuals accounting for a higher proportion in the tropical metacommunity, probably related to its higher species richness, but also because of lower limnological heterogeneity (Leibold and Chase 2018), as shown by the homogeneity test of multivariate dispersion. Higher limnological heterogeneity may therefore account for a stronger influence of environmental selection processes in the mediterranean ponds, while in the richer tropical communities, under shorter environmental gradients, we may expect a higher influence of ecological redundancy. On the other hand, biotic interactions are known to be important mechanisms structuring metacommunities (García-Girón et al. 2020), especially in the tropics where these interactions are presumably stronger than at higher latitudes (Roslin et al. 2017; Zvereva and Kozlov 2021). Besides biotic variables, which have been neglected for years in metacommunity studies, the loss of environmental information due to model selection in GAMs, may give rise to misleadingly high proportions of unexplained residual variation (and/or of pure spatial effects) (Livingston et al. 2017).

Despite some potential limitations, we found that environment and space-related processes (e.g. selection and dispersal) played an important role in structuring metacommunities of tropical and temperate temporary ponds, although environmental effects dominated in the mediterranean metacommunity (i.e. in the more heterogeneous limnological environment). Contrary to expectations underlying spatial processes, the type of dispersal ability of the studied taxa (active or passive) did not relate to the proportion of spatial or environmental control on their metacommunities. We found no general pattern among taxonomic groups between regions, with very variable and idiosyncratic responses, even though mediterranean organisms respond more similarly to those patterns described in the literature; organisms are usually more environmentally than spatially controlled, and more so in temperate than in tropical metacommunities. This is however a snapshot study at a time characterized by high stochasticity at the beginning of the hydroperiod. In order to further disentangle the actual role of each process in shaping metacommunities, we need studying their temporal dynamics to better quantify not only the relative role of environmental and spatial components along a temporal series, but also of time per se in structuring metacommunities in highly dynamic ecosystems (Rojo et al. 2016; Gálvez et al. 2020; Gomes-Mello et al. 2021).

ACKNOWLEDGEMENTS

This study was sustained by the Spanish Ministry of Economy, Industry and Competitivity–AEI, and FEDER (EU), through project METACOM-SET (CGL2016-78260-P). Ángel Gálvez was also supported by an FPI fellowship BES-2017-080022 from the Spanish Ministry of Economy, Industry and Competitiveness. Berenice de Manuel is thanked for her help in laboratory analyses.

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Laguna de Talayuelas, Cuenca

CAPÍTULO 5

Temporal dynamics in mediterranean and tropical temporary pond metacommunities: a multi-taxon approach.

ABSTRACT

Snapshot surveys have dominated empirical metacommunity literature, neglecting the role of temporal effects in the organization of these systems. When time has been considered, it has been generally included under a spatial focus, comparing consecutive snapshot surveys, looking for temporal variation in environmental and spatial effects. However, a spatio-temporal focus, analysing the whole metacommunity variation and including time as a predictor of interest has been rarely carried out. Here, we compared the role of environment, space and time, under a spatial and a spatio-temporal focus, in the organization of two metacommunities of 30 tropical and 32 mediterranean temporary ponds. We compared multiple freshwater taxa (bacteria to amphibians), sampled using the same methodology thrice in the same hydrological year. For that purpose, we performed variation partitioning analyses using Generalized Additive Models (GAMs). In the spatial focus, our results show a decay in pure environmental effects with time, probably not related with changes in environmental heterogeneity or connectivity. We hypothesize that unmeasured biotic interactions may gain relevance with time. Pure environmental effects are stronger in the mediterranean metacommunity, maybe due to higher limnological heterogeneity. Contrarily, spatial and spatially structured environmental effects are higher in the tropical metacommunity, perhaps related with higher climatic heterogeneity, higher dispersal limitation and patchy species and environment distributions. In the spatio-temporal focus, pure time was as important as pure environmental effects, so that succession might play a key role in metacommunity organization, being more relevant in the mediterranean metacommunity and in organisms with intermediate body size and generation times. However, pure spatial effects become the most important pure component in both metacommunities, suggesting that this spatio-temporal focus can detect new spatial patterns, unperceived in the spatial focus. On the other hand, temporally and spatio-temporally structured environment are important in the mediterranean and the tropical metacommunities, respectively, suggesting an important role of seasonal variability of environment (or of spatially structured environment). Thus, this research shows how important time is in the structure of metacommunities, and how useful it is using a spatio-temporal focus to better capture the real processes organizing metacommunities.

Key words: dispersal limitation, environmental selection, freshwater ecology, spatial focus, spatio-temporal focus, succession, time.

INTRODUCTION

The metacommunity concept has reframed the study of species distribution in ecology. Under its established theoretical framework, multiple processes determine metacommunity composition, including environmental selection, dispersal or ecological drift (Vellend 2010; Vellend et al 2014; Leibold and Chase 2018). However, despite being highly dynamic systems, with increasing variability through time (Bengtsson et al. 1997), empirical metacommunities have traditionally been studied from a static point of view, as a group of sites sampled just once, also known as snapshot surveys (e.g. Beisner et al. 2006; De Bie et al. 2012). Nevertheless, analyses of temporal metacommunity patterns could be crucial for a more complete understanding of these complex systems and the processes structuring them (Guzman et al. 2020).

Previous studies have already introduced time in metacommunity analysis in various ways, depending on the study aims. Some studies focused on how spatial variation in metacommunities changes through time, i.e., what we can term as with a “spatial focus”. In these type of studies, metacommunities are analyzed at different sampling periods, and the results among these consecutive snapshot surveys are compared (e.g. Langenheder et al. 2012; Fernandes et al. 2014; Delciellos et al. 2018). Generally, this spatial focus reveals that temporal fluctuations of landscape connectivity and spatial environmental heterogeneity can influence the observed metacommunity spatial variation. An increase in connectivity drives community homogenization, decreasing spatial beta diversity, and modifying the relationship between species and environmental variables (i.e. environmental fit increases from low to intermediate connectivity and decreases from intermediate to high connectivity; Heino et al. 2015a). On the other hand, higher spatial environmental heterogeneity favours spatial beta diversity and tightens the environmental fit to the spatial distribution of species. Nevertheless, with these type of studies we only contemplate changing spatial variation with a spatial focus, and consequently the spatio-temporal metacommunity variation remains partially unanalyzed.

Other studies have considered the whole metacommunity spatio-temporal variation, therefore with a more focused “spatio-temporal” view. These studies deal with the relative importance of environmental, spatial and also temporal (e.g. succession, historical events) processes structuring metacommunities, using for instance variation partitioning to disentangle these influences. Most of them found that environmental and spatial processes (e.g. dispersal) were more relevant than temporal ones in determining metacommunity variation, although temporal effects were also significant (see e.g. Padial et al. 2014; Castillo-Escrivà et al.2017; Gálvez et al. 2020; but Wu et al.

2017). Moreover, temporal effects were widely overlapped with environment, indicating broad temporal scale effects of the environmental factors changing through time. However, these analyses with a spatio-temporal focus are still scarce and suitable statistical methods are currently under development (e.g., computing eigenfunctions for spatio-temporal variables; Castillo-Escrivà et al., 2020).

Temporary ponds are especially interesting for the study of temporal processes in metacommunities (e.g. dormancy, priority effects or seasonal dynamics associated with hydroperiod; Williams 2005; Chase 2007; Antón-Pardo et al. 2016; Rojo et al. 2016; Castillo-Escrivà et al. 2017b). However, although these ponds share the important characteristic of periodical water loss, they are not homogeneous systems around the world, due to distinct precipitation and temperature regimes between regions. Some authors have considered that temperate regions show higher environmental heterogeneity (in space and time) than the tropics (MacArthur 1972), and this has been proposed as the main reason behind stronger environmental (or temporally structured environmental) effects in temperate than in tropical metacommunities (Myers et al. 2013). However, changes in metacommunity connectivity can be especially drastic in tropical freshwater ecosystems, due to seasonal heavy rains (e.g. Thomaz et al. 2007; Brasil et al. 2020), driving major temporal (or spatio-temporal) overlapped effects on metacommunity variation.

Few previous studies have explored the role of environmental and spatial effects in aquatic metacommunities from different bioclimatic regions using the same methodology (e.g. Souffreau et al. 2014; Gálvez et al. 2021a). As Myers et al. (2013) do, these works also highlight the greater influence of the environment in the temperate metacommunities, while the tropical metacommunities are more spatially controlled (Souffreau et al. 2014; Gálvez et al. 2021a). These stronger spatial effects in the tropics (interpreted as dispersal processes such as dispersal limitation) can be explained by stronger orographic barriers (Janzen 1967) or patchy species distribution, apparently independent from local environmental constraints (MacArthur 1972). However, the processes structuring metacommunities can be very variable through time (Gálvez et al. 2020; Gomes-Mello et al. 2021), and the results of the above-mentioned snapshot studies should be contrasted incorporating temporal dynamics.

In this study, we aim at disentangling how environmental, spatial and temporal effects structure metacommunities of temporary ponds comparing two set of ponds from two distant biogeographical regions. For that purpose, we studied the metacommunity organization of a group of tropical and mediterranean ponds using both a spatial and a spatio-temporal focus, comparing multiple freshwater groups of organisms and using a common methodology.

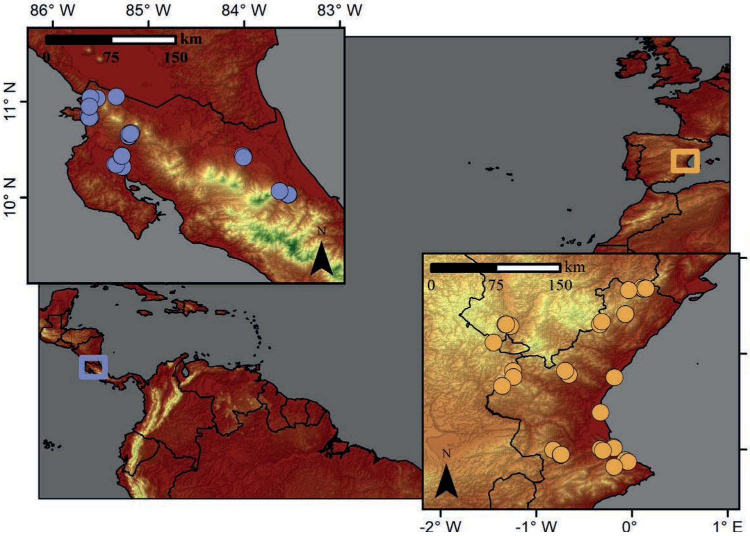

Figure 1: Map of the study area with the location of the ponds sampled in each region: Costa Rica (a) and eastern Spain (b).

We hypothesise that 1) the relative role of environmental and spatial effects on metacommunity structure will be variable across sampling seasons 2) environmental effects will be higher in the mediterranean metacommunity, while spatial effects will be higher in the tropical metacommunity, in every sampling period; 3) when incorporating time in our analyses, it will be an essential component, but not as important as environmental or spatial effects; 4) temporally structured environmental effects will be higher in the mediterranean metacommunity, due to seasonal changes in temperature.

MATERIAL AND METHODS

Study area and sampling methods

We surveyed 30 tropical and 32 mediterranean temporary ponds in Costa Rica and Eastern Spain (***Figure 1***). For that purpose, we included shallow (<2 meters of depth) and fresh or oligohaline (<7,000 µS/cm) waterbodies, such as small naturalized farmland ponds, inland shallow lakes and coastal wetlands. The ponds had different hydroperiod lengths: most of them presented an annual dry period of few months, but some of them have semipermanent hydroperiods of some years. The tropical ponds are located in a region with almost constant warm temperatures during the whole year (24.9 ± 1.3 ºC) and high but seasonally variable precipitation (2486 ± 934.7 mm). In contrast, the mediterranean ponds are distributed in a region with cooler mean annual temperature (12.9 ± 3.0 ºC) and also seasonally variable but reduced annual precipitation (537 ± 68.3 mm; Fick and Hijmans 2017). Each pond was visited during the flooding period three times along the same hydrological year: early (approximately two weeks after the infilling of the ponds, in May 2017 and January 2018, for Costa Rica and Spain respectively), mid (October 2017 and April 2018, respectively) and late hydroperiod (before desiccation of the ponds with shorter hydroperiod; January 2018 and June 2018, respectively). These ponds were distributed over a similar spatial extent in both regions (10,000 km^2 and 13,000 km^2, respectively), from sea level up to 1,500 m a.s.l.

We obtained presence-absence data for seven groups of aquatic organisms, representing the main forms inhabiting these ponds: bacteria and archaea from the water column, phytoplankton, rotifers, microcrustaceans (branchiopods, copepods and ostracods), benthic macroinvertebrates and amphibians. Bacteria and archaea community composition was characterised with abundances of different ZOTUs (Zero-radius Operational Taxonomic Units), by means of next-generation sequencing, following Picazo et al. (2019). The other groups were identified to species level (when possible). More details of the sampling methods and sample processing are provided in Gálvez et al. (2021a).

We measured different limnological, hydrogeomorphological, biotic, climatic and landscape variables for environmental characterisation (***Table 1***), as detailed in Olmo et al. (2022) and Gálvez et al. (2021a). For further analyses, environmental variables were inspected and transformed logarithmically or with the arcsine of the square root, depending on their frequency distribution, reducing leverage and skewness of extreme values (McDonald 2014). Pond characterization and biological data are available at Figshare (doi.org/10.6084/m9.figshare.16586348.v2).

Statistical analyses

We used metacommunity variation partitioning analyses in order to disentangle the role of environmental selection and spatial and temporal processes in metacommunity structure (Peres-Neto 2006) of different groups of organisms, using Generalized Additive Models (GAMs; Wood 2011; Gálvez et al. 2021a). Analyses were first performed using a spatial focus, analysing each sampling season separately as three temporally consecutive snapshot surveys. With this approach, we can know how the relevance of environment and space change across time. We used environmental and spatial variables as predictor matrices. In addition, we analysed the metacommunity structure with a spatio-temporal focus, partitioning the variation of the whole metacommunity observed in the three sampling seasons altogether (but again separately for each region and group of organisms), using three predictor matrices con-taining environmental, spatial and temporal data respectively (Anderson and Gribble 1998).

Table 1: Summary of measured environmental variables in each pond

Variable	Category	Unit
Alkalinity (Alk)	Limnological	meq L^{-1}
Chloride concentration (Cl^-)	Limnological	meq L^{-1}
Sulphate concentration (SO_4^{2-})	Limnological	meq L^{-1}
Nitrite concentration (NO_2^-)	Limnological	meq L^{-1}
Nitrate concentration (NO_3^-)	Limnological	meq L^{-1}
Ammonium concentration (NH_4^+)	Limnological	meq L^{-1}
Soluble reactive phosphorus concentration (SRP)	Limnological	meq L^{-1}
Alk/Cl^- ratio	Limnological	-
Alk/SO_4^{2-} ratio	Limnological	-
NO_3^-/NH_4^+ ratio	Limnological	-
NO_3^-/NO_2^- ratio	Limnological	-
Water temperature	Limnological	ºC
pH	Limnological	-
Electric conductivity	Limnological	µS cm^{-1}
Dissolved oxygen concentration	Limnological	mg L^{-1}
Water transparency	Limnological	cm
Average depth	Hydrogeomorphological	cm
Maximal depth	Hydrogeomorphological	cm
Pond length	Hydrogeomorphological	m
Pond width	Hydrogeomorphological	m
Pond area	Hydrogeomorphological	m^2
Morphology	Hydrogeomorphological	-
Granulometry	Hydrogeomorphological	Proportions
Organic matter content of the sediment	Hydrogeomorphological	Proportion
Carbonate content of the sediment	Hydrogeomorphological	Proportion
Seasonal hydroperiod	Hydrogeomorphological	Binary
Origin of the water (rain, river, phreatic)	Hydrogeomorphological	Factor
Chlorophyll a concentration	Biotic	µg L^{-1}
Helophytic vegetation coverage	Biotic	Proportion
Submerged vegetation coverage	Biotic	Proportion
Floating vegetation coverage	Biotic	Proportion
Fish presence	Biotic	Binary
Livestock presence	Biotic	Binary
Annual temperature range	Climate	ºC
Mean annual temperature	Climate	ºC
Annual maximum temperature	Climate	ºC
Annual minimum temperature	Climate	ºC
Annual precipitation	Climate	L m^{-2}
Precipitation seasonality	Climate	-
Agricultural land cover	Landscape	Proportion
Low grass land cover	Landscape	Proportion
High grass land cover	Landscape	Proportion
Scrub land cover	Landscape	Proportion
Forest land cover	Landscape	Proportion
Human infrastructures land cover	Landscape	Proportion
Landscape heterogeneity	Landscape	-
Altitude	Landscape	m a.s.l.

In the spatial focus, we used as response matrices the predicted values from Generalized Linear Latent Variable Models (GLLVM with binomial distribution) with the lowest AIC (Niku et al. 2017). This allowed us to concentrate on the common sources of variation among species and reduce computational time for extracting GAMs for a large number of taxa. As environmental matrix, we used the PCs of the environmental data, and as spatial variables, we used longitude and latitude coordinates. When applying GAMs, the number of explanatory variables was limited by the number of samples (about 30 samples in each region and period) to three maximum variables, because of the generation of nine splines per variable by GAMs. For that reason, we reduced the number of environmental variables selecting the first three principal components (PCs) in a Principal Component Analysis. In addition, we reduced the number of environmental PCs and spatial variables introduced in the models, using a forward selection with a double-stopping criterion (Blanchet et al. 2008). First, we selected only significant variables (p-value<0.05). Secondly, the adjusted R^2 of the selected variables had to be lower than the adjusted R^2 of the model with the whole set of variables. This procedure was repeated for the environmental (three PCs) and spatial variables (latitude and longitude) separately. We included at least one single environmental or spatial variable in rare cases that no variable was selected because the double-stopping criterion was not satisfied, as long as the included variable was significant. Because of the limitation to three predictor variables (due to the small sampling size), if more variables were selected, we manually reduced the number of variables (either spatial or environmental) by removing the selected variables that less contributed to explaining the observed variation, until reaching the maximum number of three selected variables.

As a result, GAMs provide information on the total proportion of metacommunity variation explained by environmental (E) and spatial (S) effects. In addition to the total explained variation by the models (E+S), the pure fractions of each component can be calculated: pure environmental effects (E|S); often associated with environmental selection) and pure spatial effects (S|E; that can be interpreted as mostly related to dispersal processes). In addition, we obtained the overlapped fraction of variation explained by environmental and spatial components (E∩S), often assigned to spatially structured environment (Cottenie 2005). The unexplained proportion or residuals represent common and uncommon sources of variation not explained by (measured) environmental or spatial variables. In order to reduce spurious correlation between species distributions and space-dependent environment, we applied the correction method for the environmental component as described in Clappe et al. (2018). To make results comparable among taxa and regions, we transformed the fractions of explained variation into their relative proportions, by dividing each pure or overlapped fraction by the total explained variation (E+S).

In the spatio-temporal focus, we incorporated some modifications to the method described above. Time was measured as a unique temporal variable, using the number of days after the sampling of each pond in the first sampling season. Instead of a maximum of three variables, the higher sampling size (about 90 samples per group and region) allowed to incorporate a maximum of nine variables in GAMs. In addition, we reduced the number of environmental variables by using Principal Component Analyses, but selecting the first six instead of the first three PCs. Incorporating the temporal component (T), variation partitioning analyses provide information about the total explained variation (E+S+T) and fractions explained by each component, independent from the others: pure environmental effects (E|(S+T)), pure spatial effects (S|(E+T)), purely temporal effects (T|(E+S); such as life-history, succession or phenology). Overlapped fractions include spatially structured environment ((E∩S)|T), temporally structured environment ((E∩T)|S), spatio-temporal overlap ((S∩T)|E) and spatio-temporal structured environment (E∩S∩T) In order to reduce spurious correlation between species distributions and space and/or time dependent environment, we applied the correction method for the environmental component as described in Clappe et al. (2018), with modifications for spatio-temporal eigenfunctions (Castillo-Escrivà et al. 2020). To make results comparable among taxa and regions, we transformed the fractions of explained variation into their relative proportions, by dividing each pure or overlapped fraction by the total explained variation (E+S+T).

Additionally, we contrasted the environmental heterogeneity between regions (for each sampling period separately, and the three periods altogether) using tests of homogeneity of multivariate dispersion (PERMDISP, Anderson 2006). In these analyses, we used the whole set of measured environmental variables, as well as the climatic variables separately (constant with time and expected to be more spatialized) and the limnological variables separately (more variable with time and expected to be more local). All analyses were performed with R (v4.0.2; R Core Team 2021) and R packages vegan (Oksanen et al. 2019), ade4 (Bougeard and Dray 2018), adespatial (Dray et al. 2019), gllvm (Niku et al. 2020) and mgcv (Wood 2017).

RESULTS

In the spatial focus (analysing each sampling season separately), we found a decay in the contribution of pure environmental effects to the total explained variation with time, while spatial effects or their overlap slightly increased in both regions (***Figure 2***). We found higher fractions of variation explained by pure environmental effects in the mediterranean metacommunity. In contrast, pure spatial and spatially structured environmental effects were generally stronger in the tropical ponds (***Figure 3***). These patterns are consistent in every sampling period. The general patterns described above are not strictly followed by every studied group of organisms, which were highly variable with time (***Figure 3***, ***Supplementary Material 1***). We found no significant differences in total environmental heterogeneity between regions at any sampling period, or between sampling periods within the same region in PERMDISP tests. However, climatic heterogeneity (mainly due to variability in rainfall) was significantly higher in the tropical ponds, while limnological heterogeneity was higher in the mediterranean metacommunity (only significant during the early and late hydroperiods) (***Supplementary Material 2***).

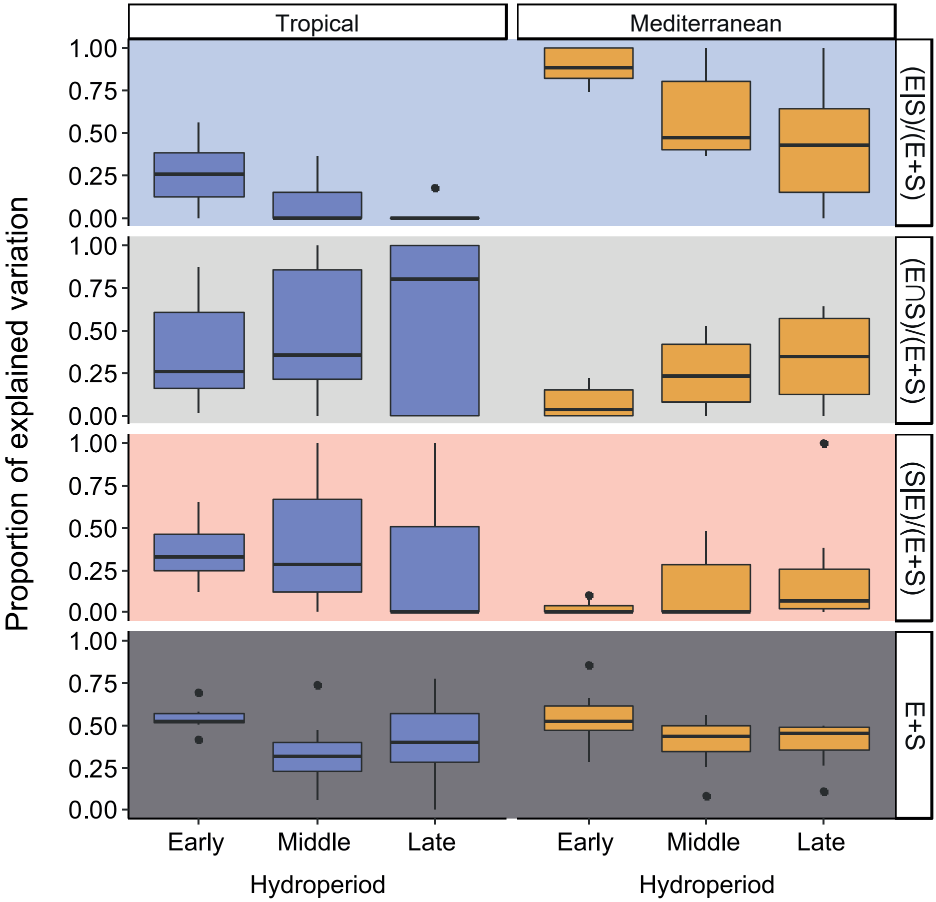

Figure 2: Results of variation partitioning analyses for each biogeographic region and sampling period. Boxplots of the relative contributions of pure environment ((E|S)/(E+S)), spatially structured environment ((E∩S)/(E+S)) and pure space ((S|E)/(E+S)) and total explained variation (E+S), represented with a different color for each region: tropical in blue and mediterranean in orange.

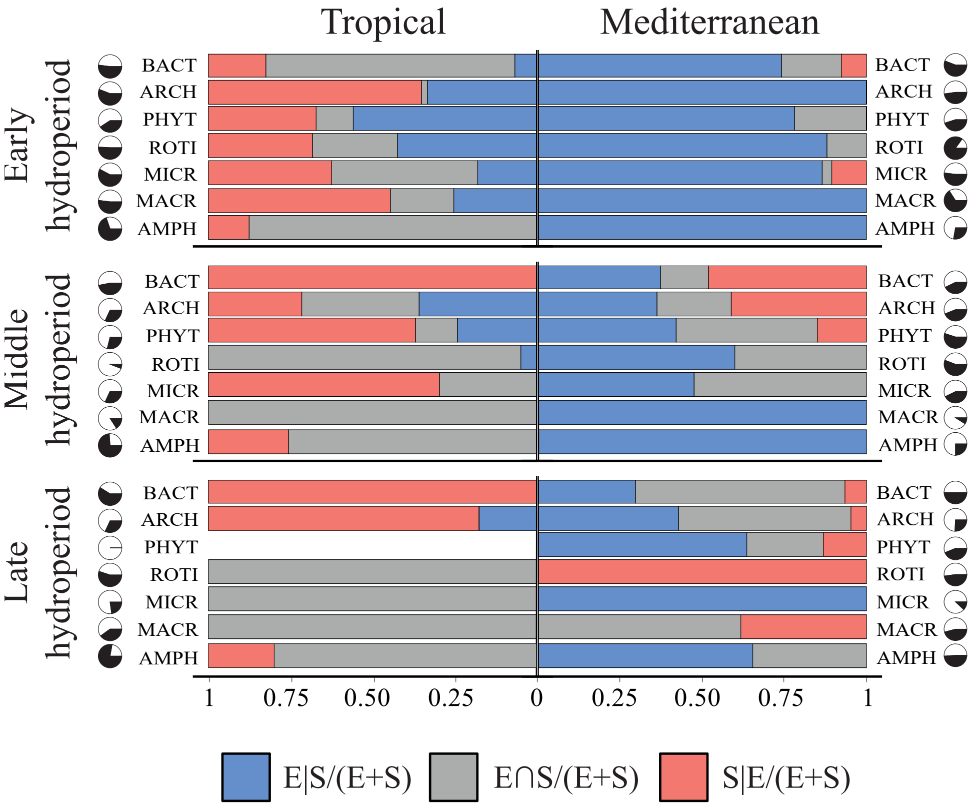

Figure 3: Results of variation partitioning analyses for each taxon in each biogeographic region and sampling period. The relative contributions of pure environment (E|S/(E+S)), spatially structured environment (E∩S/(E+S)) and pure space (S|E/(E+S)) are represented with a different color. Black portions in pie charts represent the total proportions of explained variation, and white portions the residual variation for each group of organisms: Bacteria (BACT), Archaea (ARCH), phytoplankton (PHYT), Rotifera (ROTI), Microcrustaceans (MICR), macroinvertebrates (MACR) and Amphibia (AMPH).

When analysing the three sampling campaigns altogether under a spatio-temporal focus, we incorporated the temporal variable as a third component in the variation partitioning analyses. Pure temporal effects were important elements in metacommunity structure, as important as pure environment, and slightly higher in the mediterranean metacommuity (***Figure 4***). However, pure spatial and spatially structured environment were the strongest effects. The effects of spatio-temporally structured environment were also important, particularly in the tropical metacommunity, and the temporally structured environment fraction was higher in the mediterranean metacommunity (***Figure 4***). The spatio-temporal overlap was negligible in both regions. As in the spatial focus, the relative proportion of pure environmental effects was higher in the mediterranean while spatially structured environment was higher in the tropical ponds. Purely spatial effects were high but not different between both sets of ponds (***Figure 4***). Pure temporal effects were insignificant in amphibians, but they showed an increasing trend with body size in the tropical invertebrates (***Figure 5***). In addition, the total explained variation was higher in the spatio-temporal than in the spatial focus.

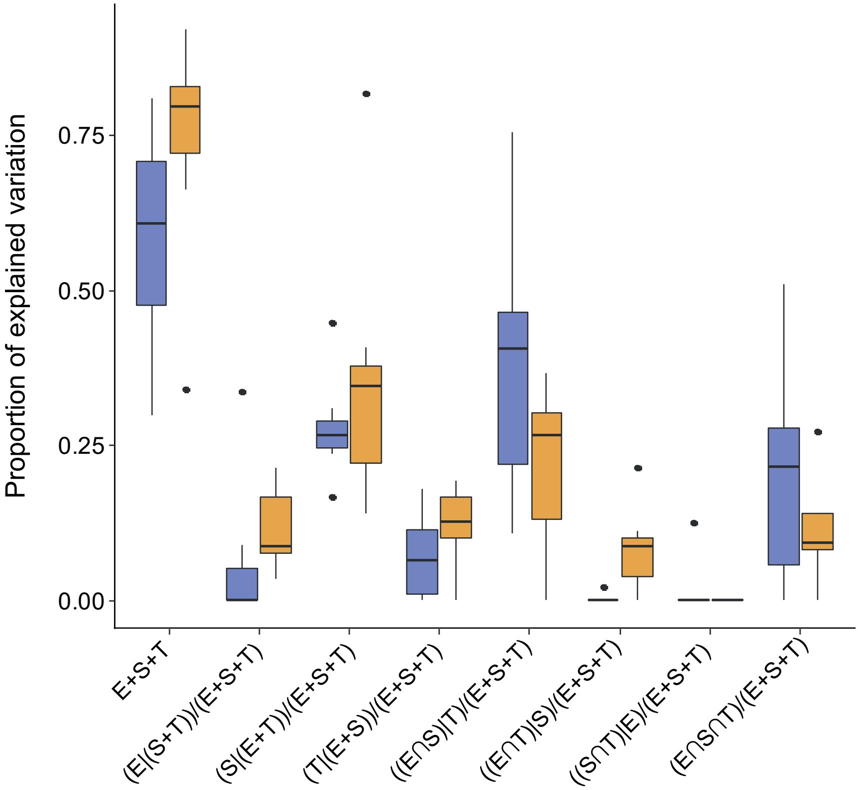

Figure 4: Boxplot results of variation partitioning analyses for each biogeographic region, incorporating the temporal component. [1] The total explained variation (E+S+T) and [2] relative contribution of pure environment ((E|(S+T))/(E+S+T)), [3] pure space ((S|(E+T))/(E+S+T)), [4] pure time ((T|(E+S))/(E+S+T)) and [5] spatially structured environmental effects (((E∩S)|T)/(E+S+T)), [6] temporally structured environmental effects (((E∩T)|S)/(E+S+T)), [7] effects of the spatio-temporal overlap (((S∩T)|E)/(E+S+T)), and [8] the spatio-temporally structured environmental effects ((E∩S∩T)/(E+S+T)), are represented with a different color for each region: tropical in blue and mediterranean in orange

Again, the explained fractions for every group of organisms was highly variable, not following the above-mentioned general patterns, and highly dissimilar to those found in the spatial focus (***Figure 5***; ***Supplementary Material 3***). However, results of amphibians are noticeable because of the absence of pure temporal effects in both regions, and the remarkable substitution of environmental effects in the spatial focus by pure spatial effects in the spatio-temporal focus. When comparing the environmental and spatial fractions of variance explained by both methods, the proportion of pure spatial effects increases in the spatio-temporal focus, while pure environmental effects are lower. These differences are more evident in the mediterranean metacommunity, and even clearer when removing the temporal proportion (***Figure 6***).

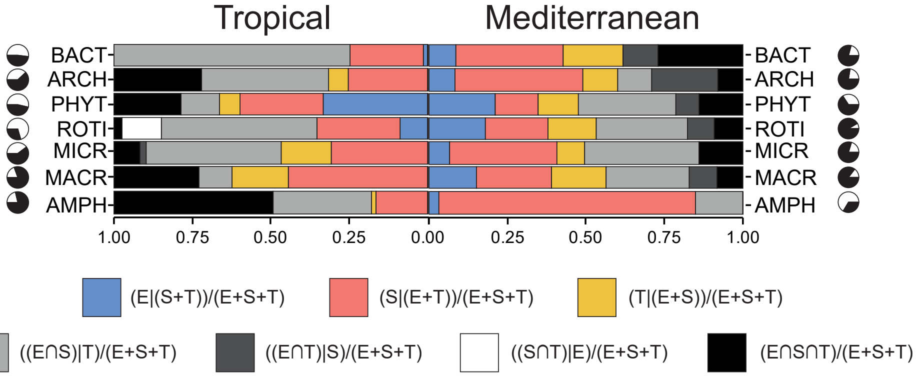

Figure 5: Results of variation partitioning analysis of all samplings periods altogether, for each group of organisms in tropical and mediterranean metacommunities. The relative contribution of [1] pure environment ((E|(S+T))/(E+S+T)), [2] pure space ((S|(E+T))/(E+S+T)), [3] pure time ((T|(E+S))/(E+S+T)) and [4] spatially structured environmental effects (((E∩S)|T)/(E+S+T)), [5] temporally structured environmental effects (((E∩T)|S)/(E+S+T)), [6] effects of the spatio-temporal overlap (((S∩T)|E)/(E+S+T)) and [7] the spatio-temporally structured environmental effects ((E∩S∩T)/(E+S+T)) are represented with a different color. Black portions in pie charts represent the total proportions of explained variation, and white portions the residual variation for each group of organisms: Bacteria (BACT), Archaea (ARCH), phytoplankton (PHYT), Rotifera (ROTI), microcrustaceans (MICR), macroinvertebrates (MACR) and Amphibia (AMPH).

DISCUSSION

In this study, we aimed at evaluating the spatial and environmental contributions to metacommunity structure in a wide variety of taxa, comparing two distant biogeographical regions, across three consecutive periods of time. Therefore, we intended to quantify the role of environmental, spatial and also temporal effects on the assemblage of metacommunities of temporary ponds along a hydrological year. Overall, we find stronger pure environmental effects in the mediterranean metacommunity, even though we found a decay in pure environmental fractions through the hydroperiod in both regions. Pure spatial effects were generally stronger in the tropical metacommunity in all three samplings periods individually, but overall similar to mediterranean ponds under the spatio-temporal focus (and slightly higher in the tropics). Pure temporal effects were also slightly higher in the mediterranean metacommunity, and (spatio-) temporally structured environmental effects were found to be also important.

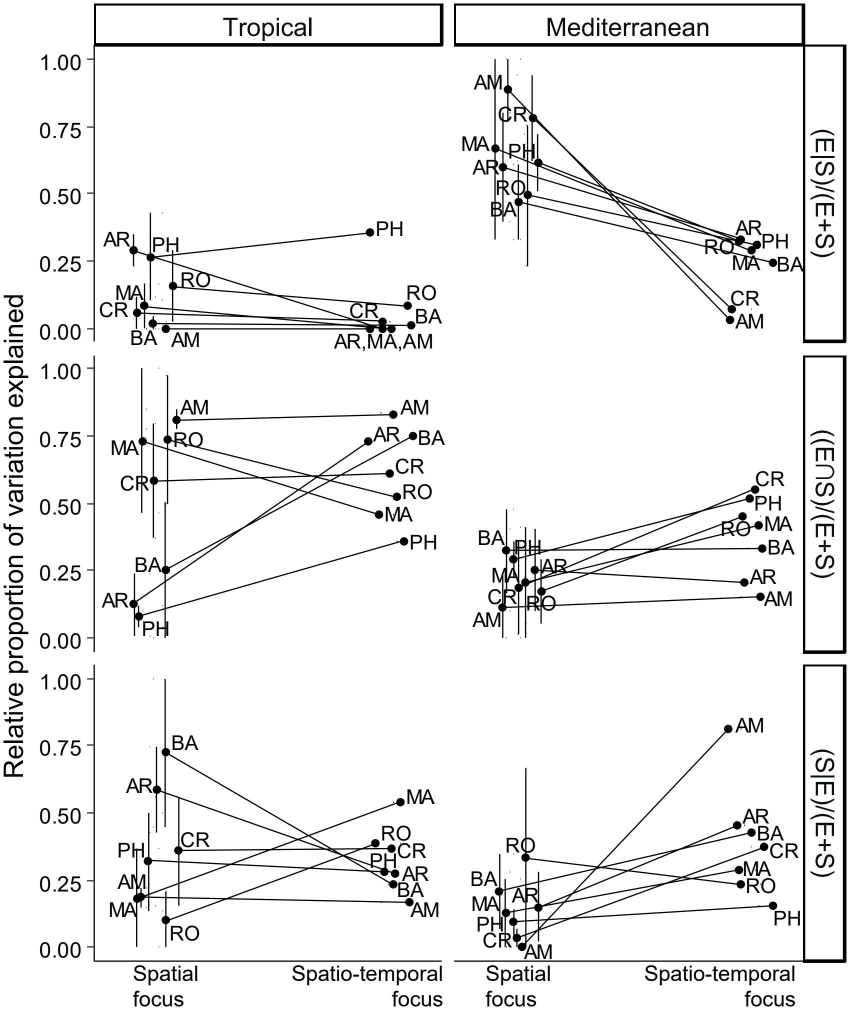

Figure 6: Comparison of results obtained for pure environmental ((E|S)/(E+S)), spatially structured environmental ((E∩S)/(E+S)) and pure spatial effects (S|E)/(E+S)) between the spatial and the spatio-temporal focus. Results of the spatial focus are represented as the average between the three sampling periods ±SE, and results of the spatio-temporal focus have been recalculated after removing the temporal component, for each group of organisms: Bacteria (BA), Archaea (AR), phytoplankton (PH), Rotifera (RO), Microcrustaceans (CR), macroinvertebrates (MA) and Amphibia (AM).

When applying the spatial focus, our results show a decay in pure environmental effects through time. Generally, two processes have been proposed to strongly influence the role of environmental effects in metacommunity organization: environmental heterogeneity and connectivity (Leibold and

Chase 2018). Previous studies considered that environmental heterogeneity increases the perception of the environmental selection (Pinha et al. 2017; Huber et al 2020). But the observed decay was not associated with a decrease in environmental heterogeneity in the studied metacommunities through time.

On the other hand, connectivity shifts can also lead to reduced environmental effects through metacommunity homogenization (Heino et al. 2015a). However, metacommunity homogenization due to connectivity shifts is less probable in the mediterranean ponds, which remain physically isolated during the whole year. Contrarily, connectivity increments could be expected in the tropical metacommunity during the rainy season, at least between close ponds (as found in other tropical studies; Brasil et al. 2020). But metacommunity homogenization due to connectivity increments should be accompanied by an environmental homogenization (Thomaz et al. 2007), not observed in any of the studied metacommunities. Apart from hydrology, active dispersal in flying insects (Boix et al. 2011) or passive dispersal mediated by mammals and birds (Waterkeyn et al. 2010, De Morais Junior et al. 2019; Fontaneto 2019) may increase as the hydroperiod progress. However, these dispersal events should be accompanied with beta diversity decreases (Fodelianakis et al. 2019), generally not observed by Gálvez et al. (in prep.; ***Capítulo 6***). Therefore, environmental heterogeneity or connectivity may not be the main processes driving temporal changes in the role of environment in these metacommunities.

One possible explanation to the observed decay in pure environmental effects through time could lie in unmeasured environmental variables, particularly biotic interactions (Thompson et al. 2020). Strong changes in metacommunity structure can be driven by community succession, with the establishment of new biotic interactions (Schneider and Frost 1996; Boix et al. 2016). As a consequence, biotic interactions might gain relevance with time, while communities become more complex (García-Girón et al. 2020). Therefore, overlooking these interactions can lead to overestimations of the residuals or even purely spatial effects (Livingston et al. 2017), which also show an increase through the hydroperiod in the studied metacommunities. Moreover, the arrival of new predators can change prey metacommunities, leading to higher apparent stochasticity due to heterogeneous prey survival in each local patch (Beisner and Peres-Neto, 2009; Vanschoenwinkel et al., 2010). Thus, environmental effects probably do not decay through time, but they are underestimated due to a relaxation of abiotic filtering in favour of the biotic filtering, and probably overestimating pure spatial effects.

Pure environmental effects were always higher in the mediterranean metacommunity, both in the spatial focus at every sampling period, and in the spatio-temporal focus. The few studies that have compared the metacommunity organization in distant biogeographical regions have also found a pattern pointing to higher environmental filtering in temperate regions (Myers et al. 2013; Souffreau et al. 2015), possibly related to their higher environmental heterogeneity, at least in terms of temperature regime (MacArthur, 1974) as the main process behind it. However, in our studied metacommunities, we found no significant differences in environmental heterogeneity between both sets of ponds. But the significantly higher limnological heterogeneity in the mediterranean region, with a stronger local influence, may explain the higher pure environmental effects in that region compared to the tropical ponds. In contrast, the significantly higher climatic heterogeneity, with a more regional influence in the tropical area, can lead to the observed higher spatially structured environmental effects in the tropical metacommunity.

We found that the tropical metacommunity seems to be more spatially controlled than the mediterranean one, supporting the findings of Myers et al. (2013) and Souffreau et al. (2015). Dispersal limitation, driven by stronger orographic barriers in the tropics (such as the Continental Divide in Costa Rica; Janzen 1967), may more effectively restrict species distribution. In this sense, the smaller extent of species distribution areas in the tropics compared with temperate regions (Rapoport, 1975) may also explain the stronger role of spatial effects in the tropics. The important role of orography for species distribution, but also (micro-)climate spatial heterogeneity, in addition to more spatially patterned environmental variables in the tropics (generally components of climate, Hawkins and Felizola Diniz-Filho 2004) may also explain the higher role of the spatially structured environmental component in the tropical metacommunity.

When incorporating the temporal component in the spatio-temporal focus, we found pure temporal effects to be as important as pure environmental effects in metacommunity organization. This result points out that metacommunity composition changes through time (e.g. succession), independently from temporal changes of environment, so that time plays a key role in metacommunity organization (Castillo-Escrivà et al. 2017a; Wu et al. 2017; Gálvez et al. 2020). In addition, these pure temporal effects were higher in the mediterranean than in the tropical metacommunity. Thus, the presence of certain species in the mediterranean metacommunity is more controlled by the moment of the hydroperiod than in the tropical metacommunity. Mediterranean ponds are characterized by a high unpredictability (Blondel et al. 2010), so successions in these ecosystems might be faster than in more stable tropical ecosystems. In addition, excluding amphibians, that do not show relevant pure temporal effects, the role of time increases with body size. This pattern is more evident in the tropical than in the mediterranean metacommunity, where pure temporal effects are more constant across groups of organisms. Thus, time-dependent processes (e.g. maturation, reproduction, senescence, etc.) are more important in organisms with longer (or at least intermediate) generation times and life cycles (Gálvez et al. 2020). In amphibians, due to extremely long generation times, that can extend from the very beginning of the hydroperiod until its end, underlying temporal dynamics (e.g. Gálvez et al. 2021b) may go unnoticed.

Pure spatial effects raise as the main pure component, not only in the tropical but also in the mediterranean metacommunity, when we included time in the analysis, probably because of the large explicit effects of temporal environmental changes that where not analysed when analysing the three sampling periods separately. Thus, pure spatial processes (mostly related to dispersal limitation, according to Cottenie 2005, although they could also be embracing unmeasured biotic factors with a spatial structure) might be the principal drivers of metacommunity organization of temporary ponds, as proposed by Heino et al. (2015b), if we exclude overlapped fractions. These results contrast to what we found in the spatial focus, where purely spatial effects were generally lower than pure environmental effects in the mediterranean metacommuniy (e.g. in macroinvertebrates or amphibians). We may therefore expect that the spatio-temporal focus, contrarily to the spatial approach, can identify as a spatial pattern the recurring presence through time of species in a particular location. As a consequence, the spatio-temporal focus can better unveil dispersal limitations related to species with restricted distributions and priority effects. Thus, the detection of new spatial patterns and the inclusion of temporal effects is translated in a reduction of the relative role of the environment in the spatio-temporal focus.

The overlapped fractions of explained variation between environment, space and time, here interpreted as spatially, temporally or spatio-temporally structured environmental effects, account for the main part of the environmental effects on the metacommunity organization of temporary ponds (Chase and Leibold 2003). Temporally structured environment, or environmental variation through time, is higher in the mediterranean metacommunity, as expected given the higher environmental variability in temperate regions (at least in terms of temperatures; Janzen 1967; MacArthur 1974; Feder 1978; Richter 2016). So, environmental changes due to strong seasonality at higher latitudes are more intensely modifying metacommunity composition. However, spatio-temporally structured environment is higher in the tropical metacommunity. This suggest that seasonality is also important in the tropical ponds, but emphasizing the role of spatially patterned environmental variables (Hawkins and Felizola Diniz-Filho 2004).

Finally, the residual (unexplained) proportion is lower in the spatio-temporal approach than in any sampling period of the spatial approach. This suggests that including time does not only allow a better detection of community composition patterns, but also provides a better explanation of the processes structuring the metacommunities. Nevertheless, differences in total explained variation may reside in the distinct sample size between both methods, so that more explanatory variables can be introduced in the spatio-temporal focus. In addition, the temporal scale is narrower than the spatial scale, so more effort through time (as suggested by Gomes-Mello et al. 2021) should be made to understand how time contributes to metacommunity structure (Castillo-Escrivà et al. 2020). However, even though some authors have found important temporal effects including large temporal series or even palaeoecological data (e.g. Castillo-Escrivà et al. 2017a), we still find a large fraction of variation, effects even larger than other studies, explained by pure temporal effects. All in all, including time in metacommunity studies is essential not only to understand how variable the structuring processes are through time, but to correctly address the role of environment, space and time in organization of the metacommunities (Guzman et al. 2020).

CONCLUSIONS

This research shows that space represents the highest pure effect in metacommunity organization, while pure temporal effects play a similar role than pure environmental effects in intra-annual changes. We also found that the importance of measured environment, mostly abiotic, decays through the hydroperiod. Given that environmental heterogeneity does not considerably change with time, that decay might mask the influence of unmeasured biotic interactions. Pure environmental effects are higher in the mediterranean metacommunity probably due to higher limnological heterogeneity. Spatially and spatio-temporally structured environmental effects and spatial effects are higher in the tropical metacommunity, maybe related to higher climatic heterogeneity, spatially patterned environment and stronger dispersal barriers that lead to dispersal limitation. On the other hand, temporally structured environmental effects are stronger in the mediterranean community, probably as a result of temporal changes in the environment related to temperature seasonality. Finally, using a spatio-temporal approach privides information about how important time per se is in the structure of metacommunities, but also how using a spatio-temporal approach is useful to unveil spatial patterns that remain unperceived.

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Laguna de Talayuelas, Cuenca

CAPÍTULO 6

Higher alpha and gamma, but not beta diversity in tropical than in mediterranean temporary ponds: a spatial and temporal analysis.

ABSTRACT

The latitudinal biodiversity gradient, one of the best described patterns in ecology, predicts that tropical regions should have higher local diversity, compositional dissimilarity between local communities and regional diversity (i.e. alpha, beta and gamma diversity) than temperate areas. However, only a few studies use a temporal framework to assess where is diversity more variable over time. In this study, we compare, using a spatial and temporal approach, the diversity of multiple taxa (from bacteria to amphibians) inhabiting two sets of tropical (Costa Rica) and mediterranean (Spain) temporary ponds, sampled on three occasions during the same hydrological year and with the same methodology. Under the spatial framework, we analysed gamma (Chao index), alpha (species richness, transformed Shannon and Simpson diversities and Pielou's evenness) and beta (Bray-Curtis or Sørensen dissimilarity indices) diversities. With a temporal approach, we compared the coefficients of variation in alpha diversity for each local community, and temporal beta diversity. Differences between regions and sampling periods were tested using GLMs. We found higher gamma diversity in the tropical ponds, as expected, and correlated with alpha diversity, but not with spatial beta diversity, which did not consistently differ between regions. However, phytoplankton and specially microinvertebrates from the mediterranean region, matched or even exceeded tropical alpha diversity in the late hydroperiod. Spatial beta diversity showed temporal decay in bacteria, micro- and macroinvertebrates and amphibians. Consequently, homogenising (e.g. flood pulse or dispersal) and heterogenising processes (isolation or environmental heterogeneity) must be balanced in both regions. The observation that temporal variation in alpha and beta diversity was similar for ponds in both regions, suggests that differences in the environmental heterogeneity of each pond through the hydroperiod do not generate major temporal differences in community composition. Exceptions to this pattern include macroinvertebrates, with higher variation in alpha diversity in the mediterranean ponds and amphibians, with higher temporal beta diversity in the tropical set of ponds.

Key words: local and regional diversity, dissimilarity, biodiversity latitudinal gradient, freshwater ecosystems, multi-taxon approach.

INTRODUCTION

The search for global patterns is one of the main aims of macroecology and biogeography. From gradients in body size and body proportions (Bergmann 1847; Allen 1876) to distribution ranges (Rapoport 1975), patterns across biogeographic regions have always been of major interest for ecologists.

The biodiversity latitudinal gradient is perhaps the best described pattern (Rosenzweig 1995; Willig et al. 2003; Hillebrand 2004). This biogeographic 'rule' establishes that biodiversity is negatively correlated with latitude, with tropical regions holding higher biodiversity than temperate ones. This pattern has been found in most of the studied taxonomic groups and ecosystems, with few exceptions in particular groups (such as soil fungal diversity; Shi et al. 2014), and is sometimes derived from historical contingencies (e.g. Gymnospermae species distribution, Barthlott et al. 2007). The processes behind this global pattern have been long debated, and are still frequently discussed. Among the factors suggested as responsible for the higher biodiversity in the tropics, are lower environmental severity (Francis and Currie 2003), lower environmental unpredictability, higher seasonal and historical stability (for example, less affected by glaciations; Brown and Lomolino 1998; Gaston and Blackburn 2000), higher evolutionary rates (Rohde 1992; "the Red Queen runs faster when she is hot", Brown 2014), or coexistence facilitated by complex biotic interactions (Roslin et al. 2017). Nevertheless, most of these studies compare only a few taxa (mostly terrestrial vertebrates or plants) across the latitudinal gradient, and those that compared several groups of organisms estimate diversity from different and heterogeneous published sources (i.e. Currie 1991).

Biodiversity is a complex concept, though. Whittaker (1972) defined three components of biological diversity: alpha (i.e. local diversity), gamma (i.e. regional diversity, considering a region as a group of localities) and beta diversity (i.e. similarity/dissimilarity between local communities). Classically, gamma diversity has been considered higher in the tropics, as most macroecology studies show when comparing regional diversities across the globe (e.g. Hillebrand 2004, Economo et al. 2018). But high gamma diversity can be the result of high alpha diversity (diverse local patches) and/or high beta diversity (dissimilar local patches). There is a wide consensus about the higher alpha diversity in the tropics (e.g. France 1992; Kaufman and Willig 1998; Rex et al. 2000; Qian and Song 2013; Gillman et al. 2014; Wang et al. 2014) and many investigations find a strong positive correlation between alpha and gamma diversities (Arellano and Halffter 2003; Mouquet and Loreau 2003; García et al. 2007). Many studies have also found spatial beta diversity to be higher in regions at lower latitudes (Qian and Ricklefs 2003; Qian and Song 2013; Cao et al. 2021; Muñoz-Mazón et al. 2021). To explain these larger dissimilarities among sites (i.e. higher spatial beta diversity) in the tropics, many authors have hypothesised that more geographically patterned environment (Rosenzweig 1995), higher speciation rates (Rohde 1992), smaller distribution ranges (Stevens 1989) or stronger dispersal barriers (mountains are "higher" in the tropics; Janzen 1967) lead to more endemicity in the tropics and, lastly, to higher species replacement and hence beta diversity (Qian and

Xiao 2012).

Large-scale empirical studies comparing biological diversity between biogeographic regions are usually addressed from a spatial focus, in the sense that they compare multiple sites without considering temporal dynamics. When time is considered, an extended spatial approach is often used, comparing snapshot multiple site data across time. In other words, multiple patches are simultaneously compared to each other, and the same procedure is repeated at different times (e.g. Soares et al. 2015). However, a purely temporal approach, comparing the variability in diversities of each single patch of a metacommunity across different times, in large spatial extents, has rarely been carried out (e.g. Liang et al. 2015; Nunes et al. 2020). In this work, to address this knowledge gap, we quantify the differences in alpha, beta and gamma diversity in freshwater ecosystems across two distant biogeographic regions (Neotropical and Mediterranean, i.e. at different latitudes). We use both a spatial approach across three sampling periods (to answer the question: which region is more diverse?) and a temporal approach (to answer the question: which region's diversity is more variable?) (***Figure 1***).

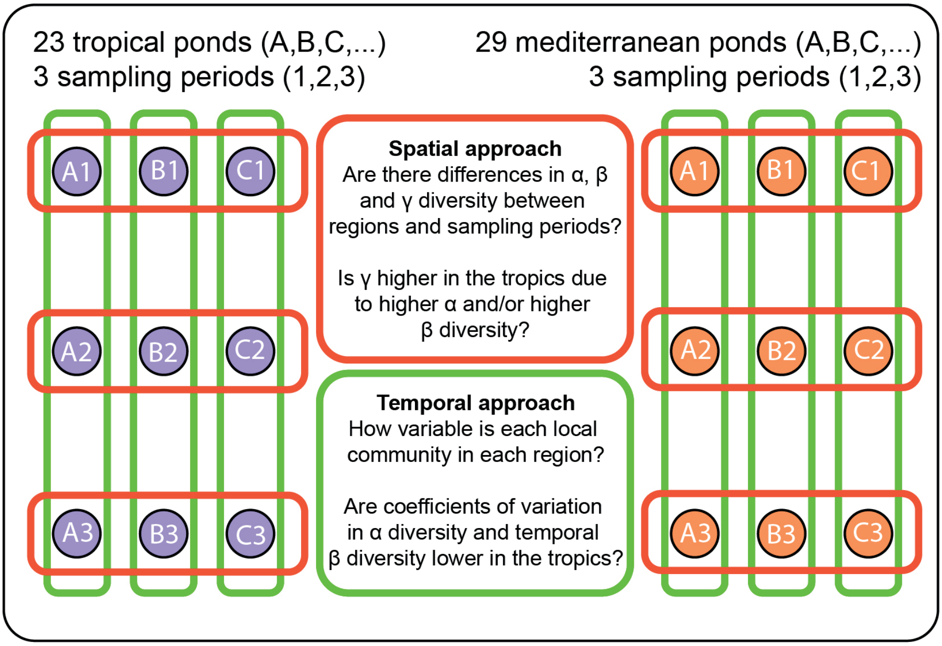

Figure 1: Summary of the sampling design, aims and structure of the diversity analyses. Different measurements of biological diversity were obtained in order to test i) for differences between regions and sampling periods and ii) for differences between regions in the variability of each local patch. The same procedure was repeated for six different groups of organisms.

When comparing the biological diversity of freshwater ecosystems in such distinct regions, the particular characteristics of each climate must be considered. While temperate climates exhibit strong seasonality in terms of temperature, this is typically more constant in the tropics. In contrast, precipitation may widely vary through the year at lower latitudes, especially in tropical climates (MacArthur 1972; Fick and Hickmans 2017), although precipitation in the temperate mediterranean climate can also be very variable (Blondel et al. 2010). Consequently, hydrology is an important driver of diversity and needs to be considered when comparing mostly isolated aquatic systems such as temporary ponds, irrespective of whether they are in the tropics or in temperate latitudes. Due to heavy precipitation in the rainy period of seasonal tropical climates, there is a hydrological connectivity shift among close water bodies, and the flood pulse can lead to environmental and metacommunity homogenization (Thomaz et al. 2007; Brasil et al. 2020). As habitat islands, ponds and lakes are considered isolated and well-delimited ecosystems allowing clear analyses of their community structure and dynamics (Hortal et al. 2014), and their strong limits reduce the potential connectivity with other systems, as it is observed in floodplain habitats. Despite the hydrological differences between regions, temporary ponds suffer from cyclic natural perturbations (generally drying), community recolonization and succession (Williams et al. 2007). Regardless of the biogeographic region, we can expect higher spatial beta diversity in early stages of the hydroperiod in some groups with resting forms, due to stochastic processes during egg bank hatching (Castillo-Escrivà et al. 2017). In contrast, as ecological succession proceeds through the hydroperiod, dispersal processes (critical in good dispersers such as some flying insects or bacteria) can contribute to homogenise communities within a region (Boix et al. 2011; Fodelianakis et al. 2019, Zeng et al. 2019).

Finally, lower variability and weaker seasonality are often argued to contribute to higher species richness in the tropics (Brown and Lomolino 1998; Gaston and Blackburn 2000). Temporal environmental heterogeneity is supposed to be lower in tropics than in temperate regions (MacArthur 1972), at least in terms of temperatures. In the same way that high spatial environmental heterogeneity generates high alpha and spatial beta diversity (Stein et al. 2014; Fernández-Aláez et al. 2020), temporal environmental heterogeneity generates temporal variability in diversity (Alves-de-Souza et al. 2017). Thus, stronger temporal environmental heterogeneity in temperate regions than in the tropics could lead to higher temporal variability of biological diversity in these regions.

In this work, we analysed how the biological diversity of a wide range of different aquatic organisms (from bacteria to amphibians) changes across space and time, using temporary ponds as model ecosystems. We approach this using the Whittaker's framework of alpha, beta and gamma diversity. Specifically, we analysed if tropical temporary ponds harbor higher biodiversity than mediterranean temporary ponds, as expected due to latitudinal differences. Moreover, we aim to assess the contributions of both temporal and spatial alpha diversity, and temporal and spatial beta diversity to the observed patterns. For this purpose, we hypothesise that i) gamma diversity will be higher in the tropical than in the mediterranean set of ponds for all taxa; ii) higher gamma diversity in the tropical set will be supported by higher alpha and higher spatial beta diversity; iii) spatial beta diversity will decrease with the progression in the hydrological cycle in the tropical ponds, due to higher hydrological connectivity; and iv) mediterranean ponds will show higher temporal beta diversity and alpha diversity variation than tropical ponds, due to higher temporal environmental heterogeneity.

MATERIAL AND METHODS

Study area

We surveyed mostly well preserved temporary ponds in two distant biogeographic regions: 23 tropical ponds in Costa Rica and 29 mediterranean ponds in Spain (***Figure 2***). These ponds were distributed in a similar spatial extent (10000 km^2 in Northern Costa Rica and 13000 km^2 in Eastern Spain) but with two distinct climates: tropical climate (almost constant warm temperatures and marked rainy and dry seasons) and mediterranean climate (mild winter and warm summer, with lower precipitation, generally concentrated in spring and autumn), respectively.

We selected natural or naturalised temporary freshwater ecosystems from sea level up to 1500 m a.s.l., including farmland ponds, coastal wetlands or inland shallow lakes. Despite hydroperiod ranging from at least six months to a few years (mostly temporary and fishless, but some semi-permanent and occasionally with fish), all these temporary ponds shared a shallow depth (always lower than 2 meters) and mostly fresh to oligohaline salinity (generally <3000 µS/cm). We visited each pond three times during the same hydrological year: once in the early hydroperiod, i.e. about two weeks after the infilling of the ponds (May 2017 in Costa Rica, January 2018 in Spain); once again in the middle of the hydroperiod (October 2017 in Costa Rica, April 2018 in Spain); and one last time by the end of the hydroperiod of temporary ponds, before their drying (January 2018 in Costa Rica, June 2018 in Spain). We characterised the environment of each surveyed pond in each period as described in Gálvez et al. (2021) and Olmo et al. (2022).

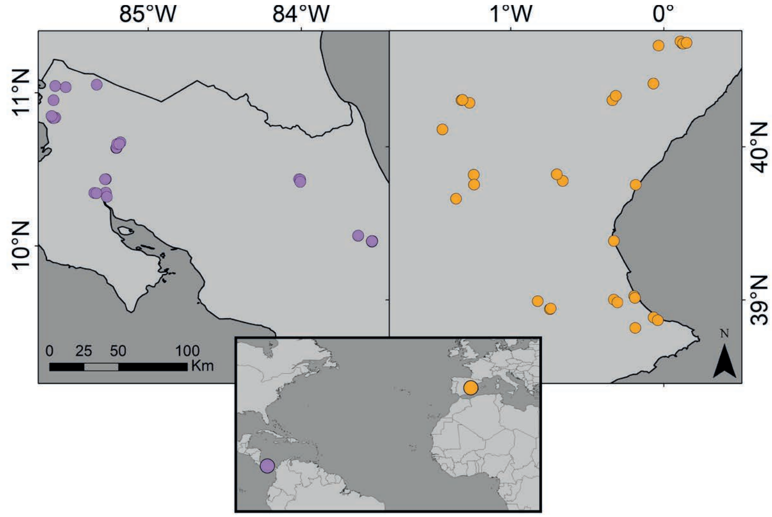

***Figure 2**:* Distribution of sampled temporary ponds in the study areas. Lilac dots represent tropical temporary ponds, located in Costa Rica, while orange dots represent mediterranean temporary ponds, in Eastern Spain.

Biological communities

In each of the three visits per pond in both regions, we characterised the biological communities of different groups of organisms, with the maximum taxonomic resolution possible: bacteria, archaea, phytoplankton, microinvertebrates (including rotifers, branchiopods, copepods and ostracods), macroinvertebrates (mainly molluscs and insects, but also including scarcer groups such as bryozoans, annelids, flatworms, crayfish, etc.) and amphibians.

Regarding bacteria and archaea, we used 1 L sterilised bottles to obtain samples from the water column. Later on, we filtered that water through 3 µm pore polycarbonate filters (Nucleopore, Whatman™) to remove large particles. We filtered the remaining water again through 0.2 µm pore polycarbonate filters (Nucleopore, Whatman™), to concentrate the DNA samples for the subsequent molecular analyses. Samples were cold-stored in microtubes filled with RNAlater™ reagent until further analysis. DNA extractions, PCR and bioinformatics for taxonomic assignments were done following Picazo et al. (2019). The obtained table of Zero-radius Operational Taxonomic Units (ZOTUs) was normalised by unifying 100 rarefactions of each sample (Edgar 2016) to the minimum threshold of 2550 reads/sample. ZOTUs with less than 1% of reads in each sample were not removed.

For phytoplankton, water samples from the water column at the centre of the ponds were sampled, stored in 100 mL amber-coloured glass bottles, and fixed with 3 mL of Lugol's solution for identification until species level whenever possible (Huber-Pestalozzi 1976-1982; Wolowski and Hindák 2005). Zooplankton invertebrates were sampled using a hand net (63 µm mesh-size) through c. 10 m of water column whenever possible, integrating all different microhabitats. We fixed these samples using formaldehyde 4% (final concentration, v/v). We identified, with the maximum taxonomic resolution possible, rotifers (following Koste 1978; and Segers 1995), branchiopods (Alonso 1996; Elías Gutiérrez et al. 2008; Błędzki and Rybak 2016; and references therein), and copepods (Dussart 1967; Dussart 1969; Elías Gutiérrez et al. 2008; Błędzki and Rybak 2016).

Benthic invertebrate samples (including ostracods, molluscs and aquatic insects, among other groups) were collected using a hand net (20 x 20 cm, 250 µm mesh-size). About 10 m were sampled integrating all microhabitats. These samples were fixed with ethanol 96% and identified to species level whenever possible using Wiederholm (1983), Tachet et al. (2010), Thorp and Covich (2010) and Springer et al. (2010), and references therein, for macroinvertebrates, and Meisch (2000), Karanovic (2012) and references therein for ostracods.

Finally, amphibian occurrence was recorded in situ by identifying adults, larvae, eggs and calls. Due to the easy detectability and low species richness, mediterranean ponds were surveyed using a hand net (800 cm^2, 2 mm mesh pore) with a constant effort of ten minutes, and examining the pond surroundings for ten more minutes. In tropical ponds, with higher species richness and lower detectability, we performed night surveys looking for individuals in the pond surroundings with an effective effort of up to 2 hours per pond, avoiding full moon nights (Wilkinson 2015).

Diversity measures and statistical analyses

We explored alpha, gamma and beta diversities of different groups of organisms, comparing between tropical and mediterranean ponds. For that reason, the analyses described below were performed separately on each group of organisms: bacteria, archaea, phytoplankton, microinvertebrates, macroinvertebrates and amphibians.

Using a spatial focus, we measured different components of biological diversity for each group of organisms at each sampling period in both regions separately. Regarding gamma diversity, we calculated the extrapolated species richness (Chao index) of the species pool for each region and sampling period using the specpool function in the vegan R package (Oksanen et al. 2019). In order to check if sampling effort covered similar proportions of the total species pool, necessary to make data comparable, we explored the sample coverage per number of sampled units using iNEXT function in iNEXT R package (Hsieh et al. 2016). As for alpha diversity, we obtained the observed values for species richness (Hill numbers of order 0), transformed Shannon (Hill numbers of order 1) (Chao et al. 2013) and Simpson (Hill numbers of order 2) (Chao et al. 2014) diversities in each pond. For this purpose, we used the ChaoRichness, ChaoShannon and ChaoSimpson functions in the iNEXT R package. Shannon and Simpson diversities were not obtained for amphibians, due to the lack of abundance data for this group. We also estimated the classical index of Pielou's evenness (J) as the ratio of the (untransformed) Shannon index to the logarithm of the number of species. We tested the relationship between gamma and alpha diversity using a Standard Major Axis regression (Legendre and Legendre 1998), with the function lmodel2 in the homonymous R package (Legendre 2018). For spatial beta diversity, we analysed the dissimilarity of each pair of local communities of each region and each sampling period independently (***Figure 1***), in order to avoid pairwise comparisons between ponds of different sampling periods, and discarding ponds without any species records. For this purpose, we used the Bray-Curtis dissimilarity index, and its partition into replacement (i.e. turnover or species substitution between sites) and richness differences (nestedness or different number of species between sites) (Legendre 2014), by means of the function beta.pair.abund in the R package betapart (Baselga and Orme 2012). Amphibian beta diversity was calculated using the Sørensen index, due to the absence of abundance data. The comparison of the different components of biological diversity (except for gamma diversity) between regions or sampling periods was performed using Generalised Linear Models (GLM; using Poisson distribution for species richness, quasi-Poisson distribution for Shannon and Simpson diversities and quasi-binomial distribution for spatial beta diversity and evenness). We contrasted the environmental heterogeneity between regions and sampling periods using tests of homogeneity of multivariate dispersion (PERMDISP, Anderson 2006), by means of the betadisper function in vegan. We tested differences in total environmental heterogeneity, and separately in local physico-chemical variables (limnological heterogeneity) and climate variables (climate heterogeneity).

Finally, using a temporal focus, and in order to compare the variability of diversity in each site, we calculated the coefficient of variation of alpha diversity (species richness and transformed Shannon and Simpson indices) across the three sampling periods, so as the dissimilarity between different sampling periods for each pond (i.e. temporal beta diversity). Temporal beta diversity was estimated with the Bray-Curtis (and Sørensen for amphibians) dissimilarity index, and its partition into replacement and richness differences, by means of the beta.multi.abund function in betapart R package. We only analysed those ponds with species records in all the three sampling periods. Temporal differences between regions (regarding temporal beta diversity and coefficients of variation of alpha diversity) were also tested using GLMs (quasi-Poisson for coefficients of variation and quasi-binomial for temporal beta diversity). In order to assess the temporal environmental heterogeneity, we calculated the distance to the centroid of each pond at different sampling periods, in a PERMDISP test. Differences in temporal environmental heterogeneity between regions were tested with a PERMANOVA test (adonis function in vegan R package). All the analyses were performed on software R 4.0.2 (R Core Team 2020).

RESULTS

When analysing diversity with a spatial focus, gamma diversity was generally higher in tropical than in mediterranean ponds (***Figure 3a***; ***Supporting Material Appendix 1, Table A1*** for extrapolated values), and highly correlated with mean alpha diversity (***Figure 4***). Sample coverage was similar across biogeographic regions and groups of organisms (***Supporting Material Appendix 2***, ***Figure A1***). However, gamma diversity of phytoplankton and microcrustaceans were very similar between regions at the middle or the end of the hydroperiod (***Figure 3***).

Alpha diversity was significantly higher in the tropical than in the mediterranean ponds in all groups, in terms of species richness and transformed Shannon and Simpson diversities, according to the GLM analyses (***Table 1***; ***Figure 3b-d***; ***Supporting Material Appendix 1***, ***Tables A1*** and ***A2*** for predicted values and estimated parameters). We found significant differences in species richness between sampling periods (that is, along the hydroperiod) in all groups of organisms except amphibians (***Table 1***). Richness of prokaryotic taxa in the mediterranean ponds declined after infilling, during the second sampling period, while mediterranean eukaryotic richness was higher in the mid or late hydroperiod compared to the beginning. These significant seasonal differences, however, disappear in Shannon and Simpson diversities in all groups analysed except for microinvertebrates. We also observed significant interactions between sampling period and biogeographic region, pointing to different trends in alpha diversity through time between regions (***Table 1***). However, regional differences were proportionally stronger than temporal effects (or interactions between region and sampling period), as shown by the large fractions of deviance explained by the regional variable (***Figure 3***). Pielou's evenness was usually higher in tropical than in mediterranean ponds (***Figure 3e***), but the difference was only significant in bacteria and microinvertebrates (***Appendix 1, Table A2***).

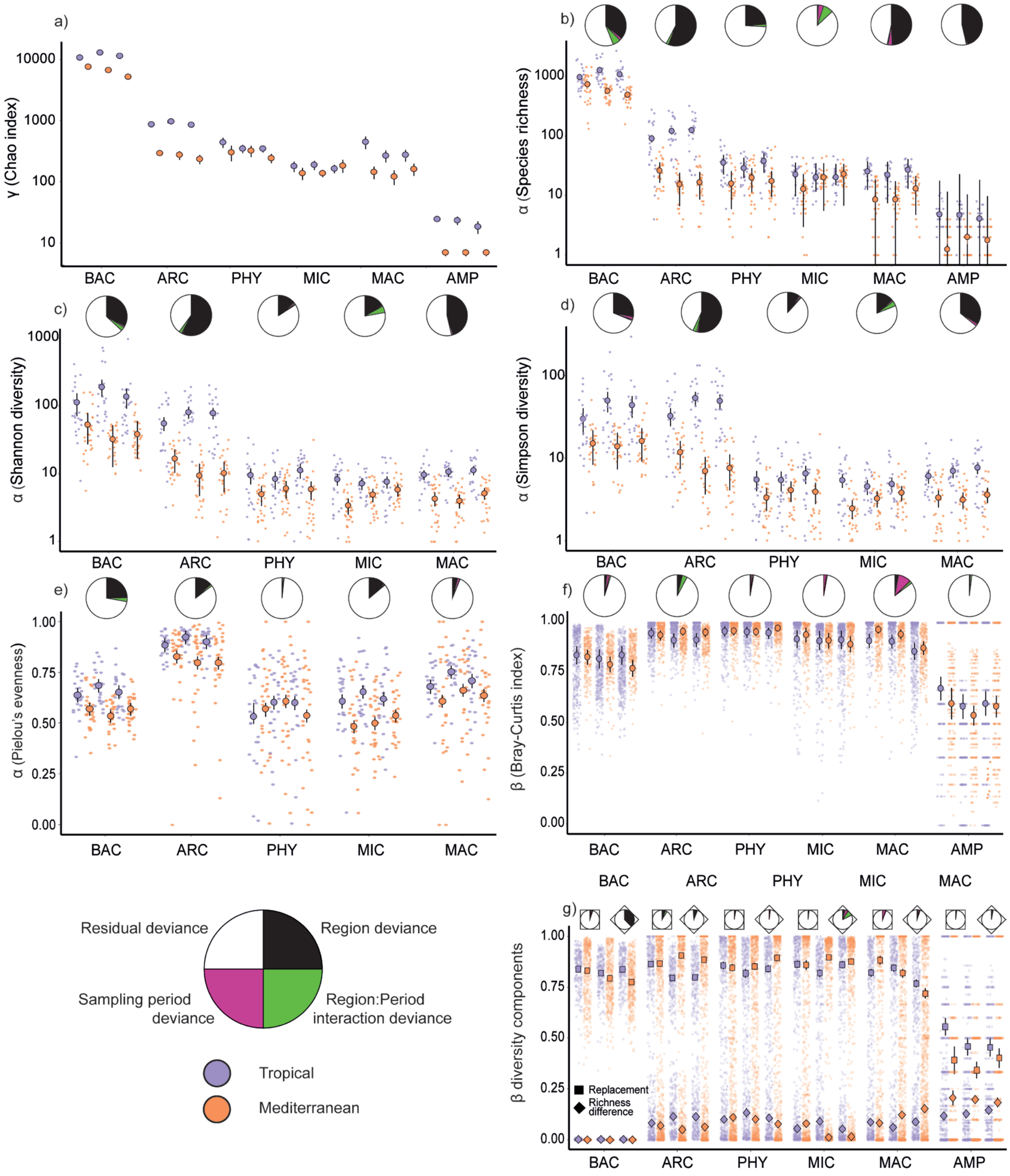

Figure 3: Observed (small dots) and predicted (large dots) values by Generalised Linear Models with 95% confidence interval for gamma (a: Chao index), alpha (b: species richness; c: transformed Shannon diversity; d: Simpson diversity, e: Pielou's evenness) and beta diversity (total beta diversity, f; beta diversity partition in replacement (squares) and richness difference (diamonds), g). Deviances are shown as pie charts (Region=black, Sampling period = pink, Region:Season interaction = green, Residuals = white). Lilac points for tropical ponds and orange points for mediterranean organisms. BAC (Bacteria), ARC (Archaea), PHY (Phytoplankton), MIC (Microinvertebrates), MAC (Macroinvertebrates), AMP (Amphibians).

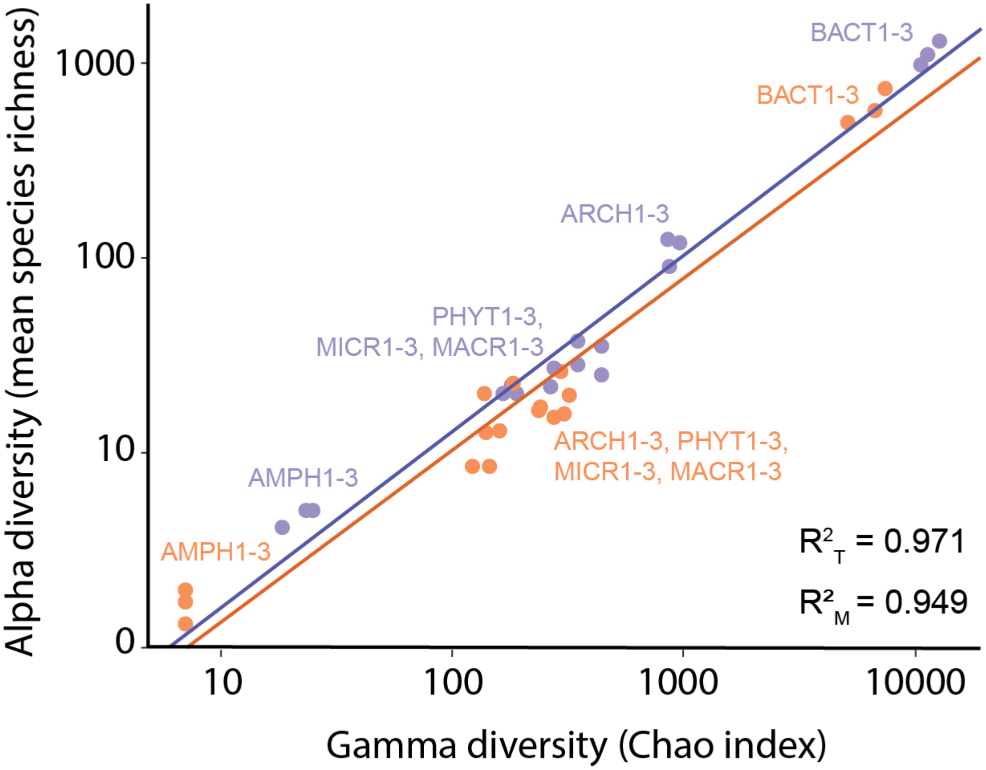

***Figure 4**:* Observed relationship between alpha diversity (as mean species richness) and gamma diversity (Chao index) for each sampling period. R^2 for tropical (R^2_T; lilac) and mediterranean (R^2_M; orange) regions in Standard Major Axis Regression are shown.

In contrast to alpha diversity, spatial beta diversity did not consistently differ between regions in most groups (***Figure 3f***; ***Table 1***; ***Supporting Material Appendix 1, Table A1*** for predicted values). Invertebrates show significantly higher beta diversity in the mediterranean-climate region, while archaea and amphibians have significantly higher beta diversity in the tropics. Temporal effects were variable and depended on the region (there were interaction effects); considering these effects, most tropical groups showed a decay in beta diversity with time, but not so in the mediterranean ponds (***Table 1***). Nevertheless, the proportion of deviance explained by temporal or regional effects on beta diversity was highly variable and generally low or even null (***Figure 3f***). Replacement was notably higher than richness differences in both regions. Nevertheless, these beta diversity components were not generally higher in one region or another. We found higher values in the tropical ponds for species replacement in amphibians and for richness differences in bacteria (***Appendix 1, Table A2***). Mediterranean ponds had higher replacement in macroinvertebrates and higher richness difference in microinvertebrates (***Figure 3g***; ***Supporting Material Appendix 1, Tables A1*** and ***A2*** for predicted values and estimated parameters). We found no differences in PERMDISP tests in total environmental heterogeneity between each sampling period within the same biogeographic region (but higher non-significant environmental heterogeneity in the first sampling period in both regions), and no differences were also found between regions within the same sampling period. However, mediterranean ponds showed higher limnological heterogeneity at every sampling period, while tropical ponds showed higher climate heterogeneity (***Supporting Material Appendix 1, Table A3***).

Table 1: Parameter estimation in Generalised Linear Models predicting alpha (species richness) and spatial beta diversity (Bray-Curtis index except Sørensen for Amphibia) for each group of organisms. Asterisks indicate significant results (p-value < 0.05). Reference levels for categorical variables are the mediterranean region and the first sampling period.

Model	Intercept	Region (Tropical)	Sampling period 2	Sampling period 3	Region (Tropical): Sampling period (2) interaction	Region (Tropical): Sampling period (3) interaction
Species richness						
Bacteria	6.603*	0.280*	-0.259*	-0.409*	0.538*	0.521*
Archaea	3.263*	1.242*	-0.535*	-0.457*	0.820*	0.780*
Phytoplankton	2.757*	0.802*	0.230*	0.098	-0.440*	-0.032
Microinvertebrates	2.552*	0.563*	0.454*	0.573*	-0.565*	-0.686*
Macroinvertebrates	2.150*	1.070*	-0.004	0.409*	-0.124	-0.333*
Amphibia	0.296*	1.338*	0.397	0.248	-0.414	0.455
Total spatial beta diversity						
Bacteria	1.596*	0.133	-0.241*	-0.354*	0.099	0.345*
Archaea	2.696*	0.190*	0.400*	0.248*	-0.960*	-0.789*
Phytoplankton	3.120*	0.011	-0.056	0.476*	-0.051	-0.684*
Microinvertebrates	2.366*	-0.317*	-0.419*	-0.612*	0.337*	0.569*
Macroinvertebrates	0.339 *	-1.043 *	-0.557*	-1.406 *	0.534*	0.902*
Amphibia	0.400*	0.329*	-0.238*	-0.053	-0.144	-0.270

Using a temporal approach, the coefficient of variation of alpha diversity barely differed between both sets of ponds in terms of species richness, Shannon and Simpson diversities, according to the GLMs (***Figure 5a-c***; ***Supporting Material Appendix 1, Tables A4*** and ***A5*** for parameter estimation and predicted values). Only macroinvertebrates showed significantly higher temporal variation in species richness in mediterranean than in tropical ponds. Regarding temporal beta diversity (***Figure 5***; ***Supporting Material Appendix 1, Tables A4*** and ***A5*** for predicted values), GLMs do not show differences between regions except for amphibians, with higher values in the tropics. The temporal replacement component was not significantly different between regions, but the richness difference component was found significantly higher only in tropical bacteria. Temporal environmental heterogeneity did not differ between regions according to a PERMANOVA test (p = 0.691).

DISCUSSION

In this study, we compared alpha, beta and gamma diversity of biological communities in two sets of temporary ponds located in two distant biogeographic regions, Neotropical and Mediterranean, with marked climate and latitudinal differences. Overall, tropical ponds harboured higher gamma diversity than mediterranean ponds in most groups and sampling periods, which is in tune with classic research describing a negative correlation between latitude and biological diversity, although phytoplankton and microinvertebrates showed similar gamma values between regions. Even though alpha diversity was also higher in the tropical ponds, spatial beta diversity was similar in both regions with the exception of a couple of groups. Temporal variability in alpha and beta diversity was also found not to differ between regions.

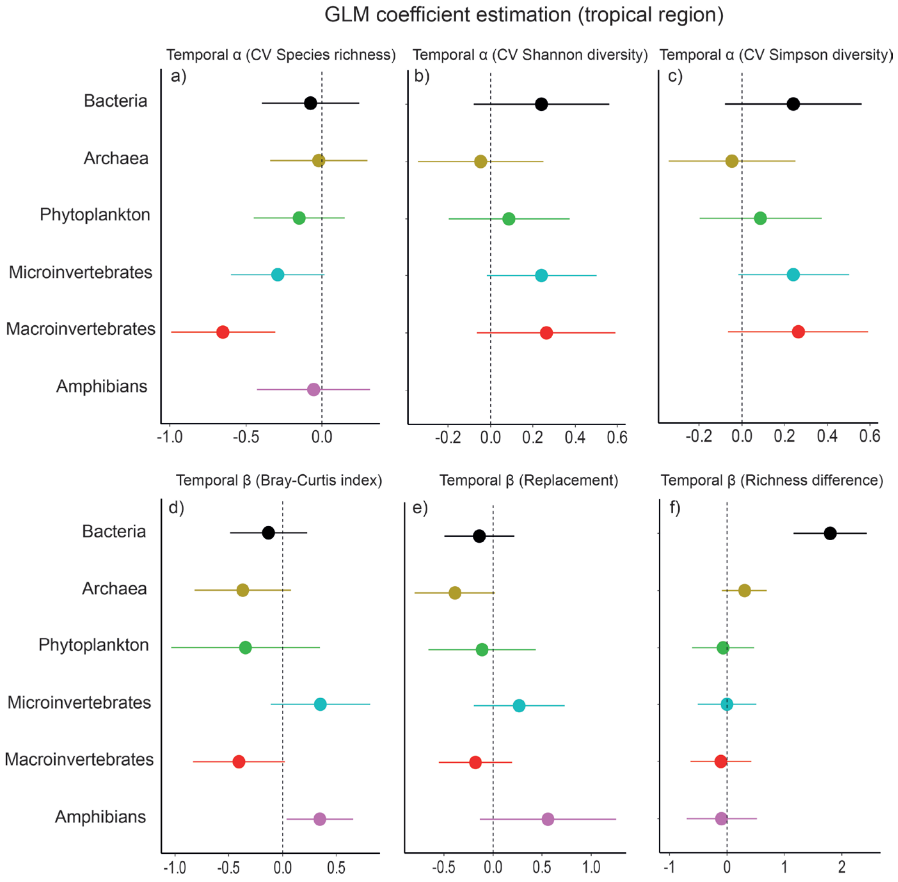

Figure 5: Coefficient estimates and 95% confidence interval for tropical ponds in Generalised Linear Models of temporal alpha and beta variation: coefficient of variation of species richness (a), transformed Shannon diversity (b), Simpson diversity (c), Bray-Curtis index (d), replacement component of beta diversity (e) and richness difference component of beta diversity (f).

Gamma and alpha diversity are higher in the tropics

As expected, the extrapolated regional species richness (gamma diversity) was generally higher in the tropical ponds, consistent with the well described biodiversity latitudinal gradient (Rosenzweig 1995; Willig et al. 2003; Hillebrand 2004). Gamma diversity was highly correlated with alpha diversity, so that a higher regional species pool in the tropics corresponded to higher local species richness, supporting previous findings (Arellano and Halffter 2003; Mouquet and Loreau 2003; García et al. 2007). Indeed, all three alpha diversity measures (i.e. order 0, 1 and 2) tended to be higher in tropical ponds in most groups.

Higher (transformed) Shannon and Simpson diversities in tropical ponds, apart from higher species richness, also reflected higher evenness in most groups, although it was only significant in microinvertebrates and bacteria. In other words, species proportions in tropical ponds were more evenly distributed (not necessarily implying less rarity but maybe less dominance), a pattern also found in tropical spider communities by Privet and Pétillon (2020). More biotic interactions in tropical ponds, such as predation, competition or facilitation, could determine the patterns observed (MacArthur 1972). For example, the absence, or low occurrence, of predators like fish in temporary ponds may allow large cladoceran species to survive and dominate the zooplankton of mediterranean communities, displacing smaller and weaker competitors (Lemma et al. 2001) such as rotifers, which are usually the component of zooplankton with more species in these regions (Olmo et al. 2016), and consequently reducing microinvertebrate evenness.

Time did not generally drive substantial changes in alpha diversity (as shown by the low explained deviances in the GLMs), but all groups except amphibians experienced a marked temporal variation in alpha diversity in the mediterranean ponds, probably driven by increasing temperatures (Parain et al. 2019; Rosset et al. 2010). In contrast, alpha diversity of tropical ponds generally shows slight changes with time. Even though tropical ponds also experience a strong environmental seasonality due to hydrological changes because of seasonal heavy rains (Ivory et al. 2019; Mitsch et al. 2020), this seasonality does not seem to be reflected in the local communities of living organisms, at least in terms of alpha diversity (species richness), except in bacteria and archaea, with higher diversity as the hydroperiod advanced, perhaps facilitated by dispersal during the flooding season and by their fast population growth.

Spatial beta diversity does not differ between regions

Regarding spatial beta diversity, we found no consistent differences between mediterranean and tropical ponds in most groups. Species replacement was the larger component of total beta diversity, in agreement with the meta-analysis of Soininen et al. (2017). Both species replacement and richness differences were not significantly different between regions or, when they were, were not always significantly higher in the same region. These results do not agree with the latitudinal rule applied to beta diversity (see Koleff et al. 2003, Soininen et al. 2017), at least for these freshwater ecosystems and at this spatial extent. Thus, it seems that the differences in gamma diversity across regions are mainly related to differences in alpha diversity, not beta diversity, in temporary ponds.

Environmental heterogeneity is considered a major mechanism generating differences in beta diversity (e.g. Melo et al. 2009), even reversing beta diversity latitudinal gradients (Alahuhta et al. 2017). The absence of differences in beta diversity in these two latitudinally distant set of ponds, in contrast to the expected higher beta diversity in the tropics, could be explained by no observed major differences in environmental heterogeneity between regions or by the higher limnological heterogeneity in the mediterranean ponds. However, the role of environmental heterogeneity can be masked by other processes (Heino et al. 2013). Connectivity may be an important explanation for these results. In a drier terrestrial matrix, mediterranean ponds can harbour more isolated communities than tropical ponds, which are often more hydrologically connected or homogenised by seasonal strong precipitation events (Thomaz et al. 2007; Rojo et al. 2016; Brasil et al. 2020). On the other hand, stronger dispersal barriers (Janzen 1967) or small species distributions (MacArthur 1972; Rapoport 1975) can lead to higher beta diversity in the tropics. Thus, a combination of different homogenising and heterogenising processes could lead to similar beta diversities in both studied sets of ponds, at least in freshwater organisms.

Spatial beta diversity shows significant decline with time in most of the groups, with lower dissimilarities between ponds during the second or the third sampling periods. This decline is especially consistent in the tropical organisms, suggesting certain metacommunity homogenization, stronger in the tropics than in the mediterranean ponds, during the rainy season (Thomaz et al. 2007). This is supported by the higher (but not significant) environmental heterogeneity during the first sampling period in both regions. However, deviances explained by this temporal variable are very low, and regional-seasonal interactions are generally not significant.

Temporal variation is not different betweeen the two regions

Temporal variability in alpha and beta diversities at the pond level did not differ between biogeographic regions in most groups, suggesting that temporal changes in each local community are similar in tropical and mediterranean ponds. In other words, if there are purely temporal effects or time-dependent environmental effects driving changes in each local community, they are equally intense in both regions. Our results, therefore, do not support the findings by Liang et al. (2015) on higher species turnover at lower latitudes, but may agree more with those of Nunes et al. (2020), who found no significant differences in temporal beta diversity in ant metacommunities at different altitudes (which could be somewhat analogous to latitudinal gradients). Therefore, differences in temporal variability in diversity between sets of ponds are not clearly observed. Although each region experiences different types of seasonal variation, with wider temperature seasonality in temperate regions and wider precipitation seasonality in tropical regions (MacArthur 1972; Fick and Hickmans 2017; Olmo et al. 2021), there are no overall differences in temporal environmental heterogeneity.

Biological diversity across taxa

Every studied group of organisms does not strictly follow the patterns described above, and some of them deserve mention apart. Among all the groups, only mediterranean microinvertebrates matched or exceeded the local species richness observed in tropical ponds and, together with phytoplankton, also gamma diversity, particularly in the mid or late hydroperiod. This has already been discussed for cladocerans (Dumont 1994), the most abundant branchiopod group. It is possible that the generally higher macroinvertebrate species richness in tropical ponds, and the more recurring presence of fish, may cause a top-down effect, reducing the planktonic microcrustacean diversity in tropical ponds (Ferreira et al. 2018). Regarding temporal variation in alpha diversity, bacteria and archaea of mediterranean ponds show a decreasing trend in alpha diversity across time with increasing temperatures through the hydroperiod, as also found by Parain et al. (2019), maybe related to competition effects (Zeng et al. 2019). Contrarily, both mediterranean micro- and macroinvertebrates had higher alpha diversity in the late hydroperiod. Winter temperatures may be a harsh enough environmental condition to limit species hatching, dispersal and survival in temperate areas, originating an increase in alpha diversity as air and water temperature rise (Rosset et al. 2010). Indeed, the sampling campaigns in our mediterranean ponds survey started with lower temperatures in winter and ended in the warmer late spring. The pattern was somehow inverted for tropical ponds, with increasing alpha diversity in prokaryotic organisms through the hydroperiod, and decreasing gamma diversity for invertebrates. Perhaps in this region the flooding events allowed rapidly growing bacteria and archaea to disperse and colonize wide areas without excluding competing species, but invertebrates may have suffered from growing populations of predators or dilution effects.

Spatial beta diversity was heterogenous across groups of organisms. While higher beta diversity in mediterranean invertebrates could be related with more isolation compared to the homogenized tropical communities (Brasil et al. 2020), higher beta diversity in tropical bacteria and amphibia could be related to fast growth coupled to high dispersal rates preventing competitive exclusion in the former (Zeng et al. 2019) or to smaller geographic ranges in the later (Whitton et al. 2012). In addition, we found the strongest decay of spatial beta diversity through time in macroinvertebrates. Higher dispersal ability (or efficiency) in active dispersers can lead to inter-season dispersal processes that produce certain metacommunity homogenization in late phases of the hydroperiod (Williams et al. 2007; Csabai et al. 2012). Species replacement was significantly higher in mediterranean macroinvertebrates, suggesting that mediterranean ponds harbour more unique macroinvertebrate communities, maybe related to stronger limnological differences between ponds. On the other hand, tropical bacteria and mediterranean microinvertebrates had higher richness difference, so that the species composition of ponds in these cases tend to be subsets of the richest ponds. Amphibians showed higher species replacement in the tropics, while richness differences were stronger in the mediterranean ponds. Even though low gamma diversity in mediterranean amphibians can favour nested patterns, Baselga et al. (2012) linked similar results to historical events. These authors related higher richness difference in temperate regions with defaunation affected by glaciations or desertification. In contrast, higher replacement in the tropics would be a sign of speciation and Pleistocene refugia, under more humid conditions.

Regarding local variability in biological diversity, variation in species richness was higher only in the macroinvertebrates of mediterranean ponds. This points to larger fluctuations in species richness due to patch colonization in the mid and late hydroperiods (Williams et al. 2007). In contrast, local communities of smaller organisms are highly influenced by egg-bank hatching and historical processes (Castillo-Escrivà et al. 2017), or they may undergo fluctuations that cannot be detected at the studied temporal scale. Contrarily, dispersal limitation modullated by connectivity shifts and dispersal barriers must be less variable in the studied tropical system. Finally, only amphibians and bacteria had significantly higher temporal beta diversity (either total beta diversity or the richness difference component, respectively) in the tropical ponds, suggesting faster succession or perhaps certain competitive exclusion in these tropical groups (Liang et al. 2015; Zeng et al. 2019).

CONCLUSIONS

Unlike meta-analyses, this research design, with different taxa being surveyed over the same time period in different regions, with the same methodology and similar sample coverages, has been successfully able to disentangle the relationship between the three components of diversity between regions at distant latitudes. Consistent with the longstanding view in the literature, the gamma diversity of temporary ponds was higher at lower latitudes, but these differences in gamma diversity across regions were mainly related to differences in alpha diversity, not spatial beta diversity, which did not differ between regions. In addition, spatial beta diversity was higher in the early hydroperiod in both regions, although this temporal effect was weak. Finally, both regions were similarly variable in terms of diversity and environmental heterogeneity through time. Thus, latitudinal differences in gamma diversity are not related to temporal but to spatial variation in diversity, specifically in alpha, not beta diversity.

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DISCUSIÓN GENERAL

A continuación, se compararán los resultados obtenidos en esta tesis en su conjunto. Primero se verá cómo los diferentes procesos ambientales, espaciales y temporales estructuran las metacomunidades de charcas temporales de ambientes tropicales y mediterráneos. Después, se comparará el efecto de estos mismos procesos en la organización de los diferentes grupos taxonómicos estudiados. Finalmente, se discutirán las limitaciones asociadas a esta tesis y se plantean futuras investigaciones que puedan derivarse de los resultados aquí obtenidos.

AMBIENTE, ESPACIO Y TIEMPO EN LA ORGANIZACIÓN DE LAS METACOMUNIDADES DE CHARCAS TEMPORALES TROPICALES Y MEDITERRÁNEAS

Los efectos ambientales son los principales procesos estructuradores de las metacomunidades, especialmente en las charcas mediterráneas

A lo largo de esta tesis hemos estudiado la contribución relativa de los efectos ambientales y espaciales (entre otros factores) en la estructuración de las metacomunidades de diferentes grupos de organismos de charcas temporales. Los dos factores han tenido un papel importante en el ensamblado de las metacomunidades, de modo que la composición de las mismas es el resultado de una combinación de diversos procesos actuando con diferentes intensidades (Grönroos et al. 2013; Devercelli et al. 2016; Brown et al. 2017).

A grandes rasgos, los efectos ambientales (asociados generalmente a la selección ambiental; Cottenie 2005) son los más importantes en las metacomunidades de las charcas temporales estudiadas, especialmente en las mediterráneas. Este resultado es todavía más evidente teniendo en cuenta la fracción de varianza explicada por el ambiente espacialmente correlacionado (***Figura 1***, **Capítulos 2, 4-5**). Estos resultados contrastan con Heino et al. (2015), donde se proponía que la estructura de las metacomunidades de charcas temporales estaría principalmente controlada por efectos espaciales (interpretados como limitación dispersiva). Sin embargo, y en consonancia con nuestros resultados, existe una extensa literatura que apoya este rol principal del ambiente frente al espacio en múltiples taxones de ecosistemas acuáticos (e.g. Cottenie et al. 2003; Souffreau et al. 2015; Rojo et al. 2016; Castillo-Escrivà et al. 2017a; Castillo-Escrivà et al. 2017b).

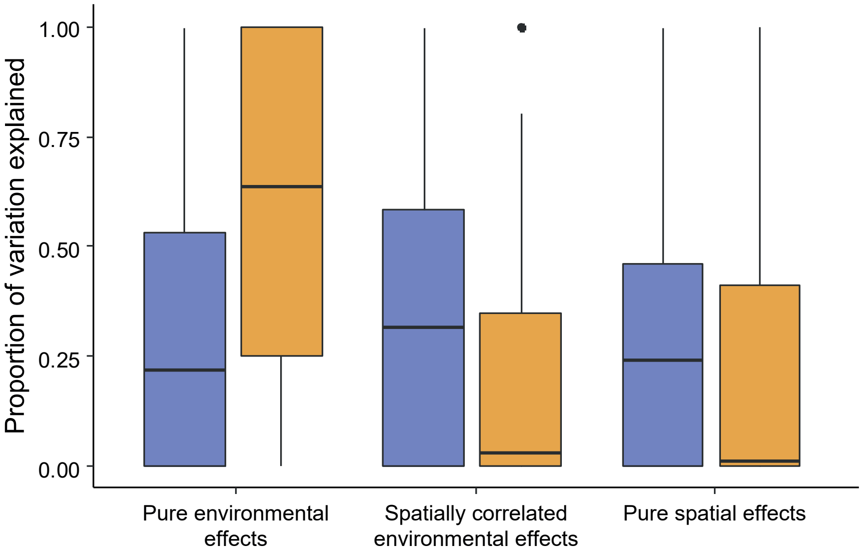

Figura 1: Proporción relativa de varianza explicada por los efectos ambientales puros ((E|S)/(E+S)), espaciales puros ((S|E)/(E+S)) y ambientales espacialmente estructurados ((E∩S)/(E+S)). En azul, los resultados para las metacomunidades tropicales y, en naranja, los resultados para la metacomunidad mediterránea. Datos procedentes de los Capítulos 2, 4-5.

La fracción de varianza explicada por el ambiente independiente del espacio es generalmente mayor en la metacomunidad mediterránea que en las tropicales (***Figura 1*****, Capítulos 2, 4-5**). Esto ha sido previamente descrito tanto en ecosistemas terrestres (Myers et al. 2013) como en acuáticos (Soffreau et al. 2005). Entre los procesos responsables de estos patrones cabe destacar las diferencias en heterogeneidad ambiental entre las dos regiones (Ai et al. 2013). La mayor heterogeneidad, al menos limnológica, de la metacomunidad mediterránea sobre la tropical es comentada en detalle en el **Capítulo 3**. Estos amplios gradientes ambientales dan lugar a diferencias entre charcas que generan diversidad de nichos ecológicos. De este modo, a mayor heterogeneidad ambiental, mayor diversidad de especies que pueden coexistir en una misma metacomunidad, incrementándose la respuesta al ambiente caracterizado en el estudio (Leibold y Chase 2018). Estos resultados deben ser interpretados con cautela, ya que los residuos constituyen una importante fracción de la varianza de la metacomunidad. Aunque existen procesos estocásticos estructurando las metacomunidades, que pueden ser bastante importantes en el caso de las charcas temporales (Jeffries 1989), los residuos también engloban la variación ambiental no medida. En esta variación no medida se incluyen las interacciones bióticas, las cuales pueden ser elementos clave en la estructura de las metacomunidades (García-Girón et al. 2020). Además, el papel de estas interacciones bióticas podría ser especialmente intenso en los trópicos, donde la depredación, la competencia o el mutualismo tienen un papel más relevante en las dinámicas poblacionales que en latitudes altas (Schemske et al. 2009; Roslin et al. 2017).

Por otro lado, la heterogeneidad ambiental entre parches también puede generar heterogeneidad de comunidades locales (Larkin 2018; Fernández-Aláez et al. 2020). Si dos parches de la metacomunidad son ambientalmente muy distintos, las comunidades locales adaptadas a esos ambientes serán más diferentes que si los dos parches son ambientalmente similares. Esta disimilitud entre parches, o diversidad beta, al igual que la diversidad local (alfa) y regional (gamma), puede estar correlacionada negativamente con la latitud, siendo por lo general mayor en las regiones tropicales que en regiones templadas (Hillebrand 2004; García et al. 2007; Qian et al. 2012). La elevada heterogeneidad limnológica en la metacomunidad mediterránea, en comparación con la tropical, puede tener un efecto compensatorio con otros procesos que permita explicar los valores similares de diversidad beta en ambas metacomunidades (**Capítulo 6**), llegando incluso a confrontar reglas macroecológicas bien establecidas como el gradiente latitudinal de biodiversidad, particularmente en el caso de la diversidad beta.

La heterogeneidad climática describía amplios patrones espaciales, lo cual fue más evidente en la región tropical que en la mediterránea. (**Capítulo 3**). Esto podría ser la causa de mayores efectos ambientales espacialmente estructurados en las charcas tropicales (***Figura 1,*** **Capítulos 2, 4-5**). Los trópicos muestran un ambiente, especialmente en lo relativo al clima, más espacialmente parcheado que en las regiones templadas (Hawkins y Diniz-Filho 2004), con especies distribuidas en áreas menores (Rapoport 1975). Estos patrones son los que pueden dar lugar a un papel mayor, en los trópicos, del ambiente espacialmente solapado. Por el contrario, esta porción de la varianza representa una fracción generalmente pequeña en la metacomunidad mediterránea, sugiriendo un papel pequeño del ambiente regional.

En resumen, la selección ambiental parece ser el principal proceso medido (obviando el papel de la deriva ecológica), aunque no el único, estructurando las metacomunidades de charcas temporales. Este proceso, parece más relevante en la metacomunidad mediterránea que en las tropicales, debido a una mayor heterogeneidad limnológica y/o a una menor redundancia ecológica. Por el contrario, los procesos ambientales climáticos, a escalas espaciales mayores que la local, parecen actuar con mayor fuerza en los trópicos.

Los efectos espaciales son esenciales, pero más fuertes en las metacomunidades tropicales.

Tal y como predice la teoría de metacomunidades (Leibold y Chase 2018), los efectos espaciales puros (a menudo asociados a procesos dispersivos; Cottenie 2005) son fundamentales en la estructura de las metacomunidades

(**Capítulos 2, 4-5**). Sin embargo, estos efectos espaciales parecen ser proporcionalmente más intensos en las metacomunidades tropicales (**Capítulos 2, 4-5**). En un primer momento hipotetizamos que los efectos espaciales serían más fuertes en la metacomunidad mediterránea, ya que un mayor aislamiento de los parches en la matriz terrestre daría lugar a una mayor limitación dispersiva (Heino et al. 2015). Además, también hipotetizábamos que las metacomunidades tropicales podrían estar muy homogeneizadas por los aumentos en la conectividad provocados por las intensas lluvias estacionales y, con ellos, efectos de masa que hicieran desaparecer los patrones espaciales (Thomaz et al. 2007; Fernandes et al. 2014; Heino et al. 2015; Brasil et al. 2020). Por otro lado, es posible que el aumento de la conectividad durante las lluvias estacionales no conecte la totalidad de la metacomunidad, eliminando así los efectos espaciales, sino que aumente la conectividad entre parches cercanos, provocando su homogeneización y generando patrones espaciales entre grupos de charcas (Heino et al. 2015).

En este sentido, encontramos el patrón opuesto al esperado (**Capítulos 2, 4-5**), con mayores efectos espaciales puros (independientes del ambiente) en la metacomunidad tropical que en la mediterránea. A lo largo de esta tesis se han expuesto varios procesos que podrían dar lugar a patrones espaciales relacionados con la limitación dispersiva. Por un lado, la distribución de las especies puede estar limitada por la orografía, la cual es una barrera dispersiva más fuerte en los trópicos que en las zonas templadas (las montañas son "más altas" en los trópicos; Janzen 1967). Al estar adaptadas a condiciones climáticas temporalmente más homogéneas (MacArthur 1972), la distribución de las especies en los trópicos está más restringida por variaciones climáticas altitudinales. Este parece ser el caso de la metacomunidad tropical estudiada, cuyas comunidades locales están separadas por la Gran Divisoria (cordillera volcánica que, en el continente americano, separa la vertiente pacífica de la atlántica), separando los charcas en dos grandes vertientes. Sin embargo, las especies de climas templados, adaptadas a rangos de temperaturas más amplios, deben de encontrar menores dificultades en su dispersión a través de barreras orográficas. En el caso de la metacomunidad mediterránea, aunque los sistemas Ibérico y Bético tienen importantes implicaciones biogeográficas, no parecen tener una influencia tan fuerte como en la metacomunidad tropical aquí estudiada.

Finalmente, y no menos importante, los rangos de distribución de las especies, probablemente debido a procesos de extinción (MacArthur 1972), son más pequeños en los trópicos (Rapoport 1972). Esto puede generar patrones espaciales aparentemente independientes del ambiente que den lugar a mayores proporciones de variación explicadas por el espacio puro. Los valores de diversidad beta similares en ambas metacomunidades (**Capítulo 6**), también sugieren que la limitación dispersiva, la cual daría lugar a mayor diversidad beta (Mouquet y Loreau 2003), no es el único o principal proceso detrás de los fuertes efectos espaciales encontrados en la metacomunidad tropical. Sin embargo, una mayor fragmentación del hábitat, lo que da lugar a limitaciones dispersivas y, eventualmente, puede traducirse en efectos espaciales (como sucede en la metacomunidad tropical), puede reducir la importancia de los procesos selectivos (efectos ambientales; Sonnier et al. 2020).

No obstante, estos resultados también deben ser interpretados con cautela. De la misma forma que los residuos pueden enmascarar efectos ambientales no medidos, los efectos espaciales puros pueden ocultar efectos ambientales espacialmente estructurados y no medidos (Gilbert y Bennet 2010; Smith y Lindholm 2010). De este modo, si las interacciones bióticas, por ejemplo, presentaran patrones espaciales, la proporción explicada por el ambiente espacialmente estructurado aumentaría en detrimento de la fracción espacial pura (Livingston et al. 2017)

Incorporando el tiempo en el estudio de metacomunidades

La mayor parte de los estudios empíricos sobre metacomunidades son estudios puramente espaciales, basados en datos de campo de un único evento de muestreo. El efecto del tiempo, obtenido por lo general estudiando cómo varían los efectos ambientales y espaciales a lo largo de una serie temporal (e.g. Rojo et al. 2016; Gomes-Mello et al. 2021), da lugar a resultados muy dispares entre diferentes momentos en el tiempo (**Capítulos 2,5**). Esta tesis refuerza la idea de que incorporar el tiempo es necesario para obtener conclusiones más robustas sobre el funcionamiento de sistemas tan dinámicos como pueden ser las metacomunidades acuáticas (Antón-Pardo et al. 2016; Benito et al. 2019; Cañedo-Argüelles et al. 2020), en este caso de charcas temporales.

Por otro lado, en el **Capítulo 5** (no así en el **Capítulo 3**) pudimos observar cómo disminuye la proporción de varianza explicada por el ambiente (mayormente abiótico) a lo largo del hidroperiodo. Esto sugiere que la selección ambiental, al menos por parte del ambiente medido, pierde relevancia con el tiempo, lo que podría estar relacionado con un aumento de la importancia de las interacciones bióticas en la estructura de las metacomunidades (García-Girón et al. 2020). Existe un ligero aumento de los efectos espaciales con el tiempo (en la metacomunidad mediterránea al menos; **Capítulo 5**), acompañado de una pequeña disminución de la diversidad beta (**Capítulo 6**). Estos resultados podrían indicar procesos dispersivos (Cottenie et al. 2005; Thomaz et al. 2007), probablemente entre localidades cercanas, manteniendo patrones espaciales de la metacomunidad pero reduciendo las diferencias entre algunas localidades. Pero también podría estar relacionado con que la variabilidad ambiental no medida podría reducir la fracción espacial pura en favor del ambiente espacialmente estructurado (Livingston et al. 2017).

Además de estudiar la variación de las fracciones ambiental y espacial en la estructura de la metacomunidad, pocos trabajos han incluido el tiempo *per se* como una variable predictora a considerar (e.g. Padial et al. 2014; Castillo-Escrivà et al. 2017b; Bortolini et al. 2019). Considerando una escala temporal pequeña (el año hidrológico; Angeler et al. 2013) encontramos que los efectos temporales puros (independientes del ambiente y el espacio) son importantes elementos estructurando las metacomunidades de charcas temporales (**Capítulos 2,5**), pudiendo llegar a ser incluso tan importantes como los efectos ambientales puros (**Capítulo 5**). Estos efectos temporales pueden constituir la principal fracción de varianza explicada para algunos grupos de organismos concretos (Bortolini et al. 2019; Wu et al. 2017). Los efectos temporales puros constituyen proporciones de varianza explicada mayores en la metacomunidades tropicales que en las mediterráneas (**Capítulo 5**), lo cual no se traduce en diferencias en variabilidad temporal en la diversidad (alfa y beta) en cada localidad de ambas regiones (**Capítulo 6**; Alves-de-Souza et al. 2017). Por tanto, a pesar de la teóricamente menor variabilidad ambiental en los trópicos a lo largo del tiempo (MacArthur 1972; pero no observada en el **Capítulo 6**), las metacomunidades no parecen ser temporalmente más variables en una región u otra. Quizás una mayor dinámica biótica en los sistemas tropicales compense los mayores cambios temporales que se dan en las metacomunidades templadas debidos a la dinámica ambiental.

La inclusión del tiempo como una variable predictora, además, reduce la proporción de varianza no explicada, permitiendo obtener mejores descripciones de los procesos que estructuran la metacomunidad (Guzman et al. 2020). Son especialmente llamativas las diferencias en la proporción de explicación ambiental encontradas entre los dos métodos descritos en el **Capítulo 5**. Incluyendo el tiempo, es posible medir patrones espaciales que pasan desapercibidos al estudiar cada periodo de tiempo por separado. Por ejemplo, se podría detectar patrones espaciales generados por especies raras que aparecen únicamente en un solo sitio, o en sitios alejados, pero de forma sostenida en el tiempo. Así, el efecto de los endemismos o de las reducciones históricas en las áreas de distribución de las especies podría verse traducido en efectos espaciales.

EFECTOS AMBIENTALES, ESPACIALES Y TEMPORALES EN DIFERENTES ORGANISMOS

Teóricamente, la capacidad dispersiva está estrechamente relacionada con la intensidad con la que actúan los efectos ambientales y espaciales (Beisner et al. 2006). Mientras que la distribución de los organismos con elevadas capacidades dispersivas está más influenciada por factores ambientales que espaciales (siempre y cuando no se den efectos de masa), en las especies cuya distribución está limitada por sus capacidades dispersivas, su distribución estará más controlada por factores espaciales (Van der Gucht et al. 2007; Astorga et al. 2012; Padial et al. 2012). Los resultados expuestos en los **Capítulos 2, 4-5** no encajan con esta perspectiva teórica (como pasa en Schulz et al. 2012). De hecho, se encontraron efectos espaciales incluso en microorganismos, que tradicionalmente han sido descritos como cosmopolitas (Finlay 2002, pero no así en Fenchel et al. 2019).

Los resultados obtenidos por los trabajos arriba mencionados, y en otros discutidos en el **Capítulo 1** son relativamente similares a los encontrados en la metacomunidad mediterránea, con efectos ambientales puros generalmente mayores que los espaciales puros, a excepción de algunos grupos más variables, en los que pueden llegar a dominar los efectos espaciales puros (diatomeas, ostrácodos o macroinvertebrados; **Capítulo 4**). Sin embargo, estos patrones son más difusos o se presentan invertidos en las metacomunidades tropicales, o incluso llegan a desaparecer en la metacomunidad mediterránea al incorporar la variación temporal (**Capítulos 2, 4-5**). Estos resultados sugieren que los patrones propuestos por De Bie et al. (2012) pueden no ser patrones generales extrapolables a cualquier metacomunidad, sino que cada ecosistema o grupo de organismos podría tener una idiosincrasia propia a tener en cuenta (Soininen 2014; Perbiche-Neves et al. 2019; Pujoni et al. 2019). No obstante, independientemente de la capacidad dispersiva en particular de cada grupo de organismos estudiado en los **Capítulos 2, 4-5**, parece que en los organismos con dispersión activa el dominio de la componente espacial pura sobre la ambiental pura es más frecuente, sugiriendo una mayor limitación dispersiva (***Figura 2***), tal y como proponen De Bie et al. (2012).

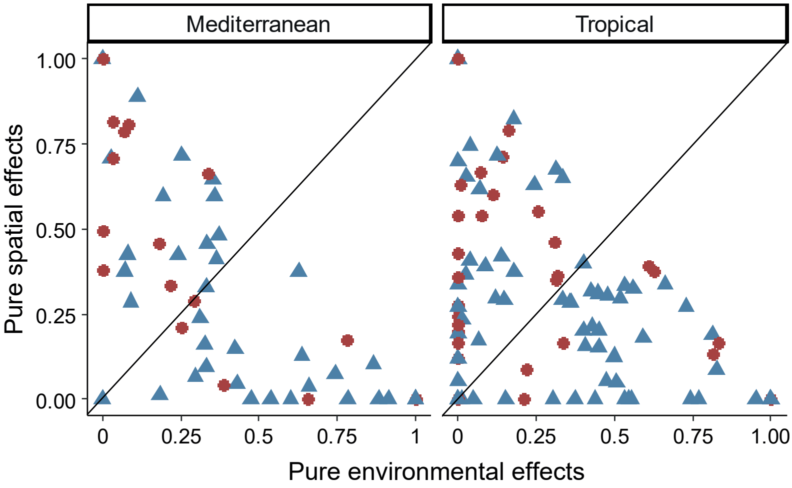

Figura 2: Relación entre la proporción relativa de varianza explicada por los efectos ambientales puros ((E|S)/(E+S)) y por los efectos espaciales puros ((S|E)/(E+S)), en grupos de organismos tropicales y mediterráneos. Los triángulos azules representan a los dispersores pasivos y los círculos granates a los dispersores activos. Datos de los Capítulos 3-5.

Sin embargo, sí observamos mayores efectos temporales en los organismos de mayor tamaño corporal (macroinvertebrados; **Capítulo 2**), sugiriendo que las especies con ciclos de vida largos (relacionado con la reproducción, senescencia, crecimiento poblacional, etc.; Brown et al. 2018) están más influenciados por dinámicas temporales. Este patrón es más claro en la región tropical que en la mediterránea (**Capítulo 5; *Figura 3***). Sin embargo, los organismos más grandes, los anfibios, con una longevidad tan alta que están presentes durante todo el hidroperiodo, presentan efectos temporales prácticamente nulos (Figura 3). Esto sugiere una relación unimodal entre los efectos temporales y el tamaño corporal, similar a la existente entre los efectos espaciales y la escala espacial o la capacidad dispersiva (Heino et al. 2015).

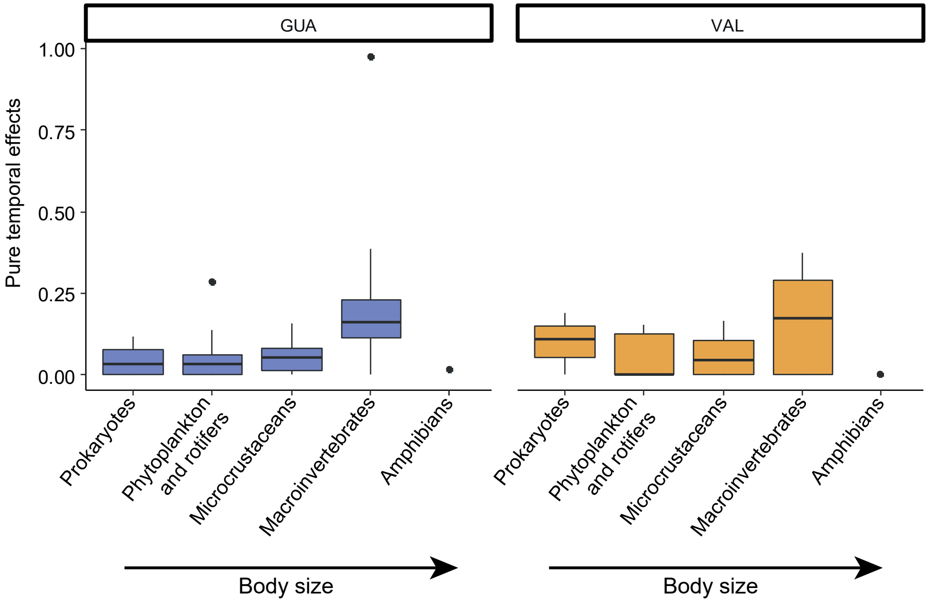

Figura 3: Proporción relativa de varianza explicada por los efectos temporales puros ((T|(E+S))/(E+S+T)) en grupos de organismos tropicales (azul) y mediterráneaos (naranja) con diferentes tamaños corporales. Datos de los Capítulos 3 y 5.

REFLEXIONES FINALES Y FUTURAS INVESTIGACIONES

En resumen, aunque la teoría de metacomunidades trata de explicar la distribución de las especies y la dinámica de sus poblaciones, englobando procesos que actúan a diferentes escalas espaciales, los trabajos de campo aún arrojan muchas incógnitas al respecto. Los efectos ambientales, espaciales, temporales y estocásticos son esenciales en la estructuración de las metacomunidades (Leibold y Chase 2018). Sin embargo, ciertos procesos, fundamentales para entender las dinámicas naturales, aún se encuentran pobremente estudiados, como son las interacciones bióticas, pudiendo esto influir en la infravaloración de los efectos ambientales (Livingston et al. 2017; García-Girón 2020). Por otro lado, el papel relativo del tiempo frente a los efectos ambientales y espaciales, aún está lejos de esclarecerse, teniendo en cuenta la amplia escala espacial y la reducida escala temporal utilizadas (Castillo-Escrivà et al. 2020). Además, sería necesaria la inclusión de más metacomunidades tropicales y mediterráneas (o templadas en general) para poder obtener patrones generales aplicables a regiones biogeográficas tan diferentes.

Aun así, en esta tesis se constata, a diferencia de otros estudios (e.g. De Bie et al. 2012), que la estructuración de las metacomunidades es muy variable en función de los grupos taxonómicos y que existen patrones más claros en función de las regiones estudiadas, estableciendo varias ideas a contrastar en posteriores estudios. Por un lado, la inclusión del tiempo es esencial para conocer mejor cómo actúan los procesos que estructuran las metacomunidades (Guzman et al. 2021; Gomes-Mello et al. 2021). Incluyendo un gradiente temporal mayor, incorporando incluso varios años hidrológicos separados por periodos de secado, permitiría llegar a conocer mejor cómo se organizan las metacomunidades de charcas temporales (Angeler et al. 2013). Además, al comparar entre regiones, se han establecido ciertos patrones, relacionados con el papel más relevante del ambiente en la metacomunidad mediterránea, y del espacio en la metacomunidad tropical (similares a Myers et al. 2012; Souffreau et al. 2015), que deberían ser contrastados en posteriores estudios. Finalmente, es necesario encontrar la forma de estimar el papel de las interacciones bióticas (i.e. mutualismo, parasitismo, depredación, competencia; García-Girón et al. 2020; Thompson et al. 2020), de forma que estos resultados pudieran ser reanalizados y reinterpretados con nuevos métodos analíticos. En cualquier caso, esta tesis y futuros estudios relacionados permitirán comprender el papel fundamental de los procesos que estructuran las metacomunidades de diferentes ecosistemas, grupos de organismos o regiones biogeográficas. Este conocimiento es, y será, fundamental para poder llevar a cabo estrategias de conservación efectivas ante la crisis ecológica actual, con importantes cambios ambientales derivados del cambio climático, fragmentación de los ecosistemas e invasiones biológicas.

CONCLUSIONES

1. A pesar del mayor esfuerzo de investigación sobre metacomunidades en regiones templadas que en tropicales, hemos constatado que existe gran interés y una creciente bibliografía en relación al estudio de estas últimas. Los trabajos llevados a cabo en sistemas tropicales demuestran un fuerte control ambiental. Por otro lado, las inundaciones periódicas durante la estación lluviosa tienen una fuerte relación con los efectos espaciales y la disminución de la diversidad beta.

2. La heterogeneidad ambiental, tal y como la hemos estimado en las regiones estudiadas, ya sea en la tropical, en Costa rica, o en las mediterráneas, en España y Chile, es similar. Sin embargo, los dos conjuntos de charcas mediterráneas muestran más heterogeneidad en los parámetros físico-químicos del agua, mientras que en el conjunto de lagunas tropicales detectamos una mayor heterogeneidad climática, principalmente debida a la variabilidad en las precipitaciones.
3. Además de las evidentes diferencias climáticas, el conjunto de charcas tropicales, en Costa Rica, difería respecto a ambos conjuntos de charcas mediterráneas, situadas en España y Chile, sobre todo en algunas variables ambientales como la conductividad, oxígeno disuelto, cobertura de vegetación acuática o los usos del suelo entorno a las charcas.
4. A pesar de sus similitudes, los dos conjuntos de charcas mediterráneas (en España y Chile) se diferenciaban entre ellos, sobre todo, en función de las coberturas vegetales o las concentraciones de nutrientes, al estar las charcas chilenas más impactadas que las españolas por actividades humanas como la agricultura o la ganadería.
5. La estructura de las metacomunidades de charcas temporales estudiadas, tanto las tropicales (en Costa Rica-Nicaragua, y en Costa Rica) como la mediterránea (en España), depende de efectos tanto ambientales como espaciales, pero también temporales, pudiendo estos ser tan importantes como los ambientales. Los efectos espaciales y ambientales son muy variables a lo largo del hidroperiodo.
6. Los efectos ambientales, puros o espacialmente estructurados, son generalmente los más importantes explicando la estructura de las metacomunidades estudiadas, aunque existe una elevada proporción de varianza que permanece sin explicar.
7. Los efectos ambientales puros son más importantes en la estructura de la metacomunidad mediterránea, situada en España, que en la tropical, en Costa Rica. Sin embargo, los efectos espaciales puros y el ambiente espacialmente estructurado son más importantes en la metacomunidad tropical. Este patrón se sostiene a lo largo del año hidrológico. El efecto del tiempo puro es ligeramente superior en la metacomunidad mediterránea.
8. No hemos detectado patrones claros en el papel de los efectos ambientales y espaciales en cuanto al tamaño corporal y habilidad dispersiva de los diferentes organismos estudiados. Sin embargo, en los sistemas tropicales se observan efectos ambientales algo mayores en los dispersores pasivos que en los activos. Las diferencias entre regiones señaladas en la conclusión anterior son más exacerbadas en los dispersores activos.
9. El papel de los efectos ambientales puros decae con el tiempo, a lo

largo del hidroperiodo, tanto en la metacomunidad tropical de Costa Rica como la mediterránea de España.

10. Los organismos de mayor tamaño corporal (macroinvertebrados) presentan, en general, efectos temporales mayores. Este patrón es más claro en los organismos tropicales (tanto de la metacomunidad de Costa Rica-Nicaragua como la de Costa Rica) que en los mediterráneos de la metacomunidad española.
11. La diversidad alfa es generalmente mayor en el conjunto de charcas tropicales de Costa Rica que en las charcas estudiadas en España. Este patrón se cumple en todos los grupos taxonómicos salvo en los microinvertebrados al final del hidroperiodo.
12. La diversidad gamma es generalmente mayor en la metacomunidad tropical de Costa Rica que en la mediterránea de España. Esta mayor diversidad gamma está correlacionada con una mayor diversidad local (diversidad alfa), pero no con una mayor disimilitud entre parches (diversidad beta)
13. La variabilidad temporal de las diversidades alfa y beta de cada charca no difiere entre las metacomunidades de Costa Rica y de España, por lo que cada charca es similarmente variable con el tiempo en ambas regiones.

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Algunas de las charcas temporales mediterráneas muestreadas en España. De arriba a abajo, Balsa Silvestre (Alcublas, Valencia), Parque Natural de la Marjal de Pego-Oliva (Pego, Alicante) y lavajo de la Vía (Camporrobles, Valencia).

ANEXOS

MATERIALES SUPLEMENTARIOS

Capítulo 2: Environment and space rule, but time also matters for the organization of tropical pond metacommunities

Supplementary Table S1: Summary of the environmental characterization of the set of studied ponds, showing the number of occurrences for dummy variables and the mean, standard deviation (SD) and minimum and maximum values for numerical variables.

Variable	Occurrences	Mean	SD	Minimum	Maximum
Seasonal_hydroperiod	49	-	-	-	-
WaterOrigin(Rain)	51	-	-	-	-
WaterOrigin(Phreatic)	36	-	-	-	-
Livestock	42	-	-	-	-
Maximum_Depth (m)	-	1.4	0.5	0.7	2.8
Average_Depth (m)	-	0.7	0.3	0.1	1.5
Area (m^2)	-	550.3	1363.5	0.1	5369.5
Perimeter (m)	-	7721.3	13057.7	134	48139
Morphology	-	1.6	0.5	1	3.3
Altitude (m a.s.l.)	-	98.1	155	3.9	486
%MacrophyteCoverage	-	61.8	35.1	5	100
%HelophyteCoverage	-	66.4	32.7	0	100
Transparency (cm)	-	22.3	10.9	5	50
WaterTemperature (ºC)	-	28.7	3.3	16.8	36.2
pH	-	7.5	0.7	6.3	9.8
O_2 (mg/L)	-	3.9	2.3	0	12.6
Chlorophyll_A (µg/L)	-	11	15.7	0.1	88.9
TDS (mg/L)	-	602.6	1379.3	91.6	11424.8
Conductivity(mS/cm)	-	1	2.5	0.1	18.5
HCO^{-3} (meq/L)	-	2.1	1.1	0.1	5.4
Cl^- (meq/L)	-	4.5	13.3	0.1	101.4
SO_4^{-2} (meq/L)	-	0.8	1	0	9.5
Ca^{+2} (meq/L)	-	2.1	2.9	0.1	16.5
Mg^{+2} (meq/L)	-	2.3	6.5	0.2	51.7
Na^+ (meq/L)	-	8.2	32.4	0.1	282.6
K^+ (meq/L)	-	0.3	0.5	0	3.7
NO_3^- (meq/L)	-	0	0	0	0.2
NO_2^- (meq/L)	-	0	0	0	0
NH_4^+ (meq/L)	-	0	0	0	0
PO_4^{-3} (meq/L)	-	0	0	0	0
Alk/Ca^{+2}	-	1.8	1.1	0.1	4.9
$Alk/(Cl^-+SO_4^{-2})$	-	1.6	1.3	0	7.1
Cl^-/SO_4^{-2}	-	21.3	95	0.1	845.1
$(Ca^{+2}+Mg^{+2})/(Na^++K^+)$	-	1.6	1.1	0.2	6.6
NO_3^-/NO_2^-	-	24.2	17.5	0.3	145.8
NO_3^-/NH_4^+	-	5.2	5.8	0.5	30.2
Ca^{+2}/Mg^{+2}	-	1.8	0.9	0.3	5.2
%LandUse(LowGrass)	-	30.9	36.3	0	100
%LandUse(HighGrass)	-	15	26.1	0	84
%LandUse(Agricultural)	-	2.6	9.5	0	50.2
%LandUse(Scrub)	-	1.4	7.7	0	42.5
%LandUse(Forest)	-	50	34.1	0	100
%LandUse(Buildings)	-	0.2	0.5	0	2.5

***Supplementary Table S1*: Continued**

LandscapeHeterogenity	-	0.5	0.3	0	1.1
AnnualAverTemperature (ºC)	-	26.7	1.3	24	28
AnnualMaxTemperature (ºC)	-	34.6	1.7	31.3	36.8
AnnualMinTemp (ºC)	-	19.9	0.9	17.7	20.6
AnnualTempRange (ºC)	-	14.8	0.9	13.3	16.2
AnnualPrecipitation (mm)	-	1810.5	220	1349	2219
PrecipitationSeasonality	-	90.1	8.5	73	102
ECELS1	-	14	5.3	0	20
ECELS2	-	13.5	3.9	8	20
ECELS3	-	8	3.1	0	10
ECELS4	-	17	6.6	5	25
ECELS5	-	7.3	3.3	3	15
ECELStotal	-	59.8	14.8	31	90

Supplementary Table S2: List of organisms found, identified with the maximum taxonomic resolution when possible. Taxa marked with an asterisk (*) were not analyzed separatedly.

Group		Species
Phytoplankton	Chlorophyceae	*Actinastrum hantzschii* Lagerheim,1882
Phytoplankton	Chlorophyceae	*Amphikrikos minutissimus* Korshikov,1953
Phytoplankton	Chlorophyceae	*Ankistrodesmus gracilis* (Reins.) Korshikov, 1953
Phytoplankton	Chlorophyceae	*Ankistrodesmus* sp.
Phytoplankton	Chlorophyceae	*Ankistrodesmus spiralis* (Turner) Lemmermann, 1908
Phytoplankton	Chlorophyceae	*Botryococcus braunii* Kützing, 1849
Phytoplankton	Chlorophyceae	*Chlamydomonas* sp.
Phytoplankton	Chlorophyceae	*Chlorella* sp.
Phytoplankton	Chlorophyceae	*Chlorolobion glareosum* (Hindák) Komárek, 1979
Phytoplankton	Chlorophyceae	Chlorophyceae 1
Phytoplankton	Chlorophyceae	*Closteriopsis acicularis* (Smith) Belch. & Swale, 1962
Phytoplankton	Chlorophyceae	*Closterium aciculare* T.West, 1860
Phytoplankton	Chlorophyceae	*Closterium acutum* Brébisson in Ralfs, 1848
Phytoplankton	Chlorophyceae	*Closterium gracile* Brébisson ex Ralfs, 1848
Phytoplankton	Chlorophyceae	*Closterium kuetzingii* Brébisson, 1856
Phytoplankton	Chlorophyceae	*Closterium lineatum* Ehrenberg ex Ralfs, 1848
Phytoplankton	Chlorophyceae	*Closterium parvulum* Nägeli, 1849
Phytoplankton	Chlorophyceae	*Coelastrum astroideum* De Notaris, 1867
Phytoplankton	Chlorophyceae	*Coelastrum microporum* Nägeli, 1855
Phytoplankton	Chlorophyceae	*Coelastrum reticulatum* (P.A.Dangeard) Senn, 1899
Phytoplankton	Chlorophyceae	*Coelastrum* sp.
Phytoplankton	Chlorophyceae	*Coenocystis* sp.
Phytoplankton	Chlorophyceae	*Cosmarium pygmaeum* W.Archer, 1864
Phytoplankton	Chlorophyceae	*Cosmarium* sp.1
Phytoplankton	Chlorophyceae	*Cosmarium* sp.2
Phytoplankton	Chlorophyceae	*Cosmarium* sp.3
Phytoplankton	Chlorophyceae	*Crucigenia tetrapedia* (Kirchn.) W. & G.S. West, 1902
Phytoplankton	Chlorophyceae	*Crucigeniella apiculata* (Lemmermann) Komárek, 1974

***Supplementary Table S2*:** Continued

Phytoplankton	Chlorophyceae	*Crucigeniella crucifera* (Wolle) Komárek, 1974
Phytoplankton	Chlorophyceae	*Crucigeniella pulchra* (W. & G.S. West) Kom., 1974
Phytoplankton	Chlorophyceae	*Crucigeniella rectangularis* (Näg.) Komárek, 1974
Phytoplankton	Chlorophyceae	*Desmatractum indutum* (Geitler) Pascher, 1930
Phytoplankton	Chlorophyceae	*Dictyosphaerium ehrenbergianum* Nägeli, 1849
Phytoplankton	Chlorophyceae	*Dictyosphaerium pulchellum* H.C.Wood, 1873
Phytoplankton	Chlorophyceae	*Dictyosphaerium* sp.
Phytoplankton	Chlorophyceae	*Dictyosphaerium subsolitarium* Van Goor, 1924
Phytoplankton	Chlorophyceae	*Dictyosphaerium tetrachotomum* Printz, 1914
Phytoplankton	Chlorophyceae	*Didymocystis comasii* Komárek, 1983
Phytoplankton	Chlorophyceae	*Didymocystis inermis* (Fott) Fott, 1973
Phytoplankton	Chlorophyceae	*Didymocystis* sp.
Phytoplankton	Chlorophyceae	*Dimorphococcus lunatus* Braun, 1855
Phytoplankton	Chlorophyceae	*Euastrum* sp.
Phytoplankton	Chlorophyceae	*Euastrum verrucosum* Ehrenberg ex Ralfs, 1848
Phytoplankton	Chlorophyceae	*Eutetramorus* sp.
Phytoplankton	Chlorophyceae	*Franceia* sp.
Phytoplankton	Chlorophyceae	*Golenkinia radiata* Chodat, 1894
Phytoplankton	Chlorophyceae	*Golenkiniopsis chlorelloides* (J.W.G.Lund) Fott, 1981
Phytoplankton	Chlorophyceae	*Gonatozygon monotaenium* De Bary, 1856
Phytoplankton	Chlorophyceae	*Gonatozygon* sp.
Phytoplankton	Chlorophyceae	*Granulocystis helenae* Hindák, 1977
Phytoplankton	Chlorophyceae	*Granulocystopsis pseudocoronata* (Korshikov) Hindák, 1977
Phytoplankton	Chlorophyceae	*Kirchneriella contorta* (Schmidle) Bohlin, 1897
Phytoplankton	Chlorophyceae	*Kirchneriella irregularis* (Smith) Korshikov, 1953
Phytoplankton	Chlorophyceae	*Kirchneriella* sp.
Phytoplankton	Chlorophyceae	*Kirchneriella subcapitata* Korshikov, 1953
Phytoplankton	Chlorophyceae	*Lagerheimia balatonica* (Scherffel) Hindák,1978
Phytoplankton	Chlorophyceae	*Lagerheimia chodatii* C.Bernard, 1908
Phytoplankton	Chlorophyceae	*Lagerheimia ciliata* (Lagerheim) Chodat, 1895
Phytoplankton	Chlorophyceae	*Micrasterias radiosa* Ralfs, 1848
Phytoplankton	Chlorophyceae	*Monomastix* sp.

***Supplementary Table S2*:** Continued

Phytoplankton	Chlorophyceae	*Monoraphidium arcuatum* (Kors.) Hindák, 1970
Phytoplankton	Chlorophyceae	*Monoraphidium circinale* (Nyg.) Nygaard, 1979
Phytoplankton	Chlorophyceae	*Monoraphidium contortum* (Thur.) Komárková-Legnerová, 1969
Phytoplankton	Chlorophyceae	*Monoraphidium komarkovae* Nygaard, 1979
Phytoplankton	Chlorophyceae	*Monoraphidium minutum* (Näg.) Komárková-Legnerová, 1969
Phytoplankton	Chlorophyceae	*Monoraphidium tortile* (West) Komárková-Legnerová, 1969
Phytoplankton	Chlorophyceae	*Nephrochlamys subsolitaria* (West) Korshikov, 1953
Phytoplankton	Chlorophyceae	*Nephrocytium agard*hianum Nägeli, 1849
Phytoplankton	Chlorophyceae	*Nephroselmis olivacea* Stein, 1878
Phytoplankton	Chlorophyceae	*Oocystis lacustris* Chodat, 1897
Phytoplankton	Chlorophyceae	*Oocystis marssonii* Lemmermann, 1898
Phytoplankton	Chlorophyceae	*Pandorina morum* (Müller) Bory, 1824
Phytoplankton	Chlorophyceae	*Pediastrum simplex* Meyen, 1829
Phytoplankton	Chlorophyceae	*Pediastrum tetras* (Ehrenb.) Ralfs, 1844
Phytoplankton	Chlorophyceae	*Planctonema lauterbornii* Schmidle, 1903
Phytoplankton	Chlorophyceae	*Pleurotaenium* sp.
Phytoplankton	Chlorophyceae	*Pteromonas* sp.
Phytoplankton	Chlorophyceae	*Quadrigula* sp.
Phytoplankton	Chlorophyceae	*Scenedesmus aculeolatus* Reinsch, 1877
Phytoplankton	Chlorophyceae	*Scenedesmus acutus* Meyen, 1829
Phytoplankton	Chlorophyceae	*Scenedesmus bicaudatus* Dedusenko, 1925
Phytoplankton	Chlorophyceae	*Scenedesmus ecornis* (Ehrenb.) Chodat, 1926
Phytoplankton	Chlorophyceae	*Scenedesmus granulatus* West & G.S.West, 1897
Phytoplankton	Chlorophyceae	*Scenedesmus intermedius* Chodat, 1926
Phytoplankton	Chlorophyceae	*Scenedesmus obtusus* Meyen, 1829
Phytoplankton	Chlorophyceae	*Scenedesmus ovalternus* Chodat, 1926
Phytoplankton	Chlorophyceae	*Scenedesmus praetervisus* Chodat, 1926
Phytoplankton	Chlorophyceae	*Scenedesmus pseudoarmatus* Hortobágyi, 1969
Phytoplankton	Chlorophyceae	*Scenedesmus quadricauda* (Turp.) Brébisson, 1835
Phytoplankton	Chlorophyceae	*Scenedesmus regularis* Svirenko, 1924

Supplementary Table S2: Continued

Phytoplankton	Chlorophyceae	*Scenedesmus semipulcher* Hortobágyi, 1960
Phytoplankton	Chlorophyceae	*Scenedesmus sempervirens* Chodat, 1913
Phytoplankton	Chlorophyceae	*Scenedesmus sooi* Hortobágyi, 1954
Phytoplankton	Chlorophyceae	*Scenedesmus* sp.
Phytoplankton	Chlorophyceae	*Scenedesmus verrucosus* Roll, 1925
Phytoplankton	Chlorophyceae	*Schroederia* sp.
Phytoplankton	Chlorophyceae	*Sorastum spinulosum* Näg., 1849
Phytoplankton	Chlorophyceae	*Spermatozopsis exsultans* Korshikov, 1913
Phytoplankton	Chlorophyceae	*Sphaerellopsis* sp.
Phytoplankton	Chlorophyceae	*Sphaerocystis* sp.
Phytoplankton	Chlorophyceae	*Staurastrum* sp.
Phytoplankton	Chlorophyceae	*Staurodesmus* sp.
Phytoplankton	Chlorophyceae	*Tetrachlorella* sp.
Phytoplankton	Chlorophyceae	*Tetraedron caudatum* (Corda) Hansgirg, 1888
Phytoplankton	Chlorophyceae	*Tetraedron minimum* (Braun) Hansgirg, 1888
Phytoplankton	Chlorophyceae	*Tetraedron triangulare* Korshikov, 1953
Phytoplankton	Chlorophyceae	*Tetraselmis* sp.
Phytoplankton	Chlorophyceae	*Tetrastrum heteracanthum* (Nordstedt) Chodat, 1895
Phytoplankton	Chlorophyceae	*Tetrastrum punctatum* (Schmidle) Ahlstrom & Tiffany, 1934
Phytoplankton	Chlorophyceae	*Tetrastrum triangulare* (Chod.) Komárek, 1974
Phytoplankton	Chlorophyceae	*Treubaria quadrispina* (G.M.Smith) Fott & Kovácik, 1975
Phytoplankton	Chlorophyceae	*Treubaria schmidlei* (Schröder) Fott & Kovácik, 1975
Phytoplankton	Chlorophyceae	*Treubaria triappendiculata* C.Bernard, 1908
Phytoplankton	Chlorophyceae	*Xanthidium* sp.
Phytoplankton	Cyanobacteria	*Anabaena* sp.
Phytoplankton	Cyanobacteria	*Anabaenopsis elenkinii* V.V.Miller, 1923
Phytoplankton	Cyanobacteria	*Aphanizomenon* sp.
Phytoplankton	Cyanobacteria	*Aphanocapsa elachista* West & West, 1894
Phytoplankton	Cyanobacteria	*Aphanocapsa incerta* (Lemm.) Cronberg & Komárek, 1994
Phytoplankton	Cyanobacteria	*Aphanocapsa* sp.
Phytoplankton	Cyanobacteria	*Aphanothece clathrata* West & G.S.West, 1906
Phytoplankton	Cyanobacteria	*Aphanothece* sp.

***Supplementary Table S2*:** Continued

Phytoplankton	Cyanobacteria	*Aphanothece stagnina* (Sprengel) A.Braun, 1863
Phytoplankton	Cyanobacteria	*Chroococcal* sp.
Phytoplankton	Cyanobacteria	*Chroococcus minutus* (Kütz.) Nägeli, 1849
Phytoplankton	Cyanobacteria	*Chroococcus* sp.
Phytoplankton	Cyanobacteria	*Chroococcus turgidus* (Kützing) Nägeli, 1849
Phytoplankton	Cyanobacteria	*Cylindrospermum* sp.
Phytoplankton	Cyanobacteria	*Geitlerinema acutissimum* (Kufferath) Anagnostidis, 1989
Phytoplankton	Cyanobacteria	*Geitlerinema amphibium* (Agardh ex Gomont) Anagnostidis, 1989
Phytoplankton	Cyanobacteria	*Geitlerinema* sp.
Phytoplankton	Cyanobacteria	*Glaucospira* sp.
Phytoplankton	Cyanobacteria	*Jaaginema geminatum* (Schwabe ex Gomont) Anagnostidis & Komárek, 1988
Phytoplankton	Cyanobacteria	*Jaaginema* sp.
Phytoplankton	Cyanobacteria	*Lyngbya* sp.
Phytoplankton	Cyanobacteria	*Merismopedia marssonii* Lemmermann, 1900
Phytoplankton	Cyanobacteria	*Merismopedia punctata* Meyen, 1839
Phytoplankton	Cyanobacteria	*Merismopedia tennuissima* Lemmermann, 1898
Phytoplankton	Cyanobacteria	*Microcystis* sp.
Phytoplankton	Cyanobacteria	*Oscillatoria ornata* Kützing ex Gomont, 1892
Phytoplankton	Cyanobacteria	*Oscillatoria* sp.
Phytoplankton	Cyanobacteria	*Oscillatoria subbrevis* Schmidle, 1901
Phytoplankton	Cyanobacteria	*Oscillatoria tenuis* Agardh ex Gomont, 1892
Phytoplankton	Cyanobacteria	Oscillatorial 1
Phytoplankton	Cyanobacteria	Oscillatorial 2
Phytoplankton	Cyanobacteria	Oscillatorial 3
Phytoplankton	Cyanobacteria	*Pannus* sp.
Phytoplankton	Cyanobacteria	*Phormidium* sp.
Phytoplankton	Cyanobacteria	*Planktolyngbya* sp.
Phytoplankton	Cyanobacteria	*Planktothrix* sp.
Phytoplankton	Cyanobacteria	*Pseudanabaena amphigranulata* (Goor) Anagnostidis, 2001
Phytoplankton	Cyanobacteria	*Pseudanabaena catenata* Lauterborn, 1915

***Supplementary Table S2*:** Continued

Phytoplankton	Cyanobacteria	*Pseudanabaena papillaterminata* (Kiselev) Kukk, 1959
Phytoplankton	Cyanobacteria	*Pseudanabaena* sp.
Phytoplankton	Cyanobacteria	*Spirulina* sp.
Phytoplankton	Cyanobacteria	*Synechococcus* sp.
Phytoplankton	Cyanobacteria	*Synechocystis aquatilis* Sauvageau, 1892
Phytoplankton	Cyanobacteria	*Woronichinia* sp.
Phytoplankton	Diatomea	*Acanthoceras zachariasii* (Brun) Simonsen, 1979
Phytoplankton	Diatomea	*Achnanthes catenata* Bily & Marvan, 1959
Phytoplankton	Diatomea	*Achnanthes hungarica* (Grunow) Grunow, 1880
Phytoplankton	Diatomea	*Achnanthes lanceolata* (Bréb.) Grunow, 1880
Phytoplankton	Diatomea	*Achnanthes* sp.
Phytoplankton	Diatomea	*Amphipleura pellucida* (Kützing) Kützing, 1844
Phytoplankton	Diatomea	*Amphora* sp.
Phytoplankton	Diatomea	*Aulacoseira granulata* (Ehr.) Simonsen, 1979
Phytoplankton	Diatomea	*Aulacoseira granulata* var. *angustissima* (Müller) Simonsen, 1979
Phytoplankton	Diatomea	*Aulacoseira* sp.
Phytoplankton	Diatomea	*Bacillaria paxillifera* (O.F.Müller) T.Marsson, 1901
Phytoplankton	Diatomea	*Caloneis* sp.
Phytoplankton	Diatomea	*Cocconeis placentula* Ehrenberg, 1838
Phytoplankton	Diatomea	*Craticula ambigua* (Ehrenberg) D.G.Mann, 1990
Phytoplankton	Diatomea	*Cyclotella meneghiniana* Kützing, 1844
Phytoplankton	Diatomea	*Cyclotella ocellata* Pantocsek, 1901
Phytoplankton	Diatomea	*Cyclotella pseudostelligera* Hustedt, 1939
Phytoplankton	Diatomea	*Cyclotella* sp.
Phytoplankton	Diatomea	*Cymbella minuta* Hilse in Rabenhorst, 1862
Phytoplankton	Diatomea	*Cymbella* sp.
Phytoplankton	Diatomea	*Diadesmis confervacea* Kützing, 1844
Phytoplankton	Diatomea	Diatomea 1
Phytoplankton	Diatomea	*Diploneis finnica* (Ehrenberg) Cleve, 1891
Phytoplankton	Diatomea	*Diploneis interrupta* (Kützing) Cleve, 1894
Phytoplankton	Diatomea	*Diploneis oblongella* (Nägeli ex Kützing) Cleve-Euler, 1922

Supplementary Table S2: Continued

Phytoplankton	Diatomea	*Diploneis* sp.
Phytoplankton	Diatomea	*Entomoneis alata* (Ehrenberg) Ehrenberg, 1845
Phytoplankton	Diatomea	*Eunotia bilunaris* (Ehr.) Mills, 1934
Phytoplankton	Diatomea	*Eunotia monodon* Ehrenberg, 1843
Phytoplankton	Diatomea	*Eunotia* sp.
Phytoplankton	Diatomea	*Fallacia pygmaea* (Kützing) Stickle & Mann, 1990
Phytoplankton	Diatomea	*Fragilaria biceps* Ehrenberg, 1843
Phytoplankton	Diatomea	*Fragilaria crotonensis* Kitton, 1869
Phytoplankton	Diatomea	*Fragilaria* sp.
Phytoplankton	Diatomea	*Fragilaria ulna* var. *acus* (Kützing) Lange-Bertalot, 1980
Phytoplankton	Diatomea	*Gomphonema augur* Ehrenberg, 1840
Phytoplankton	Diatomea	*Gomphonema gracile* Ehrenberg, 1838
Phytoplankton	Diatomea	*Gomphonema parvulum* (Kütz.) Kützing, 1849
Phytoplankton	Diatomea	*Gomphonema* sp.
Phytoplankton	Diatomea	*Gyrosigma acuminatum* (Kützing) Rabenhorst, 1853
Phytoplankton	Diatomea	*Hantzschia amphioxys* (Ehr.) Grunow, 1880
Phytoplankton	Diatomea	*Melosira varians* Agardh, 1827
Phytoplankton	Diatomea	*Navicula cryptocephala* Kützing, 1844
Phytoplankton	Diatomea	*Navicula leptostriata* Jørgensen, 1948
Phytoplankton	Diatomea	*Navicula pusio* Cleve, 1895
Phytoplankton	Diatomea	*Navicula radiosa* Kützing, 1844
Phytoplankton	Diatomea	*Navicula* sp.
Phytoplankton	Diatomea	*Navicula subrhynchocephala* Hustedt, 1935
Phytoplankton	Diatomea	*Navicula veneta* Kützing, 1844
Phytoplankton	Diatomea	*Nitzschia acicularis* (Kützing) Smith, 1853
Phytoplankton	Diatomea	*Nitzschia amphibia* Grunow, 1862
Phytoplankton	Diatomea	*Nitzschia clausii* Hantzsch, 1860
Phytoplankton	Diatomea	*Nitzschia closterium* (Ehrenberg) W.Smith, 1853
Phytoplankton	Diatomea	*Nitzschia denticula* Grunow, 1880
Phytoplankton	Diatomea	*Nitzschia dissipata* (Kütz.) Grunow, 1862
Phytoplankton	Diatomea	*Nitzschia filiformis* (Smith) Van Heurck, 1896
Phytoplankton	Diatomea	*Nitzschia gracilis* Hantzsch, 1860

***Supplementary Table S2*: Continued**

Phytoplankton	Diatomea		*Nitzschia microcephala* Grunow, 1880
Phytoplankton	Diatomea		*Nitzschia obtusa* W.Smith, 1853
Phytoplankton	Diatomea		*Nitzschia palea* (Kütz.) Smith, 1856
Phytoplankton	Diatomea		*Nitzschia reversa* Smith, 1853
Phytoplankton	Diatomea		*Nitzschia sigma* (Kütz.) Smith, 1853
Phytoplankton	Diatomea		*Nitzschia sigmoidea* (Nitzs.) Smith, 1853
Phytoplankton	Diatomea		*Nitzschia* sp.
Phytoplankton	Diatomea		*Pinnularia acrosphaerica* Smith, 1853
Phytoplankton	Diatomea		*Pinnularia* sp.
Phytoplankton	Diatomea		*Pinnularia subcapitata* Gregoy, 1856
Phytoplankton	Diatomea		*Pinnularia viridis* (Nitzsch) Ehrenberg, 1843
Phytoplankton	Diatomea		*Pleurosigma* sp.
Phytoplankton	Diatomea		*Rhizosolenia longiseta* O.Zacharias, 1893
Phytoplankton	Diatomea		*Rhopalodia gibba* (Ehr.) Müller, 1895
Phytoplankton	Diatomea		*Rhopalodia gibberula* (Ehr.) Müller, 1895
Phytoplankton	Diatomea		*Sellaphora pupula* (Kütz.) Mereschkovsky, 1902
Phytoplankton	Diatomea		*Stauroneis phoenicenteron* (Nitzs.) Ehrenberg, 1843
Phytoplankton	Diatomea		*Stauroneis* sp.
Phytoplankton	Diatomea		*Synedra ulna* (Nitzsch) Ehrenberg, 1832
Phytoplankton	Diatomea		*Tryblionella* sp.
Phytoplankton	Mixotrophic phytoplankton	Chrysophyceae*	*Chromulina* sp.
Phytoplankton	Mixotrophic phytoplankton	Chrysophyceae*	*Chrysococcus* sp.
Phytoplankton	Mixotrophic phytoplankton	Chrysophyceae*	*Desmarella* sp.
Phytoplankton	Mixotrophic phytoplankton	Chrysophyceae*	*Kephyrion* sp.
Phytoplankton	Mixotrophic phytoplankton	Chrysophyceae*	*Mallomonas* sp.
Phytoplankton	Mixotrophic phytoplankton	Chrysophyceae*	*Ochromonas* sp.
Phytoplankton	Mixotrophic phytoplankton	Cryptophyceae*	*Chroomonas* sp.
Phytoplankton	Mixotrophic phytoplankton	Cryptophyceae*	*Cryptomonas erosa* Ehrenberg, 1932
Phytoplankton	Mixotrophic phytoplankton	Cryptophyceae*	*Cryptomonas marssonii* Skuja, 1948
Phytoplankton	Mixotrophic phytoplankton	Cryptophyceae*	*Cryptomonas ovata* Ehrenberg, 1932
Phytoplankton	Mixotrophic phytoplankton	Cryptophyceae*	*Cryptomonas phaseolus* Skuja, 1948
Phytoplankton	Mixotrophic phytoplankton	Cryptophyceae*	*Cryptomonas rostratiformis* Skuja, 1956

Supplementary Table S2: Continued

Phytoplankton	Mixotrophic phytoplankton	Cryptophyceae*	*Cryptomonas* sp.
Phytoplankton	Mixotrophic phytoplankton	Cryptophyceae*	*Plagioselmis nannoplanctica* (Skuja) Novarino, 1994
Phytoplankton	Mixotrophic phytoplankton	Dinophyceae*	*Gymnodinium* sp.
Phytoplankton	Mixotrophic phytoplankton	Dinophyceae*	*Katodinium* sp.
Phytoplankton	Mixotrophic phytoplankton	Dinophyceae*	*Peridiniopsis* sp.
Phytoplankton	Mixotrophic phytoplankton	Dinophyceae*	*Peridinium umbonatum* Stein, 1883
Phytoplankton	Mixotrophic phytoplankton	Dinophyceae*	*Peridinium willei* Huitfeld-Kaas, 1900
Phytoplankton	Mixotrophic phytoplankton	Dinophyceae*	*Peridinium* sp.
Phytoplankton	Mixotrophic phytoplankton	Dinophyceae*	Cyste
Phytoplankton	Mixotrophic phytoplankton	Dinophyceae*	Dinophyceae 1
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Cryptoglena* sp.
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Euglena acus* (O.F.Müller) Ehrenberg, 1830
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Euglena ehrenbergii* Klebs, 1883
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Euglena gaumei* Allorge & Lefèvre, 1931
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Euglena* cf. *gymnodinioides* Zakrys, 1986
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Euglena oxyuris* Schmarda, 1846
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Euglena spirogyra* Ehrenberg, 1838
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Euglena* sp.1
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Euglena* sp.2
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Lepocinclis fusiformis* (Carter) Lemmermann, 1901
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Lepocinclis ovum* (Ehrenb.) Lemmermann, 1910
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Lepocinclis texta* (Duj.) Lemmermann, 1934
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Phacus inflexus* (Kisselev) Pochmann, 1942
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Phacus curvicauda* Swir., 1915
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Phacus longicauda* (Ehrenb.) Dujardin, 1841
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Phacus orbicularis* Hübn., 1886
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Phacus parvulus* Klebs, 1883
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Phacus polytrophos* Pochmann, 1942
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Phacus pyrum* (Ehrenberg) W.Archer, 1871
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Phacus suecicus* Lemmermann, 1913
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Phacus* sp.
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Strombomonas fluviatilis* (Lemm.) Deflandre, 1930

***Supplementary Table S2*:** Continued

Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Strombomonas maxima* (Skvortzov) Deflandre, 1930
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Strombomonas verrucosa* (Daday) Deflandre, 1930
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Strombomonas* sp.
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Trachelomonas armata* (Ehr.) Stein, 1878
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Trachelomonas globularis* (Awer.) Lemmermann, 1910
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Trachelomonas hispida* (Perty) Stein, 1878
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Trachelomonas* cf *pulcherrima* Playfair, 1915
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Trachelomonas robusta* Svirenko, 1914
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Trachelomonas* cf *verrucosa* Stokes, 1887
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Trachelomonas volvocina* Ehrenberg, 1838
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Trachelomonas volvocinopsis* Svirenko, 1914
Phytoplankton	Mixotrophic phytoplankton	Euglenoidea*	*Trachelomonas* sp.
Phytoplankton	Xanthophyceae*		*Centritractus belenophorus* Lemmermann, 1900
Phytoplankton	Xanthophyceae*		*Centritractus* sp.
Phytoplankton	Xanthophyceae*		*Gonichloris* sp.
Phytoplankton	Xanthophyceae*		Xanthophyceae 1
Rotifera			*Anuraeopsis fissa* Gosse, 1851
Rotifera			*Asplanchna sieboldii* (Leydig, 1854)
Rotifera			*Beauchampiella eudactylota* (Gosse, 1886)
Rotifera			*Brachionus bidentatus* Anderson, 1889
Rotifera			*Brachionus calyciflorus* Pallas, 1766
Rotifera			*Brachionus caudatus* Barrois & Daday, 1894
Rotifera			*Brachionus falcatus* Zacharias, 1898
Rotifera			*Brachionus havanaensis* Rousselet, 1911
Rotifera			*Brachionus quadridentatus* Hermann, 1783
Rotifera			*Brachionus quadridentatus* Hermann, 1783
Rotifera			*Cephalodella exigua* (Gosse, 1886)
Rotifera			*Cephalodella forficula* (Ehrenberg, 1830)
Rotifera			*Cephalodella gibba* (Ehrenberg, 1830)
Rotifera			*Cephalodella intuta* Myers, 1924
Rotifera			*Cephalodella misgurnus* Wulfert, 1937

Supplementary Table S2: Continued

Rotifera	*Cephalodella* sp.
Rotifera	*Cephalodella stenroosi* Wulfert, 1937
Rotifera	*Cephalodella ventripes* (Dixon-Nuttall, 1901)
Rotifera	*Colloteca* sp.
Rotifera	*Colurella obtusa* (Gosse, 1886)
Rotifera	*Colurella uncinata* (Müller, 1773)
Rotifera	*Dicranophoroides claviger* (Hauer, 1965)
Rotifera	*Dicranophorus grandis* (Ehrenberg, 1832)
Rotifera	*Dipleuchlanis propatula* (Gosse, 1886)
Rotifera	*Encentrum* sp.
Rotifera	*Eosphera* sp.
Rotifera	*Euchlanis incisa* Carlin, 1939
Rotifera	*Euchlanis meneta* Myers, 1930
Rotifera	*Euchlanis* sp.
Rotifera	*Filinia terminalis* (Plate, 1886)
Rotifera	*Gastropus hyptopus* (Ehrenberg, 1838)
Rotifera	*Harringia rousseleti* de Beauchamp, 1912
Rotifera	*Hexarthra fennica* (Levander, 1892)
Rotifera	*Keratella americana* Carlin, 1943
Rotifera	*Keratella serrulata* (Ehrenberg, 1838)
Rotifera	*Lecane aeganea* Harring, 1914
Rotifera	*Lecane bulla* (Gosse, 1851)
Rotifera	*Lecane candida* Harring & Myers, 1926
Rotifera	*Lecane clara* (Bryce, 1892)
Rotifera	*Lecane closterocerca* (Schmarda, 1859)
Rotifera	*Lecane cornuta* (Müller, 1786)
Rotifera	*Lecane crepida* Harring, 1914
Rotifera	*Lecane curvicornis* (Murray, 1913)
Rotifera	*Lecane decipiens* (Murray, 1913)
Rotifera	*Lecane elegans* Harring, 1914
Rotifera	*Lecane elsa* Hauer, 1931
Rotifera	*Lecane flexilis* (Gosse, 1886)

Supplementary Table S2: Continued

Rotifera	*Lecane furcata* (Murray, 1913)
Rotifera	*Lecane hamata* (Stokes, 1896)
Rotifera	*Lecane hastata* (Murray, 1913)
Rotifera	*Lecane hornemanni* (Ehrenberg, 1834)
Rotifera	*Lecane inopinata* Harring & Myers, 1926
Rotifera	*Lecane leontina* (Turner, 1892)
Rotifera	*Lecane ludwigii* (Eckstein, 1883)
Rotifera	*Lecane luna* (Müller, 1776)
Rotifera	*Lecane lunaris* (Ehrenberg, 1832)
Rotifera	*Lecane monostyla* (Daday, 1897)
Rotifera	*Lecane nana* (Murray, 1913)
Rotifera	*Lecane obtusa* (Murray, 1913)
Rotifera	*Lecane papuana* (Murray, 1913)
Rotifera	*Lecane pertica* Harring & Myers, 1926
Rotifera	*Lecane punctata* (Murray, 1913)
Rotifera	*Lecane pyriformis* (Daday, 1905)
Rotifera	*Lecane quadridentata* (Ehrenberg, 1830)
Rotifera	*Lecane rhytida* Harring & Myers
Rotifera	*Lecane scutata* (Harring & Myers, 1926)
Rotifera	*Lecane stenroosi* (Meissner, 1908)
Rotifera	*Lecane stichaea* Harring, 1913
Rotifera	*Lecane tenuiseta* Harring, 1914
Rotifera	*Lecane ungulata* (Gosse, 1887)
Rotifera	*Lepadella acuminata* (Ehrenberg, 1834)
Rotifera	*Lepadella ovalis* (Müller, 1786)
Rotifera	*Lepadella patella* (Müller, 1773)
Rotifera	*Lepadella rhomboides* (Gosse, 1886)
Rotifera	*Lophocharis oxysternon* (Gosse, 1851)
Rotifera	*Macrochaetus sericus* (Thorpe, 1893)
Rotifera	*Monommata arndti* Remane, 1933
Rotifera	*Mytilina bisulcata* (Lucks, 1912)
Rotifera	*Mytilina ventralis* (Ehrenberg, 1830)

Supplementary Table S2: Continued

Rotifera		*Notommata copeus* Ehrenberg, 1834
Rotifera		*Plationus patulus* (Müller, 1786)
Rotifera		*Platyias leloupi* Gillard, 1957
Rotifera		*Polyarthra* sp.
Rotifera		*Proales* sp.
Rotifera		*Ptygura* sp.
Rotifera		*Scaridium* sp.
Rotifera		*Sinantherina* sp.
Rotifera		*Sinantherina spinosa* (Thorpe, 1893)
Rotifera		*Synchaeta* sp.
Rotifera		*Testudinella mucronata* (Gosse, 1886)
Rotifera		*Testudinella patina* (Hermann, 1783)
Rotifera		*Trichocerca bidens* (Lucks, 1912)
Rotifera		*Trichocerca capucina* (Wierzejski & Zacharias, 1893)
Rotifera		*Trichocerca pusilla* (Jennings, 1903)
Rotifera		*Trichocerca rattus* (Müller, 1776)
Rotifera		*Trichocerca similis* (Wierzejski, 1893)
Rotifera		*Trichocerca* sp.
Rotifera		*Trichocerca tenuidens* (Hauer, 1931)
Rotifera		*Trichotria tetractis* (Ehrenberg, 1830)
Rotifera		*Tripleuchlanis plicata* (Levander, 1894)
Rotifera		*Trochosphaera* cf.
Crustacea	Branchiopoda	*Alona* cf. *affinis* (Leydig, 1860)
Crustacea	Branchiopoda	*Alona* cf. *intermedia* Sars, 1862
Crustacea	Branchiopoda	*Alona* cf. *setulosa* Megard, 1967
Crustacea	Branchiopoda	*Alona guttata* Sars, 1862
Crustacea	Branchiopoda	*Antalona* cf. *verrucosa* (Sars, 1901)
Crustacea	Branchiopoda	*Bosmina longirostris* (O. F. Müller, 1776)
Crustacea	Branchiopoda	*Camptocercus* sp.
Crustacea	Branchiopoda	*Ceriodaphnia cornuta* Sars, 1885
Crustacea	Branchiopoda	cf. *Alona*
Crustacea	Branchiopoda	Chydoridae 1

Supplementary Table S2: Continued

Crustacea	Branchiopoda	*Chydorus brevilabris* Frey, 1980
Crustacea	Branchiopoda	*Cyclestheria hislopi* (Baird, 1859)
Crustacea	Branchiopoda	*Diaphanosoma brevireme* Sars, 1901
Crustacea	Branchiopoda	*Dunhevedia odontoplax* Sars, 1901
Crustacea	Branchiopoda	*Dunhevedia setigera* (Birge, 1879)
Crustacea	Branchiopoda	*Ephemeroporus barroisi* (Richard, 1894) :
Crustacea	Branchiopoda	*Ephemeroporus hybridus* (Daday, 1905)
Crustacea	Branchiopoda	*Ilyocryptus spinifer* Herrick, 1882
Crustacea	Branchiopoda	*Karualona penuelasi* Dumont & Silva-Briano, 2000
Crustacea	Branchiopoda	*Kurzia longirostris* (Daday, 1898)
Crustacea	Branchiopoda	*Kurzia media* (Birge, 1879)
Crustacea	Branchiopoda	*Leydigia louisi* Jenkin, 1934
Crustacea	Branchiopoda	*Leydigia striata* Birabén, 1939
Crustacea	Branchiopoda	*Leydigiopsis* sp.
Crustacea	Branchiopoda	*Macrothrix elegans* Sars, 1901
Crustacea	Branchiopoda	*Macrothrix spinosa* King, 1853
Crustacea	Branchiopoda	*Moina micrura* Kurz, 1875
Crustacea	Branchiopoda	*Moinodaphnia macleayi* (King, 1853)
Crustacea	Branchiopoda	*Oxyurella longicaudis* (Birge, 1910)
Crustacea	Branchiopoda	*Pleuroxus varidentatus* Frey, 1993
Crustacea	Branchiopoda	*Sarsilatona* sp.
Crustacea	Branchiopoda	*Scapholeberis armata* Herrick, 1882
Crustacea	Branchiopoda	*Simocephalus vetulus* (O. F. Müller, 1776)
Crustacea	Branchiopoda	*Streblocerus* sp.
Crustacea	Copepoda	*Acanthocyclops robustus* (G.O. Sars, 1863)
Crustacea	Copepoda	*Acanthocyclops smithae* Reid & Suárez-Morales, 1999
Crustacea	Copepoda	Cyclopoida 1
Crustacea	Copepoda	*Diacyclops* sp.
Crustacea	Copepoda	*Eucyclops agilis* (Koch, 1838)
Crustacea	Copepoda	*Leptodiaptomus* sp.
Crustacea	Copepoda	*Mesocyclops brasilianus* Kiefer, 1933
Crustacea	Copepoda	*Mesocyclops longisetus* Dussart, 1987

**_Supplementary Table S2_: **Continued

Crustacea	Copepoda	*Mesocyclops* sp.3
Crustacea	Copepoda	*Mesocyclops thermocyclopoides* Harada, 1931
Crustacea	Copepoda	*Metacyclops* sp.1
Crustacea	Copepoda	*Metacyclops* sp.2
Crustacea	Copepoda	*Microcyclops ceibaensis* (Marsh, 1919)
Crustacea	Copepoda	*Prionodiaptomus* sp.
Crustacea	Copepoda	*Thermocyclops inversus* (Kiefer, 1936)
Crustacea	Ostracoda	*Candobrasilopsis* sp.
Crustacea	Ostracoda	*Chlamydotheca* cf. *arcuata* (Sars, 1901)
Crustacea	Ostracoda	*Chlamydotheca* cf. *mckenziei* Kotzian, 1974
Crustacea	Ostracoda	*Chlamydotheca unispinosa* (Baird, 1862)
Crustacea	Ostracoda	*Chrissia* sp.
Crustacea	Ostracoda	*Cypretta* sp.
Crustacea	Ostracoda	Cyprididae 1
Crustacea	Ostracoda	Cyprididae 2
Crustacea	Ostracoda	*Cypridopsis arcuata* Sars, 1901
Crustacea	Ostracoda	*Cypridopsis vidua* (O.F. Müller, 1776)
Crustacea	Ostracoda	*Cypris decaryi* Gauthier, 1933
Crustacea	Ostracoda	*Cytheridella ilosvayi* Daday, 1905
Crustacea	Ostracoda	*Darwinula* cf. *stevensoni* (Brady & Robertson, 1870)
Crustacea	Ostracoda	*Darwinula stevensoni* (Brady & Robertson, 1870)
Crustacea	Ostracoda	Darwinulidae 1
Crustacea	Ostracoda	Darwinulidae 2
Crustacea	Ostracoda	Darwinulidae 3
Crustacea	Ostracoda	Darwinulidae 4
Crustacea	Ostracoda	*Diaphanocypris meridana* (Furtos, 1936)
Crustacea	Ostracoda	*Eucypris bispinosa* (Victor & Michael, 1975)
Crustacea	Ostracoda	*Hemicypris pyxidata* (Moniez, 1892)
Crustacea	Ostracoda	*Ilyocypris gibba* (Ramdohr, 1808)
Crustacea	Ostracoda	*Keysercypria xanabanica* (Furtos, 1936)
Crustacea	Ostracoda	*Limnocythere stationis* Vávra, 1891
Crustacea	Ostracoda	*Potamocypris smaragdina* (Vávra, 1891)

Supplementary Table S2: Continued

Crustacea	Ostracoda		*Pseudostrandesia asymmetros* (Rome, 1962)
Crustacea	Ostracoda		*Stenocypris bolieki* Ferguson, 1962
Crustacea	Ostracoda		*Stenocypris major* (Baird, 1859)
Crustacea	Ostracoda		*Strandesia* cf. *bicuspis* (Claus, 1892)
Crustacea	Ostracoda		*Vestalenula botocuda* Pinto et al., 2003
Crustacea	Ostracoda		*Vestalenula irajai* Pinto et al., 2003
Macroinvertebrates	Annelida*		*Aulophorus pectinatus* Stephenson, 1931
Macroinvertebrates	Annelida*		*Aulophorus vagus* Leidy, 1880
Macroinvertebrates	Annelida*		*Dero* sp.
Macroinvertebrates	Annelida*		*Erpobdella costata* Sawyer & Shelley, 1976
Macroinvertebrates	Annelida*		Erpobdellidae sp.
Macroinvertebrates	Annelida*		Glossiphoniidae sp.
Macroinvertebrates	Annelida*		Haplotaxidae sp.
Macroinvertebrates	Annelida*		*Helobdella* sp.
Macroinvertebrates	Annelida*		*Helobdella stagnalis* (Linnaeus, 1758)
Macroinvertebrates	Annelida*		*Pristina* sp.
Macroinvertebrates	Arachnida*		Hydracari 1
Macroinvertebrates	Arachnida*		Hydracari 2
Macroinvertebrates	Arachnida*		Oribatida 1
Macroinvertebrates	Cnidaria*		*Hydra* sp.
Macroinvertebrates	Collembola*		Entomobryomorpha 1
Macroinvertebrates	Collembola*		Sminthuridae 1
Macroinvertebrates	Decapoda*		Atyidae 1
Macroinvertebrates	Decapoda*		Palaemonidae 1
Macroinvertebrates	Decapoda*		Pseudothelphusidae 1
Macroinvertebrates	Ectoprocta*		*Plumatella* sp.
Macroinvertebrates	Insecta	Coleoptera	*Berosus* sp.
Macroinvertebrates	Insecta	Coleoptera	Coleoptera 1
Macroinvertebrates	Insecta	Coleoptera	Colymbetinae 1
Macroinvertebrates	Insecta	Coleoptera	*Cybister* sp.
Macroinvertebrates	Insecta	Coleoptera	Dytiscidae 1

Supplementary Table S2: Continued

Macroinvertebrates	Insecta	Coleoptera	Dytiscidae 2
Macroinvertebrates	Insecta	Coleoptera	Dytiscidae 3
Macroinvertebrates	Insecta	Coleoptera	Dytiscidae 4
Macroinvertebrates	Insecta	Coleoptera	Dytiscidae 5
Macroinvertebrates	Insecta	Coleoptera	Dytiscidae 6
Macroinvertebrates	Insecta	Coleoptera	Dytiscinae 1
Macroinvertebrates	Insecta	Coleoptera	*Enochrus* 1
Macroinvertebrates	Insecta	Coleoptera	Haliplidae 1
Macroinvertebrates	Insecta	Coleoptera	*Helochares* sp.
Macroinvertebrates	Insecta	Coleoptera	*Heterelmis* sp.
Macroinvertebrates	Insecta	Coleoptera	Hydraenidae 1
Macroinvertebrates	Insecta	Coleoptera	Hydrochidae 1
Macroinvertebrates	Insecta	Coleoptera	Hydrophilinae 1
Macroinvertebrates	Insecta	Coleoptera	*Hydrophilus* sp.
Macroinvertebrates	Insecta	Coleoptera	Hydrophylidae 1
Macroinvertebrates	Insecta	Coleoptera	Hydrophylidae 1
Macroinvertebrates	Insecta	Coleoptera	Hydrophylidae 2
Macroinvertebrates	Insecta	Coleoptera	*Hyphydrus* sp.1
Macroinvertebrates	Insecta	Coleoptera	*Hyphydrus* sp.2
Macroinvertebrates	Insecta	Coleoptera	Laccophilinae 1
Macroinvertebrates	Insecta	Coleoptera	*Noterus* sp.
Macroinvertebrates	Insecta	Coleoptera	*Ochthebius* sp.
Macroinvertebrates	Insecta	Coleoptera	*Paracymus* sp.
Macroinvertebrates	Insecta	Coleoptera	*Tropisternus* sp.
Macroinvertebrates	Insecta	Diptera	*Aedeomyia squamipennis* (Lynch Arribálzaga, 1878)
Macroinvertebrates	Insecta	Diptera	*Anopheles* sp.
Macroinvertebrates	Insecta	Diptera	*Anopheles albimanus* Wiedemann, 1820
Macroinvertebrates	Insecta	Diptera	*Chaoborus flavicans* (Meigen, 1830)
Macroinvertebrates	Insecta	Diptera	*Chironomus* sp.
Macroinvertebrates	Insecta	Diptera	*Corethrella appendiculata* Grabham, 1906
Macroinvertebrates	Insecta	Diptera	*Culex* sp.
Macroinvertebrates	Insecta	Diptera	*Culex dunni* Dyar, 1918

Supplementary Table S2: Continued

Macroinvertebrates	Insecta	Diptera	*Culex erraticus* (Dyar & Kanb, 1906)
Macroinvertebrates	Insecta	Diptera	*Culex nigripalpus* Theobald, 1901
Macroinvertebrates	Insecta	Diptera	*Culex zeteki* Dyar, 1918
Macroinvertebrates	Insecta	Diptera	*Culex pilosus* (Dyar and Knab, 1906)
Macroinvertebrates	Insecta	Diptera	Culicidae 1
Macroinvertebrates	Insecta	Diptera	*Culicoides* sp.
Macroinvertebrates	Insecta	Diptera	Ephydridae 1
Macroinvertebrates	Insecta	Diptera	Forcypomyinae sp.1
Macroinvertebrates	Insecta	Diptera	*Hydrellia* 1
Macroinvertebrates	Insecta	Diptera	Limonidae 1
Macroinvertebrates	Insecta	Diptera	*Mansonia titillans* (Walker, 1848)
Macroinvertebrates	Insecta	Diptera	*Odonthomyia* sp.
Macroinvertebrates	Insecta	Diptera	*Odontomyia ornata* (Meigen, 1822)
Macroinvertebrates	Insecta	Diptera	*Oplodontha viridula* (Fabricius, 1775)
Macroinvertebrates	Insecta	Diptera	Orthocladiinae sp.
Macroinvertebrates	Insecta	Diptera	Psychodidae 1
Macroinvertebrates	Insecta	Diptera	Rhagionidae 1
Macroinvertebrates	Insecta	Diptera	Sciomyzidae 1
Macroinvertebrates	Insecta	Diptera	Statiomyidae 1
Macroinvertebrates	Insecta	Diptera	*Stratiomys longicornis* (Scopoli, 1763)
Macroinvertebrates	Insecta	Diptera	Syrphidae 1
Macroinvertebrates	Insecta	Diptera	Tabanidae 1
Macroinvertebrates	Insecta	Diptera	Tipulidae 1
Macroinvertebrates	Insecta	Diptera	*Uranotaenia* sp.
Macroinvertebrates	Insecta	Heteroptera	*Belostoma* sp.
Macroinvertebrates	Insecta	Heteroptera	*Belostoma micantulum* Stål, 1860
Macroinvertebrates	Insecta	Heteroptera	*Buenoa* sp.
Macroinvertebrates	Insecta	Heteroptera	Corixinae 1
Macroinvertebrates	Insecta	Heteroptera	*Hydrometra* sp.
Macroinvertebrates	Insecta	Heteroptera	*Lethocerus* sp.
Macroinvertebrates	Insecta	Heteroptera	*Meriagata* sp.
Macroinvertebrates	Insecta	Heteroptera	*Mesovelia* sp.

Supplementary Table S2: Continued

Macroinvertebrates	Insecta	Heteroptera	*Micronecta* sp.
Macroinvertebrates	Insecta	Heteroptera	*Microvelia* sp.
Macroinvertebrates	Insecta	Heteroptera	*Neoplea* sp.
Macroinvertebrates	Insecta	Heteroptera	*Paraplea puella* (Barber, 1923)
Macroinvertebrates	Insecta	Heteroptera	*Pelocaris* sp.
Macroinvertebrates	Insecta	Heteroptera	*Potamobates* sp.
Macroinvertebrates	Insecta	Heteroptera	*Ranatra* sp.
Macroinvertebrates	Insecta	Heteroptera	*Rheumatobates bergrothi* Meinert, 1895
Macroinvertebrates	Insecta	Heteroptera	*Rheumatobates minutus* subsp. *flavidus* Drake & Harris, 1942
Macroinvertebrates	Insecta	Heteroptera	*Trepobates* sp.
Macroinvertebrates	Insecta	Heteroptera	Veliidae 1
Macroinvertebrates	Insecta	Neuroptera*	*Sisyra apicalis* Banks, 1908
Macroinvertebrates	Insecta	Paleoptera (Ephemeroptera*)	Caenidae 1
Macroinvertebrates	Insecta	Paleoptera (Ephemeroptera*)	Caenis sp.1
Macroinvertebrates	Insecta	Paleoptera (Ephemeroptera*)	Caenis sp.2
Macroinvertebrates	Insecta	Paleoptera (Ephemeroptera*)	*Callibaetis* sp.
Macroinvertebrates	Insecta	Paleoptera (Ephemeroptera*)	*Campsurus* sp.
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	*Acanthagrion* sp.1
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	*Acanthagrion* sp.2
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	Aeshnidae 1
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	Anisopterinae 1
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	*Argia* sp.
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	*Coryphaeschna* sp.
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	*Epigomphus* sp.
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	*Erythemis* sp.
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	*Erythrodiplax* sp.
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	*Leptobasis vacillans* Hagen, 1877
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	*Libellula* sp.
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	Libellulidae 2
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	Libellulidae 1
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	*Miathyria* sp.
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	*Micrathyria* sp.

Supplementary Table S2: Continued

Macroinvertebrates	Insecta	Paleoptera (Odonata*)	*Nehalennia* sp.
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	*Nehalennia minuta* (Selys, 1857)
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	*Nephepeltia* sp.
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	*Orthemis* sp.
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	*Perithemis* sp.
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	*Protoneura* sp.
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	Protoneuridae 1
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	Pseudostigmatidae 1
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	*Remartinia* sp.
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	*Remartinia luteipennis* (Burmeister, 1839)
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	*Sympetrum* sp.
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	*Tauriphila* sp.
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	*Tramea* sp.
Macroinvertebrates	Insecta	Paleoptera (Odonata*)	Zygoptera 1
Macroinvertebrates	Insecta	Trichoptera*	Hydropsychidae 1
Macroinvertebrates	Insecta	Trichoptera*	Hydroptilidae 1
Macroinvertebrates	Insecta	Trichoptera*	Leptophlebiidae 1
Macroinvertebrates	Insecta	Trichoptera*	Limnephilidae 1
Macroinvertebrates	Insecta	Trichoptera*	*Oecetis* sp.
Macroinvertebrates	Insecta	Trichoptera*	*Oxyethyra* 1
Macroinvertebrates	Insecta	Trichoptera*	Trichoptera 1
Macroinvertebrates	Isopoda*		Oniscidea 1
Macroinvertebrates	Mollusca		Ancylidae 1
Macroinvertebrates	Mollusca		*Drepanotrema depressissimum* (Moricand, 1839)
Macroinvertebrates	Mollusca		*Drepanotrema kermatoides* (d'Orbigny, 1835)
Macroinvertebrates	Mollusca		*Drepanotrema lucidum* (Pfeiffer, 1839)
Macroinvertebrates	Mollusca		*Eupera* sp.
Macroinvertebrates	Mollusca		*Ferrissia* sp.
Macroinvertebrates	Mollusca		Gasteropoda 1
Macroinvertebrates	Mollusca		*Hebetancylus excentricus* (Morelet, 1851)
Macroinvertebrates	Mollusca		Hydrobiidae
Macroinvertebrates	Mollusca		Lymnaeidae 1

Supplementary Table S2: Continued

Macroinvertebrates	Mollusca	*Melanoides tuberculata* (O. F. Müller, 1774)
Macroinvertebrates	Mollusca	*Oxyloma elegans* (Risso, 1826)
Macroinvertebrates	Mollusca	*Physella acuta* Draparnaud, 1805
Macroinvertebrates	Mollusca	*Pisidium* sp.
Macroinvertebrates	Mollusca	*Planorbella duryi* (Wetherby, 1879)
Macroinvertebrates	Mollusca	Planorbiidae 1
Macroinvertebrates	Mollusca	Planorbiidae 2
Macroinvertebrates	Mollusca	*Pomacea flagellata* (Say, 1827)
Macroinvertebrates	Mollusca	*Stenophysa impluviata* (Morelet, 1849)
Macroinvertebrates	Nemertea*	*Prostoma* sp.
Macroinvertebrates	Platyhelminthes*	*Bothromesostoma* sp.
Macroinvertebrates	Platyhelminthes*	Dugesiidae 1
Macroinvertebrates	Platyhelminthes*	Typhloplanidae sp.
Macroinvertebrates	Porifera*	*Corvoheteromeyenia heterosclera* (Ezcurra de Drago, 1974)
Macroinvertebrates	Porifera*	*Radiospongilla cerebellata* (Bowerbank, 1863)
Macroinvertebrates	Porifera*	*Radiospongilla crateriformis* (Potts, 1882)

Supplementary Table S3: Spatial (S), environmental (E) and temporal (T) variables selected in variation partitioning analyses for each group including the three sampling periods together.

Phytoplankton
S: MEM2, MEM3, MEM6, MEM5, Region, MEM1, MEM10, MEM21, MEM8, MEM 19, MEM7, MEM14
Ca^{+2}, pH, Chlorophyll-a concentration, Precipitation seasonality, Water temperature, Area, E: Heterogeneity, Macrophyte cover, Water transparency, Maximum depth, NO$_2^-$, Minimum temperature, Livestock presence, Dissolved oxygen concentration
T: Period 2

Cyanobacteria
S: Region, MEM6, MEM3, MEM7, MEM17, MEM2
E: Maximum temperature, Ca^{+2}/Mg^{+2}, Area, Water transparency, Chlorophyll-a
T: Period 1, Period 2

Chlorophyceae
S: MEM13, MEM2, Region, MEM22, MEM6, MEM1
E: Precipitation seasonality, pH, Cl-, ECELS1, ECELS2, Seasonal hydroperiod, Phreatic origin, Rain origin, Ca^{+2}/Mg^{+2}, (Ca^{+2}+Mg^{+2})/(Na$^+$+K$^+$), Dissolved oxygen concentration
T: Period 1

Mixotrophic phytoplankton
S: Region, Connectivity, MEM1, MEM2
Average temperature, Water transparency, Heterogeneity, pH, Average depth, ECELS3, E: E: ECELS1
T: Period 1, Period 2

Diatomea
S: MEM8, Region, MEM2, MEM1, MEM9, MEM12
E: Conductivity, pH, Seasonal hydroperiod, Maximum depth, Perimeter, ECELS4, Average depth, Macrophyte cover, High grass land use, Cl$^-$, Transparency
T: Period 2

Rotifera
S: MEM2, Region, MEM5, MEM14, MEM6, MEM6, MEM7
E: Annual precipitation, Minimum temperature, K$^+$, Macrophyte cover, High grass land use, Average depth, pH, ECELS4, NO$_3^-$, Chlorophyll-a, ECELS1, PO$_4^{-3}$
T: Period 1

Branchiopoda
S: MEM1
E: Mg^{+2}, K$^+$, Cl$^-$, Total dissolved solids, Seasonal hydroperiod, Conductivity, Morphology, Water temperature, NO$_3^-$/NO$_2^-$
T: Period 1, Period 2

Copepoda
S: Region, MEM13, MEM5, MEM4
E: Building land use, NO$_2^-$, Livestock, Range of temperatures, Dissolved oxygen concentration, Average depth
T: Period 2

Ostracoda
S: Region, MEM4, MEM7, MEM16, MEM2
E: Annual precipitation, pH, Range of temperatures, Altitude, Perimeter, Maximum depth, Alk/(Cl$^-$*SO$_4^{-2}$), Average temperature, HCO$_3^-$, Heterogeneity, Maximum temperature,
T: Period 2

Crustacea
S: Region, MEM13, MEM2, MEM16, MEM14, MEM19, MEM22, MEM6, MEM3
E: Cl$^-$, Helophyte cover, Livestock presence, Morphology, Annual precipitations, Alk/(Cl-+SO$_4^{-2}$), NO$_2^-$, NO$_3^-$/NH$_4^+$, Maximum depth, Forest land use, Building land use, PO$_4^{-3}$, ECELS1, Dissolved oxygen concentration
T: Period 2, Period 1

Macroinvertebrates
S: MEM7, MEM3, Region, MEM2, MEM17, MEM4, MEM5, MEM6, MEM16
E: Range of temperatures, Annual precipitation, Area, Livestock, ECELS2, Helophyte cover
T: Period 1, Period 2

Mollusca
S: MEM2, MEM5, MEM8, MEM1
E: Livestock, Agricultural land use, Range of temperatures, Chlorophyll-a, Dissolved oxygen concentration, Seasonal hydroperiod
T: Period 1

Supplementary Table S3: Continued

Insecta	
	S: MEM7, MEM5, MEM6, MEM3, MEM4
	E: Annual precipitation, Altitude, ECELS3
	T: Period 1
Paleoptera	
	S: MEM3, MEM1, Region
	E: Total ECELS, $Alk/(Cl^{-}+SO_4^{-2})$, Low grass land use, Building land use, Precipitation seasonality
	T: Period 1
Heteroptera	
	S: MEM7, MEM3, MEM6, MEM5
	E: Annual precipitation, NO_3^{-}
	T: Period 1
Coleoptera	
	S: Connectivity
	E: SO_4^{-2}, Helophyte cover, Low grass land use, Maximum temperature
	T: Period 2
Diptera	
	S: MEM11
	E: Livestock, High grass land use, HCO_3^{-}
	T: Period 1, Period 2

Supplementary Table S4: Spatial (S) and environmental (E) variables selected in variation partitioning analyses for each group, analyzing each sampling period separately.

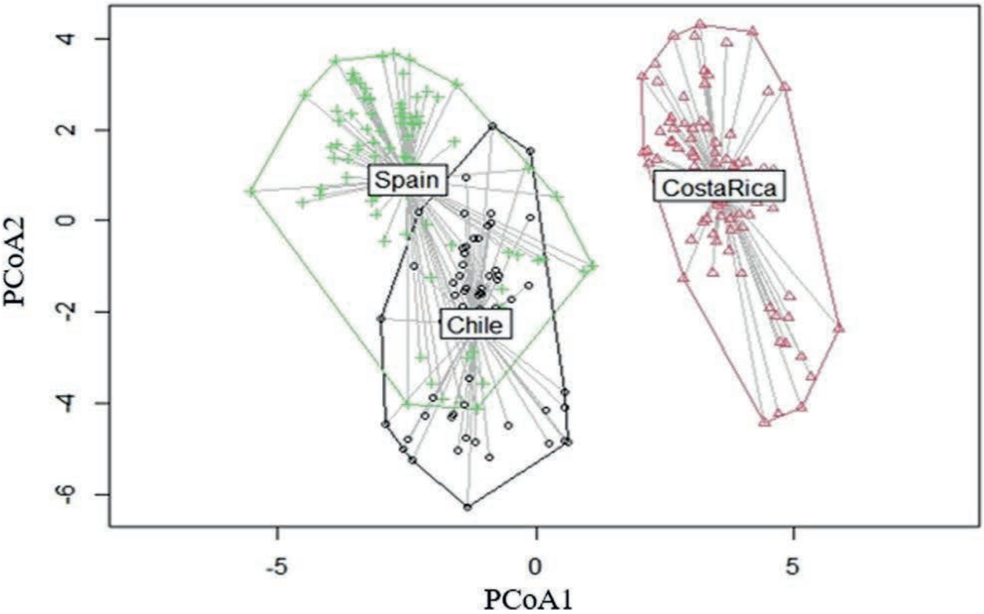
- Phytoplankton
  - Period 1
    - S: MEM3, MEM5. MEM9, MEM4
    - E: Maximum depth, pH, Precipitation seasonality, Chlorophyll-a, Area, Agricultural land use, $(Ca^{+2}+Mg^{+2})/(Na^{+}+K^{+})$
  - Period 2
    - S: MEM9, MEM3
    - E: Seasonal hydroperiod, Altitude, Macrophyte concentration, K^{+}, Helophyte cover, pH, Average depth
  - Period 3
    - S: Region, MEM2
    - E: Conductivity, Dissolved oxygen concentration
- Rotifera
  - Period 1
    - S: Region, MEM5
    - E: Annual precipitation, Range of temperatures, Chlorophyll-a
  - Period 2
    - S: MEM6, Region, MEM2, MEM3, MEM12
    - E: Transparency, Seasonal hydroperiod, Eccels4, Low grass land use, PO_4^{-3}
  - Period 3
    - S: MEM2, Region, MEM4
    - E: Cl^{-}, Dissolved oxygen concentration, ECELS4, Annual precipitation, Minimum temperature, Average depth
- Crustacea
  - Period 1
    - S: MEM1, Region, MEM2
    - E: Maximum temperature, Building land use, Average temperature, HCO3-
  - Period 2
    - S: Region
    - E: Helophyte cover, Dissolved oxygen concentration, Annual precipitation, Phreatic origin
  - Period 3
    - S: MEM2
    - E: Dissolved oxygen concentration, Conductivity, Rain origin
- Mollusca
  - Period 1
    - S: MEM3
    - E: Heterogeneity, Forest land use
  - Period 2
    - S: MEM1
    - E: Livestock, Chlorophyll-a, Range of temperatures, Transparency
  - Period 3
    - S: MEM3
    - E: High grass land use, Altitude
- Insecta
  - Period 1
    - S: Region, MEM7, MEM3
    - E: NO_3^{-}, ECELS4
  - Period 2
    - S: MEM10, MEM8, MEM7
    - E: Transparency
  - Period 3
    - S: MEM8, MEM2, MEM4, MEM7
    - E: Perimeter, Minimum temperature, NO_3^{-}/NH_4^{+}

Capítulo 3: The environmental framework of temporary ponds: A tropical-mediterranean comparison.

Supplementary Material I: Median and range (within brackets) values of all variables for the three regions. Abbreviations are shown in the caption of **Figure 5.**

	CR	**CH**	**SP**
TRAN (ºC)	9.8 (4.5-13.6)	19.3 (17.2-26.4)	25.5 (22.4-28.7)
TMIN (ºC)	22.4 (20.9-23.7)	7.1 (3.1-8.5)	0 (-3.2-6.9)
TMAX (ºC)	32.3 (27.9-34.5)	26.8 (24.0-30.2)	26.2 (24.0-31.4)
TAVE (ºC)	24.8 (22.0-26.7)	16.3 (13.4-17.6)	11.7 (9.0-18.2)
PREC (mm)	2059 (1644-4023)	436 (259-632)	522 (434-668)
SEAS	78 (23-94)	106 (102-115)	28 (25-54)
WTEM (ºC)	26.9 (21.3-39.6)	19.8 (6.4-32.9)	19.3 (3.2-30.8)
pH	7.3 (4.4-9.9)	8.1 (6.4-10.0)	8.1 (6.8-10.6)
COND (µS cm^{-1})	155 (8-1345)	1357 (49-14050)	378 (61-7920)
OXYG (mg L^{-1})	4.0 (0.3-15.1)	11.3 (2.2-20.5)	9.1 (0.7-17.1)
WTRA (cm)	15 (3-48)	15 (0.1-59)	23 (4-49)
ALKA (mg L^{-1})	45.8 (12.2-177.0)	109.8 (18.3-390.5)	110.0 (12.2-573.6)
CLOR (mg L^{-1})	8 (6-95)	42 (0.4-5914)	28 (6-2560)
NH4 (mg L^{-1})	0.09 (0.03-1.14)	0.13 (0.00-107.2)	0.19 (0.00-9.62)
NO2 (mg L^{-1})	0.01 (0.00-0.65)	0.03 (0.00-2.81)	0.03 (0.16-24.92)
NO3 (mg L^{-1})	3.78 (0.00-66.52)	10.42 (0.00-278.14)	11.07 (1.00-120.51)
SRP (mg L^{-1})	0.40 (0.00-3.69)	0.15 (0.00-9.91)	0.12 (0.05-4.10)
SO4 (mg L^{-1})	1.6 (0.0-47.5)	33.9 (0.6-261.0)	22.3 (0.5-326.2)
ALKCL	2.4 (0.3-11.8)	1.1 (0.02-115.2)	2.3 (0.1-11.1)
ALKSO4	21.1 (0.4-144.1)	2.2 (0.2-72.4)	4.0 (0.1-128.0)
NO3NH4	8.4 (1.1-386.3)	27.5 (0.01-3746.7)	8.5 (0.3-480.3)
NO3NO2	117.0 (1.9-2467.8)	285.9 (0.9-10550.2)	184.6 (3.6-1377.4)
VSUB (%)	0 (0-90)	0 (0-100)	18 (0-100)
VFLO (%)	4 (0-99)	0 (0-95)	0 (0-100)
VHEL (%)	40 (0-100)	2 (0-100)	30 (0-100)
CHLA (µg L^{-1})	7.6 (1.0-94.5)	10.8 (0.5-187.0)	1.3 (0.0-134.8)
MXDE (m)	85 (25-200)	50 (20-200)	49 (14-183)
MDDE (m)	58 (10-150)	22 (10-183)	29 (7-107)
MXDI (m)	52 (5-4840)	76 (10-465)	21 (6-455)
MIDI (m)	39 (3-2540)	31 (6-160)	14 (4-246)
SURF (m^2)	1429 (16-9655369)	1774 (47-44820)	265 (25-68911)
ORGM (%)	14.5 (6.3-37.1)	7.3 (1.0-17.3)	8.5 (3.2-30.5)
CARB (%)	17.1 (6.9-38.3)	1.9 (0.3-10.4)	25.9 (6.1-47.9)
ALTI (m)	309 (5-830)	145 (10-460)	979 (0-1235)
AGRI (%)	0 (0-0)	0 (0-80)	13 (0-92)
SHGR (%)	31 (0-100)	58 (0-95)	15 (0-97)
TAGR (%)	0 (0-100)	0 (0-83)	0 (0-100)
SCRU (%)	0 (0-0)	6 (0-96)	2 (0-70)
FORE (%)	40 (0-100)	6 (0-96)	3 (0-84)
BUIL (%)	0 (0-5)	5 (0-39)	0 (0-22)
HETE	0.5 (0-1.1)	0.6 (0.2-1.3)	0.7 (0.0-1.3)

Supplementary Material II

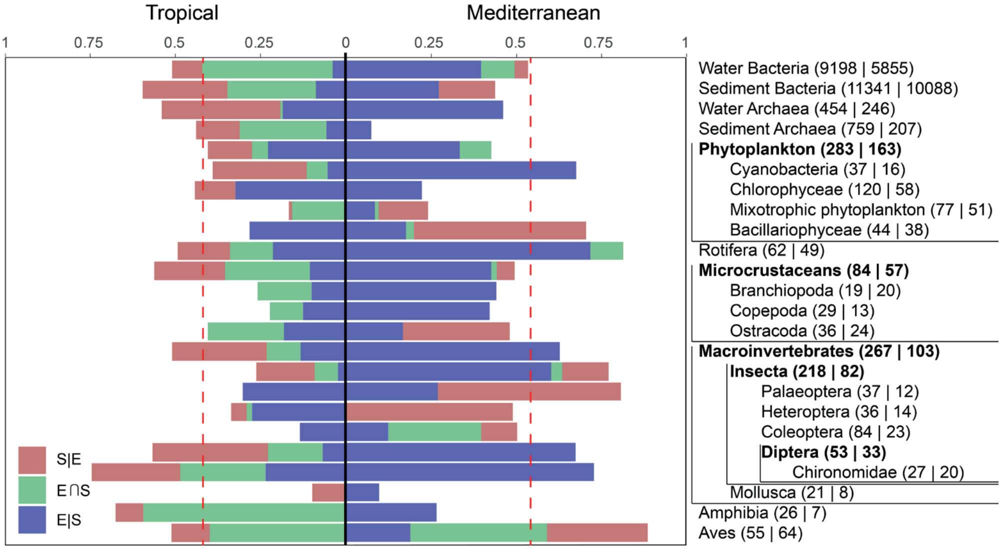


Capítulo 4: Pond metacommunities from bacteria to birds: heterogeneous response among taxa but with overall stronger environmental effects in a mediterranean than in a tropical setting

Appendix S1: Table S1: Results of variation partitioning analysis for each group. The table shows the proportion of variation (R^2_{adj}) explained by each pure component (E|S and S|E), the overlaps between components or spatialized environment (E∩S), and the total explained variation (E+S) in tropical and mediterranean metacommunities.

Group of organisms	E|S		E∩S		S|E		E+S	
Region	Trop	Med	Trop	Med	Trop	Med	Trop	Med
Water Bacteria	0.03	0.42	0.40	0.10	0.09	0.04	0.52	0.56
Sediment Bacteria	0.09	0.29	0.27	0.00	0.26	0.17	0.62	0.46
Water Archaea	0.19	0.48	0.01	0.00	0.36	0.00	0.56	0.48
Sediment Archaea	0.05	0.08	0.26	0.00	0.13	0.00	0.45	0.08
Phytoplankton	0.23	0.35	0.05	0.10	0.14	0.00	0.41	0.45
Cyanobacteria	0.05	0.71	0.06	0.00	0.29	0.00	0.40	0.71
Chlorophyceae	0.33	0.24	0.00	0.00	0.12	0.00	0.45	0.24
Mixotrophic flagellate	0.00	0.09	0.16	0.01	0.01	0.15	0.17	0.26
Bacillariophyceae	0.29	0.19	0.00	0.02	0.00	0.53	0.29	0.74
Rotifera	0.22	0.75	0.13	0.10	0.16	0.00	0.51	0.85
Microcrustaceans	0.10	0.45	0.26	0.02	0.22	0.05	0.58	0.52
Branchiopoda	0.10	0.46	0.16	0.00	0.00	0.00	0.26	0.46
Copepoda	0.13	0.44	0.10	0.00	0.00	0.00	0.23	0.44
Ostracoda	0.18	0.18	0.23	0.00	0.00	0.33	0.42	0.51
Macroinvertebrates	0.13	0.66	0.10	0.00	0.29	0.00	0.52	0.66
Insecta	0.02	0.63	0.07	0.03	0.18	0.14	0.27	0.81
Palaeoptera	0.31	0.28	0.00	0.00	0.00	0.56	0.31	0.85
Heteroptera	0.28	0.00	0.02	0.00	0.05	0.52	0.34	0.52
Coleoptera	0.14	0.13	0.00	0.29	0.00	0.11	0.14	0.53
Diptera	0.07	0.71	0.17	0.00	0.35	0.00	0.59	0.71
Chironomidae	0.24	0.76	0.26	0.00	0.27	0.00	0.77	0.76
Mollusca	0.00	0.10	0.00	0.00	0.10	0.00	0.10	0.10
Amphibia	0.00	0.28	0.61	0.00	0.08	0.00	0.70	0.28
Aves	0.00	0.20	0.41	0.42	0.11	0.31	0.53	0.93

Appendix S1: Figure S1: Results of variation partitioning analysis for each group of organisms in tropical and Mediterranean metacommunities. The proportion of variation explained by each com-ponent is represented with a different color. Taxa in bold type include species from the fol-lowing groups enclosed in the corresponding line. Red dashed line represents average total explained variation. Number of identified species (Tropical | Mediterranean species) are shown next to each group label.



Capítulo 4: Temporal dynamics in mediterranean and tropical temporary pond metacommunities: a multi-taxon approach.

Supplementary Material 1: Results of variation partitioning analyses with the spatial focus. Total explained variation (E+S), pure environmental ((E|S)/(E+S)), spatially structured environmental ((E∩S)/(E+S)) and pure spatial effects ((S|E)(E+S)) obtained in the three sampling periods are shown for each metacommunity (tropical-mediterranean). Big taxonomic groups, whose results are described and discussed in the main manuscript, appear in bold font.

Group of organisms	Sampling period 1				Sampling period 2				Sampling period 3			
	E+S	(E|S)/(E+S)	(E∩S)/(E+S)	(S|E)(E+S)	E+S	(E|S)/(E+S)	(E∩S)/(E+S)	(S|E)(E+S)	E+S	(E|S)/(E+S)	(E∩S)/(E+S)	(S|E)(E+S)
Bacteria	0.52-0.56	0.07-0.74	0.76-0.18	0.17-0.07	0.47-0.43	0-0.37	0-0.15	1-0.48	0.59-0.5	0-0.3	0-0.64	1-0.06
Archaea	0.56-0.48	0.34-1	0.02-0	0.65-0	0.32-0.44	0.36-0.36	0.36-0.23	0.28-0.41	0.32-0.26	0.18-0.43	0-0.53	0.82-0.04
Phytoplanton	0.41-0.45	0.56-0.78	0.11-0.22	0.33-0	0.29-0.55	0.24-0.42	0.13-0.43	0.63-0.15	0-0.44	0-0.64	0-0.23	0-0.13
Cyanobacteria	0.4-0.71	0.13-1	0.16-0	0.72-0	0.46-0.2	0.31-1	0.01-0	0.67-0	0.14-0.35	1-1	0-0	0-0
Chlorophyceae	0.45-0.24	0.73-1	0-0	0.27-0	0.61-0.68	0.66-1	0-0	0.34-0	0.37-0.51	0-1	1-0	0-0
Mixotrophic phytoplankton	0.17-0.26	0-0.36	0.95-0.04	0.05-0.6	0.49-0.22	0.04-0.11	0.21-0	0.75-0.89	0.13-0.5	0-1	0-0	1-0
Bacillariophyceae	0.29-0.74	1-0.25	0-0.03	0-0.72	0.78-0.59	0.15-0.33	0.85-0.34	0-0.33	0.11-0.32	1-1	0-0	0-0
Rotifera	0.51-0.85	0.43-0.88	0.26-0.12	0.31-0	0.06-0.56	0.05-0.6	0.95-0.4	0-0	0.55-0.48	0-0	1-0	0-1
Microcrustaceans	0.58-0.52	0.18-0.87	0.45-0.03	0.37-0.1	0.32-0.43	0-0.47	0.3-0.53	0.7-0	0.23-0.12	0-1	1-0	0-0
Branchiopoda	0.26-0.46	0.37-1	0.63-0	0-0	0.35-0.62	0-0.19	0.66-0.21	0.34-0.6	0.3-0.12	0.01-1	0.99-0	0-0
Copepoda	0.23-0.44	0.55-1	0.45-0	0-0	0.06-0.36	0-1	0-0	1-0	0.25-0.11	1-1	0-0	0-0
Ostracoda	0.42-0.51	0.44-0.35	0.56-0	0-0.65	0.15-0.36	0-0.54	0-0.46	1-0	0.1-0.26	1-0.33	0-0.57	0-0.1
Macroinvertebrates	0.52-0.66	0.25-1	0.2-0	0.55-0	0.16-0.09	0-1	1-0	0-0	0.4-0.46	0-0	1-0.62	0-0.38
Insecta	0.27-0.81	0.07-0.78	0.26-0.04	0.67-0.18	0.3-0.06	0-1	1-0	0-0	0.34-0.23	0.21-0	0.79-0.5	0-0.5
Palaeoptera	0.31-0.85	1-0.34	0-0	0-0.66	0.28-0.31	1-0.08	0-0.11	0-0.81	0.42-0.27	0-1	0.72-0	0.28-0
Heteroptera	0.34-0.52	0.82-0	0.05-0	0.13-1	0.1-0.14	1-1	0-0	0-0	0.38-0.14	0-1	0-0	1-0
Coleoptera	0.14-0.53	1-0.25	0-0.54	0-0.21	0.22-0.06	1-0	0-0	0-1	0.53-0.13	1-1	0-0	0-0
Diptera	0.59-0.71	0.11-1	0.29-0	0.6-0	0.45-0	0-0	0-0	1-0	0.26-0.17	0.61-0.39	0-0.57	0.39-0.04
Chironomidae	0.77-0.76	0.31-1	0.34-0	0.35-0	0.07-0	1-0	0-0	0-0	0-0.07	0-0	0-0	0-1
Mollusca	0.1-0.1	0-1	0-0	1-0	0.15-0.63	0-1	0-0	1-0	0.16-0.23	0-1	1-0	0-0
Amphibia	0.7-0.28	0-1	0.88-0	0.12-0	0.74-0.25	0-1	0.76-0	0.24-0	0.78-0.49	0-0.65	0.8-0.35	0.2-0

Supplementary Material 2: Results of PERMDISP test in total environmental, limnological and climate heterogeneity. Comparisons between sampling periods within the same biogeographic region, and between regions at different sampling periods are shown, including the heterogeneity difference and the significance values (p values).

	Total environmental heterogeneity		**Limnological heterogeneity**		**Climate heterogeneity**	
	Difference	**p value**	**Difference**	**p value**	**Difference**	**p value**
Between sampling periods (within tropical region)						
Period 2 - Period 1	-0.244	0.859	-0.548	0.476	-	-
Period 3 - Period 1	-0.173	0.927	-0.520	0.511	-	-
Period 3 - Period 2	0.071	0.987	0.027	0.998	-	-
Between sampling periods (within mediterranean region)						
Period 2 - Period 1	-0.149	0.965	-0.460	0.595	-	-
Period 3 - Period 1	-0.312	0.856	-0.835	0.187	-	-
Period 3 - Period 2	-0.163	0.958	-0.375	0.708	-	-
Between regions (across sampling periods, mediterranean - tropical)						
All periods	0.419	0.2435	1.294	<0.001	-0.338	<0.001
Period 1	0.087	0.880	0.959	0.049	-0.336	0.0453
Period 2	0.477	0.387	1.434	0.002	-0.336	0.0453
Period 3	0.70	0.481	1.236	0.002	-0.336	0.0453

***Supplementary Material 3**:* Results of variation partitioning analyses with the spatio-temporal focus. Total explained variation (E+S+T), pure environmental ((E|(S+T))/(E+S+T)), pure spatial ((S|(E+T))(E+S+T)), pure temporal ((T|(E+S))(E+S+T)), spatially correlated environmental (((E∩S)|T)/(E+S+T)), spatio-temporal overlapped (((S∩T)|E)/(E+S+T)), temporally structured environmental (((E∩T)|S)/(E+S+T)) and spatio-temporally structured environmental effects ((E∩S∩T)/(E+S+T)), obtained for each metacommunity (tropical-mediterranean). Big taxonomic groups, whose results are described and discussed in the main manuscript, appear in bold font.

Group of organisms	E+S+T	(E|(S+T))/(E+S+T)	(S|(E+T))(E+S+T)	(T|(E+S))(E+S+T)	((E∩S)|T)/(E+S+T)	((S∩T)|E)/(E+S+T)	((E∩T)|S)/(E+S+T)	(E∩S∩T)/(E+S+T)
Bacteria	0.48-0.79	0.01-0.09	0.24-0.34	0-0.19	0.75-0	0-0	0-0.11	0-0.27
Archaea	0.62-0.78	0-0.08	0.25-0.41	0.06-0.11	0.4-0.11	0-0	0-0.21	0.28-0.08
Phytoplanton	0.47-0.66	0.33-0.21	0.26-0.14	0.07-0.13	0.12-0.31	0-0	0-0.07	0.21-0.14
Cyanobacteria	0.33-0.61	0.51-0.91	0.05-0	0-0	0.44-0.09	0-0	0-0	0-0
Chlorophyceae	0.41-0.5	1-0.83	0-0	0-0	0-0	0-0	0-0.17	0-0
Mixotrophic phytoplankton	0.31-0.38	0.07-0.66	0.37-0.04	0-0	0.13-0.3	0.25-0	0-0	0.19-0
Bacillariophyceae	0.21-0.4	0.03-0.18	0.64-0.01	0.02-0	0.13-0.8	0-0	0-0	0.18-0
Rotifera	0.3-0.92	0.09-0.18	0.27-0.2	0-0.15	0.5-0.29	0.12-0	0-0.09	0.03-0.09
Microcrustaceans	0.61-0.8	0-0.07	0.31-0.34	0.16-0.09	0.43-0.37	0-0	0.02-0	0.08-0.14
Branchiopoda	0.53-0.57	0.15-0.09	0.25-0.29	0-0	0.37-0.62	0.04-0	0-0	0.19-0
Copepoda	0.78-0.34	0-0.03	0.17-0.71	0.02-0	0.32-0.27	0.02-0	0-0	0.48-0
Ostracoda	0.37-0.75	0-0.07	0.12-0.35	0-0.17	0.88-0.17	0-0	0-0	0-0.24
Macroinvertebrates	0.81-0.86	0-0.15	0.44-0.24	0.18-0.18	0.11-0.26	0-0	0-0.09	0.27-0.08
Insecta	0.8-0.68	0.01-0.13	0.53-0.33	0.16-0.27	0.07-0.05	0-0	0-0	0.24-0.22
Palaeoptera	0.14-0.58	0.22-0.06	0.09-0.65	0-0.17	0.69-0	0-0	0-0	0-0.12
Heteroptera	0.54-0.34	0-0.37	0-0	0.97-0.36	0-0	0.03-0	0-0.27	0-0
Coleoptera	0.37-0.34	0-0.03	0.27-0.71	0.24-0	0.1-0.26	0-0	0-0	0.38-0
Diptera	0.55-0.11	0-0.63	0.41-0	0.05-0.37	0.28-0	0-0	0-0	0.26-0
Chironomidae	0.35-0.07	0-1	1-0	0-0	0-0	0-0	0-0	0-0
Mollusca	0.6-0.27	0.03-0	0.28-0	0.32-0	0-1	0-0	0-0	0.38-0
Amphibia	0.79-0.34	0-0.03	0.16-0.81	0.02-0	0.31-0.15	0-0	0-0	0.51-0

Capítulo 6: Higher alpha and gamma, but not beta diversity in tropical than in mediterranean temporary ponds: a spatial and temporal analysis.

Appendix 1: Parameter estimation and predicted diversity values by GLMs or Chao index, including both spatial and temporal approaches. Summarized results of PERMDISP analyses.

Table A1: Values with standard errors predicted by GLMs of alpha (species richness, transformed Shannon and Simpson diversities, and Pielou's evenness), spatial beta (Bray-Curtis index and the replacement and richness difference components) and gamma (Chao index) diversities. These are the values represented in Figure 3, for each taxon and region (tropical | mediterranean).

	Bacteria	**Archaea**	**Phytoplankton**	**Microinvertebrates**	**Macroinvertebrates**	**Amphibia**
Sampling period 1						
Alpha diversity						
Species richness	974.9±6.5 | 737.0±5.0	90.5±2.0 | 26.1±0.9	35.1±1.2 | 15.8±0.7	22.5±1.0 | 12.8±0.7	25.0±1.0 | 8.6±0.5	5.1±0.5 | 1.3±0.2
Shannon diversity	111.4±20.9 | 52.0±12.7	54.8±6.4 | 16.5±3.2	9.4±1.3 | 4.9±0.8	8.2±0.8 | 3.4±0.5	9.5±0.8 | 4.2±0.5	-
Simpson diversity	29.8±5.5 | 15.1±3.5	32.6±4.1 | 11.8±2.3	5.5±0.8 | 3.3±0.5	5.4±0.5 | 2.5±0.3	6.0±0.6 | 3.3±0.4	-
Pielou's evenness	0.65±0.02 | 0.57±0.02	0.88±0.01 | 0.83±0.03	0.53±0.05 | 0.57±0.04	0.61±0.04 | 0.48±0.04	0.68±0.02 | 0.61±0.05	-
Spatial beta diversity						
Bray-Curtis index	0.84±0.02 | 0.83±0.02	0.95±0.01 | 0.94±0.01	0.96±0.01 | 0.96±0.01	0.92±0.02 | 0.94±0.01	0.91±0.02 | 0.97±0.01	0.67±0.03 | 0.60±0.04
Replacement	0.84±0.02 | 0.83±0.02	0.86±0.02 | 0.87±0.02	0.86±0.02 | 0.85±0.02	0.86±0.02 | 0.86±0.02	0.82±0.02 | 0.88±0.02	0.56±0.03 | 0.39±0.04
Richness difference	0.00±0.00 | 0.00±0.00	0.08±0.02 | 0.07±0.01	0.10±0.02 | 0.11±0.02	0.05±0.01 | 0.08±0.01	0.09±0.02 | 0.08±0.01	0.12±0.02 | 0.21±0.03
Gamma diversity						
Chao index	10616.0±155.0 | 7485.4±107.0	862.4±24.3 | 293.6±16.1	443.1±42.4 | 302.8±43.7	179.0±17.2 | 138.9±15.9	443.7±52.9 | 143.5±16.8	24.7±1.2 | 7.0±0.4
Sampling period 2						
Alpha diversity						
Species richness	1288.7±7.5 | 569.0±4.4	120.4±2.3 | 15.3±0.7	28.5±1.1 | 19.8±0.8	20.2±0.9 | 20.2±0.8	22.0±1 | 8.6±0.5	5±0.5 | 2.0±0.3
Shannon diversity	188.5±27.2 | 32.1±10.0	79.7±7.8 | 9.3±2.4	8.3±1.2 | 6.0±0.9	7.1±0.7 | 4.9±0.5	10.5±0.8 | 3.9±0.5	-
Simpson diversity	49.9±7.1 | 13.8±3.3	53.5±5.3 | 7.0±1.7	5.4±0.8 | 4.1±0.6	4.5±0.5 | 3.2±0.4	7.0±0.6 | 3.1±0.4	-
Pielou's evenness	0.68±0.02 | 0.53±0.01	0.92±0.01 | 0.8±0.03	0.60±0.04 | 0.61±0.04	0.65±0.03 | 0.50±0.03	0.75±0.02 | 0.66±0.04	-
Spatial beta diversity						
Bray-Curtis index	0.82±0.02 | 0.79±0.02	0.91±0.02 | 0.96±0.01	0.95±0.01 | 0.95±0.01	0.91±0.02 | 0.91±0.01	0.91±0.02 | 0.94±0.01	0.59±0.03 | 0.54±0.02
Replacement	0.82±0.02 | 0.79±0.02	0.80±0.03 | 0.91±0.01	0.82±0.02 | 0.85±0.02	0.82±0.02 | 0.90±0.02	0.85±0.02 | 0.82±0.02	0.46±0.03 | 0.34±0.02
Richness difference	0.00±0.00 | 0.00±0.00	0.11±0.02 | 0.05±0.01	0.13±0.02 | 0.10±0.01	0.09±0.02 | 0.01±0.01	0.06±0.02 | 0.12±0.02	0.13±0.02 | 0.20±0.02
Gamma diversity						
Chao index	12852.2±164.6 | 6683.5±114.4	958.9±26.0 | 273.1±23.2	346.1±27.9 | 320.8±33.9	187.8±16.2 | 138.0±8.9	266.3±29.8 | 120.8±16.3	23.3±1.8 | 7.0±0.4

Table A1: Continued

Sampling period 3						
Alpha diversity						
Species richness	1090.9±6.9 | 489.7±4.1	125.0±2.3 | 16.6±0.8	37.5±1.3 | 17.4±0.8	20.1±0.9 | 22.8±0.9	27.0±1.1 | 12.9±0.7	4.2±0.4 | 1.7±0.2
Shannon diversity	135.0±23.0 | 37.7±10.8	77.5±7.7 | 10.1±2.5	11.2±1.4 | 5.8±0.9	7.5±0.8 | 5.8±0.6	11.1±0.8 | 5.1±0.5	-
Simpson diversity	44.1±6.6 | 16.1±3.6	49.4±5.1 | 7.6±1.8	6.5±0.8 | 3.9±0.6	4.9±0.5 | 3.8±0.4	7.7±0.6 | 3.6±0.4	-
Pielou's evenness	0.65±0.02 | 0.57±0.01	0.90±0.01 | 0.80±0.03	0.60±0.04 | 0.54±0.05	0.62±0.03 | 0.54±0.02	0.71±0.03 | 0.64±0.03	-
Spatial beta diversity						
Bray-Curtis index	0.84±0.02 | 0.78±0.02	0.91±0.02 | 0.95±0.01	0.95±0.01 | 0.97±0.01	0.91±0.02 | 0.89±0.02	0.86±0.02 | 0.87±0.02	0.60±0.03 | 0.59±0.03
Replacement	0.84±0.02 | 0.78±0.02	0.80±0.03 | 0.89±0.02	0.84±0.02 | 0.89±0.02	0.86±0.02 | 0.88±0.02	0.77±0.03 | 0.72±0.02	0.45±0.03 | 0.40±0.03
Richness difference	0.00±0.00 | 0.00±0.00	0.11±0.02 | 0.06±0.01	0.11±0.02 | 0.08±0.01	0.05±0.01 | 0.02±0.01	0.09±0.02 | 0.15±0.02	0.15±0.02 | 0.18±0.02
Gamma diversity						
Chao index	11382.0±152.0 | 5145.1±82.8	852.1±20.8 | 233.8±20.5	345.0±23.0 | 240.6±21.1	164.4±13.1 | 182.5±22.2	273.3±29.8 | 160.4±18.2	18.4±2.2 | 7.0±0.4

Table A2**:** Parameter estimation in Generalised Linear Models predicting alpha (transformed Shannon and Simpson diversities, and Pielou's evenness) and spatial beta diversity (species replacement and richness difference partitions, using Bray-Curtis index except Sørensen for Amphibia) for each group of organisms. Asterisks indicate significant results (p-value < 0.05). Reference levels for categorical variables are the mediterranean region and the first sampling period.

Model	**Intercept**	**Region (Tropical)**	**Sampling period 2**	**Sampling period 3**	**Region (Tropical): Sampling period (2) interaction**	**Region (Tropical): Sampling period (3) interaction**
Shannon diversity						
Bacteria	3.952*	0.761*	-0.484	-0.322	1.01*	0.514
Archaea	2.806*	1.199*	-0.573	-0.490	0.947*	0.837*
Phytoplankton	1.598*	0.644*	0.192	0.166	-0.323	0.004
Microinvertebrates	1.220*	0.884*	0.362*	0.535*	-0.505*	-0.626*
Macroinvertebrates	1.445*	0.811*	-0.073	0.185	0.172	-0.034
Simpson diversity						
Bacteria	2.713*	0.682*	-0.087	0.069	0.603	0.322
Archaea	2.465*	1.018*	-0.522	-0.442	1.019*	0.858*
Phytoplankton	1.198*	0.499*	0.205	0.165	-0.214	0.010
Microinvertebrates	0.896*	0.788*	0.281	0.434*	-0.455*	-0.539*
Macroinvertebrates	1.193*	0.605*	-0.056	0.088	0.196	0.150
Pielou's evenness						
Bacteria	0.273*	0.292*	-0.139	0.002	0.344*	0.061
Archaea	1.558*	0.459	-0.197	-0.197	0.650	0.368
Phytoplankton	0.273	-0.146	0.160	-0.131	0.120	0.402
Microinvertebrates	-0.076	0.508*	0.071	0.217	0.130	-0.169
Macroinvertebrates	0.437*	0.314	0.233	0.119	0.126	0.012
Species replacement						
Bacteria	1.593*	0.062	-0.240*	-0.354*	0.0970	0.344*
Archaea	1.868*	-0.015	0.401*	0.180*	-0.891*	-0.658*
Phytoplankton	1.706*	0.082	0.052	0.436*	-0.331*	-0.562*
Microinvertebrates	1.805*	0.035	0.368*	0.151	-0.688*	-0.170
Macroinvertebrates	2.024*	-0.499*	-0.513*	-1.081*	0.685*	0.758*
Amphibia	-0.441*	0.666*	-0.212	0.044	-0.181	-0.455*

Table A2: Continued

Richness difference						
Bacteria	-7.811*	1.560*	-0.459*	0.110	0.598*	-0.053
Archaea	-2.578*	0.172	-0.356*	-0.101	0.721*	0.460*
Phytoplankton	-2.086*	-0.105	-0.065	-0.386*	0.419*	0.459*
Microinvertebrates	-2.442*	-0.403*	-1.961*	-1.636*	2.505*	1.617*
Macroinvertebrates	-2.409*	0.061	0.439*	0.705*	-0.819*	-0.692*
Amphibia	-1.342*	-0.665*	-0.056	-0.149	0.143	0.392*

Table A3: Results of PERMDISP test in total environmental, limnological and climate heterogeneity. Comparisons between sampling periods within the same biogeographic region, and between regions at different sampling periods are shown, including the heterogeneity difference and the significance values (p values).

	Total environmental heterogeneity		**Limnological heterogeneity**		**Climate heterogeneity**	
	Difference	**p value**	**Difference**	**p value**	**Difference**	**p value**
Between sampling periods (within tropical region)						
Period 2 - Period 1	-0.244	0.859	-0.548	0.476	-	-
Period 3 - Period 1	-0.173	0.927	-0.520	0.511	-	-
Period 3 - Period 2	0.071	0.987	0.027	0.998	-	-
Between sampling periods (within mediterranean region)						
Period 2 - Period 1	-0.149	0.965	-0.460	0.595	-	-
Period 3 - Period 1	-0.312	0.856	-0.835	0.187	-	-
Period 3 - Period 2	-0.163	0.958	-0.375	0.708	-	-
Between regions (across sampling periods. mediterranean - tropical)						
All periods	0.419	0.2435	1.294	<0.001	-0.338	<0.001
Period 1	0.087	0.880	0.959	0.049	-0.336	0.0453
Period 2	0.477	0.387	1.434	0.002	-0.336	0.0453
Period 3	0.70	0.481	1.236	0.002	-0.336	0.0453

Table A4: Parameter estimation in Generalised Linear Models temporal variation of alpha (coeffient of variation of species richness, transformed Shannon and Simpson diversities) and beta diversity (total and its partition into species replacement and richness difference, using Bray-Curtis index except Sørensen for Amphibia) in each pond for each group of organisms. Asterisks indicate significant results (p-value < 0.05). Reference level is the mediterranean region.

Model	Intercept	Region (Tropical)	Model	Intercept	Region (Tropical)
Temporal α (CV species richness)			Temporal β (Bray-Curtis index)		
Bacteria	-1.127*	-0.075	Bacteria	1.207*	-0.128
Archaea	-0.682*	-0.022	Archaea	2.072*	-0.367
Phytoplankton	-0.880*	-0.149	Phytoplankton	2.532*	-0.342
Microinvertebrates	-0.917*	-0.291	Microinvertebrates	0.352*	0.352
Macroinvertebrates	-0.671*	-0.651*	Macroinvertebrates	2.105*	-0.402
Amphibia	-0.056*	-0.056	Amphibia	-0.391*	0.347*
Temporal α (CV Shannon diversity)			Temporal β (Replacement)		
Bacteria	-0.763*	0.161	Bacteria	1.205*	-0.138
Archaea	-0.644*	-0.058	Archaea	1.446*	-0.388
Phytoplankton	-0.635*	0.036	Phytoplankton	1.312*	-0.110
Microinvertebrates	-0.893*	0.157	Microinvertebrates	0.900*	0.268
Macroinvertebrates	-0.962*	0.007	Macroinvertebrates	1.162*	-0.179
Amphibia	-	-	Amphibia	-1.444*	0.559
Temporal α (CV Simpson diversity)			Temporal β (Richness difference)		
Bacteria	-0.931*	0.242	Bacteria	-7.867*	1.794*
Archaea	-0.586*	-0.047	Archaea	-2.460*	0.305
Phytoplankton	-0.680*	0.087	Phytoplankton	-1.828*	-0.068
Microinvertebrates	-0.950*	0.242	Microinvertebrates	-2.398*	-0.004
Macroinvertebrates	-1.049*	0.264	Macroinvertebrates	-1.903*	-0.106
Amphibia	-	-	Amphibia	-1.309*	-0.097

Table A5: Values with standard errors predicted by GLMs of alpha (species richness and transformed Shannon and Simpson diversities) coefficient of variation and temporal beta (Bray-Curtis index and the replacement and richness difference components) diversities. These are the predicted values by the models whose predictor coefficient estimation is represented in Figure 5, for each taxon and region (tropical | mediterranean).

	Bacteria	Archaea	Phytoplankton	Microinvertebrates	Macroinvertebrates	Amphibia
Alpha diversity CV						
Species richness	0.30±0.04 | 0.32±0.03	0.49±0.06 | 0.51±0.06	0.36±0.04 | 0.41±0.04	0.30±0.04 | 0.40±0.04	0.27±0.04 | 0.51±0.05	0.33±0.05 | 0.35±0.06
Shannon diversity	0.55±0.06 | 0.47±0.05	0.50±0.06 | 0.53±0.06	0.55±0.06 | 0.53±0.05	0.48±0.04 | 0.41±0.04	0.38±0.05 | 0.38±0.05	-
Simpson diversity	0.50±0.06 | 0.39±0.05	0.53±0.06 | 0.56±0.06	0.55±0.06 | 0.51±0.05	0.49±0.05 | 0.39±0.04	0.46±0.05 | 0.35±0.04	-
Temporal beta diversity						
Bray-Curtis index	0.75±0.09 | 0.77±0.08	0.85±0.08 | 0.89±0.06	0.90±0.06 | 0.93±0.05	0.85±0.08 | 0.79±0.08	0.85±0.08 | 0.90±0.06	0.49±0.10 | 0.38±0.12
Replacement	0.74±0.09 | 0.77±0.08	0.74±0.09 | 0.79±0.08	0.77±0.09 | 0.79±0.08	0.76±0.09 | 0.71±0.08	0.73±0.09 | 0.77±0.08	0.29±0.09 | 0.18±0.10
Richness difference	0.00±0.01 | 0.00±0.00	0.10±0.06 | 0.10±0.06	0.13±0.07 | 0.14±0.06	0.08±0.06 | 0.08±0.05	0.12±0.07 | 0.12±0.06	0.20±0.08 | 0.20±0.10

Appendix 2: Sample coverage by taxa and region

Figure A1: Proportion of sample coverage (in terms of species richness) by number of sampling units (pond samples) for each group of organisms at both tropical (lilac) and mediterranean (orange) regions, in sampling period 1 (A), 2 (B) and 3 (C). Solid line for observed coverage and dashed line for extrapolated coverage.

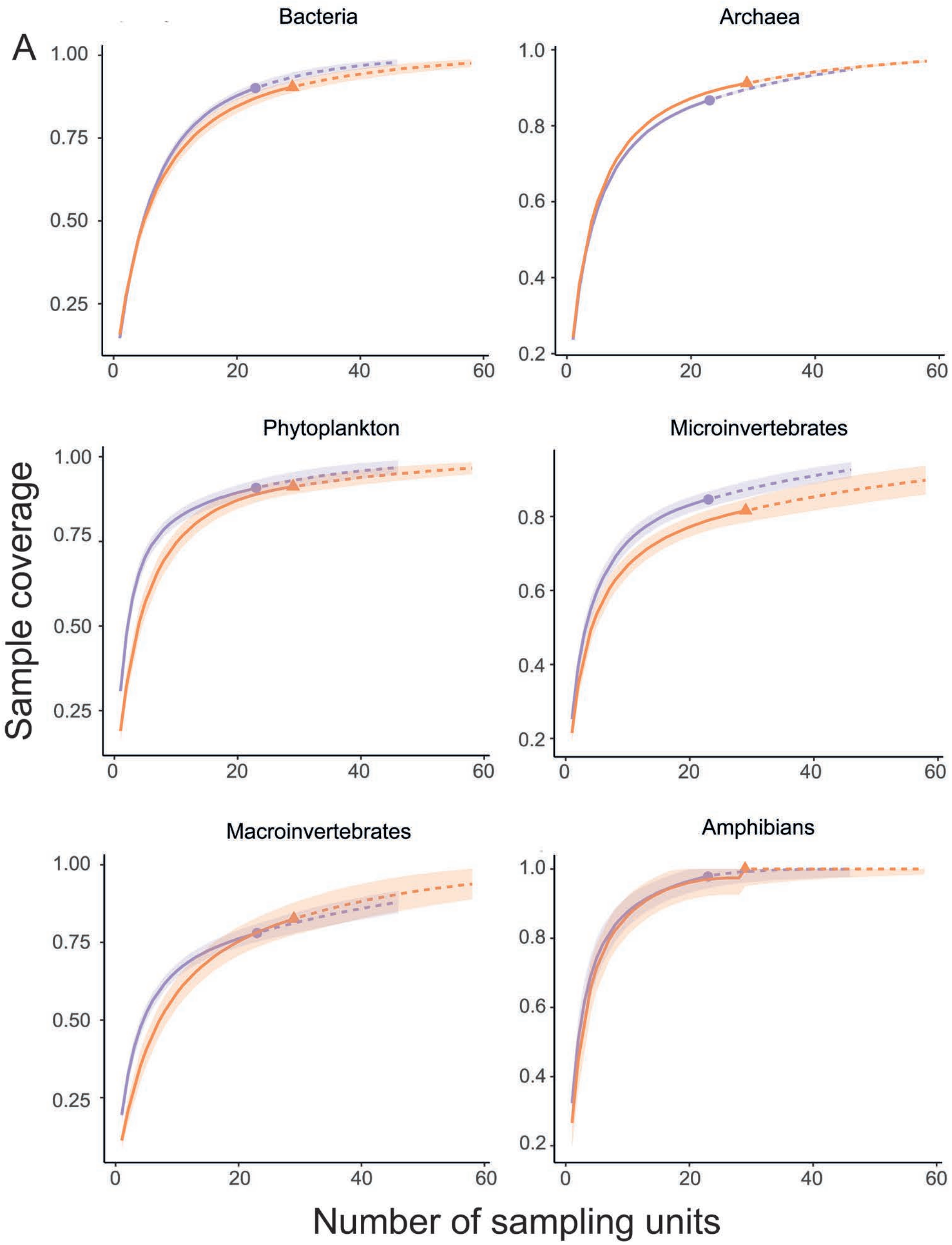


Figure A1: Continued

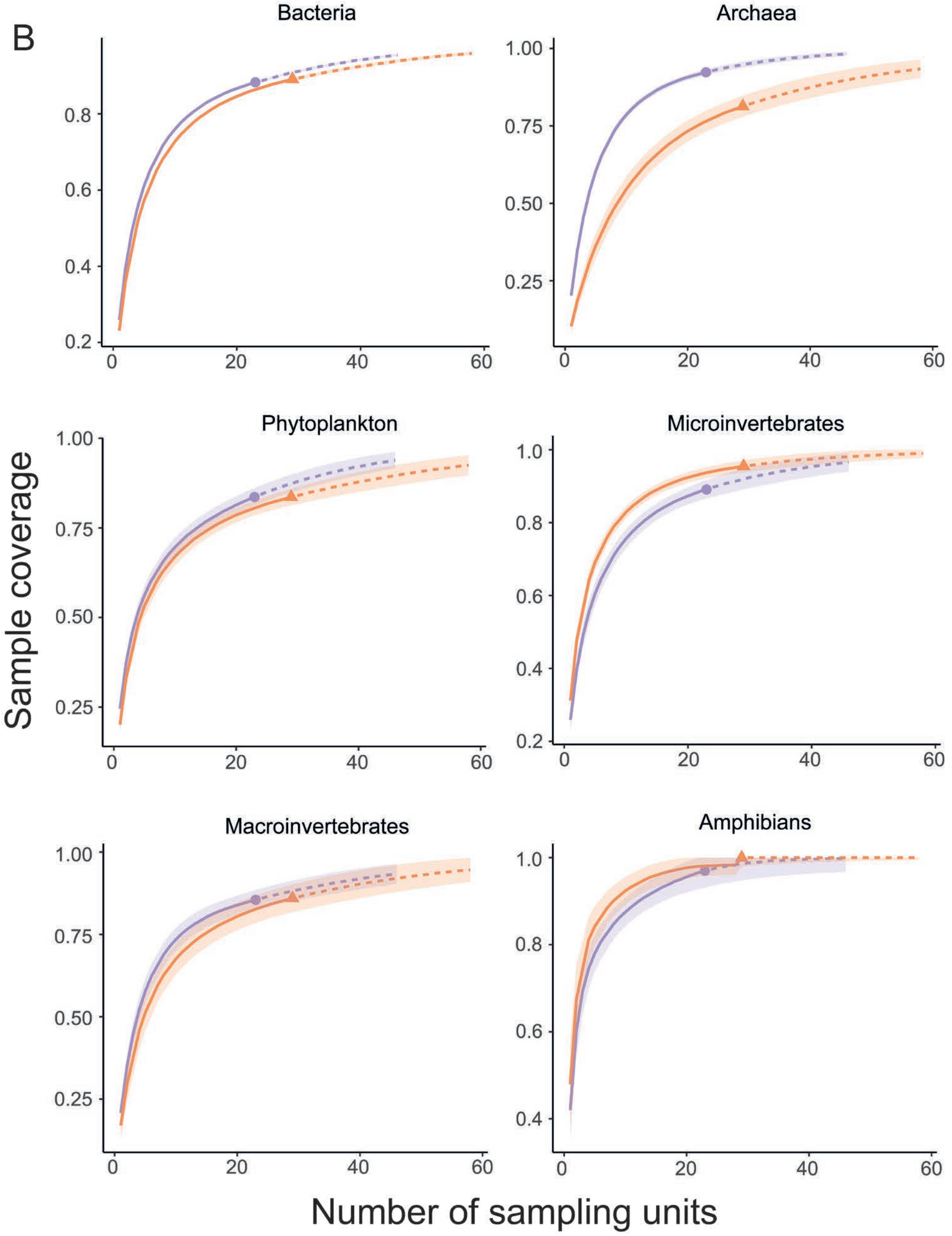


Figure A1: Continued