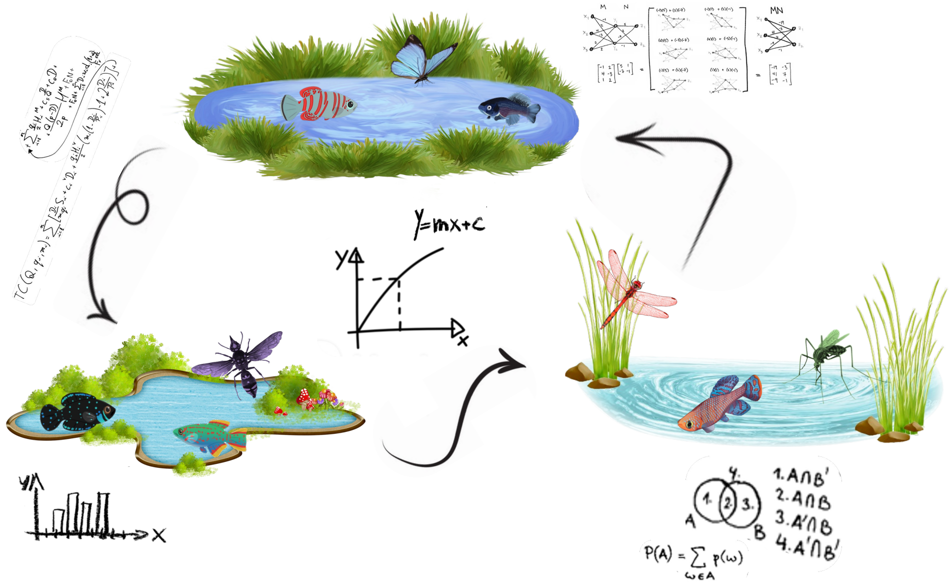
Tamaño corporal, dispersión y ensamblaje de metacomunidades

Hacia una comprensión mecanicista de procesos atributo-dependientes en un contexto metacomunitario

Tesis de Doctorado



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Tamaño corporal, dispersión y ensamblaje de metacomunidades

Hacia una comprensión mecanicista de procesos atributo-dependientes en un contexto metacomunitario

Tesis para la obtención de grado de Doctor en Ciencias Biológicas por el Programa de Desarrollo de las Ciencias Básicas (PEDECIBA), Universidad de la República (UdelaR).

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Resumen general

1. Entender la dinámica de ensamblaje de especies y redes de interacciones requiere comprender la interrelación entre los atributos de las especies, los procesos de dispersión y deriva, y la diversidad regional. Esto implica un cambio en la visión tradicional en ecología de comunidades basada en procesos locales y en la identidad taxonómica de las especies hacia una teoría que vincule procesos locales y regionales, comprendiendo el rol de los atributos y el azar en el desempeño de las especies. En las últimas dos décadas, la Teoría de Metacomunidades ha consolidado ese papel. Sin embargo, su desarrollo es incipiente, y en varias áreas está basada principalmente en evidencias teóricas y los estudios empíricos rara vez alcanzan un análisis explícito de los mecanismos involucrados.

2. Esta tesis se enfoca en la evaluación teórica y empírica de los mecanismos involucrados en el proceso de ensamblaje de comunidades y redes tróficas, basados en la dispersión y atributos de las especies. Específicamente, se utilizaron herramientas de simulación y modelado estadístico para evaluar cómo el tamaño corporal, a través de su efecto en la dispersión, densidad, diversidad y procesos de selección de presas, determina la estructura y diversidad de metacomunidades y sus redes tróficas.

3. La teoría de metacomunidades ha identificado a la dispersión, la diversidad regional y la cantidad de individuos en una comunidad como determinantes primarios de los patrones de biodiversidad. Si bien la dependencia de la capacidad de dispersión con el tamaño corporal ha sido explícitamente considerada, el efecto de los bien reportados escalamientos en densidad local y diversidad regional con el tamaño corporal sobre la diversidad han sido mayoritariamente ignorados. En el Capítulo 1, por medio de un modelo metacomunitario neutral, se evaluó cómo la interacción entre estos escalamientos determina la diversidad α, β y γ de las metacomunidades. El escalamiento positivo entre dispersión y tamaño corporal tiende a incrementar la diversidad α y reducir la diversidad β con el aumento en tamaño corporal. Este efecto contrarresta las consecuencias opuestas de la reducción en diversidad regional y densidad con el tamaño de los organismos.

4. La existencia de una relación negativa entre diversidad beta y dispersión ha sido ampliamente considerada en la teoría ecológica. Naturalmente, la teoría de

metacomunidades asume esta relación sesgando la forma en que ha sido puesta a prueba. No obstante, diversas evidencias empíricas y teóricas sugieren que la asociación diversidad beta-dispersión podría ser más compleja. En el segundo capítulo se evaluaron diversos mecanismos con el potencial de generar una relación positiva entre dispersión y diversidad beta. Para esto, se trabajó con un modelo metacomunitario que incorpora un gradiente en capacidad de dispersión (por ejemplo, asociado al tamaño corporal) y en la fuerza de selección local, en donde el desempeño de los individuos está determinado por el acople entre sus atributos y las características del ambiente (i.e. arreglo de especies). Se evaluó de forma explícita cómo el efecto prioridad (i.e. efecto de los tiempos y orden de llegada de las especies a cierta comunidad sobre sus abundancias finales) y el arreglo de especies interactúan con el efecto de masa (i.e. aumento en la probabilidad de persistencia local y recolonización dado por inmigración) en la determinación de la diversidad beta metacomunitaria. Los resultados de este capítulo muestran que los mecanismos evaluados tienen el potencial de generar un patrón en joroba en la diversidad beta a lo largo de un gradiente de dispersión, permitiendo avanzar en la comprensión mecanicista de este fenómeno. Estos resultados contradicen la conceptualización hegemónica de la dispersión como un proceso que homogeniza las comunidades, mientras que al mismo tiempo logran explicar una creciente masa de evidencia empírica que reporta un efecto positivo de la dispersión sobre la diversidad beta.

5. En el último capítulo, se analizó el sustento empírico hacia tres mecanismos no excluyentes con el potencial de generar patrones ampliamente reportados en redes tróficas. La evaluación de estos mecanismos (i.e. requerimiento energético, limitación en consumo por tamaño corporal y forrajeo óptimo) ha sido principalmente indirecta. Utilizando abordajes estadísticos provistos por la Teoría de Ensamblaje de Comunidades por Selección de Atributos (CATS), se evaluó de forma explícita el sustento a cada mecanismo en base a los patrones de selección de presas predichos por cada uno de ellos. Para esto se utilizó información de la dieta de un gremio de peces anuales que habitan una metacomunidad de charcos temporales en Rocha, Uruguay. Los resultados muestran que la estructura de la red trófica de los charcos temporales está determinada por la acción conjunta de estos tres mecanismos, pero que su acción depende del grupo trófico y tamaño de las presas consumidas.

6. El conjunto de abordajes empíricos y teóricos aquí desarrollados permiten avanzar en la conexión mecanicista entre dispersión, atributos y el ensamblaje de comunidades y redes tróficas. Esta tesis intenta contribuir al desarrollo de la teoría ecológica y a la comprensión de los patrones de diversidad de especies y estructuramiento de comunidades incorporando mecanismos poco atendidos hasta el momento, generando una conexión explícita entre la TM y marcos teóricos complementarios.

Introducción general

Entender el fenómeno de la biodiversidad requiere, necesariamente, entender los mecanismos de ensamblaje de comunidades y redes ecológicas (Arim *et al.* 2023; Shipley 2010; Shipley *et al.* 2006). Para ello, es preciso considerar explícitamente el rol que los atributos de las especies tienen en su desempeño, y cómo estos interactúan con procesos que operan a escala tanto local como regional (e.g. selección local vs. dispersión) en la determinación de los patrones de diversidad. El foco en las interacciones basadas en atributos para entender la diversidad es la esencia de la teoría de nicho clásica y contemporánea (Chase & Leibold 2003; Clements *et al.* 1929; Darwin 1859; Gause 1934; Hutchinson 1959). Sin embargo, la ecología de comunidades ha estudiado el proceso de ensamblaje desde una perspectiva fundamentalmente taxonómica (Cadotte *et al.* 2015; Mcgill *et al.* 2006; Shipley 2010). En este contexto, el foco ha estado en las dinámicas poblacionales y estabilidad de las interacciones entre pocas especies en base a su identidad taxonómica más que en sus atributos (Mcgill *et al.* 2006; Schmitz 2017). Si bien esta aproximación permitió entender la esencia de las interacciones directas o de bajo orden, no resulta adecuado para obtener principios generales sobre el proceso de ensamblaje de comunidades altamente diversas (Lawton 1999; Simberloff 2004). Esto se debe principalmente a tres motivos. Primero, evaluar de forma tanto teórica como empírica la dinámica poblacional de una gran cantidad de pares de especies es sumamente costoso en términos del número de parámetros que es necesario estimar y medir (Maurer 1999). Segundo, una aproximación taxonómica restringe las conclusiones obtenidas únicamente a los propios casos de estudio, perdiendo así poder predictivo y explicativo más allá de las idiosincrasias propias de los modelos de estudio utilizados (Lawton 1999; Marquet *et al.* 2014; Simberloff 2004). Tercero, utilizar como criterio de selección la identidad taxonómica de las especies no garantiza que realmente existan interacciones ecológicas entre ellas, ni que necesariamente respondan de manera similar a las mismas condiciones ambientales (Morin 2011; Vellend 2016). En este sentido, en las últimas dos décadas se ha puesto de manifiesto la necesidad re-enfocar la atención hacia el rol de los atributos de las especies como forma de entender de forma mecanicista el proceso de ensamblaje de comunidades (Des Roches *et al.* 2018; Enquist *et al.* 2015; Mcgill *et al.* 2006; Verberk *et al.* 2013; Violle *et al.* 2012).

Históricamente, el estudio del ensamblaje de las comunidades ecológicas estuvo centrado en la acción de procesos y mecanismos operantes a escala local, considerando a las comunidades como entidades aisladas ensambladas por interacciones especie-especie y especie-ambiente (Leibold *et al.* 2004). Sin embargo, durante las dos últimas décadas se ha producido un notable avance conceptual al reconocer que los patrones de diversidad y el estructuramiento de las redes ecológicas depende fuertemente de la interacción entre procesos que operan a escala tanto local como regional, dando paso a la teoría de metacomunidades (Leibold *et al.* 2004; Leibold & Chase 2018; Thompson *et al.* 2020; Thompson & Gonzalez 2017; Vellend 2016). Una metacomunidad puede definirse como un conjunto de comunidades locales conectadas por dispersión de individuos pertenecientes a diferentes especies con el potencial de interactuar entre sí (Gilpin & Hanski 1991; Leibold *et al.* 2004; Wilson 1992). Este marco conceptual permite integrar de forma explícita procesos que ocurren a diferentes escalas a través del flujo de individuos entre comunidades. Así mismo, permite realizar predicciones robustas acerca de los patrones de diversidad esperados en función de la tasa de dispersión entre comunidades (Economo & Keitt 2010; Mouquet & Loreau 2002, 2003), y su interacción con procesos de selección ambiental e interacciones bióticas (Cunillera-Montcusí *et al.* 2020; García-Girón *et al.* 2020; Heino 2013; Hill *et al.* 2017; Mouquet *et al.* 2006; Vanschoenwinkel *et al.* 2013).

El proceso de dispersión es un factor clave en el ensamblaje de comunidades y redes ecológicas a escala local y regional (Borthagaray *et al.* 2023b; Economo & Keitt 2010; Leibold & Chase 2018; Pillai *et al.* 2011). Por un lado, permite que especies con determinados atributos lleguen a aquellas comunidades donde son positivamente seleccionadas según las condiciones ambientales locales. Esto favorece que cada comunidad se ensamble con diferentes sub-conjuntos de especies según los atributos seleccionados localmente, a través del mecanismo de arreglo de especies el cual determina el ensamblaje de comunidades por procesos de nicho (Arim *et al.* 2023; Cunillera-Montcusí *et al.* 2020; Gianuca *et al.* 2017; Leibold *et al.* 2004; Suzuki & Economo 2021). A su vez, la dispersión aumenta la probabilidad de que las comunidades sean colonizadas por diferentes especies favoreciendo distintas composiciones alternativas a través del efecto prioridad, por el cual las abundancias locales de las especies están determinadas por sus tiempo y orden de llegada (Fukami 2005, 2015). Sin embargo, altas tasas de dispersión determinan que especies seleccionadas negativamente puedan persistir a nivel local por medio del mecanismo de efecto de masa, al disminuir la probabilidad de extinción local y permitir eventos de recolonización en función del nivel de inmigración desde comunidades vecinas (Leibold *et al.* 2004; Leibold & Chase 2018). Así, el mecanismo de efecto de masa disminuye la magnitud de los procesos de ensamblaje basados en atributos (i.e. arreglo de especies) permitiendo un ensamblaje comunitario dominado por procesos de deriva (Arim *et al.* 2023; Loke & Chisholm 2023; Suzuki & Economo 2021). En este sentido, la teoría de metacomunidades representa un marco teórico adecuado para analizar el rol de los atributos de las especies en el proceso de ensamblaje de comunidades y redes ecológicas (Arim *et al.* 2023; Cunillera-Montcusí *et al.* 2020, 2021; Leibold *et al.* 2017; Ortiz *et al.* 2023a). A pesar de esto, el avance teórico en esta área ha estado restringido por tres aspectos. En primer lugar, la mayoría de los estudios se han limitado a considerar atributos directamente asociados a la capacidad o modo de dispersión de los individuos, sin incorporar interacciones entre diferentes tipos de atributos o explorar como un mismo atributo puede afectar simultáneamente diferentes aspectos de las metacomunidades (Ortiz *et al.* 2023a). Segundo, incluso cuando el foco ha estado puesto en el rol de atributos asociados a la dispersión en el estructuramiento de comunidades, la forma en que esta ha sido manipulada en trabajos de campo y laboratorio elimina las diferencias en capacidades de dispersión entre especies (Grainger & Gilbert 2016; Logue *et al.* 2011; Vannette & Fukami 2017). La técnica más usada para simular eventos de dispersión entre parches consiste en la transferencia manual de una porción de una comunidad hacia otra (e.g. determinado volumen de agua en estudios acuáticos), forzando indefectiblemente a que todas las especies estén sujetas a la misma tasa de dispersión independientemente de sus atributos (Grainger & Gilbert 2016). En la misma línea, una gran parte de los trabajos empíricos diseñados para evaluar el rol de los atributos en el ensamblaje de las comunidades han trabajado con parches homogéneos, evitando así cualquier efecto asociado a la selección local (Grainger & Gilbert 2016). Esto inhibe que las comunidades sean ensambladas a través de mecanismos que involucran una interacción entre la dispersión y los procesos de selección local diferenciados entre comunidades, limitando así el avance de la teoría (Grainger & Gilbert 2016).

Tamaño corporal y tasas biológicas

Dentro de la amplia variedad de atributos observados en la naturaleza, el tamaño corporal es reconocido como una de las características más influyentes en el desempeño de las especies y estructuramiento de las comunidades y redes ecológicas (Brown 1995; Brown *et al.* 2004; Peters 1983; Woodward *et al.* 2005a, b). A través de su asociación positiva con la tasa metabólica de los organismos (Brown *et al.* 2004; Gillooly *et al.* 2001), el tamaño corporal está directamente relacionado con un gran número de tasas biológicas. Por ejemplo, grupos de mayor tamaño presentan una mayor demanda energética (Brown *et al.* 2004; Gillooly *et al.* 2001), mayor tasa de crecimiento somático (Hatton *et al.* 2019), una mayor percepción de la escala espacial del paisaje (Borthagaray *et al.* 2014, 2015a; Ritchie 2010; Ritchie & Olff 1999; Rodríguez-Tricot & Arim 2020) y menor tasa de mortalidad (Hatton *et al.* 2019). Además, depredadores más grandes presentan un aumento en el tamaño (Brose *et al.* 2006a, 2019) y biomasa (Perkins *et al.* 2022) de presas consumidas, así como un incremento en las tasas de consumo asociado a la reducción en los tiempos de manipulación de sus presas (Pawar *et al.* 2015). A su vez, el tamaño corporal es un atributo fácilmente medible por lo que resulta sencillo obtener datos fidedignos a partir de estudios de campo y laboratorio.

Tamaño corporal y ensamblaje de metacomunidades #1: relación tamaño-diversidad

En un contexto metacomunitario, el tamaño corporal ha estado en el centro de atención debido a su asociación positiva con la capacidad de dispersión (i.e. tasa de intercambio de individuos entre comunidades locales) (De Bie *et al.* 2012; Heino *et al.* 2017a; Jenkins *et al.* 2007) y locomoción (e.g. velocidad máxima y maniobrabilidad) (Cloyed *et al.* 2021; Domenici 2001; Hirt *et al.* 2017) de los individuos. Un incremento moderado en la tasa de dispersión entre comunidades favorece la diversidad local por efecto de masa pero homogeniza a las comunidades (Borthagaray *et al.* 2020; Cadotte 2006; Carrara *et al.* 2012; Economo & Keitt 2010; Grainger & Gilbert 2016; Mouquet & Loreau 2003). Consecuentemente, organismos con mayor tamaño corporal deberían presentar una mayor diversidad α así como una menor diversidad β respecto a taxa de menor tamaño. Sin embargo, es reconocido que aquellos taxa más grandes también presentan una menor densidad local (Arim *et al.* 2011; Damuth 1981; Marquet *et al.* 1990; White *et al.* 2007) y menor diversidad a escala regional (Gaston & Blackburn 2000). La reducción en densidad local con el tamaño aumenta la probabilidad de extinción de poblaciones locales, haciendo que taxa de mayor tamaño presenten menor diversidad α que taxa pequeños (Storch *et al.* 2018). Así mismo, dado que es esperable que estas extinciones afecten mayoritariamente a las especies raras, las comunidades estarían representadas principalmente por aquellas especies comunes reduciendo también la diversidad β y γ. Adicionalmente, el escalamiento negativo en diversidad regional con el tamaño corporal lleva a que aquellos taxa de mayor tamaño estén representados por un número reducido de especies en el pool regional, limitando nuevamente la diversidad α, β y γ de grupos grandes respecto a taxa chicos a escala metacomunitaria. De esta forma, es esperable que los patrones de diversidad en metacomunidades estén determinados por la acción conjunta de estos tres escalamientos. Sin embargo, y a pesar de estar en el centro de la teoría, a la fecha ningún trabajo se ha enfocado en su evaluación formal.

Tamaño corporal y ensamblaje de metacomunidades #2: relación diversidad β-dispersión

Por otro lado, la relación entre diversidad β y dispersión también ha estado en el centro de la teoría ecológica desde hace décadas, en especial en el marco de metacomunidades. El proceso de dispersión ha sido conceptualizado como una fuerza que tiende a homogenizar las comunidades locales reduciendo la diversidad β (Grainger & Gilbert 2016; Gu *et al.* 2023; Heino & Tolonen 2017; Loreau 2000; Loreau & Mouquet 1999; Mouquet & Loreau 2003; Soininen *et al.* 2007). El sustento empírico hacia el efecto homogeneizador de la dispersión es notable (Catano *et al.* 2017; Grainger & Gilbert 2016; Lu 2021). A pesar de esto, trabajos teóricos y empíricos recientes han evidenciado relaciones más complejas entre la dispersión y diversidad β, incluyendo tendencias positivas o en joroba (Lu 2021; Vannette & Fukami 2017). Uno de los mecanismos planteados para explicar la relación positiva entre diversidad β y dispersión es el efecto prioridad, donde el orden y tiempo de llegada de las especies a las comunidades tiene el potencial de generar composiciones alternativas (i.e. contingencia histórica) (Fukami 2010, 2015). Un incremento moderado en la tasa de dispersión favorece que las comunidades sean potencialmente colonizadas por una mayor variedad de especies, las cuales tienden a dominar localmente al tener mayor tiempo para acaparar los recursos disponibles y/o modificar el ambiente a su favor (Fukami 2015). La diferenciación comunitaria mediada por efecto prioridad ha sido particularmente propuesta bajo un escenario en donde las especies presenten capacidades de dispersión similares. De lo contrario, las comunidades locales serían ensambladas siguiendo una secuencia de colonización determinista, en donde las mismas especies con alta capacidad de dispersión colonizarían y dominarían gran parte de las comunidades (Fukami 2015). Notablemente, y en oposición a este planteo, la variabilidad en capacidad de dispersión entre especies ha sido recientemente identificada como un determinante del nivel de diferenciación entre comunidades (Vannette & Fukami 2017). Esta variabilidad, la cual puede estar asociada a diferencias en tamaño corporal entre taxa, permite que las comunidades sean colonizadas por especies con diferentes capacidades de dispersión cuando la dispersión alcanza valores intermedios, favoreciendo diferentes composiciones alternativas a través del efecto prioridad (Vannette & Fukami 2017). A pesar de la importancia que tendría este novedoso mecanismo en el ensamblaje de metacomunidades, a la fecha solamente ha sido inferido de forma indirecta faltando aún una evaluación formal del mismo.

Tamaño corporal y ensamblaje de redes tróficas #3: mecanismos de selección de presas basados en atributos

En el área de las redes tróficas, el tamaño corporal ha sido identificado con un atributo clave en su estructuramiento y estabilidad (Allhoff *et al.* 2015; Arim *et al.* 2011; Brose *et al.* 2006b; Ortiz *et al.* 2023b; Ortiz & Arim 2016; Ramos-Jiliberto *et al.* 2011; Woodward *et al.* 2005b). Existen tres patrones estructurales ampliamente reportados en la literatura asociados al tamaño corporal de los depredadores. Específicamente, depredadores de mayor tamaño presentan un aumento en su posición trófica (Arim *et al.* 2010; Dantas *et al.* 2019; Potapov *et al.* 2019; Romanuk *et al.* 2011), así como un aumento en la diversidad y tamaño de las presas que consumen (Araújo *et al.* 2010; Arim *et al.* 2010; Brose *et al.* 2019; Cohen *et al.* 1993, 2003; Miller-ter Kuile *et al.* 2022; Nordström *et al.* 2015; Ortiz & Arim 2016; Ramos-Jiliberto *et al.* 2011; Woodward & Hildrew 2002). Estos patrones han sido explicados a través de la acción de tres mecanismos no excluyentes asociados a los atributos de presas y depredadores. El primero consiste en el aumento en demanda energética asociada al tamaño corporal el cual determina que depredadores de mayor tamaño consuman un mayor número de presas independientemente de sus atributos (Brown *et al.* 2004; McNab 2002). Segundo, el progresivo relajamiento en la restricción de consumo a medida que los depredadores aumentan su tamaño (i.e. gape limitation) permite un aumento gradual tanto en la diversidad como tamaño de presas consumidas (Hairston 1993; Layman *et al.* 2005). Por último, a través del mecanismo de forrajeo óptimo, depredadores más grandes consumen presas de mayor tamaño y retorno energético respecto a depredadores más pequeños (Carbone *et al.* 1999; Mittelbach 1981; Sherwood *et al.* 2002). Estos tres mecanismos generan patrones de selección de presas claramente distinguibles en función del tamaño de los depredadores y atributos de sus presas. El mecanismo de demanda energética supone que las presas no están sometidas a ningún tipo de selección basada en sus atributos, lo que determina un consumo atributo-independiente. Bajo el mecanismo de restricción de consumo por tamaño corporal se espera que depredadores chicos consuman únicamente presas de pequeño tamaño, siendo las presas grandes negativamente seleccionadas. Esta preferencia hacia presas pequeñas es progresivamente relajada hacia depredadores de mayor tamaño, los cuales seleccionan tanto presas chicas como grandes por igual. Alternativamente, y dado que el contenido energético de una presa está asociado a su tamaño y nivel trófico (Lazzaro 1987; McNab 2002; Sih 1980), bajo el mecanismo de forrajeo óptimo se espera que depredadores grandes seleccionen sistemáticamente presas grandes en posiciones tróficas altas (e.g. presas carnívoras) respecto a depredadores pequeños, los cuales seleccionan presas chicas pertenecientes a niveles tróficos bajos (e.g. productores primarios). Esta distinción entre las predicciones hechas por cada mecanismo permitiría evaluar directamente su importancia relativa en la determinación del aumento sistemático en posición trófica, diversidad y tamaño de presas de los depredadores. Sin embargo, su evaluación se ha realizado mayoritariamente de forma indirecta a partir de la interpretación de patrones de representación de atributos de presas en la dieta de los depredadores respecto a los atributos observados en el ambiente (e.g. (Devries *et al.* 1998; Schael *et al.* 1991; Werner & Hall 1974)).

Esta tesis

La presente tesis se centra en la identificación, formalización y evaluación de mecanismos atributo-dependientes claves en el ensamblaje de las metacomunidades. Se pone el foco en mecanismos poco explorados por la teoría de metacomunidades o inferidos indirectamente a partir de patrones. Para esto se utiliza una variedad de aproximaciones metodológicas basades en herramientas de simulación y análisis estadístico de datos obtenidos en una metacomunidad de charcos temporales ubicados en la cuenca de la Laguna de Castillos, Rocha.

Objetivo general

Contribuir a la comprensión mecanicista de los procesos de ensamblaje de metacomunidades y redes tróficas basados en la interacción entre los atributos de las especies y procesos de selección y dispersión.

Objetivos específicos

OE_1: Evaluar el potencial efecto de los escalamientos con el tamaño corporal en dispersión, densidad local y diversidad regional sobre los patrones de diversidad y la relación diversidad–tamaño corporal en metacomunidades.

OE_2: Evaluar el papel de la dispersión en la magnitud del efecto prioridad y del arreglo de especies, así como sus consecuencias, en la relación diversidad β-dispersión en metacomunidades.

OE_3: Evaluar la importancia relativa que tienen los mecanismos de demanda energética, restricción de consumo por tamaño corporal y forrajeo óptimo en el ensamblaje de las redes tróficas en metacomunidades.

Estos objetivos se abordan a lo largo de los siguientes capítulos aplicando aproximaciones metodológicas complementarias. En el Capítulo 1 se aplica un modelo de lotería que simula el ensamblaje de metacomunidades considerando el efecto del tamaño corporal en la capacidad de dispersión, densidad local y diversidad regional de un grupo de taxa de alta jerarquía taxonómica (e.g. órdenes o familias) que varían en su tamaño corporal. De esta forma, se evalúa cómo la interacción entre estos tres escalamientos determina los patrones de diversidad α, β y γ a lo largo del gradiente de tamaño corporal de los taxa. Los resultados asociados a este capítulo se encuentran publicados en Biology Letters (DOI: 10.1098/rsbl.2022.0618). En el Capítulo 2 se aplica un modelo de lotería que también simula el proceso de ensamblaje de metacomunidades incluyendo selección local y dispersión diferencial entre especies. Así, se analiza cómo el tiempo de llegada de las especies a las comunidades locales y la selección diferencial de atributos determina la relación diversidad β−dispersión a través de los mecanismos de efecto prioridad y arreglo de especies. En el Capítulo 3 se aplica el abordaje estadístico CATS (i.e. Ensamblaje de Comunidades por Selección de Atributos) para analizar los patrones de selección de presas a lo largo de un gradiente de tamaño corporal de depredadores, evaluando explícitamente la importancia relativa de los mecanismos de selección de rasgos de presas involucrados. Para esto se utiliza como modelo de estudio un ensamble de peces anuales que habitan una metacomunidad de charcos temporales, el cual ha sido ampliamente analizado en estudios anteriores (Arim *et al.* 2010, 2011; Canavero *et al.* 2014; Ortiz & Arim 2016). Los resultados de este tercer capítulo se encuentran publicados en Plos One (DOI: 10.1371/journal.pone.0292374). Por último, se presenta una síntesis de los principales resultados de la tesis, y se plantean preguntas y perspectivas importantes a transitar en el futuro.

Capítulo 1:

Escalamiento de tasas biológicas con el tamaño corporal como columna vertebral en el ensamblaje de patrones de diversidad en metacomunidades

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Community ecology

Scaling of biological rates with body size as a backbone in the assembly of metacommunity biodiversity

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The dispersal–body mass association has been highlighted as a main determinant of biodiversity patterns in metacommunities. However, less attention has been devoted to other well-recognized determinants of metacommunity diversity: the scaling in density and regional richness with body size. Among active dispersers, the increase in movement with body size may enhance local richness and decrease β-diversity. Nevertheless, the reduction of population size and regional richness with body mass may determine a negative diversity–body size association. Consequently, metacommunity assembly probably emerges from a balance between the effect of these scalings. We formalize this hypothesis by relating the exponents of size-scaling rules with simulated trends in α-, β- and γ-diversity with body size. Our results highlight that the diversity–body size relationship in metacommunities may be driven by the combined effect of different scaling rules. Given their ubiquity in most terrestrial and aquatic biotas, these scaling rules may represent the basic determinants—backbone—of biodiversity, over which other mechanisms operate determining metacommunity assembly. Further studies are needed, aimed at explaining biodiversity patterns from functional relationships between biological rates and body size, as well as their association with environmental conditions and species interactions.

Introduction

Body size is a key attribute that shapes community assembly at several scales [1–4]. In a metacommunity context, body size is related to three well-recognized determinants of metacommunity diversity: dispersal ability, local density and regional species richness (figure 1*a*) [5]. Despite their recognized potential for shaping diversity, metacommunity theory has devoted more attention to the scaling in dispersal ability than to other scaling relations [5–7]. For taxa exhibiting active dispersal strategies, dispersal ability increases with body mass [6,8]. Besides, dispersal has the potential to increase local diversity and to reduce β-diversity, provided that it is not large enough to homogenize the system [9–11]. Consequently, if the positive dispersal ability–mass scaling is considered in isolation, larger sized taxa should present higher local richness and lower β-diversity, as compared to smaller sized taxa.

In addition to the positive relation between body size and dispersal, the well-reported negative scaling in population density and regional richness with taxon body mass may contribute to explain the among-taxa differences in metacommunity diversity. Local density scales negatively with the mass of individuals [2,12,13]. Consequently, larger sized taxa present lower potential numbers of

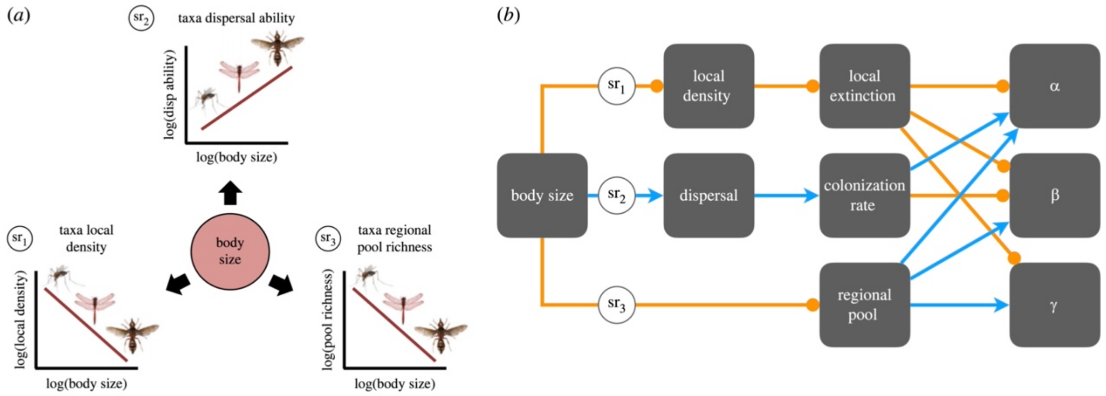

Figure 1. (*a*) Schematic representation showing empirical body size-scaling rules on local density (sr$_1$), dispersal ability (sr$_2$) and regional pool richness (sr$_3$). As taxa body size becomes larger, there is an increase in dispersal ability, while the richness of the regional pool and local and regional density scales negatively with taxa body size. Any of these scaling rules or their combined effects have the potential to determine metacommunity assembly and diversity patterns. (*b*) Theoretical chains of effects between body size and α-, β- and γ-diversity. Blue/orange arcs ending in arrows/circles represent positive/negative effects. While body size is expected to negatively affect β- and γ-diversity, there are countervailing indirect effects on α-diversity. Empirical body size-scaling rules sr$_1$, sr$_2$ and sr$_3$ are indicated.

occurring species in a community because local populations tend to be smaller and more prone to extinction, which leads to a reduction in α-diversity [2,3,14]. In addition, extinctions will disproportionately affect rare species, increasing the representation of common species across different communities, thus reducing β- and γ-diversity. Similarly, regional richness, which enhances local richness [15,16], usually decreases with body mass [17]. That is, large sized taxa are poorly represented in regional pools as compared to small sized ones, and the same species tend to be observed across local communities. Consequently, if the negative density- and regional richness-mass scaling are considered in isolation, α-, β- and γ-diversity of larger sized taxa should be lower than those of smaller sized taxa. In summary, it could be hypothesized the existence of countervailing effects of body size on diversity patterns, which are dependent on the expected influence that the local density scaling, dispersal scaling and regional pool richness scaling have on diversity when they are combined. This framework predicts a negative relationship between body size and β- and γ-diversity due to the reduced number of species that could potentially reach each community from the regional pool, the homogenizing effect of dispersal and the higher local extinction rate of rare species. However, body size could reduce α-diversity because of the higher extinction risk and the lower colonization rate of novel species from the regional pool, but could enhance it because of the higher colonization rates of larger species. Figure 1*b* shows a visual representation of our hypothesis.

Here we theoretically formalize this hypothesis, exploring the expected interaction between scaling of dispersal, density and regional pool richness as determinants of the diversity–body size relationship. We used a lottery-based metacommunity model that incorporates these three scaling relationships for analysing the expected trends in α-, β- and γ-diversity with taxon body size.

Material and methods

The metacommunity was assembled with a lottery model in two stages (electronic supplementary material, appendix S1 and figure S1). First, communities were filled with coalescent dynamics starting with the random sampling of one individual from the regional species pool for colonizing each community, and then, filling communities with J individuals each, progressively chosen either from the regional pool, from adjacent communities—neighbouring dispersal—or from the updated community—local recruitment (following [18–20]). After local communities were filled, the lottery dynamics started. At each time step and in each local community, a single individual was randomly removed and replaced with a new one which could also be chosen either from the regional pool, from adjacent communities or from the updated community. Under the lottery dynamics, local extinctions and recolonizations may occur. Dispersal among adjacent (i.e. neighbour) communities was assumed as inversely proportional to the distance between them. This is a spatially explicit model involving neutrality only among species of the same taxon (see [21–24] for similar approximations).

The metacommunity dynamic was simulated for 10 hypothetical taxa representing high-ranking taxonomic groups (e.g. orders), to which a different body size value was assigned. These 10 body size values were uniformly drawn from the interval [1,200]. The model was run considering the potential effect of body size on the parameters representing regional pool richness (S_{pool_i}), local density (J_i) and dispersal ability ($Disp_i$), as

$$S_{pool_i} = aM_i^{b.pool};$$

$$J_i = cM_i^{b.local};$$

$$Disp_{i|p,q} = M_i^{b.disp} * 1/dist_{pq},$$

where a and c are scaling constants, M_i represents the mean body size of the taxon i, $dist_{pq}$ is the geographical distance between communities p and q, and $b.pool$, $b.local$ and $b.disp$ are scaling exponents that relate the richness of the regional pool, local density and dispersal ability of taxon i to its mean body size.

The lottery model was run along gradients of values for $b.pool$, $b.local$ and $b.disp$ that surpassed the range of empirically reported scaling. We run five replicates for each combination of $b.pool$, $b.local$ and $b.disp$. At the beginning of each simulation, a random metacommunity network of 20 local communities was generated. Communities were randomly placed within a landscape in which the geographical distance between each pair of communities could range from 1 to 2000 m. The lottery dynamics were run until both the mean α- and γ-diversity stabilized, eliminating transient dynamics (electronic supplementary material, appendix S1 and figure S2).

For each simulation, we obtained the expected relationship between taxa mean α-, β- and γ-diversity and their body size. It should be noted that γ-diversity refers to the total richness at the metacommunity level, which may differ from the richness in the regional pool. β-diversity was estimated by the difference between the expected value of mean α- and γ-diversity ([25] and electronic supplementary material, appendix S1). We did not include interactions among size–classes in these simulations because our attempt was to visualize the pure effect of the size–scaling on biodiversity. That is, how body size promoted a particular structure of the metacommunity diversity, over which other mechanisms may operate (see [18] for a modelling with size–classes interaction).

We used linear models to evaluate the expected associations between metacommunity α-, β- and γ-diversity and mean body size of taxa. All analyses were performed using R software (v. 4.0.4) [26].

Results

The scaling in dispersal, regional richness and local density with body size affected diversity, both when considered isolated or through their combined effects (figure 2; electronic supplementary material, table S1 and figure S3). When scaling relationships were individually considered, the increase in dispersal with body size enhanced local richness but had negative effects on β- and γ-diversity (figure 2*a*–*c*). Conversely, the negative scaling in both local density and regional pool size determined a negative effect of body size on all diversity metrics (figure 2*a*–*c*). These results fully matched our expectations (figure 1*b*). When the scaling relationships were combined, both β- and γ-diversity consistently showed a negative relationship with body mass (figure 2*e*,*f*). However, the negative effect of scaling of local density + regional pool richness on local diversity could be reverted when the positive scaling in dispersal ability was considered (figure 2*d*). Finally, when no scaling relationship was included, body size was not associated with diversity (figure 2*f*–*h*). These trends were consistent over a wide range of the parameter space (figure 2*j*–*l*; electronic supplementary material, figure S3).

Discussion

In a metacommunity context, the role of body size on shaping diversity has been mainly associated with its effect on taxon-independent dispersal ability [5–7,27]. However, our analyses showed that the interaction among the size-scaling in local density, dispersal ability and regional pool richness may represent a main determinant of the variation in metacommunity diversity among organisms with different body size. That is, our results support that the negative effect of scaling in density and regional pool richness on biodiversity can be counterbalanced by the positive effect of dispersal scaling with body size. While the local richness–body size relationship was qualitatively sensitive to the scaling rule considered, trends in β-, and consequently γ-diversities were not. In agreement with several empirical studies which reported a negative association between dispersal and β-diversity [11], we found a negative effect of the scaling in dispersal on the β-diversity–body size relation. However, a strong effect of the scaling in density and regional richness on the β-diversity–body size association was also captured, a relationship that is poorly considered in the metacommunity literature.

The strength of our modelling approach relies upon its simplicity. Basal neutrality among species of the same taxon, and population dynamics guided by basic ecological processes (i.e. local recruitment, death, dispersal and colonization), allowed us to test our working hypotheses with the minimum of underlying assumptions, which commonly obscure model outcomes. However, some limitations regarding some assumptions of our model should be considered. Simulations were run for hypothetical taxa differing only in body size, although the interaction with other traits could also be important to consider [6,13,28]. A simplified association between dispersal ability and body size was assumed. Nevertheless, variation in dispersal modes suggests that a general scaling may represent a gross approximation to the dispersal ability of each taxon [6]. Additionally, dispersal ability may be nonlinearly related to metacommunity connectivity [29,30] or with changes between life stages [31], determining negative correlations between dispersal distance, frequency and body size. Complex population dynamics and a narrow range of body sizes in local communities may determine weak density–mass scaling at local communities [13,32], but see [33]. The scaling in regional richness with body size may vary among taxa, even presenting unimodal trends [34]. We simulated metacommunity networks with random spatial structures and homogeneous patches. However, more realistic metacommunity configurations can direct dispersal, diminishing the differences in recruitment among taxa [35,36]. Also, local filters could affect the probability of local extinctions [37,38]. These factors may alter the relative effect of each scaling rule in the assembly process. Despite this, the general scaling relationships point to an expected trend in metacommunity diversity with body mass that is congruent with patterns reported elsewhere [39,40]. Our findings suggest that the combination of the three scaling relationships could represent a backbone in metacommunity assembly, upon which the action of idiosyncratic assembly mechanisms and deviations from general scaling rules may operate.

Our focus was on the putative role of sound scaling relationships with body size on metacommunity diversity. In this context, some perspectives deserve attention. First, scaling parameters in ecological rates with body size may differ among systems, explaining differences in diversity among metacommunities, higher taxonomic groups or trophic levels (e.g. [13,41–43]). Second, other biological rates that also scale with mass may be crucial for the regulation of metacommunity diversity [2,44]. Individual turnover rate [45], assimilation efficiency [46], growth rate [47], trophic interactions [48], size and number of dormant structures [49], niche breadth [50] and landscape perception [3,4,29,51] were all related to metacommunity diversity and showed systematic size-dependences. Third, we assumed independence among taxa through our simulations, even though interactions among them could enhance or attenuate expected patterns (see [18]). Fourth, the temperature-dependence of biological rates [52] provides a mechanistic avenue for understanding how climate modulates diversity in a metacommunity framework [2]. Finally, and beyond body size differences, although the model was based on a neutral approach, we also highlight the importance of non-neutral and particularly size-dependent processes in general [4,30]. Consequently, there are several mechanisms by which the integration of metacommunity, niche and metabolic theories may enhance our understanding of biodiversity [22]. Considering biological scaling relationships represents an exceptional opportunity for progress in the mechanistic understanding of the

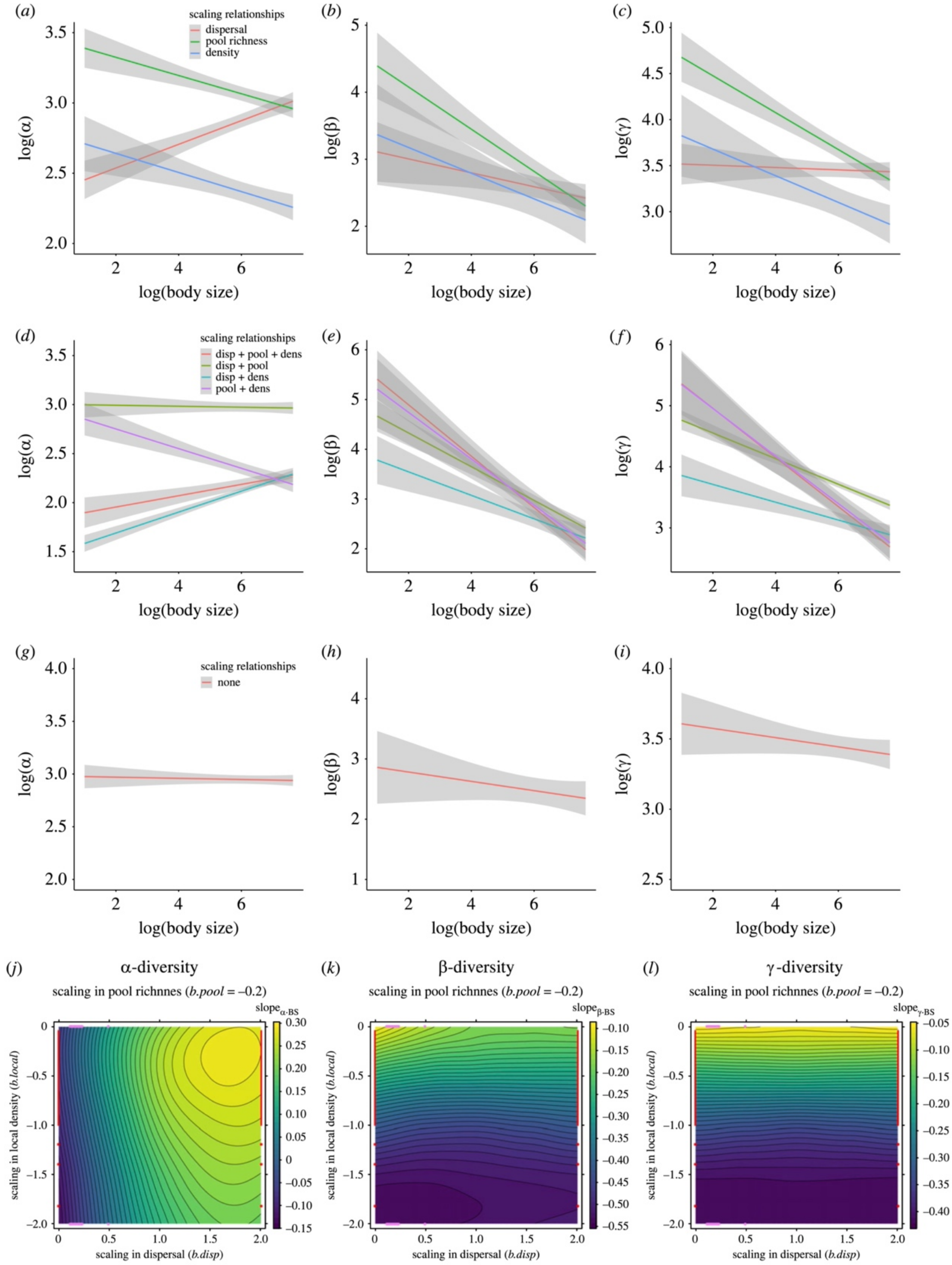

Figure 2. Theoretical results showing the relationships between diversity and taxon body size. (*a–i*) Expected relationship between α-, β- and γ-diversity with taxon body size for different scaling combinations: (*a–c*) the isolated effects of scaling in dispersal ability, regional pool richness and local density on metacommunity diversity; (*d–f*) combined effects of different scaling relationships; (*g–i*) body size–diversity relation resulting when no scaling relationship was included in the model. Parameter values used in simulations: $a = 100$, $c = 50$, $b.disp = 0.5$, $b.pool = -0.4$, $b.local = -0.75$. (*j–l*) Parameter space for the association between α-, β- and γ-diversity with taxon body size along a gradient in the scaling exponent between local density (*y*-axis) and dispersal ability (*x*-axis) with mass. Pool richness–body size-scaling value (*b.pool*) was set to −0.2. Each point within the parameter space corresponds to the average of the regression slopes between mean α-, β- and γ-diversity obtained from the five replicates run for each parameter combination. Red and purple marginal dots indicate the range of empirical scaling exponents reported in the literature for the relationship between local density and dispersal ability with body mass, respectively (see electronic supplementary material, tables S2 and S3). Patterns are robust to changes in *b.pool* (see electronic supplementary material, figure S3).

interrelationships between body size and diversity in metacommunities, and more generally, for unravelling the mechanisms shaping biodiversity patterns and processes.

Data accessibility. R scripts are freely available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.rjdfn2zhd [53].

The data are provided in the electronic supplementary material [54].

Authors' contributions. E.O.: conceptualization, formal analysis, funding acquisition, investigation, methodology, visualization, writing—original draft and writing—review and editing; A.I.B.: investigation, visualization, writing—original draft and writing—review and editing; R.R.-J.: investigation, visualization, writing—original draft and writing—review and editing; M.A.: conceptualization, formal analysis, funding acquisition, investigation, methodology, supervision, visualization, writing—original draft and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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Supplementary material

Supplementary Appendix 1

The lottery-based metacommunity model (LBMM) and simulations

The LBMM reconstructs the structure of a set of local communities within a metacommunity by recruiting individuals from three different sources: a regional pool of species, the neighboring (i.e. connected) communities, and the communities themselves (i.e. local recruitment) (Figure S1). The LBMM is a spatially explicit model since it considers the effect of the relative spatial position of the communities on dispersal. That is, the observed geographic distance between each pair of communities in the metacommunity influences the probability of selecting a new recruit from a neighboring community. For example, if the spatial configuration of the metacommunity determines that community *i* is closer to community *j* than to community *k*, the probability of recruiting an individual from community *j* is higher than the probability of selecting a recruit from community *k*. In addition, the model allows that the size of the regional pool, local density, and dispersal ability of each taxon scale with its body size.

The LBMM works in two stages (Figure S1). In the first stage, communities are filled under coalescent dynamics [1–3] by adding to each community one new individual at a time until a certain local abundance/density value (J) is reached. In the first step of the coalescent dynamics, each community is colonized with a different individual that is chosen equiprobably from one of the species in the regional pool. After each community has been colonized, the rest of the individuals to be added can be chosen from the regional pool, from the descendants generated by the species in other communities (i.e. dispersers within the metacommunity) or from a direct descendant of the species that are already present (i.e. local recruitment). When all communities have reached a total abundance of J individuals, the lottery dynamics start [1,4,5]. In each time step (i.e. iteration), an individual is randomly eliminated from each community and replaced with a new recruit which, as in the coalescent dynamics, can be chosen either from the regional pool, from adjacent communities, or from the descendant of the species that are already present in the updated communities. The sampling procedure by which individuals are chosen and added to each community resembles three basic ecological processes: (i) migration from a regional pool; (ii) migration from within the metacommunity; and (iii) local recruitment. In addition, under the lottery stage local populations can become extinct allowing the recolonization from the regional pool or from the metacommunity. The model is neutral for the species that belong to the same taxonomic group (e.g. order), so the establishment of the individuals is not affected by environmental filters or differential dispersal ability [4]. Then, all local communities follow migration-drift dynamics without selection. However, it is important to note that there exist differences in dispersal ability, local density, and pool richness among taxonomic groups because of the effect of their body sizes on the scaling relationships.

The metacommunity dynamics were simulated for ten hypothetical taxa representing high-ranking taxonomic groups (e.g. orders), to which a different body size value was assigned. These 10 body size values were uniformly drawn from the interval [1;200], being: 1, 23, 45, 67, 89, 112, 134, 156, 178, 200. For each taxon i, the procedure is as follows: first, we set its regional pool richness (S_{pool_i}), local density (J_i) and dispersal ability ($Disp_i$) as:

$$S_{pool_i} = aM_i^{b.pool};$$

$$J_i = cM_i^{b.local};$$

$$Disp_{i|p,q} = M_i^{b.disp} * 1/dist_{pq}$$

Parameters a and c represent scaling constants, M_i represents the body size of taxon i, $dist_{pq}$ is the geographic distance between two communities p and q according to their relative position on the landscape, and $b.pool$, $b.local$ and $b.disp$ are scaling exponents that relate the size of the regional pool, local density and dispersal ability of taxon i with its respective mean body size. These three variables have been shown to follow a power law relationship with body size [6–12] (see Table S2 and S3). After S_{pool_i}, J_i and $Disp_i$ are set, the coalescent dynamics start by adding individuals until J_i is reached in each community. The probability that a new recruit comes from the regional pool is determined by the dispersal ability of the taxon to which it belongs, as: $Disp_{i_{pool}} = M_i^{b.disp}$. Similarly, the probability that the recruit is selected from the metacommunity is determined by the dispersal ability of the taxon to which it belongs and the geographic distance between each pair of communities p and q, as:

$Disp_{i_{meta}} = \sum_{q \neq p}^{N_{com}} M_i^{b.disp} / dist_{pq}$. Finally, the probability of local recruitment is: $Local_i = 1 - Disp_{i_{pool}} - Disp_{i_{meta}}$. Note that the probability of recruitment from both the regional pool and the metacommunity increases for those larger taxa, due to the positive scaling between dispersal ability and body size. After all communities are filled with J_i individuals, lottery dynamics start by randomly removing an individual from each community with a probability proportional to the abundance of its local population. The removed individuals are replaced with new recruits sampled either from the regional pool, from neighboring communities or from the focal communities with the same probabilities as in the coalescent dynamics. This procedure is repeated N_{it} number of iterations. The LBMM simulates the dynamics of all local communities simultaneously. This means that the processes of colonization, dispersal, death and recruitment occur in all communities at the same time.

The lottery model was run along different gradients of *b.pool*, *b.local* and *b.disp* that surpassed empirically reported scalings (Supplementary Table S2, Table S3 and Figure S3). We run five replicates for each combination of *b.pool (range [0;-1], binned at 0.2)*, *b.local (range [0;-2], binned at 0.1)* and *b.disp (range [0;2], binned at 0.1)*. At the beginning of each simulation, a random metacommunity network of 20 local communities was generated. Communities were randomly placed within a landscape in which the geographic distance between each pair of communities could range from 1 to 2000 m. Both the body size values assigned to each taxon and the spatial scale of the random metacommunities are congruent with data reported in several natural systems [13–16]. In order to control for the effect of possible transient states of diversity on the results, we explored the number of iterations (N_{it}) needed for the diversity metrics to stabilize. The lottery dynamics were run during 10.000 iterations for several scaling relationship combinations and the minimum number of iterations needed for the mean alpha and gamma diversity to stabilize was determined (Figure S2). Simulations showed that the time needed for the model to converge into stable diversity values is dependent on taxa body size, since small taxa require more time to reach stability. We detected that 5000 iterations are enough to let the diversity of all taxa stabilize. Therefore, all simulations were run for 5000 time steps.

When the lottery dynamics end, the standardized alpha diversity per community is obtained for a common level of abundance that equals the double of the minimum taxon´s abundance (minimum J_i) (following [17]) using the iNEXT package of R [18]. For each hypothetical taxon, the mean alpha diversity (i.e., average number of species per community) was estimated. Beta diversity was estimated from the standardized alpha and total gamma diversity as: $\beta = \gamma - \bar{\alpha}$ [19].

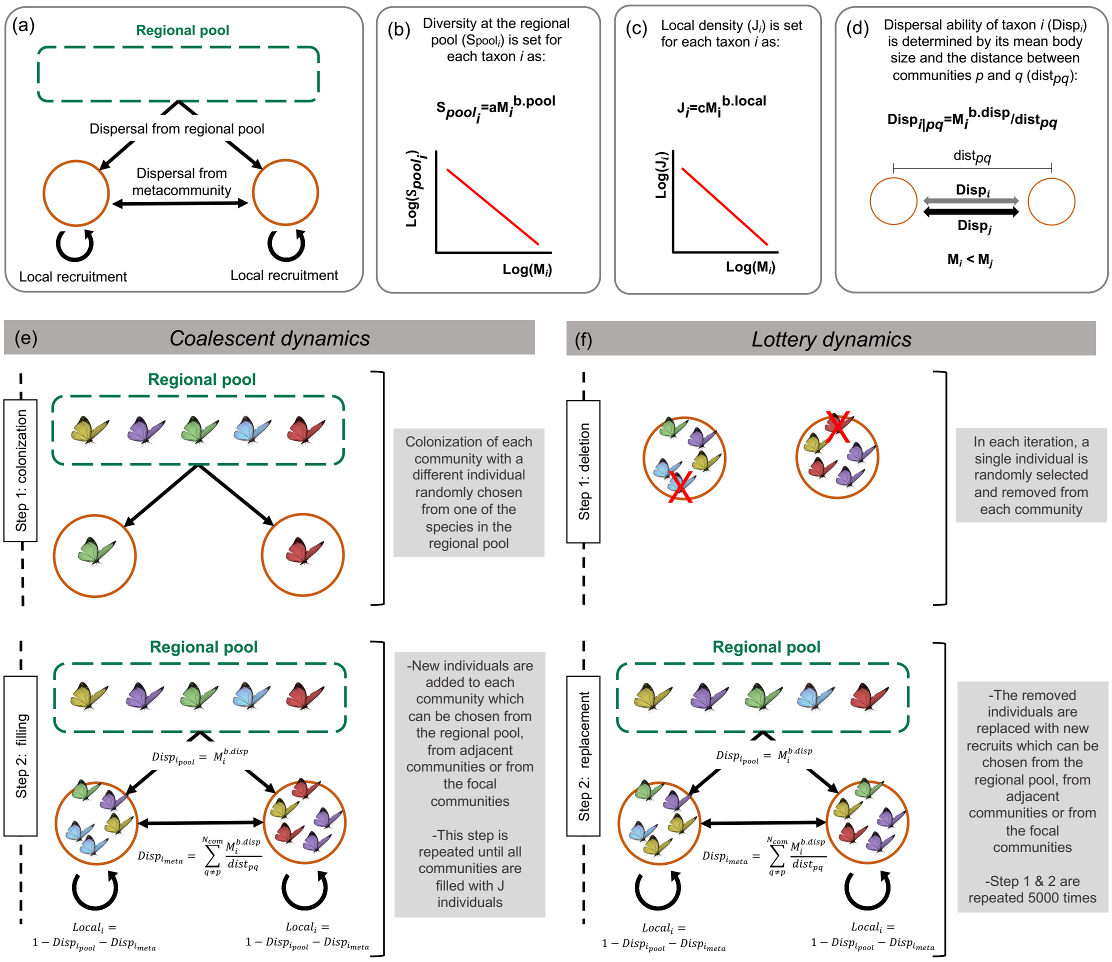

Figure S1 Lottery-based metacommunity model (LBMM) pseudocode. (a) Local community structure is assembled by recruiting individuals from the regional pool, the metacommunity (i.e. adjacent, connected communities) and/or the local community itself. For each taxon i: (b) its regional pool richness (S_{pool_i}), (c) its local density (J_i) and (d) dispersal ability ($Disp_i$) are set following the scaling relationships with its mean body size (M_i). (e) The first stage (i.e. coalescent dynamics) consists of colonizing each local community with one different individual that is randomly chosen from the species in the regional pool. After that, the coalescent dynamics start by adding new individuals to each community until the density of taxon i (J_i) is reached. Now, individuals can be sampled from the regional pool (with probability $Disp_{i_{pool}} = M_i^{b.disp}$), from the metacommunity (with probability $Disp_{i_{meta}} = \sum_{q \neq p}^{N_{com}} M_i^{b.disp} / dist_{pq}$) or the communities themselves (with probability $Local_i = 1 - Disp_{i_{pool}} - Disp_{i_{meta}}$). (f) After local communities reached J_i, the lottery dynamics start. Now, in each time step (i.e., iteration) a single individual is randomly removed from each community and replaced with a new recruit which can also be sampled either from the regional pool, from the metacommunity or from the updated communities with the same probabilities as in the coalescent stage. This routine is repeated for each taxon included in the analysis.

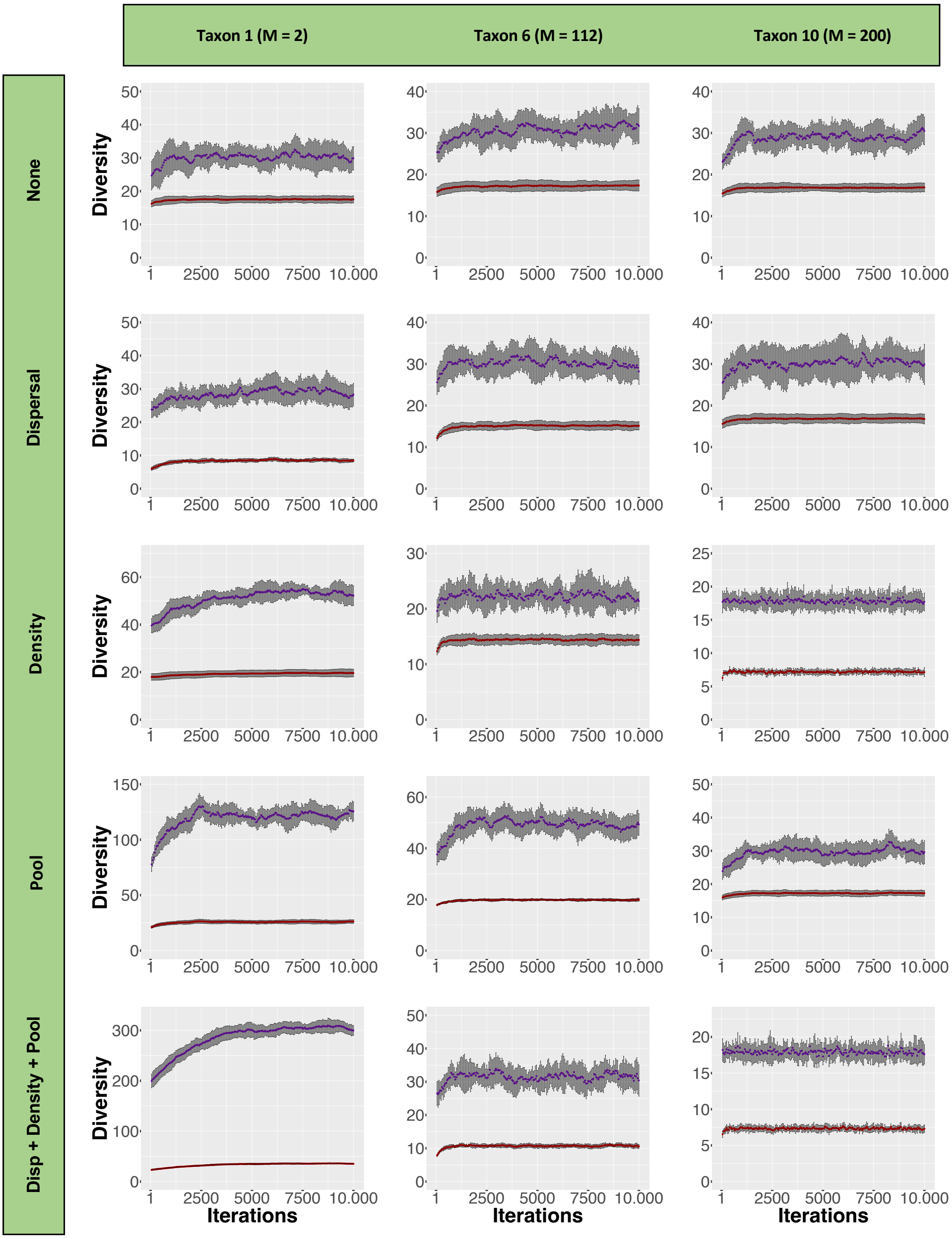

Figure S2 Convergence analysis of the lottery-based metacommunity model. Mean alpha (red) and gamma (purple) diversity values during the lottery dynamics along 10.000 iterations for three of the ten hypothetical taxa (columns) under different combinations of the scaling relationships (rows). Diversity metrics were averaged from 10 replicates (error lines correspond to their standard deviation). Taxa 1, 6 and 10 represent small, medium, and large body size classes. Note that both diversity metrics stabilize after 5000 iterations.

Parameter values used in these simulations: *a*=100, *c*=50, *b.disp* = 0.5, *b.pool* = -0.4, *b.local* = -0.75 (same values used for Figure 2a-i). Convergence results are congruent for different scaling parameter values.

Table S1. Linear models from the simulation results shown in Figure 2a-i (main text). Parameter values used in the simulations: a=100, c=50, $b.disp$ = 0.5, $b.pool$ = -0.2, $b.local$ = -0.75.

Theoretical analysis						
Scaling relationship	Diversity metric	Estimate	SE	t-value	p-value	R2
Dispersal + Pool + Density						
	Alpha	0.058	0.013	4.58	0.0018	0.72
	Beta	–0.52	0.033	–15.61	<0.001	0.97
	Gamma	–0.4	0.041	–9.76	<0.001	0.92
None						
	Alpha	–0.0054	0.009	–0.61	0.56	0.044
	Beta	–0.077	0.049	–1.58	0.15	0.23
	Gamma	–0.032	0.018	–1.83	0.1	0.29
Dispersal						
	Alpha	0.084	0.011	7.6	<0.001	0.88
	Beta	–0.1	0.036	–2.88	0.021	0.51
	Gamma	–0.013	0.018	–0.7	0.51	0.06
Pool						
	Alpha	–0.065	0.011	–5.73	<0.001	0.80
	Beta	–0.31	0.04	–7.83	<0.001	0.88
	Gamma	–0.2	0.022	–9.25	<0.001	0.91
Density						
	Alpha	–0.068	0.016	–4.3	0.0026	0.70
	Beta	–0.19	0.061	–3.15	0.014	0.55
	Gamma	–0.15	0.036	–4.02	0.004	0.67
Dispersal + Pool						
	Alpha	–0.005	0.011	–0.47	0.65	0.027
	Beta	–0.34	0.025	–13.34	<0.001	0.96
	Gamma	–0.21	0.013	–16.22	<0.001	0.97
Dispersal + Density						
	Alpha	0.11	0.0069	15.44	<0.001	0.97
	Beta	–0.24	0.039	–6.03	<0.001	0.82
	Gamma	–0.15	0.028	–5.27	<0.001	0.78
Pool + Density						
	Alpha	–0.1	0.013	–7.46	<0.001	0.87
	Beta	–0.45	0.063	–7.42	<0.001	0.87
	Gamma	–0.39	0.045	–8.62	<0.001	0.90

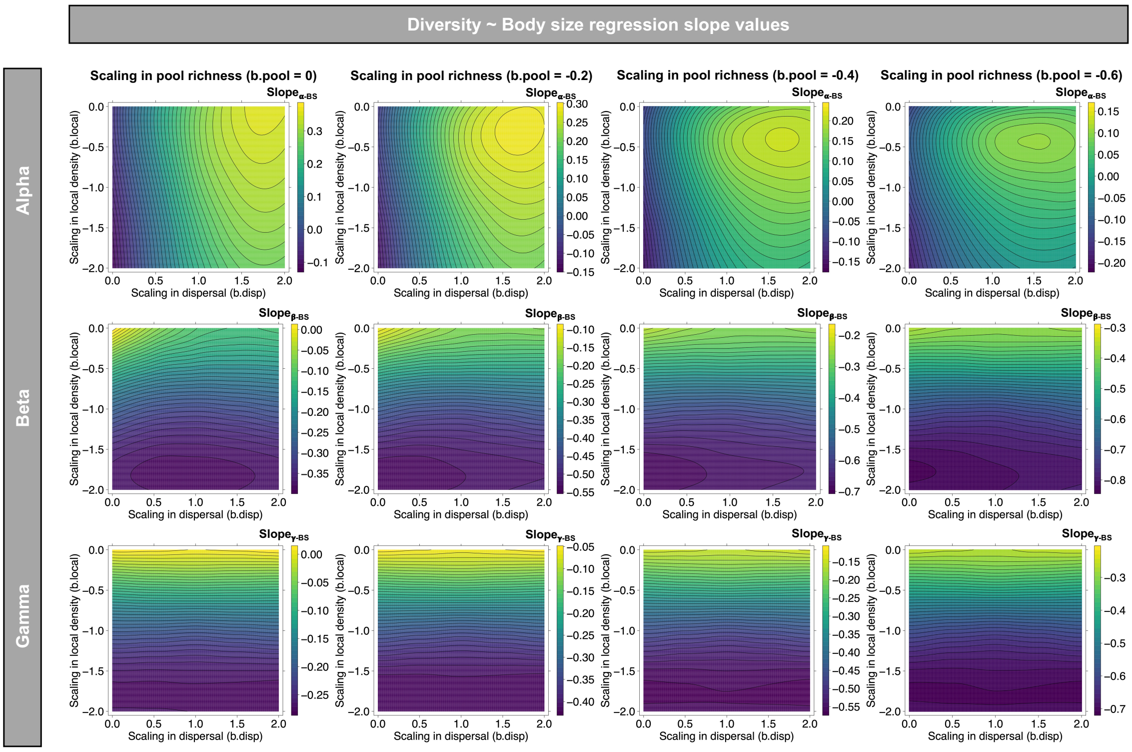

Figure S3. Interrelationship between trends in alpha, beta and gamma diversity with body size and the parameter space defined by the size-scaling in dispersal, local density and regional richness. The plots show the average slope values of the diversity-body size associations obtained from 5 replicates along gradients in the scaling of dispersal ability (x-axis), local density (y-axis), and regional richness (columns) with body size. The upper row of panels shows the effect on alpha diversity, the middle one on beta diversity, and the lower row shows results for gamma diversity. Color bar indicates the slopes of the diversity-body size relationships.

Table S2 Different scaling exponents estimated from the relationship between body size and local density gathered from different published studies. Scaling exponents were estimated using OLS (i.e. ordinary least squares regression), OLS$_{BIS}$ (i.e. ordinary least squares-bisector regression) or RMA (i.e. reduced major axis regression). Reference ID: [8] (1), [20] (2), [21] (3), [7] (4), [22] (5), [23] (6), [6] (7).

Major taxa	Method	Scaling exponent	SE	CI	Body size measure	Reference ID
Dung beetles from South Africa (Hluhluwe)	OLS	−0.364	–	−0.58; −0.15	Weight	1
	RMA	−1.396	–	–	Weight	1
Dung beetles from South Africa (Mkuze)	OLS	−0.287	–	−0.53; −0.04	Weight	1
	RMA	−1.368	–	–	Weight	1
Benthic invertebrates	OLS	−0.702	–	−0.77; −0.63	Dry mass	2
	OLS$_{BIS}$	−1.03	–	−1.09; −0.97	Dry mass	2
Mammals (primary consumers)	OLS	−0.75	0.026	–	Mass	1,3
Mammals	RMA	−1.193	–	–	Weight	1,4
Rocky intertidal communities	OLS	−0.77	0.11	–	Mass	5
Swidish birds	OLS	−0.771	–	−1.0 ; −0.54	Weight	1,6
	RMA	−1.822	–	–	Weight	1,6
Pond macroinvertebrates, fish and amphibians	OLS	−0.64	–	−1 ; −0.28	Volumen	7

Table S3. Different scaling exponents estimated from the relationship between body size and dispersal ability gathered from different published studies. Reference ID: [11] (1), [12] (2), [24] (3), [25] (4).

Major taxa	Scaling exponent	SE	CI	Dispersal ability measure	Units	Body size measure	Reference ID
Invertebrates	0.19	0.04	–	Exploratory speed	mm/s	Mass	1
Bacteria, arthropods, vertebrates	0.2	–	0.186-0.214	Routine speed	m/s	Mass	2
Birds, Bats, Insects	0.13	–	0.11-0.15	Muscle mass-specific induced power	W/Kg	Mass	3
Fish, Whales	0.49	–	–	Maximum speed	m/s	Length	4

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Capítulo 2:

Interacción entre dispersión, arreglo de especies y efecto prioridad como determinante de un patrón en joroba entre diversidad β y dispersión

El contenido de este capítulo está en proceso de ser enviado a revisión y se presenta en formato manuscrito.

Title: The interactive effect between dispersal, species sorting, and priority effects determines a humped pattern between beta diversity and immigration rates.

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Abstract

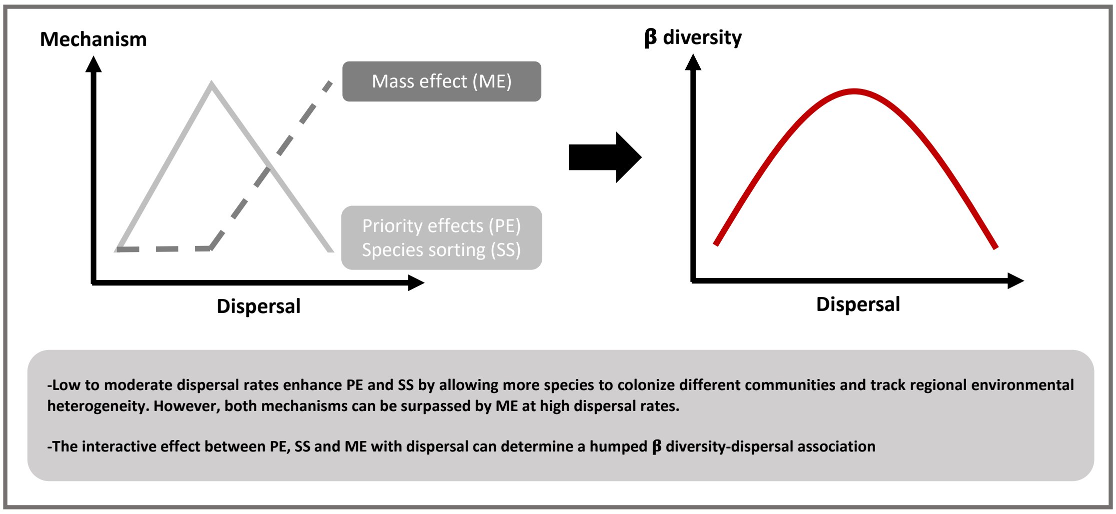
Contrary to the dominant view that dispersal homogenizes communities, recent studies have reported a positive relationship between dispersal and beta diversity. Although this result has been associated with the action of priority effects and species sorting, it remains unclear how the interaction between these mechanisms with dispersal affects the beta diversity-dispersal relationship. We theoretically evaluate how priority effects and species sorting shape beta diversity in metacommunities subject to external immigration from a regional pool of species. Both mechanisms foster community differentiation at intermediate immigration rates, but only when internal dispersal between communities is considered. Additionally, the interaction between internal and external dispersal homogenizes communities at low and high immigration rates through mass effects determining a humped pattern in beta diversity along the immigration gradient. These results contribute to our mechanistic understanding of metacommunity assembly and account for contradictory empirical results challenging the classic conceptualization of dispersal as a homogenizing process.

Introduction

Detecting the mechanisms that determine biodiversity patterns is still a major goal in ecology (Leibold and Chase 2018). The metacommunity theory has provided a robust conceptual framework that combines the interaction between local and regional processes to explain the emergence of diversity at several scales (Leibold et al. 2004; Thompson et al. 2020; Suzuki and Economo 2021). In this context, the beta diversity-dispersal relationship has been a major focus of attention. Dispersal has been conceptualized as a homogenizing process that increases community similarity (Loreau and Mouquet 1999; Loreau 2000; Soininen et al. 2007; Mouquet and Loreau 2003; Grainger and Gilbert 2016; Heino and Tolonen 2017; Gu et al. 2023). Congruently, foundational theoretical studies have predicted that beta diversity decreases monotonically along a gradient in dispersal intensity among communities (Mouquet and Loreau 2003; Leibold et al. 2004; Soininen et al. 2007), and a large body of field and experimental studies have remarkably supported this prediction (Grainger and Gilbert 2016; Catano et al. 2017). However, recent empirical and theoretical studies have evidenced more complex relationships between dispersal and beta diversity, even involving positive associations (Lu 2021).

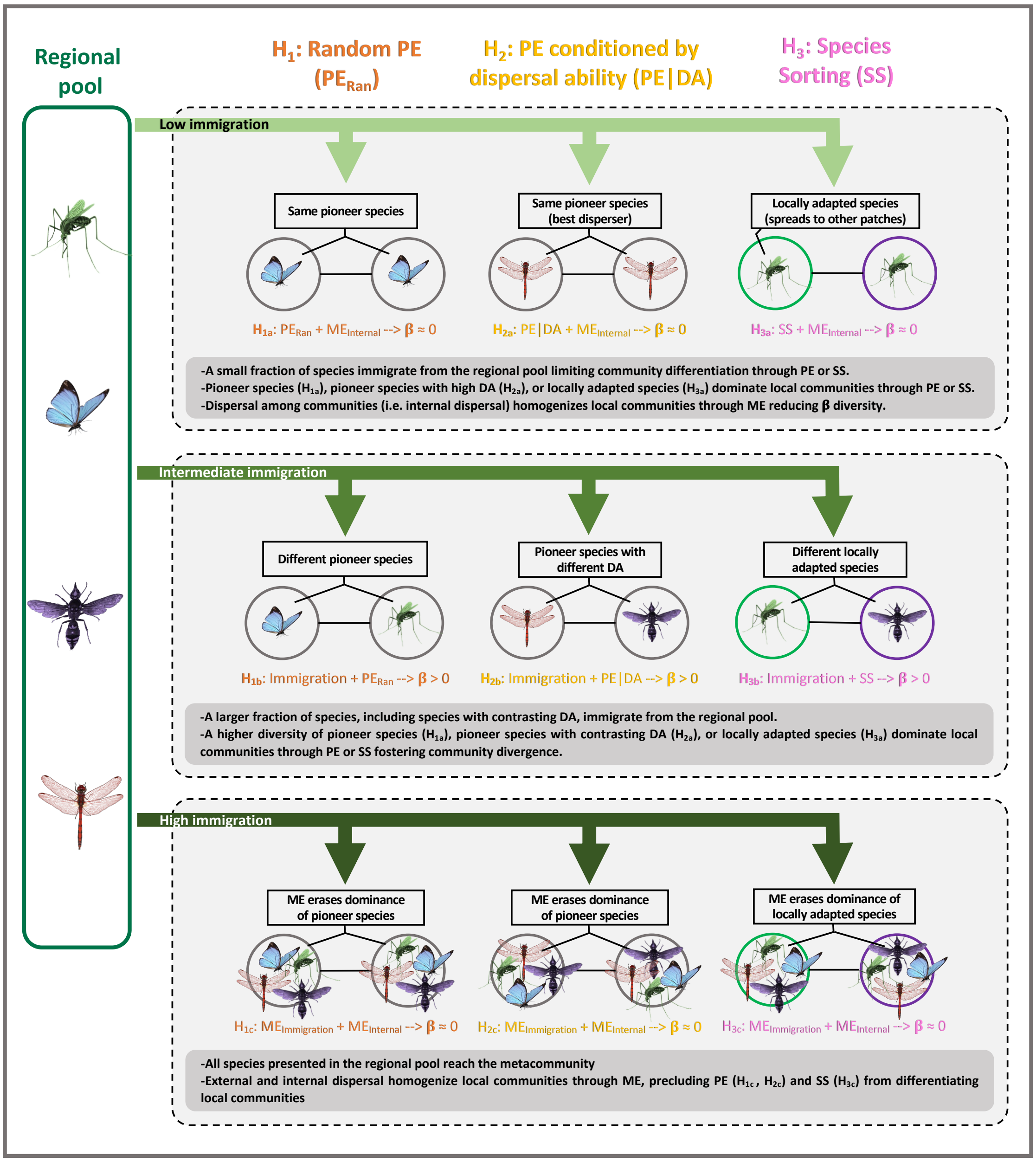
In experiment with protist communities, dispersal reduces beta diversity at high disturbance intensities but not at low or intermediate perturbation rates (Ojima and Jiang 2017), a result not evidencing the expected monotonic decline in beta diversity with dispersal. In the same line, a meta-analysis of experimental results about the interaction between dispersal, disturbance, and beta diversity in herbaceous communities found a lack of evidence for the expected homogenizing effect of dispersal on beta diversity (Catano et al. 2017). Furthermore, while beta diversity is expected to emerge from the combined action of stochastic drift and differences in selection regimen between communities—species sorting—, this last effect was not supported by the evidence (Catano et al. 2017). This result highlights the need for a better understanding of the relative role and interaction between stochastic and niche mediated determinants of beta diversity (Catano et al. 2017; Arim et al. 2023). Furthermore, a positive effect of dispersal on beta diversity was reported by empirical studies in which dispersal and local conditions were naturally allowed to vary. In a metacommunity of nectar microbes, dispersal between flowers promoted beta diversity due to strong priority effects when pollinators with different dispersal abilities were considered (Vannette and Fukami 2017). Similarly, pond connectivity—a proxy of dispersal rate—was found to increases beta diversity in amphibian assemblies (Werner et al. 2007). In addition, recent theoretical models point to the potential existence of negative, positive, and even humped effects of dispersal on beta diversity (Lu 2021). This variety of possible associations between dispersal and beta diversity is determined by the relative effect of dispersal on the mean and variance probability of species spatial occupancy, which can be associated with biotic interactions and disturbance intensity determining different selective regimes (Lu 2021).

Having been shown that a wide range of beta diversity-dispersal associations can be expected and are effectively observed, the explicit effect of dispersal on the final determinants of communities´ differentiation, that is species sorting and stochastic dynamics due to differences in assembly history, must be better understood. Low to intermediate dispersal rates have the potential to enhance the action of species sorting and priority effects by allowing more species to track regional environmental heterogeneity (Heino 2011; Soininen 2014; Alahuhta et al. 2014), and by increasing the diversity of species that act as potential colonizers of communities (Chase 2003; Fukami 2015; Vannette and Fukami 2017) (Figure 1a). This allows local communities to reach alternative species compositions increasing beta diversity. However, both species sorting and priority effects can be surpassed by mass effect at high dispersal rates increasing community homogenization (Fukami 2005, 2015; Gianuca et al. 2017; Loke and Chisholm 2023) (Figure 1a). Therefore, along a gradient in dispersal intensity a humped pattern in beta diversity is expected due to the interactive effect between species sorting, priority effects and mass effect with dispersal (Figure 1a).



-Low to moderate dispersal rates enhance PE and SS by allowing more species to colonize different communities and track regional environmental heterogeneity. However, both mechanisms can be surpassed by ME at high dispersal rates.

-The interactive effect between PE, SS and ME with dispersal can determine a humped β diversity-dispersal association



-A small fraction of species immigrate from the regional pool limiting community differentiation through PE or SS.
-Pioneer species (H_{1a}), pioneer species with high DA (H_{2a}), or locally adapted species (H_{3a}) dominate local communities through PE or SS.
-Dispersal among communities (i.e. internal dispersal) homogenizes local communities through ME reducing β diversity.

-A larger fraction of species, including species with contrasting DA, immigrate from the regional pool.
-A higher diversity of pioneer species (H_{1a}), pioneer species with contrasting DA (H_{2a}), or locally adapted species (H_{3a}) dominate local communities through PE or SS fostering community divergence.

-All species presented in the regional pool reach the metacommunity
-External and internal dispersal homogenize local communities through ME, precluding PE (H_{1c}, H_{2c}) and SS (H_{3c}) from differentiating local communities

Figure 1. (a) Mechanisms hypothesized to determine a humped pattern between beta diversity and dispersal. Low to intermediate dispersal rates enhance priority effects and species sorting by allowing more species to colonize different communities and track environmental heterogeneity at the regional scale increasing beta diversity. However, high dispersal rates homogenize local communities through mass effects surpassing priority effects and species sorting. (b) Hypotheses under which a humped pattern between beta diversity and dispersal from the regional pool of species is predicted through the mechanisms of random priority effects (H_1), priority effects conditioned by species dispersal ability (H_2) and species sorting (H_3).

An additional factor that has limited the identification of alternative beta diversity-dispersal associations in both theoretical and experimental studies is the simplification of the dispersal process. On one hand, studies have mainly focused on the dispersal gradient between communities (i.e., internal dispersal) obviating the potential effects that the immigration from a regional pool of species to the metacommunity (i.e., external dispersal) could have on diversity (Grainger and Gilbert 2016). External dispersal provides a flux of individuals differing in their traits that act as the source of diversity upon which species sorting (Cottenie and De Meester 2004; Gianuca et al. 2017) and priority effects (Chase 2003; Fukami 2015) operate. However, community homogenization due to mass effect can occur either by internal or external dispersal, and their interactive effect on beta diversity is often overlooked (Fukami 2005). On the other, studies have eliminated the natural differences in dispersal ability among species (Granger and Gilbert 2016; Vannette and Fukami 2017; Lu 2021), even though large variations in species dispersal rates are typically observed in metacommunities (de Bie et al. 2012; Vannette and Fukai 2017; Cunillera et al. 2020). At low dispersal rates, differences in dispersal ability can determine a specific sequence in the arrival of species to local communities favoring the same set of good dispersers (Fukami 2015), preventing species sorting and priority effects from increasing community differentiation. Nevertheless, increasing dispersal can favor the early arrival of species with contrasting dispersal abilities to local communities enhancing beta diversity. In conclusion, a major effort to formalize how species sorting, priority effects, the natural differences in dispersal ability among species and the interaction between internal and external dispersal could determine different associations between beta diversity and dispersal is still needed.

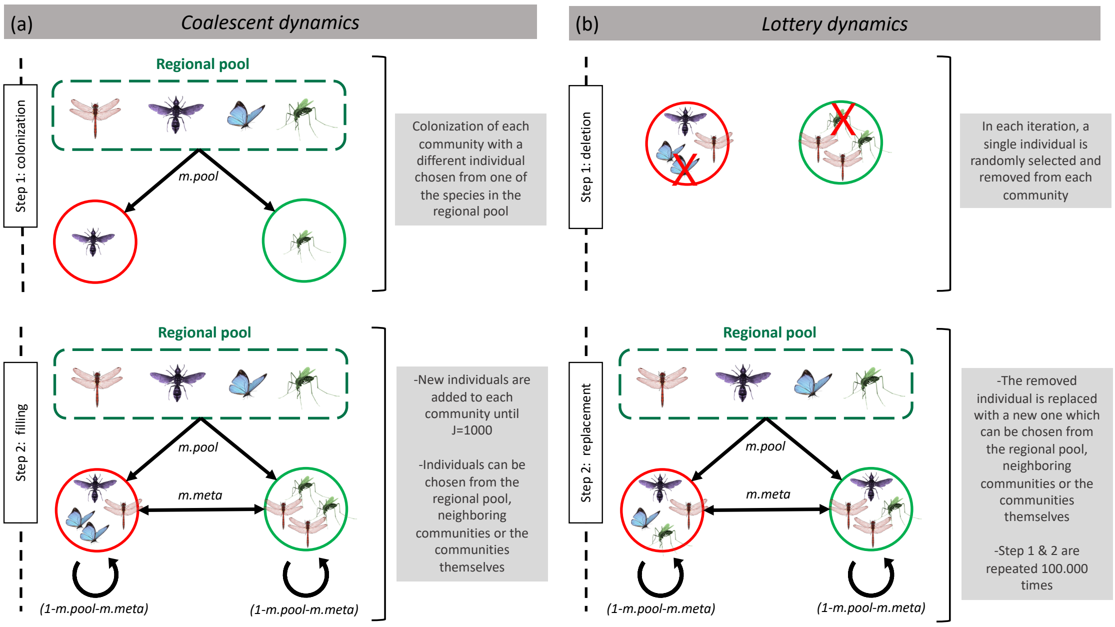
Considering a metacommunity connected to a regional pool of species (Figure 1b), a humped pattern in beta diversity is expected along the immigration gradient under three scenarios: purely random priority effects (H_1), priority effects conditioned by species dispersal ability (H_2), and species sorting (H_3). Low immigration rates restrain the diversity of species that arrive to each local patch limiting community differentiation. Communities could be dominated by the same set of pioneer species through stochastic priority effects (H_{1a}), by the same set of pioneer species with high dispersal ability (H_{2a}), or by a reduced set of locally adapted species through species sorting (H_{3a}). In any case, internal dispersal homogenizes local communities through mass effect reducing beta diversity. Contrary, intermediate immigration rates increase the diversity of species that arrive to the metacommunity enhancing priority effects and species sorting. Communities can differentiate through priority effects by being dominated by different pioneer species (H_{1b}) which can also have contrasting dispersal abilities (H_{2b}), or through species sorting due to the differential selection of species with distinctive traits (H_{3b}). Finally, high immigration rates, together with internal dispersal, homogenize local communities through mass effects surpassing both priority effects (H_{1c}, H_{2c}) and species sorting (H_{3c}).

Here, we theoretically formalized these hypotheses analyzing the effect that the arrival time of species to local communities, the differences in their dispersal abilities, and species local performances have in the beta diversity-dispersal relationship. We used a lottery model that simulates the dynamics of metacommunities connected to a regional pool of species and analyzed the expected trend in beta diversity along the immigration gradient under the scenarios of purely random priority effect (H_1), priority effects conditioned by differences in dispersal ability (H_2), and species sorting (H_3) (Figure 1b).

Methods

The lottery-based metacommunity model

Metacommunities were assembled with a lottery model (Hubbell 2001; Borthagaray et al. 2014; Worm and Tittenson 2018; Cunillera-Montcusí et al. 2021; Ortiz et al. 2023) which simulates the dynamics of a set of local communities connected between them, and to a regional pool of species, through dispersal (Figure 2). In addition, our model can incorporate variations in dispersal ability among species and environmental filtering during the assembly process of the metacommunities. In its simplest form, the model works in two stages (Figure 2). The first stage consist of community filling with coalescent dynamics where each community was first colonized with a different individual randomly sampled from the regional pool (Figure 2a, Step 1), and then filled with J individuals each by progressively adding a new individual randomly selected either from the regional pool (with dispersal rate *m.pool*), from neighboring communities (with dispersal rate *m.meta*), or from the updated community (i.e. local recruitment) (with rate 1 – *m.pool* – *m.meta*) (Figure 2a, Step 2) (Worm and Tittenson 2018; Cunillera-Montcusí et al. 2021; Borthagaray et al. 2023a, b; Ortiz et al. 2023). After all communities reached J individuals, the lottery dynamics started (Figure 2b) (Hubbell 2001; Worm and Tittenson 2018; Cunillera-Montcusí et al. 2021; Ortiz et al. 2023). Now, at each time step and in each local community a single individual was randomly deleted (Figure 2b, Step 1) and replaced by a different recruit randomly selected either from the regional pool, from neighboring communities or from the communities themselves with the same rates as before (Figure 2b, Step 2). This procedure was repeated N_{it} number of iterations. The model simulates the dynamics of all local communities simultaneously. This means that the processes of colonization, dispersal, death and recruitment occur in all communities at the same time.



Colonization of each community with a different individual chosen from one of the species in the regional pool

-New individuals are added to each community until J=1000

-Individuals can be chosen from the regional pool, neighboring communities or the communities themselves

In each iteration, a single individual is randomly selected and removed from each community

-The removed individual is replaced with a new one which can be chosen from the regional pool, neighboring communities or the communities themselves

-Step 1 & 2 are repeated 100.000 times

Figure 2. Lottery-based metacommunity model pseudocode. Metacommunities were assembled by recruiting individuals from the regional pool of species, from adjacent,

connected communities (i.e. the metacommunity) and from the focal local communities (i.e. local recruitment). The model works in two stages. (a) The first stage (i.e. coalescent dynamics) consists of colonizing each local community with one different individual that is randomly chosen from the species in the regional pool with dispersal rate *m.pool* (Step 1). After that, new individuals are progressively added to each community until the density J is reached in each one of them (Step 2). Now, individuals can be sampled either from the regional pool (with fixed dispersal rate *m.pool*), from other communities within the metacommunity (with fixed dispersal rate *m.meta*), or the communities themselves (with fixed rate 1 – *m.pool* – *m.meta*). (b) After local communities reached J individuals each, lottery dynamics start. Now, in each time step (i.e., iteration) a single individual is randomly removed from each community (Step 1) and replaced with a new recruit (Step 2) which can also be sampled either from the regional pool, from other connected communities or from the updated communities with the same rates as in the coalescent stage. This routine is repeated N_{it} number of iterations until local populations stabilize.

Evaluation of mechanisms

Hypothesis 1: Random priority effects

To evaluate how purely random priority effects modulate the relationship between beta diversity and dispersal, we run a neutral version of the model in which species were equivalent in their dispersal abilities and local performances. In this scenario, the probability of recruiting an individual of species *i* from the regional pool $(Disp_{i,pool})$, or from an adjacent community *q* $(Disp_{i,q})$ are determine simply by its local abundance and the dispersal rates *m.pool* and *m.meta*, as:

$$Disp_{i,pool} = m.pool * N_{i,pool}$$

$$Disp_{i,q} = m.meta * N_{i,q}.$$

The probability of local recruitment of an individual of species *i* from any focal community p $(Local_{i,p})$, and the probability of local death $(Death_{i,p})$ are defined as:

$$Local_{i,p} = \left(1 - Disp_{i,pool} - \sum_{q \neq p}^{N_{com}} Disp_{i,q}\right) * N_{i,p}$$

$$Death_{i,p} = N_{i,p}.$$

Hypothesis 2: Priority effects conditioned by dispersal ability

To evaluate the effect of the differences in dispersal ability among species on the beta diversity-dispersal relationship, each species was assigned a dispersal ability value DA_i drawn from the interval [0,1] (supplementary material, Figure S1a). Here, larger DA_i values determine larger dispersal abilities. The magnitude in the difference in dispersal ability among species is set by a parameter Q, which changes the shape of its functional relationship (supplementary material, Figure S2a). Now, the probability of recruiting an individual of species *i*, either from the regional pool ($Disp_{i,pool|DA_i}$) or any adjacent community q ($\mathrm{Disp}_{i,q|DA_i}$), is defined by its dispersal ability value as:

$$Disp_{i,pool|DA_i} = m.pool * N_{i,pool} * DA_i$$

$$Disp_{i,q|DA_i} = m.meta * N_{i,q} * DA_i.$$

Consequently, the probability of recruiting an individual of species *i* from any focal community p $\left(Local_{i,p}\right)$ is now:

$$Local_{i,p} = \left(1 - Disp_{i,pool|DA_i} - \sum\nolimits_{q \neq p}^{N_{com}} Disp_{i,q|DA_i}\right) * N_{i,p},$$

but the probability of local death ($Death_{i,p}$) remains the same:

$$Death_{i,p} = N_{i,p}.$$

Hypothesis 3: Species sorting

To incorporate the effect of species sorting within the dynamics, a different environmental and trait value distribution was assigned to each local community and species respectively (supplementary material, Figure S1b). The mean value μ of each distribution was placed within the interval [0,1] with constant standard deviation σ. The degree of overlap between the trait value distribution of species i and the filter value distribution of community p (i.e., match filter-trait—$MFT_{i,p}$—) determines its local performance. That is, the larger the $MFT_{i,p}$, the stronger the positive local selection over species i. Under this scenario, the probabilities of recruiting a new individual of species i, either from the regional pool ($Disp_{i,pool}$) or from an adjacent community q ($Disp_{i,q}$), are:

$$Disp_{i,pool} = m.pool * N_{i,pool}$$

$$Disp_{i,q} = m.meta * N_{i,q}.$$

However, the probabilities of local recruitment and death are now defined by the $MFT_{i,p}$ value, as:

$$Local_{i,p|MFT_{i,p}} = \left(1 - Disp_{i,pool} - \sum_{q \neq p}^{N_{com}} Disp_{i,q}\right) * N_{i,p} * MFT_{i,p}$$

$$Death_{i,p|MFT_{i,p}} = N_{i,q} * (1 - MFT_{i,p}).$$

Data analysis

We simulated metacommunities of five interconnected local communities with $J = 1000$ individuals each connected to a regional pool of 100 species. Simulations were run along the immigration gradient from the regional pool (i.e. external dispersal—range [0;0.5]—) considering different dispersal rates vales between communities (i.e. internal dispersal), with 10 replicates per parameter combination for each scenario. In addition, we run simulations considering different magnitudes in differences in dispersal ability and local filters (supplementary material, Figure S2). In all scenarios, lottery dynamics were run 100.000 time steps allowing species abundances to stabilize, eliminating transient dynamics (supplementary material, Figure S3).

After each simulation, we obtained the mean α, mean β (Jaccard) and γ diversity in the metacommunity. Additionally, we analyzed how random priority effects (H_1), priority effects conditioned by species dispersal ability (H_2), and species sorting (H_3) determined community assembly and species abundance. For this, we compared the final local abundance $N_{i,p}$ of species according to their arrival times to local communities ($AT_{i,p}$), dispersal abilities (DA_i) and local performances ($MFT_{i,p}$) along the *m.pool* dispersal gradient to determined how these variables influenced species abundances. All analysis were performed using R Software v.4.0.4 (R Core Team 2021).

Results

Beta diversity-dispersal relationship

Beta diversity showed complex trends along the immigration gradient (*m.pool* gradient), dependent on the dispersal rate between communities ($m.meta$) (Figure 3). At low $m.meta$ values, beta diversity decreased monotonically along the *m.pool* gradient (Figure 3a). However, beta diversity showed a humped pattern at intermediate (Figure 3b) and high (Figure 3c) $m.meta$ values. This pattern was qualitatively consistent under the three scenarios simulated, although its magnitude was higher when differences in dispersal ability and local selection were considered. Additionally, an increase in α (Figure 3d-f) and γ (Figure 3g-if) diversity was observed in all cases. See supplementary material Figure S4-6 for the results of β, α and γ diversity over the parameter space.

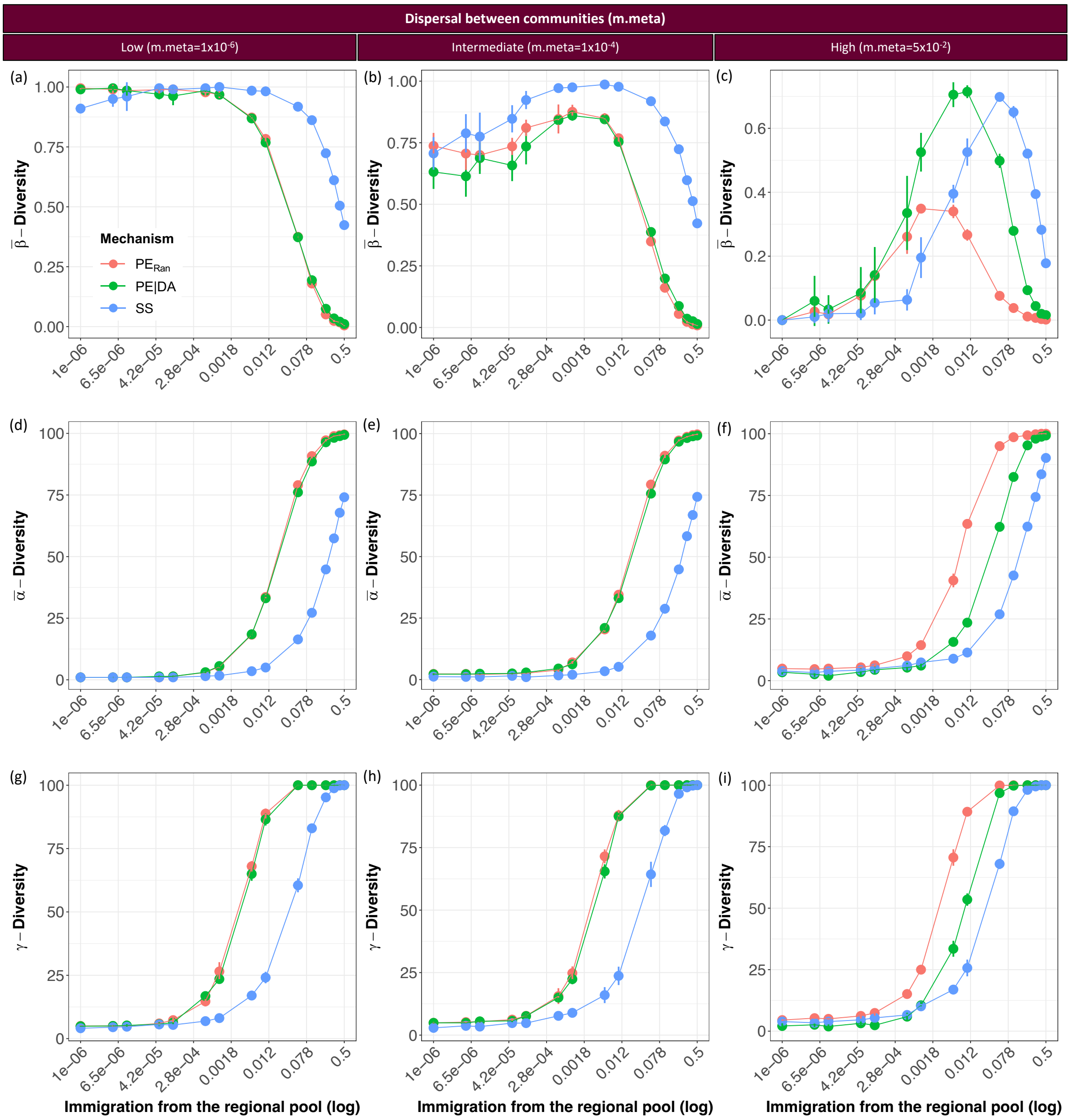


Figure 3. Trends in beta (a-c), alpha (d-f) and gamma (g-i) diversity along the immigration gradient from the regional pool of species to the metacommunity (*m.pool* gradient), considering different intensities of internal dispersal between local communities (*m.meta* values). Each point corresponds to the average (and 95% confidence interval) of the mean beta (a-c), alpha (d-f) and gamma (g-i) diversity obtained from the 10 replicates run for each parameter combination. Along the gradient in *m.pool*, beta diversity decreased monotonically when *m.meta* was low (a), but showed a humped pattern at intermediate (b) and high (c) *m.meta* values. In addition, mean alpha and gamma diversity increased monotonically in all cases. These patterns were qualitatively consistent under the action of the three mechanisms evaluated.

Hypotheses

Hypothesis 1: Random priority effect

The arrival times of species to local communities ($AT_{i,p}$) (Figure 4a) determined species abundance ($N_{i,p}$) and community differentiation through priority effects. At low and intermediate immigration rates from the regional pool, the abundance of those species that arrived at early stages of the dynamics was markedly higher than the abundance of the species that arrived at last (Figure 4b). However, high immigration rates determined similar abundance levels between species arriving at the beginning and at the end of the dynamics, erasing the effects of priority effects on species abundances.

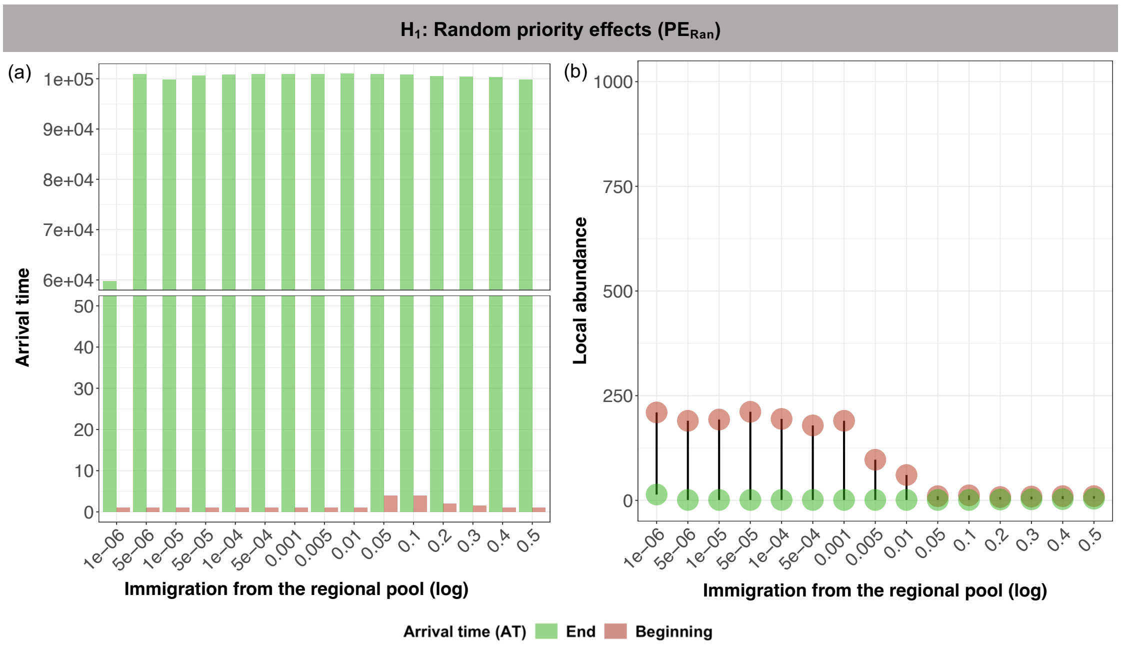


Figure 4. Effect of the arrival time of species to local communities ($AT_{i,p}$) on community structure and differentiation along the immigration gradient from the regional pool of species to the metacommunity (*m.pool* gradient), at high dispersal rates between communities (*m.meta* = 5x10^{-2}). After the dynamics ended, species present in each metacommunity were sorted according to their $AT_{i,p}$ and the arrival times corresponding to the percentile 0.01 ($AT_{P0.01}$) and 0.99 ($AT_{P0.99}$) defined. (a) Red and green bars represent the (median) arrival time of those species that arrived at the beginning ($AT_{i,p} \leq AT_{P0.01}$) and at the end ($AT_{i,p} \geq AT_{P0.99}$) of the dynamics

respectively. (b) Local abundance (median) ($N_{i,p}$) of the species shown in (a). At low to intermediate *m.pool* rates, communities were dominated by those pioneer species (red dots). However, the effect of $AT_{i,p}$ on $N_{i,p}$ progressively vanished as *m.pool* increased, homogenizing species abundances.

Hypothesis 2: Priority effects conditioned by species dispersal ability

Species dispersal ability (DA_i) determined species abundances and community differentiation favoring the early arrival of species with high dispersal rates to the metacommunity (Figure 5). Species with large DA_i values systematically showed higher local abundances than species with low dispersal abilities (Figure 5a), although the difference in abundance between good and bad dispersers was strongly reduced at high *m.pool* values. Furthermore, species with high DA_i values either colonized local communities or arrived earlier in the dynamics than species with low DA_i (Figure 5b). In addition, immigration rate determined the distribution of DA_i values among species (Figure 5c). Low immigration rates favored the early arrival of species with maximal dispersal abilities whereas intermediate immigration rates allowed species with high and intermediate dispersal abilities to colonize local communities. Contrary, high m.pool values determined the arrival of a larger number of species with low dispersal ability values.

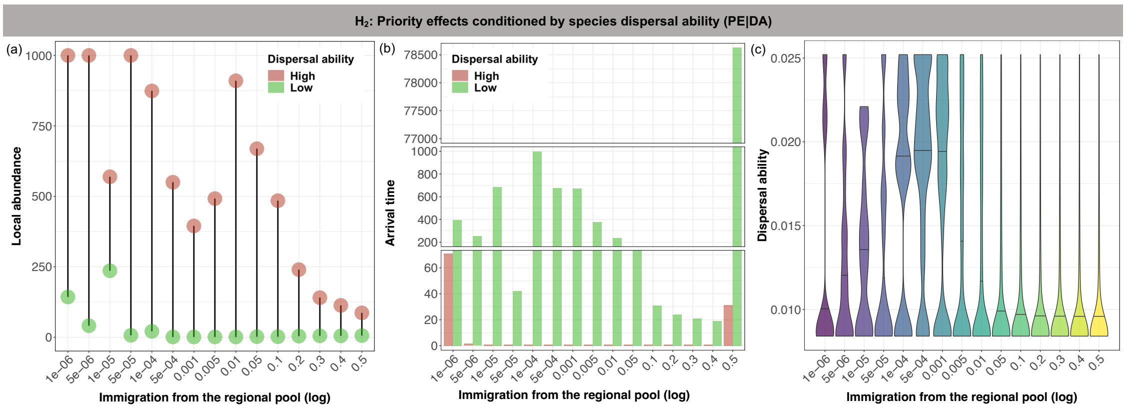


Figure 5. Effect of dispersal ability of species (DA_i) on community structure and differentiation along the immigration gradient from the regional pool of species to the metacommunity (*m.pool* gradient), at high dispersal rates among communities

(*m.meta* = 5x10^{-2}). After the dynamics ended, species present in each metacommunity were sorted according to their DA_i and the dispersal ability values corresponding to the percentile 0.01 ($DA_{P0.01}$) and 0.99 ($DA_{P0.99}$) defined. (a) Red and green dots represent the (median) abundance of the best ($DA_i \geq DA_{P0.99}$) and worst ($DA_i \leq DA_{P0.01}$) dispersers. Species with large DA_i showed abundance values markedly higher than species with low DA_i. However, differences in local abundance between good and bad dispersers were reduced as *m.pool* increased. (b) Arrival time values ($AT_{i,p}$) for the species shown in (a). Red and green bars indicate the arrival times of those good and bad dispersers respectively. (c) Distribution of DA_i values within the metacommunity. Low immigration rates favored the early arrival of species with high dispersal ability, whereas species with intermediate DA_i values were allowed to colonized local communities at intermediate immigration rates. Nevertheless, high m.pool rates determined the arrival of a larger number of species with low dispersal abilities.

Hypothesis 3: Species sorting

Species local performance ($MFT_{i,p}$) determined species abundance ($N_{i,p}$) and community differentiation through species sorting (Figure 6). Species with large $MFT_{i,p}$ values systematically showed higher local abundances than species with low local performance (Figure 6a), although these differences were reduced at high *m.pool* values. Furthermore, species abundance was not associated with their arrival times (Figure 6b), indicating that species sorting surpassed priority effects during the assembly process.

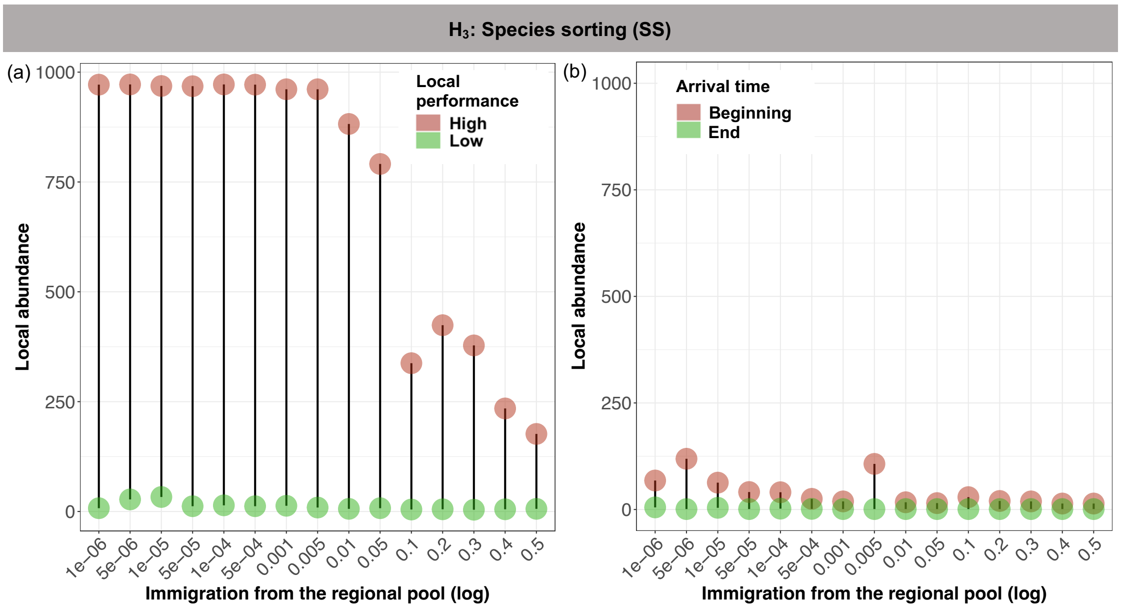


Figure 6. Effect of species local performance ($MFT_{i,p}$) on community structure and differentiation along the immigration gradient from the regional pool of species to the metacommunity (*m.pool* gradient), at high dispersal rates among communities (*m.meta* = 5x10^{-2}). After the dynamics ended, species present in each metacommunity were independently sorted according to their $MFT_{i,p}$ and arrival times ($AT_{i,p}$) values. From this two vectors, the $MFT_{i,p}$ and $AT_{i,p}$ values corresponding to the percentile 0.01 ($MFT_{P0.01}$; $AT_{P0.01}$) and 0.99 ($MFT_{P0.99}$; $AT_{P0.99}$) were defined. (a) Red and green dots represent the (median) abundance of the most ($MFT_{i,p} \geq MFT_{P0.99}$) and less ($MFT_{i,p} \leq MFT_{P0.01}$) adapted species in each metacommunity. Species with high $MFT_{i,p}$ showed abundance values markedly higher than species with low $MFT_{i,p}$. However, differences in local abundance between species were reduced as *m.pool* increased. (b) Red and green dots indicate the (median) abundance of those species that arrived at the beginning ($AT_{i,p} \leq AT_{P0.01}$) and at the end ($AT_{i,p} \geq AT_{P0.99}$) of the dynamics. Under a scenario of species sorting, local abundance was not associated with species arrival times.

Discussion

Stochasticity in the arrival times of species to local patches (Lepori and Malmqvist 2009; Fukami 2015; Vannette and Fukami 2017), differences in dispersal ability between species (De Bie et al. 2012; Jones et al. 2015; Hill et al. 2017; Ortiz et al 2023) and local selection due to heterogeneity in local filters (Cottenie and De Meester 2004; Mouquet et al. 2006; Gianuca et al. 2017; Cadotte and Tucker 2017) interact with dispersal shaping beta diversity. Nevertheless, the potential role of dispersal on community differentiation has been overlooked by most empirical studies (Logue et al. 2011; Grainger and Gilbert 2016; Vannette and Fukami 2017) by ignoring these sources of variation. Typically, experimental setups predefine the initial composition of species avoiding communities from being stochastically colonized, consider patches with homogenous environmental conditions limiting community assembly by species sorting, and eliminate any natural differences in dispersal ability between species (Logue et al. 2011; Grainger and Gilbert 2016; Vannette and Fukami 2017). Here, we showed that these sources of variation can determine a humped pattern in beta diversity along the immigration gradient from the regional pool, but only when sufficient dispersal among communities is considered (Figure 3b-c). Beta diversity was highest when immigration rates: (i) optimized the number of species that colonized local communities determining different assembly histories though priority effects (Figure 4); (ii) allowed the arrival and establishment of species with contrasting dispersal abilities in local communities which would be otherwise dominated only by good dispersers (Figure 5); and (iii) allowed the arrival of species with different traits to those local communities where they were best adapted determining community divergence through species sorting (Figure 6). Furthermore, community homogenization occurred from the interaction between external and internal dispersal through mass effects. When immigration from the regional pool was low, internal dispersal facilitated the spread within the metacommunity of the reduced set of species that arrived from the regional pool. Contrary, high immigration rates homogenized local communities surpassing priority effects and species sorting. These results are in line with our hypotheses (Figure 1b).

Under priority effects, community structure and differentiation results from variations in the arrival times of species to local communities (Fukami 2015). Species arriving at early stages of the assembly process dominate local communities by monopolizing limiting resources (i.e. niche preemption), reducing the abundance and viability of those species that arrive later during the dynamics (Fukami 2015). The importance of colonization history in structuring communities is expected to be particularly important when species present high niche overlap (Vannette and Fukami 2014), and at intermediate immigration rates from the regional pool (Chase 2003; Fukami 2005). This provides more time to pioneer species to stablish and grow before the arrival of other species, and avoids posterior competitive exclusions associated to species local performances. This was the case for our simulations when metacommunities were neutrally assembled (Figure 4), detecting high beta diversity at intermediate immigration rates. However, priority effects are usually conceived under a source-sink conceptualization, in which species arrive to a set of local, unconnected communities from an external source of immigrants (Fukami 2015). Under this scenario, beta diversity is expected to decrease as immigration rates from the regional pool increases due to species accumulation through mass effect (Chase 2003; Fukami 2015). This prediction is in line with our results when dispersal among communities was practically null (Figure 3a). However, by considering the interaction between external and internal dispersal, we were able to also detect a positive relationship between beta diversity and dispersal (Figure 3b-c). Future empirical studies are needed aiming at disentangling how biodiversity patters are modulated by priority effects and the interplay between immigration from the regional pool and metacommunity dispersal.

Priority effects are typically expected when species present similar dispersal abilities (Fukami 2015). If species differ in their dispersal rates, a deterministic sequence in the arrival of species to local communities is expected, being good dispersers the first ones to arrive limiting community divergence through historical contingency (Fukami 2015). However, our results show that beta diversity can also be increased under a scenario in which species differ in their dispersal abilities. At low dispersal rates from the regional pool, communities where colonized and dominated by the same set of species with high dispersal ability (Figure 5c). Yet, intermediate immigration rates allowed the arrival of a larger set of species with sub-optimal dispersal abilities to the metacommunity. The increase in community differentiation can be explained either by historical contingency if the species with sub-optimal dispersal abilities are able to colonize and dominate different communities, of by rescue effect (Hanski 1982; Gotelli 1991) since the local populations of these sub-optimal dispersers are expected to receive more immigrants. More investigation is needed in this area, since the interaction between these two mechanisms, and their effect on community diversity may have been overlooked by experimental studies by eliminating the variability in dispersal ability among species.

In agreement with several empirical studies (Cottenie and De Meester 2004; Gianuca et al. 2017), the increment from low to intermediate immigration rates enhanced the importance of species sorting in the structuring of communities, being surpassed by mass effect at high immigration rates. Communities subject to low and intermediate immigration rates were strongly structured by species sorting overcoming priority effects (Figure 6). This result reinforces the idea that both external and internal dispersal plays a major role in allowing species to arrive to suitable communities where they are positively selected (Cottenie and De Meester 2004; Leibold et al. 2004; Gianuca et al. 2017) favoring beta diversity. It is important to note that although our model incorporates species sorting due to environmental filtering, it can also be conceptually expanded to any biotic interaction that could generate differential selection between species throughout the metacommunity (e.g., interference competition, predation, mutualisms) (García-Girón et al. 2020; Ortiz et al. 2023b). However, the explicit evaluation of the effects of biotic interactions on the beta diversity-dispersal relationship in multitrophic metacommunities is still needed.

The influence of a stable, independent regional pool of species that supplies the metacommunities with an external set of species has been highlighted as an important determinant of community assembly (Fukami 2005, 2010; Harrison and Cornell 2008). However, a concrete interpretation of what the regional pool represents in different empirical scenarios is not always straightforward. Under our conceptualization, the regional pool of species can represent either a source of immigrants at a biogeographical scale that arrive to a specific metacommunity, or a spatially delimited portion of a metacommunity that acts as a source of individuals to a minor sub-set of local communities within the same metacommunity. In any case, it is important that the dynamics within the regional pool are decoupled from the dynamics within the metacommunity to explore how beta diversity is affected by dispersal (Fukami 2015). Empirical studies have frequently neglected the importance of considering an external source of immigrants by working with closed metacommunities (Grainger and Gilbert 2016). We draw attention to this issue and highlight that more empirical research is needed to detect how the regional pool of species interact with metacommunity dispersal determining community structure and diversity patterns.

Our modelling approach allowed us to evaluate how different mechanisms determine the relationship between beta diversity and dispersal relying only on basic ecological processes (i.e., local recruitment, death, dispersal, colonization, and local selection). This facilitates the interpretation of the model outcomes and contributes to our mechanistic understanding of how dispersal can determine novel patterns of beta diversity. Furthermore, it incorporated different factors that are logistically challenging to include in experimental setups. Specifically, we were able to consider a continuous gradient in dispersal intensity rather than a limited number of discrete dispersal levels, and evaluated the influence of an external regional pool of species on metacommunity dynamics (Grainger and Gilbert 2016). However, some limitations regarding the assumptions of our model should be considered. First, simulations were run on metacommunities containing only a small number of interconnected communities. Nevertheless, different metacommunity structures and directional dispersal influence colonization rates affecting beta diversity differentially among patches (Brown and Swan 2010; Carrara et al. 2012; Altermatt et al. 2013; Seymour and Altermatt 2014). Second, we obviated biotic interactions among species which have the potential to strongly affect community structure (Haegeman and Loreau 2014; Soininen et al. 2017; García-Girón et al. 2020; Lu 2021; Ortiz et al, 2023b). Third, we simulated dispersal as a purely stochastic process, although active dispersal can affect diversity at several scales (Ye and Wang 2023). Finally, we focused on a specific type of priority effects based on niche preemption in which pioneer species only reduced the amount of resource available (i.e., space) to later dispersers. However, priority effects based on niche modification, where early-arriving species modify local environmental conditions should also be considered (Fukami 2015). The theoretical and empirical analysis of these factors represent future venues that could revel novel mechanisms guiding the relationship between dispersal and beta diversity in metacommunities.

Founding

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Supplementary Material

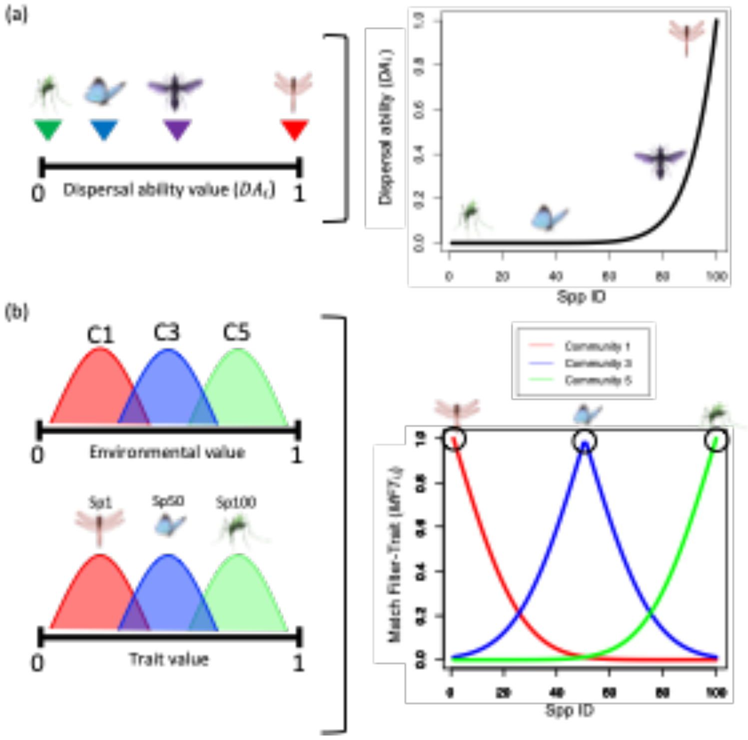

Figure S1. Determination of species dispersal ability (a) and species local performance (b). (a) Species dispersal ability (DA_i) was defined by assigning to each species a value drawn from the interval [0,1], where larger DA_i values determine higher dispersal abilities. (b) Species local performance was determined by assigning to each local community and species an environmental and trait value distribution respectively with mean μ drawn from the interval [0,1] and constant standard deviation σ. The local performance of a species i in a local community p was defined as the overlap between the trait distribution of i and the environmental distribution of j (i.e. Match Filter-Trait, $MFT_{i,p}$). If $MFT_{i,p} = 1$, the overlap between the two distributions is maximum which means that i is the species best adapted to community p showing the highest local performance.

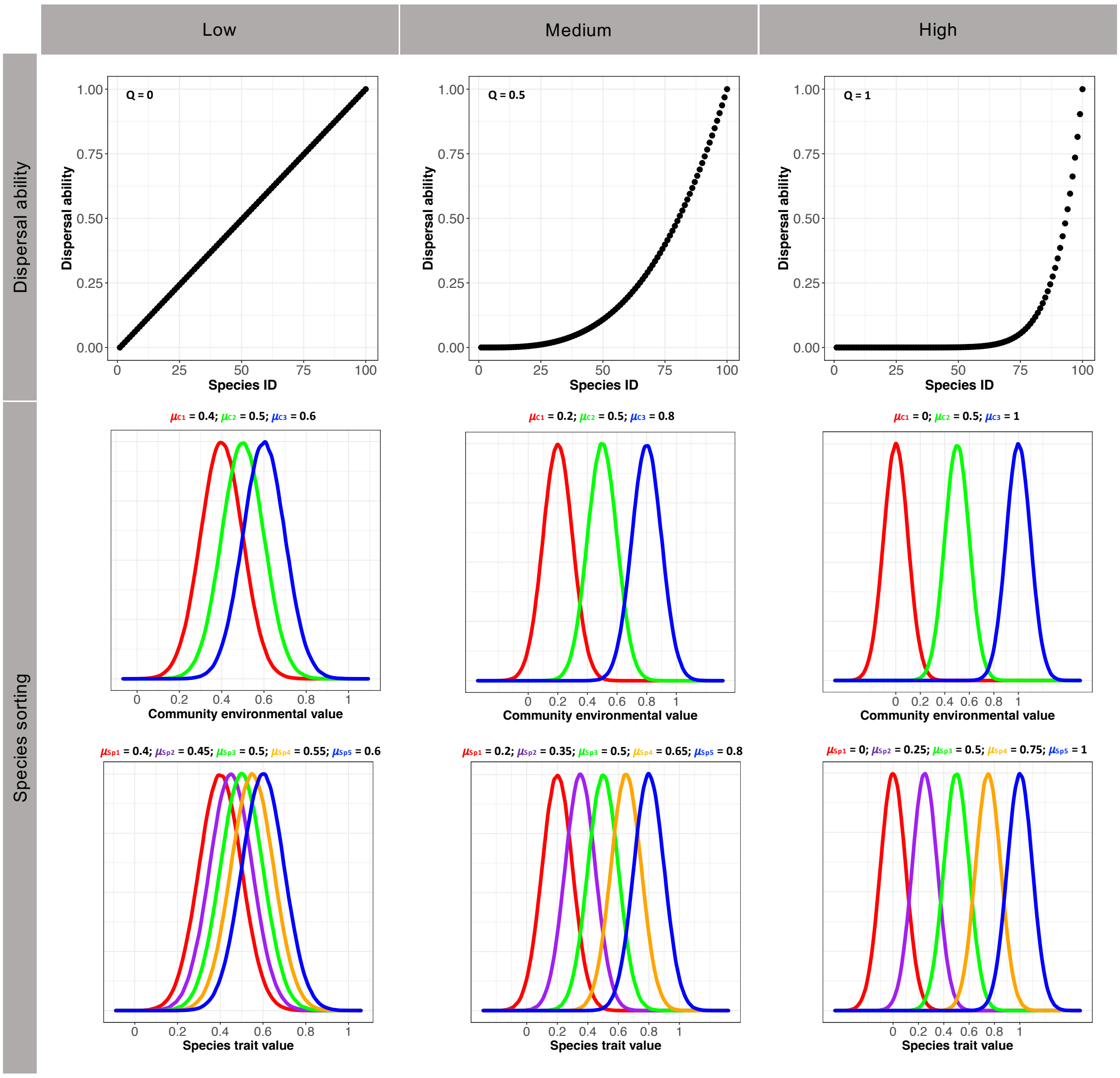

Figure S2. (a) Variations in dispersal ability between species were determined by parameter Q. Large Q values magnify the differences in dispersal ability between good and bad dispersers. (b) Variations in species local performance were determined by the distance between the mean μ of each distribution. The longer the distance between the values of μ, the more different local communities and species are in terms of their environmental conditions and traits respectively.

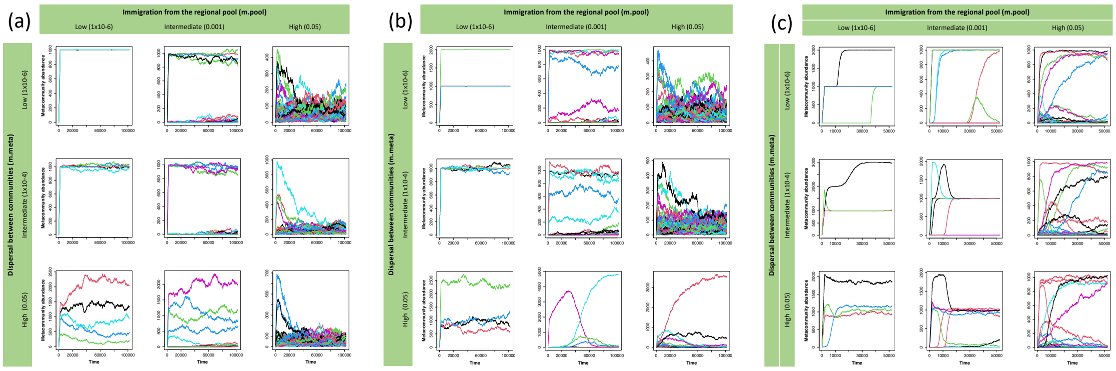

Figure S3. Species abundances during the lottery dynamics under the scenarios of random priority effects (H_1), priority effects conditioned by species dispersal ability (H_2) and species sorting (H_3) for different m.pool and m.meta dispersal rates. Each line corresponds to the dynamics of a different species.

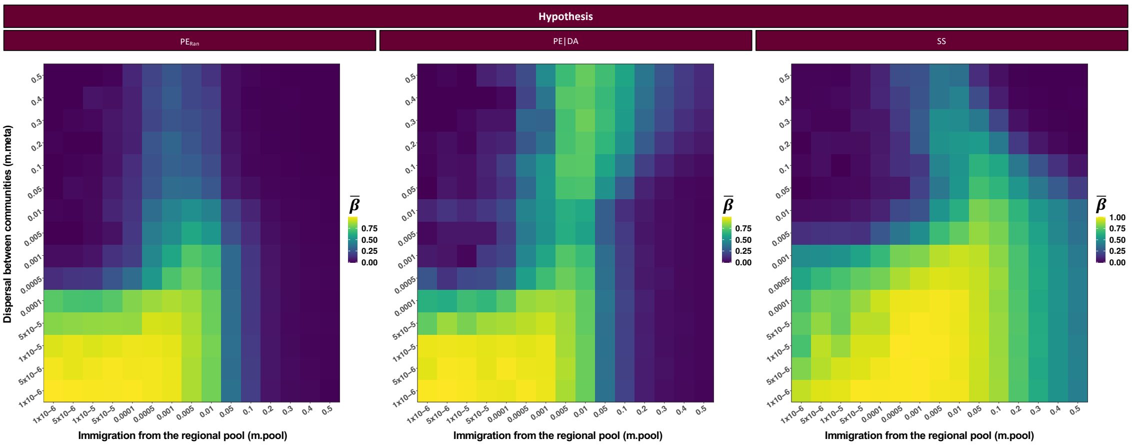

Figure S4. Mean β diversity for different combinations of immigration (m.pool) and internal dispersal (m.meta) rates.

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Capítulo 3:

Patrones de selección de presas a lo largo de un gradiente de tamaño corporal de depredador evidencian el rol de diferentes mecanismos basados en atributos en la organización de redes tróficas

El contenido de este capítulo se encuentra publicado en la revista Plos One y se presenta en el formato original del artículo:

Ortiz, E., Ramos-Jiliberto, R. & Arim, M. (2023b). Prey selection along a predators' body size gradient evidences the role of different trait-based mechanisms in food web organization. PLOS ONE, 18, e0292374.

PLOS ONE

RESEARCH ARTICLE

Prey selection along a predators' body size gradient evidences the role of different trait-based mechanisms in food web organization

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Abstract

An increase in prey richness, prey size and predator trophic position with predator body size has been consistently reported as prime features of food web organization. These trends have been explained by non-exclusive mechanisms. First, the increase in energy demand with body size determines that larger predators must reduce prey selectivity for achieving the required number of resources, being consumption relationships independent of prey traits. Second, when consumption is restricted by gape limitation, small predators are constrained to select among small prey. However, this selection weakens over large predators, which progressively consume more and larger prey. Finally, the optimal foraging mechanism predicts that larger predators optimize their diet by selecting only large prey with high energy reward. Each one of these mechanisms can individually explain the increase in prey richness, prey size and predator trophic position with predator body size but their relative importance or the direct evidence for their combined role was seldom considered. Here we use the community assembly by trait selection (CATS) theory for evaluating the support for each one of these mechanisms based on the prey selection patterns that they predict. We analyzed how prey body size and trophic guild determine prey selection by predators of increasing body size in a killifish guild from a temporary pond system. Results support the combination of the three mechanisms to explain the structural trends in our food web, although their strength is contingent on prey trophic group. Overall, high energy prey are preferred by larger predators, and small predators select small prey of all trophic status. However, large predators prefer large primary producers and avoid large carnivorous prey, probably because of the inherent risk of consuming other carnivorous. Our study provides a mechanistic understanding of how predator traits determine the selection of prey traits affecting food web assembly.

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Introduction

Species interactions are highly influenced by species body size [1–3]. Predator-prey body size relationships determine variations in community-level properties such as the distribution of interaction strength [4, 5], secondary extinctions after species loss [6], and community stability [7]. Consequently, empirical studies have reported robust trends in trophic interaction properties with increasing body size of predators (Fig 1A). Of most importance, the increases in prey richness and in prey size were widely reported at the intra and interspecific level [1, 3, 8–15], and have been identified as important determinants of food web structure and stability [2, 3, 11, 12, 16–18]. Therefore, body size, through determining predator-prey interactions, potentially shapes community level structural and functional attributes beyond pairwise ecological relationships.

Prey selection is a leading process modulating predator-prey relationships [19]. Specific mechanisms have been proposed to explain observed trends in prey selection as a function of the body size of predators and their prey [12, 20]. These mechanisms include: first, the increase in the number of prey items consumed due to the need to satisfy the increase in energy demand at larger body sizes [21, 22] (Fig 1B); second, the progressive relaxation of gape limitation, which allows the gradual consumption over more and larger prey [23, 24] (Fig 1C); and third, the optimal foraging mechanism, which predicts strengthening the preference for prey of larger size–with greater energy reward–as predator become larger [25–27] (Fig 1D). These mechanisms determine specific prey selection patterns governed by the interaction between prey traits and predator body size [12, 20], and may operate either individually or through their combined action. The increase in energy demand with predator body size determines that larger predators progressively incorporate prey items into their diet independently of prey traits—e.g. predators become less selective and more generalists [12]. This mechanism does not involve changes in the selection of prey with different traits and represents a null hypothesis from the perspective of prey traits (Fig 1B). However, gape limitation is expected to mediate the association between predator and prey body sizes [1, 8, 12, 23, 28]. The mechanism of gape limitation operates through excluding large prey from being consumed by small predators, determining a negative selection on these items and a preference over small prey. This selection pattern progressively weakens as predators become larger being both small and large prey equally preferred by large predators (Fig 1C). Finally, since the energetic content of a prey is positively associated with its trophic level and body size [21, 29, 30], the higher energy demand of large predators may consequently determine a selection for larger-bodied prey that provide greater energetic return (e.g. animals over basal resources) (Fig 1D) [25–27]. These three prey selection models evidence the basic mechanisms underlying body size dependent trends in predator trophic position [24], prey richness [8, 17], and prey size [28] (Fig 1A), and indirectly, emergent structural community properties such as nestedness [13, 14] and modularity [27]. Remarkably, although these mechanisms generate explicit predictions about the body size dependent prey selection behavior, they have often been indirectly evaluated. This has been done mainly through interpretating patterns of over–versus under–representation of prey traits relative to the environmental offer, along a gradient of predator body size (e.g. [31–33]).

New methods for analyzing trait selection along ecological gradients have been extensively developed. Among them, the community assembly through trait selection (CATS) theory [34–36] introduced techniques for directly evaluate the role of traits as determinants of the relative abundance of species along environmental gradients. Essentially, by means of generalized linear models, species abundances are related to species traits, environmental conditions, and the interaction among them [35–37]. This method is also suited for the analysis of trends in trophic interactions with predator body size mediated by prey traits. In this context, predator

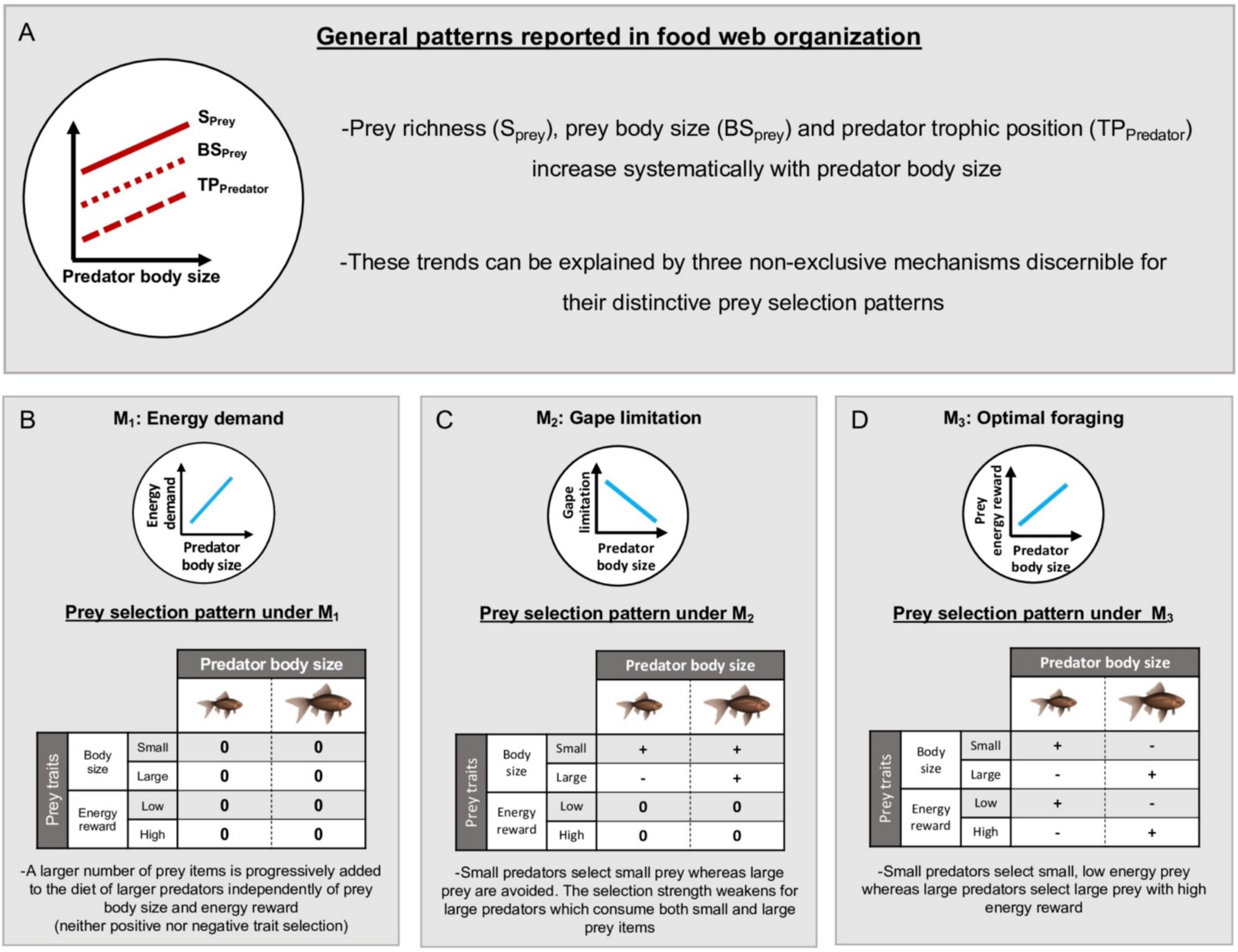

Fig 1. Mechanisms and hypotheses. (A) Common structural patters broadly reported in food webs. Along a gradient in predator body size, an increase in prey richness, prey body size and predator trophic position have been systematically observed in numerous food webs. These trends can be explained by three non-exclusive mechanisms discernible for their distinctive prey selection patterns based on predator body size and prey traits (i.e. size and energy reward). (B-D) Mechanisms proposed to explain the structural trends shown in (A). (B) Under the energy demand mechanism (M_1), the increase in prey consumption by large predators is determined by the positive association between predator´s energy demand and body size. The progressive incorporation of prey items into the diet of larger predators is not associated with prey traits, involving a trait-independent consumption pattern. (C) The gape limitation mechanism (M_2) allows large predators to consume over more and larger prey items due to the relaxation of gape limitation. This mechanism determines a selection pattern in which small predators select only small prey, with large prey being excluded from the diet. This preference for small prey weakens as predator body size increases, since large predators are able to consume all size classes of prey. (D) Under the optimal foraging mechanism (M_3), prey items are consumed according to their energy reward. This mechanism determines that larger predators select larger prey with higher energy reward.

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body size represents the environmental gradient and prey traits determine a selection process in consumption that could systematically change along the gradient of predator body size. Additionally, the identity of the observed prey items in the diet represents the complete prey pool consumed by all predators in the defined system. This approach overcomes the classic limitation of identifying the total available prey set, needed to infer selection mechanisms through traditional methods [25, 38, 39].

In using the CATS framework, we advance our understanding of trophic relationships by directly evaluating the support for the three alternative mechanisms that could explain the patterns of prey consumption as a function of predator body size and prey traits. The combination of the three alternative mechanisms of prey selection gives rise to seven competing hypotheses that guide our study (Fig 1D). H_1: the increase in energy demand by larger predators determines the increase in prey abundance and the consequent diversification of diet items independently of prey traits. H_2: consumption is determined by restrictions imposed by consumers body size (i.e. gape limitation). The banned consumption of large prey determines a negative selection for these items and/or a positive selection for smaller ones by small predators, and the progressive attenuation of this selection regimen along larger consumers. H_3: consumption is determined by a maximization of energy acquisition. Large predators positively select big prey with high energy reward (e.g. animal prey) and avoid the consumption of small prey with low energy reward (e.g. primary producers). H_4: relaxation of gape limitation and the increase in energy demand jointly determine the trend in diet with body size. H_5: the increase in energy demand and the maximization of energy reward guide consumers diet, increasing selection for large prey along large consumers. H_6: the relaxation of gape limitation and the maximization of energy reward determine that large predators select over large prey with high energy reward and small predators select small prey. H_7: in addition to gape limitation and maximization of energy reward, the increase in energy demand with predator body size also explains the change in trophic interactions by an increase in consumption. We test the above hypotheses by analyzing our own dietary trait data from a guild of annual killifish species. This empirical system has been thoroughly studied and employed as a research model to reveal how trait-based trophic interactions affect food web structure [12, 14, 40, 41].

Materials and methods

Ethic statement

We used the data collected and published in [12, 42], and no additional animals were sampled or euthanized for the current study. Fish sampling in [42] was carried out in strict accordance with the recommendations of "Comisión Honoraria de Experimentación Animal (CHEA)" in 2006. Fish individuals were sampled with a hand net, euthanized with an overdose of 2-phenoxyethanol, and fixed with 4% formaldehyde. All efforts were made to minimize suffering. All specimens analyzed were placed in the Fish Collection of Facultad de Ciencias (Faculty of Science), Montevideo, Uruguay, under the Institutional Code: ZVC-P. Fishes were collected on a private land in the region of Humedales del Este (Eastern Wetlands) which was declared Biosphere Reserve by UNESCO (program MAB). Permissions to collect had been granted by the landowners.

Study system

Predators and prey for analysis come from a set of temporary ponds located in grassland in the Laguna de Castillos basin, Rocha, Uruguay. Ponds are formed from ground depressions during the rainy season, when rainwater supply surpasses water loss due to evaporation [42]. The aquatic system shows a high diversity of macrophyte, macroinvertebrate and vertebrate species [40, 43]. Our analyses are based on the diet information collected from stomachs of 619 individuals belonging to the four killifish species that inhabit the ponds: *Austrolebias viarius*, *A. cheradophilus*, *A. lutheoflammulatus* and *Cynopoecilus melanotaenia* [12, 43]. In our study system, these species are the top predators, showing a strong positive intraguild relationship between their body mass and their trophic position, along with prey richness and number of energy sources (i.e. plants, detritus, phytoplankton and terrestrial prey) [12]. In addition, we detected a smooth incorporation of prey items with increasing body size, determining the emergence of a strong nested size-dependent organization of trophic interactions [14]. Fish individuals were sampled during winter 2006, identified at the species level and their standard length was measured following established procedures [40, 42, 44]. Following [12] and [14], individual predators were sorted by size and classified into 20 body size classes, each of them composed of 31 individuals (30 in the largest class) (S1 Fig).

Prey items in the stomach content of each individual fish were identified to the highest possible taxonomic resolution and categorized into trophic groups as primary producers, herbivorous and detritivores, and carnivorous (data published in [12, 42]). We used the membership to a trophic group as a categorical trait of prey, subsequently included in the predator selection analyses. The trophic groups represent an increasing gradient in the energy quality of prey form primary producers to carnivorous species [12, 21]. Prey size was the second trait of prey considered in the selection analyses. Prey size was estimated from a dataset of invertebrates that inhabit the pond system, that were collected in October 2008 [40] (S2 Fig). In addition, we obtained from literature [45–49] the body sizes of those items that appeared in the killifish diet but that were not collected in the field survey. These data represented less than 1% of prey items in terms of richness and abundance.

Prey trait representation in predator body size classes

The representation of traits in communities along an environmental gradient is usually visualized through the trend exhibited by the "community-weighted mean" along the gradient [50]. This metric captures the average representation of traits in each community. In analogy, we estimated a "diet-weighted mean" (DWM), indicating the representation of prey traits across predator size classes. For quantitative traits, $DWM = \sum_{i=1}^{n} p_i * trait_i$, where p_i is the relative abundance of the trophic item i in a killifish size class and $trait_i$ is the mean trait value of that item—that is the average prey trait value independently of its taxonomic identity. For categorical traits with n levels, $trait_i$ represents a particular level i of the trait and p_i is the relative abundance of all prey items within i—that is the frequency of a categorical prey level (e.g. carnivorous prey) in predator diet, independently of prey taxonomy [50]. Here, DWM provides an estimation of the relative frequency of primary producers, herbivorous and detritivores, and carnivorous prey items, and the average prey size (combining all trophic groups) in the diet of each killifish body size class [51].

CATS regression model and hypotheses evaluation

In the present analysis we employed CATS regression model to relate the abundance of a prey item with the interaction between its traits and the body size of consumers [34–36, 51, 52]. This technique allows to evaluate how influential the traits of a prey item are in determining its abundance in the diet of consumers with different body sizes. The CATS regression model consists of a generalized linear mixed model of Poisson family, with an offset that represents a prior abundance distribution of prey items. That is, the frequency of each prey item along all size classes of predators combined [36]. Using this approach, the abundances of prey items in each predator body size class were related to predator body size, prey traits—size and trophic group—and the interaction among them. The sign of the model coefficients (β) directly translates into positive ($\beta > 0$), null ($\beta = 0$) or negative ($\beta < 0$) prey selection according to their traits [36]. In addition, the numeric value of the model coefficients represents a measure of the relative selection for some kind of prey over others (e.g. small vs large prey). That is, the larger the magnitude of the coefficient, the larger the selection strength for a certain prey category [35, 37]. This allowed us to analyze whether and to what extent predators with different body sizes prefer different prey items (e.g. vegetable vs. animal prey) and whether this selection is affected by prey traits (e.g. body size and trophic category).

We used the CATS regression model to evaluate the prey selection patterns expected under the three alternative mechanisms, and then the support for the seven competing hypotheses (Fig 1). The inclusion of the predators and prey traits as fixed effects in the model represents a direct way of testing the predictions associated with mechanisms M_2 and M_3 (Fig 1B and 1C). Under the gape limitation mechanism M_2, small predators are expected to select small prey for all trophic categories (i.e. $\beta_{\text{small prey}} > \beta_{\text{large prey}}$), whereas this preference should weaken for large predators (i.e. $\beta_{\text{small prey}} \approx \beta_{\text{large prey}}$) (Fig 1B). Under the optimal foraging mechanism M_3, large predators should select prey with high energy reward (i.e. large, animal prey—$\beta_{\text{small prey}} < \beta_{\text{large prey}}$ and $\beta_{\text{primary producers prey}} < \beta_{\text{animal prey}}$), but small predators may comparatively prefer prey items with low energy reward (i.e. small, primary producer prey—$\beta_{\text{small prey}} > \beta_{\text{large prey}}$ and $\beta_{\text{primary producers prey}} > \beta_{\text{animal prey}}$) (Fig 1C). The prediction associated to the energy demand mechanism M_1 was tested by including the identity of predator body size class as random effect [53] (Fig 1A). Under this mechanism, it is expected that prey items are incorporated into the diet of large predators independently of prey traits. The random effect associated to the predator size class controls for the variation in consumption rate among body size classes of predators not related to prey traits. That is, trends in diet are explained by differences in consumption rate along predator body size classes due to the increasing energy demand of larger predators and are independent of changes in the selection of prey traits. Since the energy demand mechanism predicts that this variation in prey consumption originates from differences in predator body size, we also computed the Pearson correlation between the number of prey items and the predator body size.

The CATS regression model including both fixed and random effects (i.e. full model) was compared with alternative simpler models that could be used to test the mechanisms herein evaluated. The full model was compared against several nested models constructed by systematically removing different terms from the full model. The criteria used to select the best model was based on the Akaike´s Information Criterion (AIC) and the estimation of the weight of evidence [54], which indicates the probability that one of the models is the real one, as compared to all the alternative models. In addition, we performed the Wilks´ likelihood ratio test, which permits comparing the degree of empirical support that two nested statistical models receive from data. Finally, the identity of prey items was also included as random effect [53] to control for the effect of the natural differences in prey abundances—i.e. those not related to predator body size. All analysis were conducted in R [55] at $\alpha = 0.05$ significance.

Data availability

All raw data and code lines used in this study are freely available at https://doi.org/10.5061/dryad.bk3j9kdjg

Results

We found significant trends for the diet weighted mean of prey traits along the gradient of predator body sizes. First, we observed a reduction in the proportion of primary producers present in the diet, down to a complete absence of this item in the largest predator size classes (Fig 2A). Second, the frequency of herbivorous and detritivores prey items did not differ among predators (Fig 2B). Third, we detected a strong increase in the frequency of carnivorous prey items with predator size (Figs 2C and S3). Finally, the representation of larger prey items systematically increased with predator body size (Fig 2D). It is important to note that these

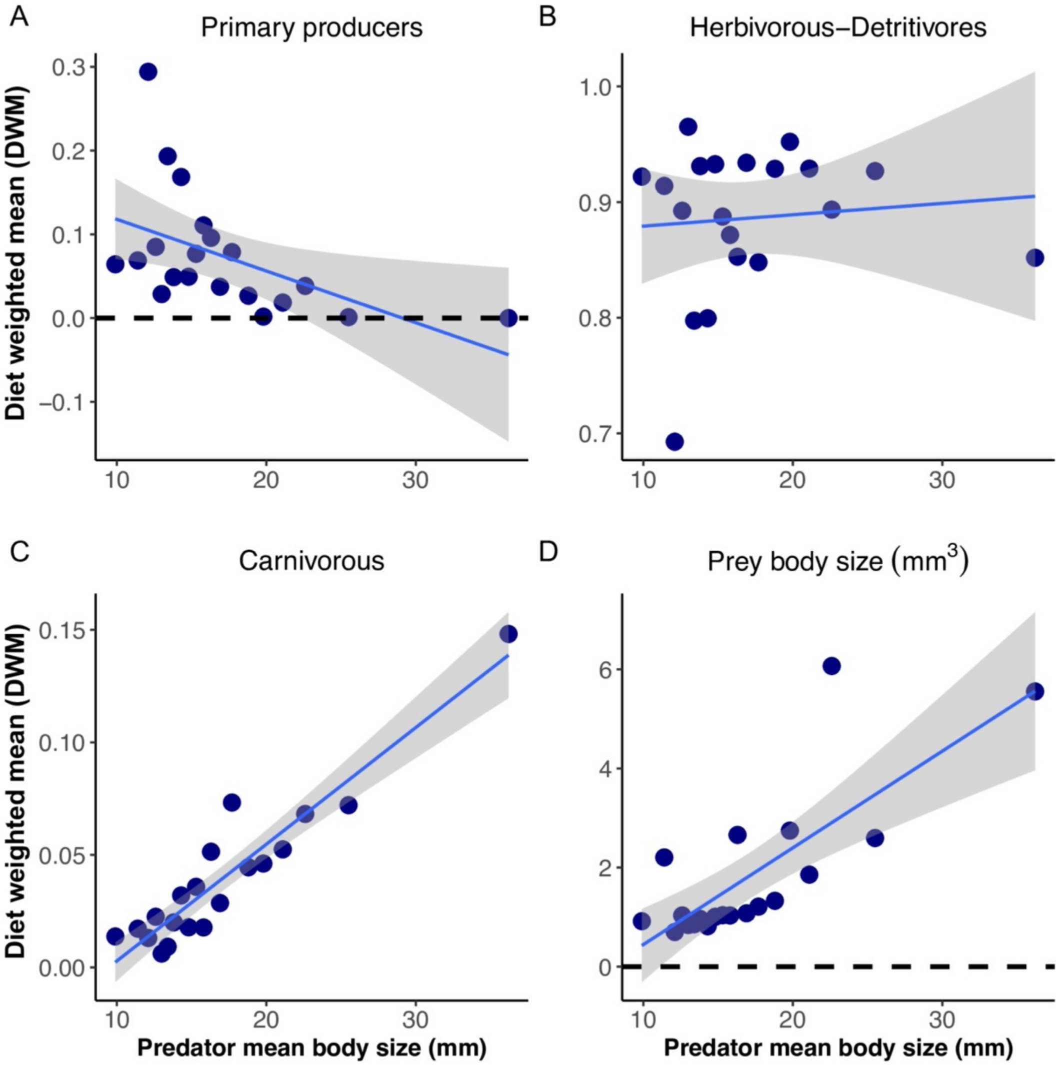

Fig 2. Diet weighted mean of prey traits along the gradient in predator body size. (A) primary producers are overrepresented in the diet of smaller predators, but their representation progressively decreases along size classes ($R^2 = 0.26$, $P = 0.02$). (B) The representation of herbivorous and detritivores prey did not change along body size classes of consumers ($R^2 = 0.01$, $P = 0.9$). (C) Carnivorous prey systematically increases with consumers body size ($R^2 = 0.88$, $P<0.01$). (D) The average body size of prey items systematically increases with predator body size ($R^2 = 0.6$, $P<0.01$).

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results only describe general patterns regarding the representation of different types of prey in the diet of predators, but do not evidence the mechanisms responsible for such patterns.

The full CATS regression model outperformed each one of the alternative models (weight of evidence = 0.998) (S1 Table) showing a good performance ($R^2 = 0.67$). This result indicates that 67% of the occurrence and strength of trophic links in this system was explained by the trait values of predators and prey here considered. Furthermore, our analysis sheds light on the prey selection mechanisms involved, by evidencing support for the three alternative mechanisms evaluated. In this context, our results support H_7, which relates the combined action of the three prey selection mechanisms considered here. The action of the first mechanism about the increase in the number of prey consumed as a determinant of differences in trophic interactions along predator size classes was strongly supported. Specifically, the regression model with a random effect associated to predator body size class outperformed a model without this effect ($\Delta AIC = 505.33$) (S1 Table). In addition, we obtained a strong positive association between the number of individual prey consumed and the predator body size ($r = 0.91$; $t_{18} = 9.2$; $P < 0.0001$). Despite this, we observed a change in the selection of prey traits (body size and trophic group) along the gradient of predator body size, also supporting the action of mechanisms M_2 and M_3 (Fig 3 and S2 Table and S4 Fig).

Supporting the prediction derived from the gape limitation mechanism, small predators positively selected small prey items from all trophic groups (i.e. $\beta_{\text{small prey}} > \beta_{\text{large prey}}$) (Fig 3). However, this selection was progressively inverted for primary producer prey ($\beta_{\text{small prey}} < \beta_{\text{large prey}}$) (Fig 3A) and reduced for herbivorous and detritivores prey ($\beta_{\text{small prey}} \approx \beta_{\text{large prey}}$) (Figs 3B and S4) as predator body size increased. Moreover, carnivorous prey of small size were always selected over large carnivorous prey ($\beta_{\text{small prey}} > \beta_{\text{large prey}}$), a pattern that was magnified in large predators (Figs 3C and S4). In this sense, the gape limitation mechanism is supported by the consistent selection over small prey by small predators, and the selection pattern observed for herbivorous and detritivores prey in which both small and large prey items were equally consumed by large predators. Interestingly, the selection pattern observed for primary producers, for which large prey were preferred by large predators (Fig 3A), is the only one that supports the action of the optimal foraging mechanism in terms of selecting large over small prey by large predators. However, this mechanism is also supported by the observed replacement among prey trophic groups along size classes of predators (see below).

As expected under the optimal foraging mechanism, as predators become larger there was a transition in the selection pattern from low (i.e. primary producers) to high energy prey (i.e. animal prey–herbivorous, detritivores and carnivorous) (Fig 3). The selection for primary producers peaked at small size classes of predators (Fig 3A), whereas the selection for herbivorous and detritivores prey peaked at intermediate body size classes (Fig 3B). The reduction in the preference for herbivorous and detritivores prey was coupled with a progressive increase in the selection for carnivorous prey that continues rising towards the lager body size class of consumers. Consequently, selection of prey traits in terms of trophic group in the predator body size gradient goes from a preference for primary producer, which are replaced by the preference for herbivorous and detritivores prey, being finally replaced by carnivorous prey (Fig 3). In this sense, the consumption pattern supports the mechanism of optimal foraging towards more energetic prey as predators become large.

Discussion

Prey selection is a basic process driving the emergence of food web structure [19, 56, 57]. Consequently, detecting the mechanisms that determine how and why prey are selected by predators is key to understand the structure and assembly of communities [2, 58]. In this framework, the increase in energy demand, the gape limitation and the optimal foraging mechanisms have been proposed to explain the role of consumers body size and prey traits on the emergence of common structural patterns among food webs. These mechanisms involve alternative trends in prey selection along predator body size gradients and were all supported by our results. Based on our analyses we found that: first, the energy demand mechanism, which refers to a trait-independent increase in number of prey at large body sizes, had strong statistical support as a determinant of trophic interactions. Second, selection on small prey for small size classes of predators associated with gape limitation is evidenced along primary

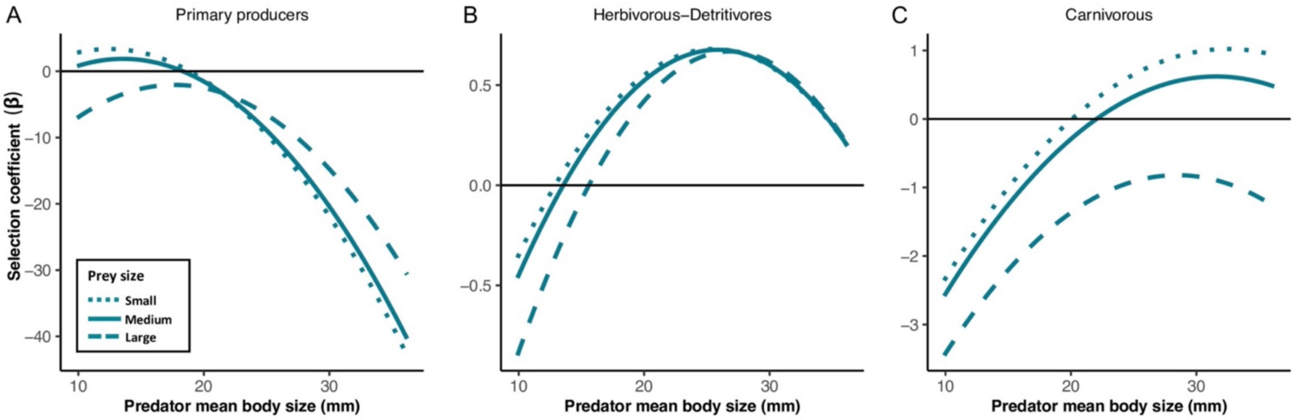

Fig 3. Selection of prey traits along the predator body size gradient. (A) primary producers, (B) herbivorous and detritivores and (C) carnivorous prey items. Line type shows the interaction between prey trophic status and prey body size. The dotted lines correspond to prey items with small body sizes (percentile 0.05 of prey body sizes), the solid lines represent medium-sized prey (percentile 0.5 of prey body sizes), and dashed lines represent large prey (percentile 0.95 of prey body sizes). Selection coefficient relates prey consumption with prey traits. Selection of prey body sizes must be interpreted observing the vertical axis of the figure. When the dotted line is at the top of curves, small prey items are selected at this size class. When the dashed line is at the top, large size classes of prey are selected. Small prey items from all trophic groups are preferred by small predators. However, large predators select large primary producer prey over the small ones. In addition, the preference for small herbivorous-detritivores prey weakens for large predators, which consume this kind of prey independently of prey size. Note that large carnivorous prey are always avoided, and that this pattern is enhanced as predator body size increases.

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producers, herbivorous and detritivores and carnivorous prey. This size preference is reduced for herbivorous and detritivores prey items as predator body size increases, additionally supporting the gape limitation mechanism. However, larger consumers progressively select smaller carnivorous prey, a pattern not expected from the hypotheses here and elsewhere evaluated and that requires considering further mechanisms—e.g. risk avoiding or enhanced escape behavior due to their higher mobility. Third, the replacement of selection among trophic categories in the gradient of consumer body size, and the switch in selection from small to large primary producer prey, support the action of the optimal foraging mechanism. From the set of seven hypotheses proposed, our results allowed to detect the most suitable one which combines the action of the three alternative mechanisms (H_7). Our study shed light on the mechanisms through which the match-mismatch of predator-prey traits shapes food webs.

The taxonomic and functional diversity of the prey pool is the substrate over which selection mechanisms operate [35, 59]. A high prey diversity with a continuous representation of body sizes, as the observed in this system [14, 40]; S2 Fig), is optimal for evidencing different selection mechanisms. Congruently, clear trends in selection patterns were detected with a gradual transition in the sign and strength of trait selection from small to large predators. These patterns provide a direct evaluation of the main body size-dependent mechanisms proposed to explain food web architecture. It should be noted that the same selection pattern operating over a system with a low prey diversity and/or with discontinuous body sizes may have low effect on food web structure or promote sharp transition in consumption patterns [13, 27, 60]. In this vein, our study adds to the existing evidence, supporting that the pond food web herein analyzed is strongly structured by processes mediated by body size [12, 14, 40, 61, 62], and serves as an optimal study model for testing mechanisms based on trophic relationships guided by body size.

The CATS regression model exhibited a high explanatory power for the occurrence and strength of trophic interactions in the pond food web ($R^2 = 0.67$). It is remarkable that only considering the body size of predators and prey, plus a general trophic categorization of these prey, was enough to explain a large fraction of the food web structure, in agreement with prior studies (e.g. [17, 63]). In addition, trait-selection analyses advance on the mechanistic understanding of the role of body size on the properties of food webs. For example, [14] detected a strong nested and antimodular pattern in this food web along the gradient in killifish body size. Nestedness has been also reported in several food webs [10, 11, 13, 64]. The gradual trend in selection of prey traits from smaller to larger consumers identifies the proximal mechanisms generating the observed nestedness in prey consumption [14]. However, it also points to a progressive substitution of prey trophic groups (Fig 3). Similarly, the relaxation in gape limitation and the increase in consumption rate explain the increase in trophic position, prey richness and number of energy sources with body size [12, 65]. It has to be highlighted that the trait selection approach is not intended to explain a particular food web pattern—e.g. nestedness, food chain length or connectance. However, 67% of the variation in weighted trophic links was explained by the model, explaining in a large extent the emergence of several features of food web architecture at higher levels. In this sense, the selection pattern of prey items should be central in modulating the stability of ecosystems, due to their connection with food webs features that were proved to determine network stability—modularity, nestedness, integration of energy channels [7, 12, 13, 17, 18, 63, 66].

The direct analysis of trait selection in trophic interactions was able to evidence the action of mechanisms not detected when the evaluation of particular food web metrics was the focus of different studies. For example, for the killifish guild herein studied, it was found that the preference of larger prey items was not a requirement for the emergence of body size-dependent food web structure [12]. Instead, the relaxation of gape limitation and the rise in prey number were able to explain the increase in prey diversity, energy paths and predator trophic position with body size. The selection pattern reported here further supports these ideas. However, trait selection analysis was also able to detect patterns congruent with optimal foraging predictions not revealed in previous studies (e.g. [12, 14]). In addition, a consistent selection for small sized carnivorous prey was here evidenced, being the consumption of large predatory prey always avoided. This trend is magnified for larger predators (Fig 3). Large carnivorous prey are less abundant [67], demand longer handling times [30], move faster and have more maneuverability [68, 69], and their consumption could be risky, either because of aggressive antipredator behavior [57, 70, 71] or due to trophically transmitted parasites [72]. The consistent avoidance of large carnivorous prey may be suggesting the action of mechanisms based on antipredator traits that would make them less profitable in terms of energy reward for large predators, in agreement with the optimal foraging mechanism [57]. In this sense, the use of CATS models for evidencing the mechanisms beyond the emergence of food web structure complements approaches based on specific metrics of food webs. Indeed, since the CATS regression predicts the elements of the weighted food web matrix, it could be potentially used for predicting a large variety of food web metrics commonly used in ecological studies.

Diet Weighted Mean (DWM) is a useful approach for evidencing how the representation of prey traits is changing along gradients of predators' traits. The community weighted mean, from which the idea of DWM was borrowed, has shown a great potential for visualizing the action of possible assembly mechanisms [35, 51]. Although community weighted mean provides information regarding patterns, it is frequently used as the main tool for inferring the mechanisms behind them, representing an indirect way of testing hypotheses and their explanatory forces [73]. However, a single pattern of traits representation in a community can originate from different assembly rules [35]. Similarly, diet weighted means, prey frequencies or food web metrics can originate by several underlying causes. For example, considering that only a fraction of the total prey items (or traits) consumed could be truly subject to selection, the information provided by the general pattern of prey consumption shown in Fig 2 is insufficient to tell between those selected and not selected prey items and the potential explanations for such selection [74]. The trait-dependent prey selection approach overcomes these limitations, providing a direct analysis of the selection processes that determine trends in diet among predators or environments. Finally, traits selection models can also overcome a canonical limitation of prey preference studies about the need to identify the species pool truly available for consumers to evidence selection mechanisms [75–77]. In the CATS regression model, the set of prey items and abundances observed among all consumers can be used as the effective species pool exploited by predators. This effective prey species pool is included as both an offset and as a random factor that indicates the expected prey frequencies in each predator body size class. Therefore, changes in the representation of these items in the diet of predators with different body sizes can be associated with a selection process based on the interaction between consumers and prey traits [36]. The CATS model represents a robust tool to analyze prey selection mechanisms based on functional, morphological and behavioral attributes that complements previous approach and overcomes some limitations from behavioral ecology and food web studies. This is key in the inference process and hypothesis testing contributing to the progress in the field of food webs [78–80].

Conclusions

Our study focused on the mechanistic basis responsible for several well-reported trends in food web structure with predator body size. These trends can be explained by different mechanisms involving trait-mediated interactions between predators and their prey, which have been indirectly inferred in the past. By using a trait-based approach we found support for the three proposed mechanisms associated with energy demand, gape limitation and optimal foraging, but also for additional mechanisms such as risk avoidance as determinants of food web structure. On this basis, our results favored the most complex of the tested hypotheses, H7, which integrates the three prey selection mechanisms considered in this study. Unveiling the connection between species traits and trophic interactions has the potential to provide mechanistic predictions about the expected effect of changes in species traits, driven either by changes in community composition or by trait evolution, on the structure of food webs.

Supporting information

S1 Table. Model selection process results. Akaike´s Information Criterion values (AIC), weight of evidence (WAIC) and Wilks´ likelihood ratio test results for the alternative models included in the selection process. Predator body size (PredBS), Predator body size^2 (PredBS2), Prey body size (PreyBS), Prey trophic group (PreyTG), Predator body size class identity (PredBSC ID).
(XLSX)

S2 Table. CATS regression model results. Selection coefficients obtained from the CATS model ($R^2 = 0.67$). Body size (BS), Trophic group (TG).
(XLSX)

S1 Fig. Predator body size classes and their range values. Range values for the 20 predator body size classes used in the analyses. Each body size class is composed of 31 killifish individuals, except for the last one which contains 30 individuals.
(TIF)

S2 Fig. Prey body size distribution. Body size distribution of potential animal prey categorized as A) herbivorous-detritivores and B) carnivorous in the study system. Body size estimations were made from a dataset of invertebrate and vertebrate individuals collected in 2008 in

the study system (see Methods section). The green line represents the body size range of primary producer prey, which was obtained from published literature.
(TIF)

S3 Fig. Prey richness and abundance. Richness (A) and abundance (B) of prey items categorized as primary producers, herbivorous-detritivores and carnivorous in the diet of each body size class of killifish.
(TIF)

S4 Fig. Selection of prey body size along the predator body size gradient. Selection of prey body size along predator body size classes for prey categorized as (A) primary producers, (B) herbivorous and detritivores and (C) carnivorous. Selection coefficient relates prey consumption based on their size with predator body size. Small predators select over small prey items of all trophic groups. However, large predators select larger primary producers meanwhile they consume herbivorous-detritivores prey items independently of their size. Contrary, as predator body size increases, large carnivorous prey are always avoided, a pattern that is magnified for those larger predators.
(TIF)

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Project administration: Esteban Ortiz, Matías Arim.

Visualization: Esteban Ortiz, Rodrigo Ramos-Jiliberto, Matías Arim.

Writing – original draft: Esteban Ortiz, Rodrigo Ramos-Jiliberto, Matías Arim.

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Supporting information

S1 Table. Model selection process results. Akaike´s Information Criterion values (AIC), weight of evidence (WAIC) and Wilks´ likelihood ratio test results for the alternative models included in the selection process. Predator body size (PredBS), Predator body size^2 (PredBS2), Prey body size (PreyBS), Prey trophic group (PreyTG), Predator body size class identity (PredBSC ID).

Model	Fixed effects							
	PredBS	**PredBS2**	**PreyBS**	**PreyTG**	**PredBS*PreyBS**	**PredBS2*PreyBS**	**PredBS*PreyTG**	**PredBS2*PreyTG**
m.full	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
m3	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
m6	Yes	No	Yes	Yes	Yes	No	Yes	No
m7	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
m8	Yes	Yes	Yes	No	Yes	Yes	No	No
m9	Yes	Yes	No	Yes	No	No	Yes	Yes

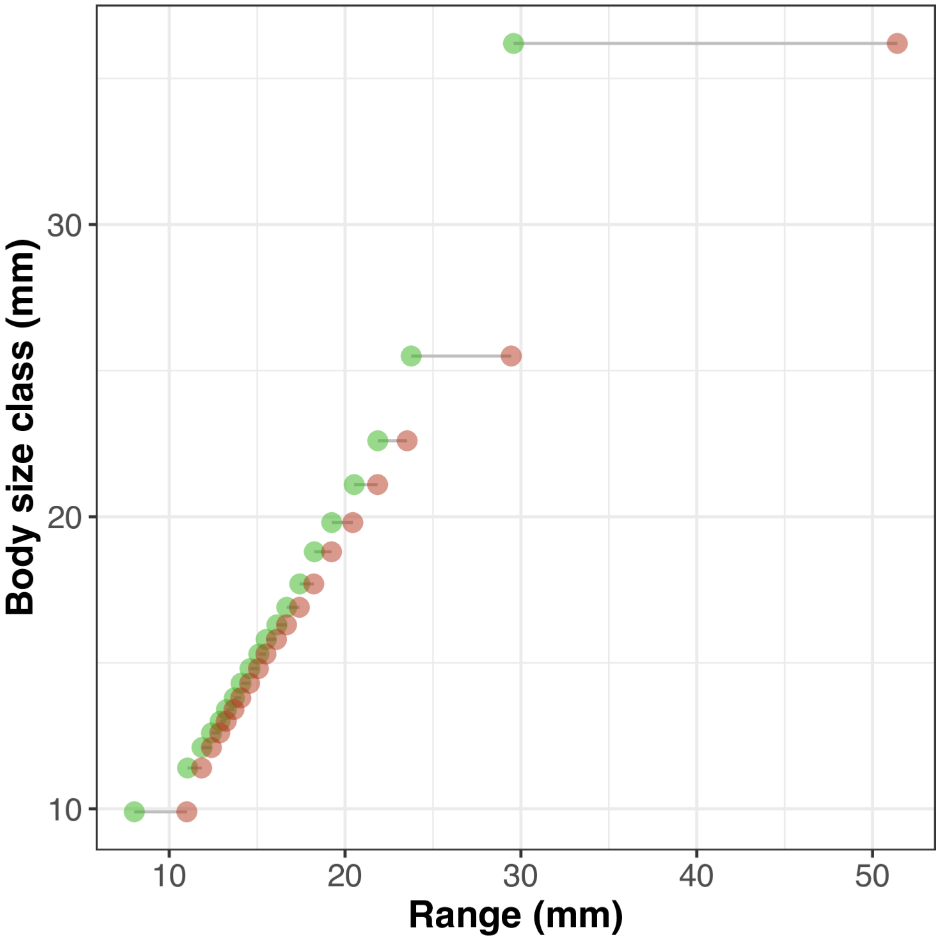
S1 Table (Continuation)

PreyBS*PreyTG	PredBS*PreyBS*PreyTG	Random effect PredBSC ID	AIC	ΔAIC	WAIC	Wilks Test Chi squared
Yes	Yes	Yes	4897.02	–	0.998	–
Yes	Yes	No	5402.34	505.33	0	507.33***
Yes	Yes	Yes	4969.54	72.52	0	80.52***
No	No	Yes	4909.16	12.14	0.002	18.14***
No	No	Yes	5472.92	575.9	0	593.9***
No	No	Yes	4934.49	37.47	0	49.47***

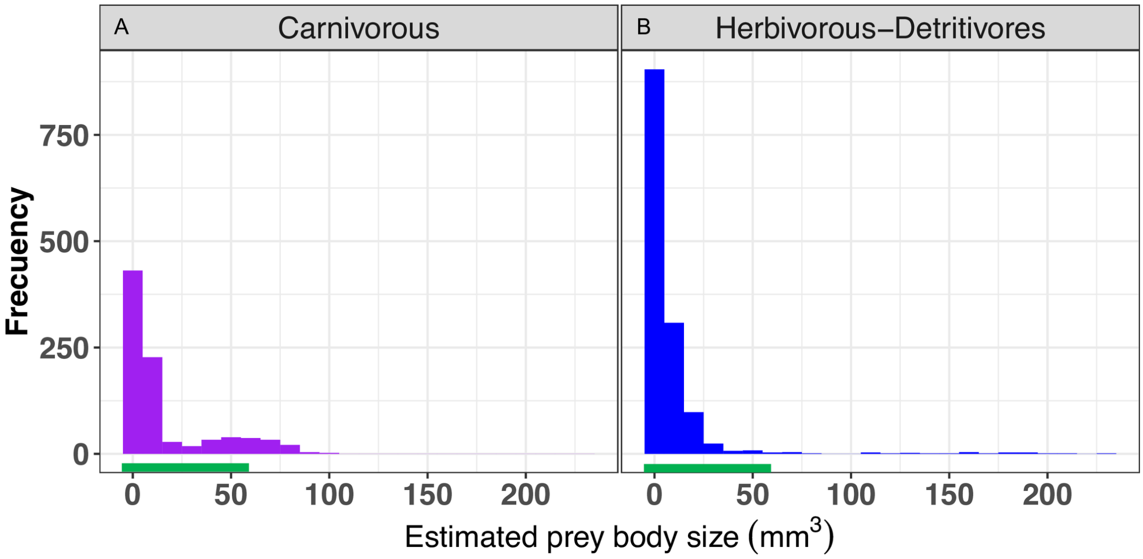
S2 Table. CATS regression model results. Selection coefficients obtained from the CATS model ($R^2 = 0.67$). Body size (BS), Trophic group (TG).

Explicative variables	Estimate	SE	Z-value	p-value
Prey TG				
Primary producers	-9.28	3.3	-2.17	0.03
Herbivorous-Detritivores	-2.09	0.68	-3.1	0.002
Carnivorous	-5.95	0.84	-4.6	<0.001
Prey TG*Prey BS				
Primary producers	-0.58	0.21	-2.61	0.009
Herbivorous-Detritivores	-3.29	0.01	-3.28	0.001
Carnivorous	-0.037	0.035	-0.11	0.9
Prey TG*Predator BS				
Primary producers	2.04	0.38	4.81	<0.001
Herbivorous-Detritivores	2.17	0.048	4.49	<0.001
Carnivorous	0.43	0.044	4.84	<0.001
Prey TG*Predator BS2				
Primary producers	-0.08	0.014	-5.64	<0.001
Herbivorous-Detritivores	-4.25	0.0011	-3.97	<0.001
Carnivorous	-0.007	0.00087	-2.71	0.007
Prey TG*Prey BS*Predator BS				
Primary producers	0.03	0.01	2.57	0.01
Herbivorous-Detritivores	0.002	0.0007	2.98	0.003
Carnivorous	0.0002	0.00064	-3.04	0.002

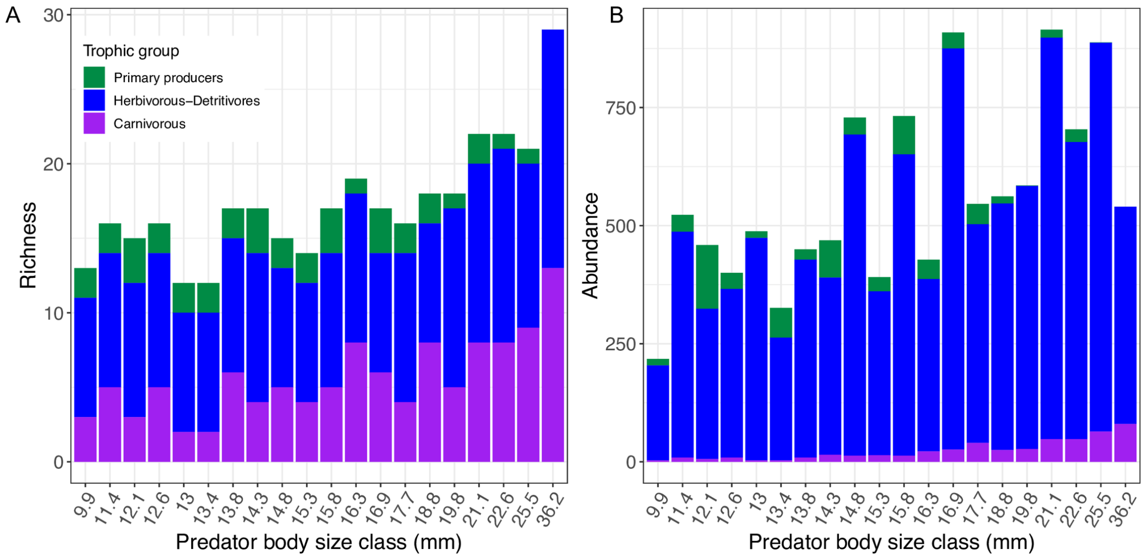
S1 Fig. Predator body size classes and their range values. Range values for the 20 predator body size classes used in the analyses. Each body size class is composed of 31 killifish individuals, except for the last one which contains 30 individuals.



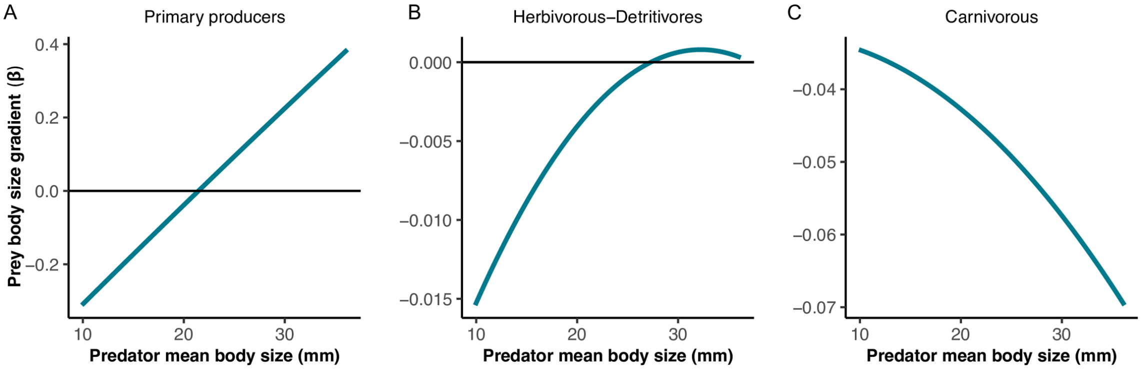
S2 Fig. Prey body size distribution. Body size distribution of potential animal prey categorized as A) herbivorous-detritivores and B) carnivorous in the study system. Body size estimations were made from a dataset of invertebrate and vertebrate individuals collected in 2008 in the study system (see Methods section). The green line represents the body size range of primary producer prey, which was obtained from published literature.



S3 Fig. Prey richness and abundance. Richness (A) and abundance (B) of prey items categorized as primary producers, herbivorous-detritivores and carnivorous in the diet of each body size class of killifish.



S4 Fig. Selection of prey body size along the predator body size gradient. Selection of prey body size along predator body size classes for prey categorized as (A) primary producers, (B) herbivorous and detritivores and (C) carnivorous. Selection coefficient relates prey consumption based on their size with predator body size. Small predators select over small prey items of all trophic groups. However, large predators select larger primary producers meanwhile they consume herbivorous-detritivores prey items independently of their size. Contrary, as predator body size increases, large carnivorous prey are always avoided, a pattern that is magnified for those larger predators.



Discusión general

En los últimos años, el análisis del rol de los atributos en el desempeño de las especies y su interacción con procesos operando a diferentes escalas ha cobrado un renovado interés en ecología de comunidades y redes ecológicas (Arim *et al.* 2023; Des Roches *et al.* 2018; Enquist *et al.* 2015; Mcgill *et al.* 2006; Shipley 2010; Shipley *et al.* 2006; Verberk *et al.* 2013; Violle *et al.* 2012). En parte, esta aproximación emerge como respuesta a las limitantes asociadas a análisis tradicionales basados en taxonomía los cuales han dominado la ecología durante décadas (Lawton 1999; Marquet *et al.* 2014; Maurer 1999; Morin 2011; Simberloff 2004; Vellend 2016). En esta línea, esta tesis contribuye al desarrollo del marco teórico al identificar, formalizar y evaluar mecanismos basados en atributos que pueden dar cuenta del ensamblaje de comunidades y redes tróficas ((Ortiz *et al.* 2023a, b) y Capítulo 2). Es importante destacar que estos mecanismos son novedosos (Capítulo 1) o han sido recientemente propuestos sin una formalización apropiada (Capítulo 2). En el Capítulo 1 se evidenció que la interacción entre el escalamiento positivo en capacidad de dispersión, y los escalamientos negativos en densidad local y riqueza del pool regional con el tamaño corporal de los taxa tiene el potencial de generar la relación diversidad–tamaño corporal observada en metacomunidades (Ortiz *et al.* 2023a). Corroborando la hipótesis planteada, la relación diversidad α–tamaño corporal emerge del balance entre los tres escalamientos mencionados, y no solo por el papel del cambio en capacidad de dispersión como ha sido resaltado en la teoría (Cadotte 2006; Grainger & Gilbert 2016; Leibold *et al.* 2004; Leibold & Chase 2018; Mouquet & Loreau 2003). En el Capítulo 2 se detectó que la acción del efecto prioridad y el arreglo de especies dependen de los procesos de dispersión metacomunitarios. Si bien ambos mecanismos son reconocidos por su potencial para incrementar el nivel de diferenciación entre comunidades (Alahuhta *et al.* 2014; Chase 2003; Fukami 2010, 2015; Gianuca *et al.* 2017; Heino 2011; Soininen 2014), la forma en que estos interactúan con la dispersión determinando la diversidad β en metacomunidades resulta poco clara. Durante décadas, se ha considerado que la diversidad β decrece con la dispersión entre comunidades. No obstante, en esta tesis se demostró que la diversidad β puede alcanzar valores máximos a niveles intermedios de dispersión desde un pool regional de especies. Estos resultados van en contraposición a la conceptualización clásica de la dispersión como proceso homogeneizador de comunidades (Grainger &

Gilbert 2016; Gu *et al.* 2023; Heino & Tolonen 2017; Loreau 2000; Loreau & Mouquet 1999; Mouquet & Loreau 2003; Soininen *et al.* 2007) logrando a su vez explicar patrones empíricos recientemente reportados en distintos sistemas (Catano *et al.* 2017; Ojima & Jiang 2017; Vannette & Fukami 2017; Werner *et al.* 2007). Los resultados proporcionan una conceptualización genuinamente novedosa la cual demanda nuevas perspectivas de investigación. Si bien el arreglo de especies y el efecto prioridad han sido recientemente propuestos como posibles determinantes de una relación positiva entre dispersión y diversidad beta, el análisis realizado en esta tesis representa la primera síntesis de los mecanismos potencialmente involucrados y su formalización en modelos metacomunitarios. Por último, en el Capítulo 3 se evidenció de forma directa que los mecanismos de demanda energética, restricción en consumo por tamaño corporal y forrajeo óptimo determinan patrones de selección de rasgos de presas que estructuran conjuntamente la red trófica aquí estudiada (Ortiz *et al.* 2023b). Esto supone una contribución importante respecto a trabajos anteriores en los cuales la evaluación de dichos mecanismos se realizó indirectamente a partir de la interpretación de patrones de distribución relativa de atributos observados en dieta respecto a atributos observados en el ambiente (e.g. (Griffiths 1975; Hart & Hamrin 1988; Mittelbach 1981)). Los resultados muestran que la acción de dichos mecanismos es dependiente del tamaño y nivel trófico de las presas consumidas. A su vez, los resultados basados en rasgos y no en la taxonomía de las especies involucradas sustentan la extrapolación de las conclusiones a otros sistemas y especies (Arim *et al.* 2010, 2011; Canavero *et al.* 2014; Ortiz & Arim 2016).

Integración de marcos teóricos como herramienta para entender el proceso de ensamblaje de comunidades y redes ecológicas basado en atributos

Desarrollar un marco teórico robusto basado en principios generales es fundamental para entender el funcionamiento de los sistemas ecológicos y predecir su comportamiento (Marquet *et al.* 2014; Scheiner & Willig 2008; Vellend 2016). Esto requiere generar vínculos explícitos entre diferentes teorías (Marquet *et al.* 2014; Ritchie 2010; Scheiner & Willig 2008). La presente tesis intenta aportar en este sentido al vincular de forma explícita diferentes marcos teóricos. En este sentido, se destaca las conexiones transitadas explícitamente entre la Teoría Metabólica de Ecología (TME) (Brown *et al.* 2004), la Teoría de Ensamblaje de Comunidades por Selección de Atributos (CATS) (Shipley 2010; Shipley *et al.* 2006; Warton *et al.* 2015), la Teoría de Metacomunidades

(TM) (Leibold *et al.* 2004; Leibold & Chase 2018; Vellend 2016) y la Teoría de Redes Tróficas (McCann 2011; Moore *et al.* 2017; Pascual & Dunne 2006; Thompson *et al.* 2012). A través del escalamiento positivo en la tasa metabólica de los individuos con su tamaño corporal (Brown *et al.* 2004), la TME explica la reducción en densidad local y diversidad con el tamaño corporal de los taxa. Estos dos factores, conjuntamente con el escalamiento positivo en capacidad de dispersión reportado en varios trabajos (De Bie *et al.* 2012; Domenici 2001; Ellington 1991; Heino *et al.* 2017b; Hirt *et al.* 2017; Jenkins *et al.* 2007), son reconocidos por la TM como piezas clave en la determinación de los patrones de diversidad (Leibold & Chase 2018; Vellend 2016). En la misma línea, el escalamiento tasa metabólica–tamaño corporal sienta la base de los tres mecanismos evaluados en el Capítulo 3 en un contexto de redes tróficas. Este contexto resalta el vínculo entre la TME y la Teoría de Forrajeo Óptimo (Beckerman *et al.* 2006; Charnov 1976) la cual intenta explicar tanto las reglas de decisión de consumo por parte de los individuos, así como sus dietas óptimas, en función del balance entre el gasto energético asociado a su tamaño y el retorno energético de las presas. Un componente adicional incluido en este capítulo es la integración de las herramientas metodológicas y conceptuales provistas por la Teoría de Ensamblaje de Comunidades por Selección de Atributos (CATS) (Shipley 2010; Shipley *et al.* 2006; Warton *et al.* 2015) para evaluar los tres mecanismos planteados. A mi entender, este trabajo es el primero en aplicar este abordaje en un contexto de redes tróficas (ver (Ortiz *et al.* 2023b)). Por último, tanto en el Capítulo 1 como en el Capítulo 2 se adoptan los conceptos y aproximación metodológica basada en modelos de lotería desarrollados por la Teoría Neutral de Biodiversidad y Biogeografía (TNDB) (Hubbell 2001; Rosindell *et al.* 2011) en el contexto de metacomunidades. La TNDB es reconocida como uno de los pilares conceptuales sobre los que se realiza la síntesis que da origen a la TM (Leibold *et al.* 2004; Leibold & Chase 2018; Vellend 2010, 2016). A su vez, desarrolla los modelos de lotería como herramienta para simular la dinámica de ensamblaje de metacomunidades basada originalmente en deriva ecológica y dispersión, incluyendo posteriormente selección local. Los modelos de lotería, así como los modelos de coalescente (utilizados y descritos en ambos capítulos) están siendo ampliamente utilizados para explorar el rol que tiene la estructura del paisaje, procesos neutrales vs. procesos basados en nicho y atributos de las especies en el estructuramiento de metacomunidades (Borthagaray *et al.* 2014, 2023b, a; Cunillera-Montcusí *et al.* 2021; Hubbell 2001; Munoz *et al.* 2018; Ortiz *et al.* 2023a; Rosindell *et al.* 2011; Worm & Tittenson 2018).

Ensamblaje de metacomunidades y redes tróficas en un contexto de cambio climático

Entender el rol que juega el tamaño corporal en el ensamblaje de metacomunidades y redes tróficas resulta imperativo en el escenario actual de cambio climático (Brose *et al.* 2012; Enquist *et al.* 2020; Martins *et al.* 2023). Específicamente, el impacto del calentamiento global sobre el ensamblaje de metacomunidades está asociado a varios de los escalamientos analizados en esta tesis. A través del aumento en tasa metabólica con la temperatura (Brown *et al.* 2004), y asumiendo que el tamaño corporal es independiente de ella, la TME predice una reducción en la abundancia de las poblaciones hacia mayores temperaturas ((Brown *et al.* 2004; Savage *et al.* 2004), pero ver (Bernhardt *et al.* 2018)). Sin embargo, existe un sustento empírico robusto hacia una reducción de los tamaños corporales con la temperatura, sobre todo de ectotermos y en ambientes acuáticos (Atkinson 1994; Atkinson *et al.* 2003; DeLong 2012; Forster *et al.* 2012; Meerhoff *et al.* 2012; Sheridan & Bickford 2011). De hecho, al incluir el escalamiento en tasa metabólica y tamaño corporal con temperatura, estudios recientes han reportado que esta relación negativa tiende a amortiguar la caída predicha originalmente por la TME en capacidad de carga de las poblaciones con la temperatura (Bernhardt *et al.* 2018). Esto se debe a la atenuación de la magnitud del escalamiento densidad–tamaño corporal. En la misma línea, existen reportes acerca de cambios en la composición de especies en función de sus tamaños corporales en el contexto del calentamiento global (Martins *et al.* 2023). Por un lado, el aumento en temperatura lleva a que las comunidades estén sujetas a una tendencia de reemplazo de taxa de mayor tamaño por taxa más pequeños. Por el otro, el aumento en temperatura de zonas templadas y frías asociado al cambio climático determina el desplazamiento de especies previamente ausentes hacia estos ambientes (e.g. (Bartley *et al.* 2019)) pudiendo favorecer la llegada de taxa grandes contrarrestando así la sobrerrepresentación de grupos pequeños (Martins *et al.* 2023). Cualquiera de estos dos escenarios tiene el potencial de modificar el escalamiento diversidad regional–tamaño corporal, pudiendo generar incluso asociaciones positivas. Esta masa de evidencia empírica jerarquiza la importancia de los resultados obtenidos en el Capítulo 1, ya que contribuyen a entender y predecir cómo es que desvíos esperados en los escalamientos en densidad local y diversidad regional con el tamaño corporal afectarían el ensamblaje de metacomunidades sometidas a un constante aumento de temperatura.

De forma similar, el aumento en temperatura puede estar asociado tanto a un incremento como a una reducción en la tasa de movimiento y actividad de los individuos, y por ende en su tasa de dispersión, dependiendo del taxon y estadio de vida en el cual la fase de dispersión ocurra. Mayores temperaturas han sido asociadas a un aumento en la velocidad de movimiento en invertebrados y vertebrados ectotermos en general (Gibert *et al.* 2016; Hurlbert *et al.* 2008), mayor distancia de movimiento en mariposas (Niitepõld *et al.* 2009), y mayores tasas de movimiento (Davidson *et al.* 2020) y dispersión (Wu & Seebacher 2022) en grandes mamíferos, aves, invertebrados y anfibios. Contrariamente, también se ha reportado una reducción en la tasa de dispersión en peces asociada al aumento en su tasa de maduración con la temperatura (Raventos *et al.* 2021). Dado que su fase de dispersión se da en etapas larvarias, el incremento en temperatura determina que las larvas maduren más rápidamente reduciendo considerablemente su tiempo y rango dispersión. Estos resultados sugieren que el aumento en temperatura asociado al calentamiento global también afectaría considerablemente la magnitud, e incluso signo, del escalamiento dispersión–tamaño corporal. Así, y en línea con lo demostrado en el primer capítulo, cambios en el escalamiento en dispersión con temperatura podrían tanto amortiguar como exacerbar la pérdida de diversidad dada por los escalamientos en densidad y diversidad regional. El balance final entre estos tres escalamientos dependerá de los cambios relativos de cada uno de ellos respecto al aumento en temperatura, lo cual puede estar asociado a las características propias de cada sistema. De todas formas, el abordaje presentado en el Capítulo 1 brinda un marco de análisis aplicable a cualquier tipo de sistema más allá de sus idiosincrasias puntuales.

Finalmente, se ha reportado que la reducción en tamaño corporal con la temperatura afecta diferencialmente a depredadores y presas según su nivel trófico generando desviaciones en la relación entre sus tamaños respecto a lo esperado (Gibert & DeLong 2014). En línea con los resultados mostrados en el Capítulo 3, estos cambios diferenciales en tamaño corporal afectarían la importancia relativa de los mecanismos estructuradores de redes tróficas. Una mayor reducción en los tamaños de los depredadores determinaría un aumento en su restricción de consumo (i.e. mayor gape limitation) limitando tanto la diversidad como abundancia de las presas a las que podrían acceder. Por otro lado, si la reducción en tamaño corporal afecta mayormente a las presas, es esperable una reducción en la oferta de ítems tróficos con alto contenido energético limitando el mecanismo de forrajeo óptimo. Esto tiene potenciales consecuencias en la estabilidad de las redes tróficas al modificarse las fuerzas de interacciones de consumo entre especies. En conclusión, el análisis del efecto de la temperatura en el ensamblaje de las comunidades ecológicas representa un área de frontera del marco teórico actual que debe ser mayormente explorado.

Perspectivas

La estructura espacial de las metacomunidades (i.e. posición relativa de las comunidades locales en el espacio) ha sido identificada como uno factor determinante del ensamblaje y estructuramiento de comunidades y redes tróficas (Borthagaray *et al.* 2020, 2023b; Chase *et al.* 2010; Chase & Shulman 2009; Economo & Keitt 2010; Häussler *et al.* 2021; Ryser *et al.* 2019; Suzuki & Economo 2021). Esta estructura espacial determina un gradiente en el aislamiento relativo de las comunidades en donde aquellas comunidades más centrales están sujetas a un mayor flujo de individuos que comunidades aisladas (Borthagaray *et al.* 2015b; Economo & Keitt 2010; Urban & Keitt 2001). Comunidades más centrales tienden a ser más diversas y homogéneas (Altermatt *et al.* 2013; Borthagaray *et al.* 2020, 2023b; Carrara *et al.* 2012; Economo & Keitt 2010), presentar menor equitatividad (Borthagaray *et al.* 2020) y mayor diversidad funcional (Favre-Bac *et al.* 2017), presentar una menor limitación energética permitiendo una mayor viabilidad de depredadores tope y cadenas tróficas más largas (Arim *et al.* 2016; Ryser *et al.* 2019), tienen una mayor relación diversidad de depredadores vs. diversidad de presas (Shulman & Chase 2007) y por ende una mayor estructuración top-down dada por depredadores tope (Chase *et al.* 2010). En función de esto, como perspectiva se plantea explorar la interacción entre la estructura espacial metacomunitaria y diferentes escalamientos asociados al tamaño corporal, y su efecto en el ensamblaje y diversidad en metacomunidades. Esto puede realizarse por medio de herramientas de simulación utilizando paisajes artificiales con estructuras espaciales contrastantes (e.g. aleatoria, cadena, lattice, dendrítica) (e.g. (Brown & Swan 2010)), o simulando la dinámica de metacomunidades con estructuras espaciales reales y comparando su estructura final respecto a metacomunidades obtenidas a partir de la aleatorización de dicha estructura (e.g. (Borthagaray *et al.* 2023b)).

Adicionalmente, se plantea profundizar en el rol que tiene el tamaño corporal en interacción con otras variables biológicas en el proceso de ensamblaje de metacomunidades como forma de explicar respuestas complejas (i.e. no lineales) observadas en la naturaleza. Esto efectivamente se realizó en el Capítulo 3 al incluir la interacción entre el tamaño corporal y nivel trófico de las presas. Esto permitió detectar la potencial acción de mecanismos asociados al comportamiento anti-depredador de las presas, los cuales no fue inicialmente priorizado en la explicación de la estructura de las redes tróficas (Ortiz *et al.* 2023b). De manera similar, se propone complementar los resultados obtenidos en el Capítulo 1 evaluando cómo diferentes modos de dispersión (i.e. pasivo vs. activo) afectan la interacción entre los tres escalamientos analizados al variar el signo del escalamiento dispersión–tamaño corporal. En el caso del Capítulo 2, se propone considerar el compromiso entre la capacidad de dispersión y el nivel de selección a escala metacomunitaria de las especies como forma de evaluar la interacción de estas dos variables en la determinación de la relación diversidad β–dispersión.

Comentarios finales

En esta tesis se evaluó diferentes mecanismos basados en atributos en el proceso de ensamblaje de metacomunidades y redes tróficas. Varios de estos mecanismos no han sido aun propiamente considerados en el marco teórico (Capítulo 1, (Ortiz *et al.* 2023a)), o han sido sugeridos, pero no formalizados (Capítulo 2) (Vannette & Fukami 2017). A su vez, los mecanismos de ensamblaje de redes tróficas analizados en el Capítulo 3 fueron evaluados de forma directa por medio de un abordaje mecanicista superando limitaciones tradicionales en esta área (Ortiz *et al.* 2023b). Es de destacar que los resultados obtenidos en esta tesis surgen de la combinación de varias aproximaciones metodológicas complementarias, abarcando desde herramientas de simulación (i.e. modelos de coalescente y lotería) hasta modelamiento estadístico (i.e. CATS). A su vez, resalta la interacción entre varios marcos teóricos como la Teoría de Metacomunidades (Cottenie 2005; Leibold *et al.* 2004; Leibold & Chase 2018; Vellend 2016), Teoría Metabólica de Ecología (Brown *et al.* 2004), Teoría de Ensamblaje de Comunidades por Selección de Atributos (Shipley 2010; Shipley *et al.* 2006; Warton *et al.* 2015), Teoría Neutral (Hubbell 2001; Rosindell *et al.* 2011) y Teoría de Forrajeo Óptimo (Beckerman *et al.*

2006; Charnov 1976) como forma de contribuir al desarrollo de una síntesis teórica en el área de la ecología (Marquet *et al.* 2014).

El rol de los atributos en el ensamblaje de sistemas ecológicos, y su interacción con procesos que operan a diferentes escalas espacio-temporales, representa un área potente para entender el funcionamiento de los sistemas naturales y predecir su comportamiento en el contexto actual de cambio climático. El tamaño corporal destaca como un atributo que permite sintetizar y conceptualizar adecuadamente la acción de una gran variedad de mecanismos y procesos determinantes del estructuramiento de comunidades y redes ecológicas. Esta tesis explora el rol del tamaño corporal en el proceso de ensamblaje de metacomunidades y redes tróficas desde varias aristas, abriendo diferentes perspectivas de investigación para trabajos futuros.

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