Algunas consecuencias ecológicas y evolutivas del movimiento animal para las interacciones bióticas

TESIS DOCTORAL

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Algunas consecuencias ecológicas y evolutivas del movimiento animal para las interacciones bióticas

Memoria presentada por Oriol Verdeny Vilalta para optar al Grado de Doctor por la Universidad de Granada

El Doctorando

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Granada, marzo de 2013

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Director/es de la Tesis	Doctorando
Fdo.:	Fdo.:

Als meus pares,
al meu germà,

i a la meva petita Ana

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Resumen

Resumen

En el mundo animal, la evolución ha dotado a distintas especies con diversas formas de dispersión, lo que les permite satisfacer sus necesidades mas básicas, como por ejemplo encontrar recursos, escapar de los depredadores o aparearse. Además, distintos patrones de movimiento de los animales conllevarán una redistribución de las poblaciones en el espacio, lo que afectará a las tasas de encuentro y a las posibles interacciones bióticas que se pueden establecer. Por este motivo las tasas de encuentro están, en última instancia, relacionadas con la eficacia biológica de los animales. Dado que las interacciones están necesariamente localizadas en el espacio, el conocimiento del movimiento de los animales y sus tasas de encuentro pueden mejorar nuestro conocimiento de las interacciones bióticas así como qué condiciones llevan a la estabilidad de las poblaciones que interaccionan. Además, la movilidad de los animales juega un papel importante en la evolución de determinados rasgos, ya que determinados fenotipos pueden determinar la eficacia de dispersión y las tasas de encuentro, así como el potencial de interacción. El objetivo de la presente tesis ha sido estudiar el papel que tienen distintos factores abióticos -haciendo hincapié sobre aquellos factores que están siendo afectados por el cambio climático- sobre las tasas de encuentro de invertebrados, así como algunas de las consecuencias ecológicas y evolutivas que pueden tener dichas tasas de encuentro. Para ello en esta tesis se desarrollan cinco objetivos específicos: (1) estudiar la importancia relativa de la distribución y disponibilidad hídrica en las tasas de encuentro y de depredación de un depredador y una presa típicos de bosques caducifolios, (2) determinar, en una red trófica de descomponedores de bosques caducifolios, los efectos de la disponibilidad de agua y de recursos basales en los patrones de agregaciones espaciales, así como sus consecuencias en las tasas de depredación, (3) investigar los roles de la complejidad estructural de la vegetación y de la fuerza de atracción de un recurso en la geometría de los movimientos del díptero *Rhagoletis pomonella*, (4) investigar las consecuencias de la movilidad en la evolución del tamaño y número de los huevos en depredadores intragremiales (5) estudiar las consecuencias de un incremento en la temperatura sobre las dinámicas eco-evolutivas en interacciones tri-tróficas. Los resultados de esta

tesis muestran la importancia de la disponibilidad hídrica y la productividad basal a la que va normalmente asociada el agua en suelos (i.e. hongos) en determinar las tasas de encuentro entre animales, la estructura de la red trófica, y los posibles efectos indirectos que los depredadores ejercen sobre las presas. También hemos visto cómo la estructura de la vegetación determina los movimientos de un insecto que forrajea a la vez que modifica el radio de percepción del insecto. Finalmente los resultados nos han mostrado que la movilidad de los animales juega un importante papel en la evolución de ciertos rasgos fenotípicos como son el tamaño y el número de los huevos, así como en las dinámicas eco-evolutivas de una red tri-trófica.

Introducción general

Introducción

En el mundo animal, la evolución ha dotado a distintas especies con diversas formas de dispersión para satisfacer sus necesidades mas básicas, como por ejemplo encontrar recursos, escapar de los depredadores o aparearse (Bell 1990, Moya-Laraño et al. 2002, Bartumeus et al. 2003, Nilsson and Bengtsson 2004). La dispersión de los animales también permite la recolonización de ciertas áreas en las que subpoblaciones no se encontraban presentes o se habían extinguido, lo que a nivel global afecta a las dinámicas de poblaciones e incrementa la persistencia de las poblaciones (Bascompte and Solé 1995, Thompson et al. 2012), especialmente en poblaciones que se encuentran en hábitats fragmentados (Zollner and Lima 1999). Además, la movilidad de las especies también afecta al flujo de material genético entre distintas áreas y por lo tanto a la diversidad genética y a su mantenimiento (Lundberg and Moberg 2003, Brown et al. 2008, Amos et al. 2012), y es un factor clave que afecta a las invasiones biológicas y a la propagación de enfermedades o plagas (Fevre et al. 2006, Nathan 2008, Stoddard et al. 2013).

La capacidad de movimiento es una característica fundamental que determina las **tasas de encuentro** de los organismos y sus interacciones bióticas potenciales. Por este motivo las tasas de encuentro también están en última instancia relacionadas con la eficacia biológica de los animales. Por lo tanto, distintos patrones de movimiento como son la velocidad de los animales, la sinuosidad de los recorridos efectuados por los mismos o la atracción hacia ciertas áreas, conllevará redistribuciones de las poblaciones que afectarán a las tasas de encuentro y a las posibles interacciones bióticas que se pueden establecer (Zollner and Lima 1999, Bartumeus et al. 2005, Scharf et al. 2006, Montoya and Raffaelli 2010, Walther 2010, Lurgi et al. 2012a). Dado que los patrones de movimiento son tan importantes en determinar el encuentro con otros organismos o territorios, muchos animales ajustan ciertas características del movimiento según el contexto ambiental con el fin de conseguir una tasa óptima de encuentros (Bartumeus et al. 2005, Humphries et al. 2010).

Para poder entender y predecir las tasas de encuentro también es necesario tener en cuenta los **factores abióticos** que afectan al movimiento de los animales. La distribución espacial de factores como por ejemplo la temperatura o la disponibilidad hídrica está generalmente ligada a la distribución de los animales y a su movilidad (Bauwens et al. 1995, Chen et al. 2011). Por lo tanto es de esperar que estos dos importantes factores ambientales que a su vez están siendo fuertemente afectados por el cambio climático (IPCC 2007), afecten a la frecuencia de encuentros, las interacciones bióticas, y al funcionamiento de los ecosistemas (Montoya and Raffaelli 2010, Moya-Laraño 2010, Walther 2010, Chen et al. 2011, Ledger et al. 2012, Lurgi et al. 2012a).

Dado que las interacciones están necesariamente localizadas en el espacio, el movimiento de los animales y sus tasas de encuentro contribuye al conocimiento de las interacciones bióticas así como al de la estabilidad de las poblaciones que interaccionan (Polis et al. 1997, McCann et al. 2005, Reichenbach et al. 2007, Amarasekare 2008). Además, la movilidad de los animales juega un papel importante en la evolución de determinados rasgos, ya que determinados fenotipos pueden determinar la eficacia de dispersión, las tasa de encuentro con la que interactúan, y por lo tanto su eficacia biológica (Moya-Laraño et al. 2002, Moya-Laraño et al. 2008, Forsman et al. 2011, Liedvogel et al. 2011). Sin embargo, aunque la relación entre el movimiento de los animales y las dinámicas de interacciones bióticas puede parecer lógica, todavía no están muy claras ciertas **implicaciones ecológicas y evolutivas** que el movimiento animal puede conllevar, especialmente si se tiene en cuenta que muchas de las interacciones ocurren en ambientes que son dinámicos y altamente heterogéneos, tanto a nivel biótico como abiótico.

A continuación se discuten algunos de los principales factores ecológicos que afectan a las tasas de encuentro, así como algunas implicaciones que las tasas de encuentro pueden tener a nivel ecológico y evolutivo (Figura 1).

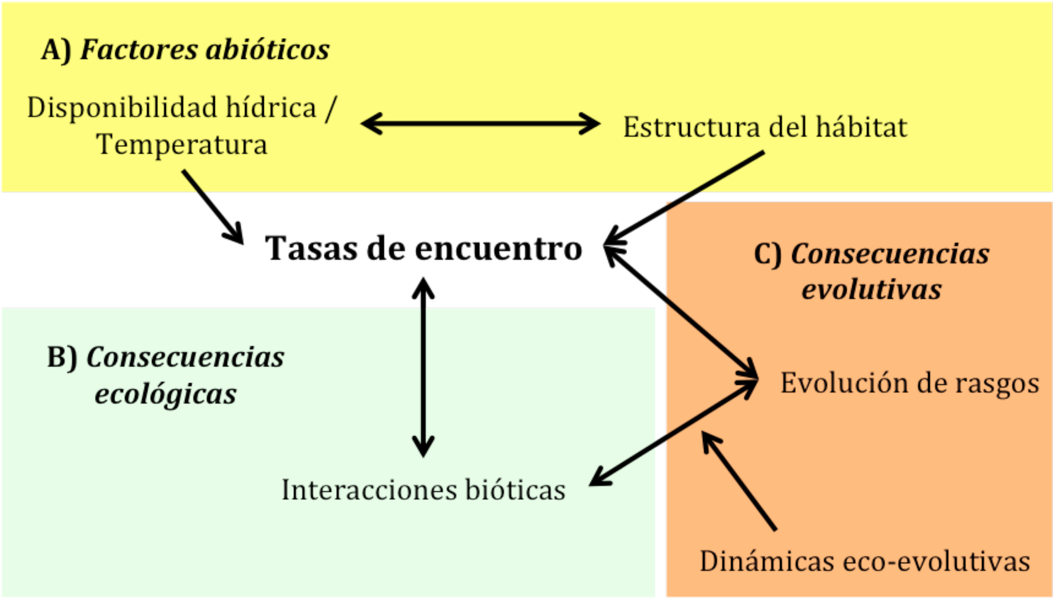

Figura 1: Representación esquemática de las relaciones entre los factores abióticos (disponibilidad hídrica, temperatura y estructura del hábitat), las tasas de encuentro, y sus implicaciones ecológicas y evolutivas, tal y como se han estudiado en la presente tesis.

A) Potenciales factores abióticos determinantes de las tasas de encuentro

Disponibilidad hídrica

Los modelos climáticos predicen un cambio en el régimen hídrico, con lluvias de un carácter mas torrencial y un incremento del tiempo de sequia entre ellas (Houghton 2004, IPCC 2007). Además, en ciertas zonas como en el norte de España por ejemplo, hay una predicción de un descenso del 20% de la pluviometría en los próximos 50 años (IPCC 2007), lo que sugiere que los bosques del norte se encuentran, o se van a encontrar en un futuro cercano, amenazados ante esta situación. El papel que juega la disponibilidad hídrica en el funcionamiento de la red trófica del suelo del bosque, así como el papel de dicha red en el ciclo de nutrientes necesario para su mantenimiento, es bastante desconocido (pero ver Lensing and Wise 2006), sobre todo en bosques en los que parecen encontrarse amenazados por el Cambio Climático, como son los hayedos del Norte de la Península Ibérica (Peñuelas and Boada 2003). Aunque los fisiólogos animales han reconocido el papel fundamental que juega el agua como recurso básico en los animales, la ecología animal de comunidades se ha preocupado muy poco de estudiar los efectos potenciales de la disponibilidad hídrica (y por lo tanto los efectos de una disminución hídrica debida al cambio global) en el movimiento de los animales, sus interacciones y el funcionamiento de los ecosistemas terrestres (McCluney and Sabo 2009).

El agua es un recurso esencial para todos los organismos, necesario para que las células realicen adecuadamente todas sus funciones fisiológicas (Chown and Nicolson 2004), y su disponibilidad determina la riqueza y abundancia de muchos organismos terrestres (Hawkins et al. 2003), así como su distribución espacial (Levings and Windsor 1984, Hopkin 1997, Chown and Nicolson 2004, Lensing et al. 2005, Melguizo-Ruiz et al. 2012). Además, el agua también actúa como recurso indirecto, ya que su abundancia puede incrementar la productividad primaria y el crecimiento de otros recursos basales como los hongos y las bacterias, lo que provocaría un efecto de abajo a arriba (*bottom-up*) en el ecosistema (Rosenzweig 1968, Webb et al. 1983, Sala et al. 1988, Huxman et al. 2004, Rousk and Baath 2011). Normalmente, en los ecosistemas terrestres el agua se encuentra distribuida de forma heterogénea, y alteraciones en la precipitación pueden provocar cambios tanto en su abundancia como en su distribución espacial (Famiglietti et al. 1998, Herbst and Diekkruger 2003, Schume et al. 2003, Jost et al. 2004, Katra et al. 2007). Debido a esta distribución heterogénea, el agua puede provocar agregaciones de animales que buscan prevenir la desecación y/o que se sienten atraídos por sus recursos basales asociados. De esta forma, cabría esperar que las densidades de los animales en parches húmedos se incrementarán mediante respuestas agregativas o un efecto de abajo a arriba mediado por los recursos basales, lo que podría potencialmente afectar a los encuentros de los animales. Por otra parte, cambios en la disponibilidad hídrica también pueden afectar a los encuentros de los animales si estos modifican sus patrones de movimiento, como por ejemplo reducir su actividad de movimiento cuando la disponibilidad hídrica decrece con el fin de disminuir las perdidas de agua (McCluney and Sabo 2009).

Temperatura

La temperatura es un importante factor abiótico que juega un papel fundamental determinando varias de las tasas biológicas de los animales, y que a su vez puede influir en la disponibilidad hídrica, ya que el agua no se encuentra disponible cuando está congelada (temperaturas bajas) o se evapora rápidamente (temperaturas altas). En los últimos 100 años se ha detectado una clara tendencia al alza la temperatura (incremento linear de +0.74°C), con temperaturas mínimas que incrementan a una tasa que es el doble que la de las temperaturas máximas (IPCC 2007). En animales ectotermos, un incremento en la temperatura conllevará a un incremento de sus tasas metabólicas lo que provocará a un incremento de la actividad biológica (Brown et al. 2004). De esta forma cabría esperar, como ya se ha visto en algunos animales, que un incremento en la temperatura aumentaría la movilidad de animales ectotermos y como consecuencia sus tasas de encuentro (Bauwens et al. 1995, Herrera 1995, Baird and May 2003, Kruse et al. 2008, Moya-Laraño 2010). No obstante, un incremento en la temperatura también puede reducir la esperanza de vida de los animales con lo que éstos podrían tener una ventana de tiempo mas pequeña para encontrar recursos o pareja. Por otra parte también se ha visto que alteraciones en la temperatura pueden cambiar de forma diferencial las áreas de distribución de los animales y por lo tanto generar nuevas combinaciones de especies que interactúan (Montoya and Raffaelli 2010, Lurgi et al. 2012a, b).

Arquitectura del hábitat

Los movimientos de una gran parte de animales vienen determinados por la complejidad de las estructuras del hábitat en donde viven. Algunos ejemplos son los monos araña buscando alimento en el bosque (Boyer et al. 2006), avispas buscando huéspedes entre la hierba (Randlkofer et al. 2010) o los invertebrados que se mueven entre la hojarasca de los bosques caducifolios (Vucic-Pestic et al. 2010, Morice et al. *submited*). De hecho muchas de las interacciones entre animales terrestres (ej. invertebrados) ocurren en un ambiente altamente estructurado y complejo como es la vegetación, lo que ha llevado a numerosos estudios a investigar el papel que juega la arquitectura del hábitat en las tasas de encuentro e interacciones bióticas de los animales. Por ejemplo la complejidad del hábitat en la que se encuentran presas y depredadores puede determinar las respuestas funcionales de los depredadores, que cuantifican su tasa de consumo per cápita (Kaiser 1983, Vucic-Pestic et al. 2010). Generalmente, para una misma densidad, a mayor complejidad del hábitat menores tasas de encuentro entre organismos (Andow and Prokrym 1990, With 1994, Casas and Djemai 2002, Gols et al. 2005). Sin embargo, todavía no se sabe cómo la estructura del hábitat afecta la geometría de los movimientos de animales que forrajean buscando recursos.

B) Tasas de encuentro e interacciones bióticas

Para que dos individuos interaccionen es necesario que éstos se encuentren. Dado que además hay una serie de combinaciones fenotípicas que tienen una probabilidad de interacción mayor que otras -por ejemplo de tamaño corporal (Brose et al. 2008)-, el estudio del movimiento animal y de las distribuciones espaciales de los individuos proporciona información esencial acerca de los fenotipos que se encuentran y por lo tanto de las potenciales interacciones bióticas. A nivel trófico, las tasas de encuentro son uno de los componentes esenciales de las respuestas funcionales, que describen la tasa de consumo *per cápita* de los depredadores en función de la densidad de presas (Holling 1959). De hecho, se ha visto que en muchas redes tróficas los depredadores tienen gran proporción de su contenido intestinal vacío (Woodward et al. 2010), lo que indica que están lejos de estar saciados y que las tasas de encuentro serían un elemento clave que determina las fuerzas de interacción entre depredador y presa (Hagen et al. 2012).

Las tasas de encuentro no solamente afectan a las interacciones bióticas, sino que también las interacciones bióticas pueden, al igual que los factores abióticos, repercutir en las tasas de encuentro de los animales. Por ejemplo, numerosas especies reducen su actividad de movimiento o cambian el área de forrajeo en función del riesgo de depredación, lo que puede disminuir sus tasas de encuentro con otros organismos teniendo importantes efectos indirectos sobre los mismos (Schmitz et al. 2004).

En general, las alteraciones en los patrones de movimiento de las especies (ej. localización, velocidad, sinuosidad) pueden producir nuevos conjuntos de interacciones que a su vez cambiarán la estructura de las redes de interacción (Montoya and Raffaelli 2010, Walther 2010, Lurgi et al. 2012a, b). Por lo tanto, determinar el efecto de un conjunto de factores ecológicos que se pueden ver potencialmente afectados por el cambio climático y que afectan a su vez a la movilidad y a las interacciones bióticas, es uno de los desafíos mas importantes para determinar la estructura, dinámica y funcionamiento de los ecosistemas frente a un mundo cambiante.

C) Evolución de rasgos mediada por la movilidad y dinámicas eco-evolutivas

A pesar de que distintos procesos ecológicos y evolutivos están íntimamente ligados, a menudo han sido tratados por separado (Fussmann et al. 2007). No obstante, los biólogos de poblaciones han cambiado recientemente este punto de vista, ya que hay algunos cambios micro-evolutivos tan rápidos que pueden afectar a las dinámicas poblacionales, y *viceversa*, de una forma muy notable (Pelletier et al. 2009). Esto ha permitido cuantificar la magnitud de los diferentes efectos recíprocos que existen entre la ecología y la evolución a una escala temporal relativamente pequeña. Sin embargo, el papel que juega la movilidad como rasgo en ecología y evolución es todavía ampliamente desconocido, sobre todo cuando nos centramos en el estudio de redes ecológicas más o menos complejas. La mayoría de los animales necesitan, en alguna fase de su vida, dispersarse para aparearse, encontrar recursos o evitar ser depredados, lo que conlleva a que la movilidad es un factor que determina la eficacia biológica de los animales. Por lo tanto, cabría esperar que la movilidad, además de un rasgo sometido a selección, sea un importante agente de selección en sí mismo, que actúa sobre determinados rasgos fenotípicos pudiendo afectar a cómo los animales van a interaccionar en el futuro (tras la actuación de la selección natural). En otras palabras, la movilidad es un rasgo sobre el que actúa la selección y además una fuente de selección sobre otros rasgos (además de sobre otros individuos), pues este rasgo determina, en gran medida, el ambiente experimentado por los individuos.

Debido a que explica las tasas de encuentro entre depredadores y presas (Huey and Pianka 1981, Werner and Anholt 1993 y las referencias en él), la movilidad puede haber jugado un papel muy importante en determinar la dirección en la evolución de dos rasgos reproductivos vitales, el número y el tamaño de los huevos. Esto puede ser especialmente relevante en uno de los grupos de depredadores terrestres mas importantes (tanto por su abundancia, como por su diversidad y distribución cosmopolita) como es el de las arañas. La razón de tamaños corporales entre un depredador y su presa es una variable que explica un gran porcentaje del éxito de ataque cuando dos individuos se encuentran (Nentwig and Wissel 1986, Brose et al. 2008). De esta forma, si un individuo incrementa su tamaño corporal puede tener un doble beneficio: incrementar el éxito de caza de sus presas y disminuir el éxito de ser cazado por otros depredadores. Esto es especialmente relevante cuando tenemos en cuenta la relación negativa entre la abundancia y el tamaño corporal en redes tróficas (Woodward et al. 2005, Mulder et al. 2009). Un pequeño incremento de tamaño en una cría puede aumentar considerablemente tanto su acceso a presas como su capacidad de evitar ser depredada al haber menos depredadores capaces de depredar sobre dicha cría.

Factores abióticos como la temperatura y la humedad tienen una gran influencia sobre las tasas de movilidad y de metabolismo de los animales (Brown et al. 2004, Moya-Laraño 2010), con lo que pueden promover la creación de nuevas interacciones bióticas o incluso alterar las ya existentes (Tylianakis et al. 2008, Lurgi et al. 2012a, b). Alteraciones en estos dos factores abióticos como consecuencia del cambio climático podría crear nuevos escenarios ecológicos, lo que tendría unos efectos relevantes en las dinámicas eco-evolutivas. Determinadas combinaciones de rasgos fenotípicos podrían ver favorecidas frente a otras, lo que a su vez podría afectar a la persistencia y el funcionamiento de las redes tróficas. Sin embargo, todavía se sabe muy poco sobre las consecuencias del cambio climático en la evolución de determinados fenotipos y el efecto de estos nuevos fenotipos sobre las interacciones bióticas y el funcionamiento de los ecosistemas. Además, para entender cómo los rasgos van a ser afectados cambiando la frecuencia de fenotipos, debemos tener en cuenta tanto el rango de variabilidad de estos rasgos relevantes para la interacción de los organismos (ej. tasa de crecimiento, fenología), como el grado de correlación entre ellos (Moya-Laraño 2011). Si los rasgos están altamente correlacionados, la selección natural no podrá optimizar todas las combinaciones posibles (Lande 1979).

Justificación y objetivos

En primer lugar, en esta tesis se ha estudiado el papel que juegan distintos **factores abióticos** -haciendo hincapié sobre aquellos factores que están siendo afectados por el cambio climático- sobre las tasas de encuentro de los invertebrados a través de cambios en sus patrones de movimiento y su distribución espacial (Figura 1A). En segundo lugar, se ha investigado cómo diferencias en la movilidad y en las redistribuciones de los animales afectarán a las **interacciones bióticas** (Figura 1B) y la **evolución** de determinadas combinaciones rasgos de los animales, que a su vez pueden afectar recíprocamente a las relaciones entre ellos mediante bucles (*feedbacks*) eco-evolutivos (Figura 1C).

Los efectos que los factores abióticos tienen sobre las tasas de encuentro se estudian en los capítulos 1, 2, 3 y 5. Concretamente, en los capítulos 1-2 se estudian los efectos del agua, en el capítulo 5 los de la temperatura, y en el 3 los efectos de la arquitectura del hábitat. A su vez, en los capítulos 1-2 se estudian las implicaciones de la movilidad de los animales sobre las interacciones bióticas (depredación), y cómo estas mismas interacciones bióticas pueden afectar a los patrones de movimiento de los animales. Finalmente, los capítulos 4, 5 conciernen a algunas de las implicaciones evolutivas de la movilidad. En el capítulo 4 se estudia el rol que puede haber jugado la movilidad sobre la evolución de los rasgos reproductivos tamaño y número de huevos, tomando la estructura de la red trófica como ambiente biótico, y en el capítulo 5 el efecto de la movilidad mediada por la temperatura en las dinámicas eco-evolutivas. A continuación se explican los objetivos específicos abordados en cada uno de estos 5 capítulos de la presente tesis.

Capítulo 1: *estudiar la importancia relativa de la distribución y disponibilidad hídrica en las tasas de encuentro y de depredación de un depredador y una presa típicos de bosques caducifolios*.

La disponibilidad hídrica es un factor que puede potencialmente afectar a las tasas de encuentro entre los invertebrados terrestres tales como los componentes de la red de descomponedores de la hojarasca. El objetivo de este capítulo es estudiar la importancia relativa de la abundancia de agua y de su distribución en determinar las tasas de encuentro y de depredación a corto plazo, lo que es especialmente importante para saber qué tipo de alteraciones hídricas podrían tener unos efectos mas importantes en las interacciones tróficas. Paralelamente también se ha estudiado cómo las interacciones bióticas previas pueden repercutir en los encuentros posteriores entre depredadores y presas, al alterar el patrón de movimiento de los individuos. Para ello se ha realizado un experimento de laboratorio en el que se midieron las tasas de actividad de depredadores y presas en solitario o en presencia de un individuo del otro nivel trófico.

Capítulo 2: *en una red trófica de descomponedores de bosques caducifolios, determinar los efectos de la disponibilidad de agua y de recursos basales en los patrones de agregaciones espaciales, así como las consecuencias posibles en la mortalidad tanto por depredación como por otras causas (ej. deshidratación).*

El objetivo de este capítulo fue manipular de manera independiente la disponibilidad hídrica del suelo y la cantidad de hongos -uno de los principales recursos basales necesarios para el funcionamiento de las redes tróficas de descomponedores- para ver 1) las redistribuciones de diferentes grupos de invertebrados y 2) las consecuencias que éstas redistribuciones tienen sobre las relaciones tróficas de los invertebrados. Para llevar a cabo este objetivo, se diseñó un experimento de campo bi-factorial en el que se manipularon estos dos recursos y se midieron las pautas de redistribución de abundancias y tamaños corporales de distintos depredadores y presas, consecuencia de su movilidad diferencial hacia uno u otro recurso.

Capítulo 3: *investigar los roles de la complejidad estructural de la vegetación y de la fuerza de atracción de un recurso en la geometría de los movimientos de la mosca* Rhagoletis pomonella*.*

Hasta la fecha todavía no es bien conocido cómo la fuerza de atracción de un determinado estímulo (ej. recurso) afecta a los patrones de movimiento de los animales que forrajean en ambientes con arquitecturas complejas, tal como la vegetación. En este estudio hemos cuantificado el impacto que tiene la estructura de la vegetación sobre el movimiento de forrajeo de un artrópodo modelo que se siente atraído por un recurso. Además hemos analizado el efecto que la densidad de la vegetación tiene sobre el radio de percepción del artrópodo. Para ello se ha trabajado con la mosca *Rhagoletis pomonella*, dado que al ser un animal que no vive escondido dentro de la hojarasca, esto nos permitió extraer las coordenadas del movimiento de los individuos.

Capítulo 4: *investigar las consecuencias de la movilidad en la evolución del tamaño y número de los huevos en arañas.*

El papel que juega la movilidad en la evolución de ciertos rasgos de historias de vida es todavía ampliamente desconocido, especialmente si nos centramos en el estudio de redes ecológicas complejas. Utilizando la teoría de forrajeo y las relaciones entre tamaño corporal y abundancia de las redes tróficas, se ha construido un modelo que predice, en función de la movilidad de los individuos, el tamaño óptimo que tendrían que tener los huevos de uno de los grupos de depredadores terrestres mas importantes, las arañas. Los resultados del modelo se contrastan utilizando el método comparativo en biología evolutiva.

Capítulo 5: *estudiar las consecuencias de un incremento en la temperatura sobre las dinámicas eco-evolutivas en interacciones tri-tróficas.*

Un incremento en la temperatura de los ecosistemas puede aumentar las tasas metabólicas y las tasas de encuentro. Esto, a su vez, puede determinar qué fenotipos van a ser mas favorables en escenarios ecológicos donde la temperatura se ha incrementado. Además, éstas nuevas combinaciones fenotípicas afectarán a las dinámicas tróficas y a las futuras presiones selectivas de los distintos fenotipos. En este estudio se ha construido un Modelo Basado en Individuos espacialmente explícito para vislumbrar las consecuencias que puede tener un incremento en la temperatura sobre las dinámicas eco-evolutivas de una interacción tri-trófica del suelo (hongo-presa-depredador caníbal). En dicho modelo, las interacciones entre individuos dependen de 13 rasgos fenotípicos que son responsables del funcionamiento de las redes. Éstos rasgos se heredan de padres a hijos de manera cuantitativa. En el estudio también se ha investigado cómo la arquitectura genética; por ejemplo, el hecho de que los rasgos estén o no correlacionados genéticamente, va a afectar a los fenotipos que se van a seleccionar, a las tasas de encuentro y a la dinámica ecológica.

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Chapter 1

Seeking for water while avoiding predators: moisture gradients can affect centipede-springtail predator-prey interactions

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Abstract

Water is an essential resource that can affect the distribution and abundance of species across ecosystems. However how water availability and its spatial heterogeneity affects animal movement, and, associated predator-prey encounter and predation rates, is still poorly understood. Using predatory centipedes and springtails (prey) from the leaf litter of a beech forest, we tested the following hypotheses in two laboratory experiments in which we manipulated water availability: 1) Do centipedes and springtails decrease their activity when moisture is limiting?, 2) Do these animals aggregate in patches were moisture is high or less limiting?, and 3) if both centipedes and springtails tend to aggregate in moistened areas, do springtails tend to avoid these otherwise suitable areas when predators are present?, and 4) since smaller animals tend to loose water at a higher rate, Do smaller springtails expose themselves to predation relatively more by expending longer time in dangerous but sufficiently wet spots? Overall, average water availability did not affect the levels of activity. However, both animal taxa were equally attracted to the moistest spots. Springtails however, switched to slightly drier spots when predators were present, and as expected from physiological constraints in water loss, smaller springtails expended more time in wet spots, incurring higher predation risk. Larger animals were more active regardless of taxonomic affiliation, however, springtails switched to a much higher activity under predation risk. This size-dependent anti-predatory behaviour could explain why predation rates were similar across treatments and also why predator-prey ratios were worse predictors of predation rates than were separate estimates of predator and prey sizes when included in the same model. Since spatial heterogeneity in moisture is widespread in terrestrial ecosystems, our findings may be relevant to understand predator prey dynamics, not only in arid environments, but also in temperate ecosystems, such as beech forests.

Key words: *water distribution; animals' mobility; encounter rates; predator-prey interactions; climate change.*

Introduction

Water is an essential resource in terrestrial ecosystems which can often become limiting (Noy-Meir 1974, Wolf and Walsberg 1996, McCluney and Sabo 2009). Water availability can actually be used to predict species richness and organism abundance (Hawkins et al. 2003), as well as the spatial distribution of taxonomic and functional groups (Levings and Windsor 1984, Chown and Nicolson 2004, Doblas-Miranda et al. 2009, Melguizo-Ruiz et al. 2012). Thus, water availability appears to strongly affect the spatial coupling of species and the potential for biotic interactions to occur. However, although the effects of water availability on plant interactions are well studied (e.g. Dawson 1993, Scholes and Archer 1997, Weigelt et al. 2000, Maestre and Cortina 2004, Pugnaire et al. 2004, Soliveres et al. 2011), studies on water-mediated interactions in animal communities have received much less attention, with most of the studies based on drylands and desert ecosystems (Noy-Meir 1974, McCluney and Sabo 2009, McCluney et al. 2011, González-Megías and Menéndez 2012; but see Lensing and Wise 2006, Spiller and Schoener 2008).

In addition to warming the globe, climate change is also altering precipitation in most terrestrial ecosystems (IPCC 2007). Variations in the amount of water can directly impact animal interactions by altering their physiology and water balances (Stenseth et al. 2002). This, in turn, may alter their consumption behavior (McCluney and Sabo 2009, Walter et al. 2012) and foraging games of animals (McCluney et al. 2011). Moreover, experimentation has shown that water availability can indirectly alter animal interactions through changes in the composition and number of links among species (e.g. Ledger et al. 2012 in freshwater food webs). Yet, it remains poorly understood how in terrestrial ecosystems the availability and distribution of water affects animal interactions through changes in the patterns of individual and population movement. Unraveling the effects of water on the patterns of animal movement will provide essential clues on how altered precipitation may impact encounter rates and subsequent predator-prey and food web dynamics.

In terrestrial ecosystems, water availability is often heterogeneously distributed at the micro-scale level (Herbst and Diekkruger 2003, Schume et al. 2003, Jost et al. 2004, Katra et al. 2007, Melguizo-Ruiz et al. 2012) and therefore climate change and associated precipitation regimes may alter both the abundance and also the spatial distribution of soil water content. Moreover, altered precipitation regimes could result in longer dry periods (Easterling et al. 2000) that would increase soil water evaporation leading to the formation of stronger water gradients that would also last for longer periods. Soil invertebrates that face such changes on water availability have evolved different physiological, morphological and behavioral traits to diminish water loss during dry periods (Chown and Nicolson 2004, Chown 2011). Behavioural responses involving the rate and direction of movement can potentially modify the rates at which animals encounter each other and the opportunity for predation. However, to our knowledge these potentially important consequences of water scarcity have been barely studied.

In general animals can, by behavioral means, either avoid loosing water by reducing their movement and metabolic rates, or increase the movement rate in order to find resources with high water content or alternatively suitable wet areas (McCluney and Sabo 2009; Moya-Laraño 2010). In fact, most invertebrates must actively seek for water sources in excess of that ingested with food (e.g. Walter et al. 2012). As a consequence, most invertebrates migrate vertically and horizontally in order to find suitable moistened areas (Swift et al. 1979, Hassall et al. 1986), probably contributing in part to explain the positive correlations between water availability and invertebrate numbers (Badejo et al. 1998, Ferguson and Joly 2002, Melguizo-Ruiz et al. 2012). Nevertheless, not all invertebrates use a moisture gradient to find a suitable place for balancing their water budget, but in some instances they do it to find other resources associated with moisture. For example, it has been found that some predatory ants hunting on springtails and termites follow moisture gradients in order to locate their prey (Dejean and Benhamou 1993, Durou et al. 2001). This is consistent with the idea that moisture content is correlated with both productivity (Rosenzweigh 1968, Webb et al. 1983, Price and Clancy 1986, Sala et al. 1988, Huxman et al. 2004, Rousk and Baath 2011) and prey densities (e.g. Levings and Windsor 1984, Melguizo-Ruiz et al. 2012), whether the latter is a consequence of increased productivity or it is an aggregation in response to water scarcity. The point of interest for the present work is that water-mediated changes in movement behavior may alter encounter rates among individuals and thus the opportunity for predation. On the one hand, if individuals become more active due to increases or decreases in the availability of water (e.g. Lensing et al. 2005, Shultz et al. 2006), they must encounter each other more frequently (Werner and Anholt 1993, Scharf et al. 2006, Moya-Laraño 2010). On the other hand, if water is heterogeneously distributed, and the animals are attracted towards the wettest areas during dry periods, higher encounter rates could be the result of an aggregative response.

However, if both prey and predators are attracted towards wet areas, prey will have to trade off the risk of desiccation with the risk of predation. Since larger arthropods can retain water more efficiently either because their lower surface to volume ratio or because they can store proportionally more water (Chown 1993, Renault and Coray 2004) smaller prey would face a stronger trade-off and would have to deal with higher predation risk to avoid desiccation.

Here, we tested the hypothesis that the distribution and amount of water largely determine encounters and predator-prey interactions of two major groups of leaf-litter invertebrates: predatory centipedes and fungivorous (prey) springtails. First, we tested if (1) a gradient of water potentially increase predator-prey encounter rates because both groups are attracted towards the wettest areas, and if (2) higher amounts of water homogeneously distributed potentially increase encounter rates by an associated increasing in the movement rates of individuals (Moya-Laraño 2010). Secondly, we assessed if these water-mediated movement patterns (i.e. micro-habitat selection and movement activity) affect in turn the encounters between predators and prey and, importantly, the probability that predators feed on prey. We also assessed the role of body size on activity and we also tested the trade-off hypothesis, by which prey avoid wet areas more likely if predators are present and smaller prey, due to water physiological constraints, are forced to expose themselves to higher predation risk in order to balance their water budgets.

Materials and Methods

Field site and animal taxa

The experiments were conducted using two well-represented invertebrate groups from the leaf litter of European beech (*Fagus silvatica*) forests: Lithobiid centipedes (*Lithobius sp.*) as the predator and the surface-dwelling collembolan (*Tomocerus sp.*) as prey (Schaefer and Schauermann 2009). Voucher specimens of the animals have been deposited in the EEZA museum (*Lithobius*, INV-134-1; *Tomoceurs*, INV-134-2). Collembolans (springtails) are widely distributed arthropods across most biomes, and can be found throughout the upper part of the soil profile, where they feed mainly on the fungal hyphae associated with the decaying vegetation (e.g. leaf litter, twigs and trunks). Lithobiids, which also occur in a wide range of biomes, are flat centipedes and common generalist, highly active predators that live in the upper soil layers pursuing prey such as collembolans (Hopkin 1997a, Coleman et al. 2004).

Springtails and centipedes were manually collected during October 2010 near Vielha in Catalonia, Spain (42° 35' 49''N, 0° 45' 11''E) by sifting the leaf litter (e.g. Lensing and Wise 2006). Animals were collected from the field as needed (see interdispersion of replicates below) and used for the experiments within the next 3-4 days. Individuals were individually kept in petri dishes containing the bottom covered with moistened plaster of Paris and activated charcoal (in a proportion of 9:1) in order to maintain the humidity. Water in the bottom of the petri dishes was provided *ad libitum*. Collembolans were fed with yeast *at libitum*. However, centipedes did not receive any prey other than the ones caught during the experiments. Therefore, predators were partially starved prior to experimentation but were not water deprived. To control for ongoing centipede starvation, we included the date of observations in all analyses (see below). The body length of all individuals was measured twice to the nearest 0.01 mm using a caliper (correlation between measures, springtails: r=0.91; centipedes r=0.94) and the mean between measures used for analysis.

Experimental set-up

For convenience, the "laboratory" experiments were conducted in a cellar-cave near the field site, in a house owned by the family of OVV. During the experiments the temperature in the cave was 10.65±0.09°C and the ambient relative humidity was 68.54±0.19%. Both environmental variables had a similar range to the one that the invertebrates were experiencing in the field during the experiments, which were opportunistically measured in a few micro-sites by placing the probe of a DeltaOHM HD2301.0 thermo-hygrometer ca. 10cm in the litter (RH range 79.8-95.3%; N=25; T range 6.5-12.1ºC, N=15). Although RH was slightly lower in the cellar cave, our experimental manipulations allowed to approach the lowest RH in the natural range (see below). Each experimental unit consisted of a 35 x 12 x 7.5 cm stainless steel container. For preventing animals climbing and escaping from the containers, we applied liquid Teflon on the walls. Each container had the bottom (5mm height) covered with plaster of Paris and activated charcoal (9:1), which served to retain the humidity applied in each water treatment. In order to divide the longitudinal space of the container in 4 equally sized regions (8.75 x 12 cm), a series of marks were painted on the walls of the containers, which delimited a 1D grid to measure activity. This subdivision allowed us to easily identify in which of the four areas the individuals were positioned at any given time. Although the animals moved in 2D (containers were 12cm width), with this space subdivision we aimed to simplify the animal movement into 1D, which was especially relevant when measuring behavioral responses in humidity gradients (see below). The experimental units were spatially arranged and oriented at random within the experimental room. After the initial setup we performed two sequential experiments.

Experiment 1: moisture preferences, rate of movement and potential encounter rates

The aim of the first experiment was to test if water availability and its distribution could potentially affect encounter rates between prey (springtails) and predators (centipedes) by the rates of mobility and micro-habitat preferences when no interactions were allowed (individuals were placed individually in the experimental containers). We explored if higher amounts of water lead to higher movement rates (a proxy of encounter rates), and if a gradient of water availability could also lead to higher encounter rates because individuals would aggregate in the wettest patches. We established three water treatments that differed in the amount of water and in its spatial distribution. The "low water" and "high water" treatments received a total of 12 ml and 48 ml of water respectively, which was homogeneously distributed along the four areas. The "gradient" treatment received 12 ml of water in area number 1. It is important to note that the water quantities used reflect similar RH as that experienced by these animals in the field in both wet (~85-95%RH) and dry (~75-85%RH) micro-sites (Melguizo-Ruiz et al. 2012). We measured RH using the same device as in the field (see above), but by putting the probe in contact with the experimental surface. Within the gradient treatment, wet experimental areas (i.e. in the section were the water was supplied) had a RH range of 85.7-89.2% and in dry areas (in the opposite extreme of the container were the water was supplied) a range of 68-80.3% (N=4). The water used in the laboratory experiments was from the Sant Clem natural fountain (42° 13' 15.9''N, 0° 55' 18.2''E) near Salàs del Pallars, in Catalonia, North-East Spain, to which we added 0.5 ppm of chlorine. Before applying the water to the experimental units we let it rest in an opened recipient for 24h in order to facilitate the chlorine evaporation.

We used 24 collembolans and 24 Lithobiids that were randomly and individually placed in one of 48 experimental units. All individuals experienced the three treatments throughout the entire duration of the experiment, which made a total of 48 x 3 total replicates to study the effects of water availability on the mobility of the predators and the prey when there are no interacting with each other. The order in which each individual entered each treatment was randomly assigned. Due to logistic constraints and the availability of animals, we established trial blocks (1 block=1 day) of 24 animals (containers) each during a total of 6 days. All treatments and taxa were well interdispersed among all experimental bouts. To prevent that cues from previous trials affected the behaviour of the individuals, each container was cleaned between individual replicates and the plastic of Paris replaced.

Experiment 2: anti-predatory use of space, and actual encounter and predation rates

In the second laboratory experiment we assessed the effect of the amount and distribution of water on predation rates through water-mediated changes in individual behaviour. Thus, for this experiment we located one centipede and one springtail in each container. If prey individuals do not display anti-predator behavior, higher predation rates were predicted to occur in situations were the potential encounter rates in Experiment 1 were higher. If, on the other hand, prey assess the risk of predation and avoid risky areas, we predicted that due to the constraint imposed by body size and water budget, individuals that avoid the wettest areas in the gradient treatment would be the largest individuals and as a consequence, predation rates would not match the potential encounter rates estimated in Experiment 1. The water treatments were the same as in experiment 1. We also used the same individuals as in the first experiment, but here each experimental unit contained two individuals: a randomly picked centipede and a springtail. If a centipede killed a springtail, we gently removed the dead body trying not to disturb the predator by using soft forceps, and introduced a new individual in a random position. We tested for differences in behaviour of second individuals (e.g. from assessing the cues of a recent predation event) relative to first individuals (those that were killed) in the containers and found no differences (not shown). All the individuals, except the dead individuals and the new collembolans that replaced them, experienced the three water treatments. Therefore, in the second experiment, we also had 48 x 3 total replicates to assess individual mobility. However, because for this experiment a predator and a prey were placed in the same experimental units, we had a total of 24 x 3 + 17 observations to assess predation rate, 17 being the number of replacements of previously preyed collembolans.

Behavioural measures

At 30-minute intervals, and for a total period of 10 hours, we recorded the area of the experimental unit in which the individual was positioned within each container. The experiments were conducted in complete darkness, and the observations were made with a red led lamp to minimize disturbance. Since most interactions among organisms within the leaf-litter occur in the dark, we believe that this approach best mimics the light conditions in the wild. Each individual was located in the experimental units 30 minutes before starting to record behaviour, with the exception of the cases in which the predator killed the prey in the second laboratory experiment, for which we introduced a new prey immediately after discovering the death of the previous one. With the data on activity within each container section, we estimated three variables for analysis: 1) location preference, 2) rate of movement, and 3) potential and actual encounter rates.

The variable "location preference" was estimated as the mean across the individual locations (sections in the container) over the period of observations (i.e. 10h, 20 observations). The four areas of each experimental unit were scored as -1, -0.5, 0.5 and 1, and for the water gradient, maximum water availability (were the actual water was supplied) was arbitrarily established to be 1. Thus, if the average location for a given individual equals 0, it means that the individual expended the same amount of time in each half of the experimental units (expected in the two homogeneous treatment – no water gradient). On the other hand, if the mean of “location preference” approaches either 1 or -1 (gradient treatment), this means that the individuals were respectively attracted to or repelled from the water area.

As in the analysis of discrete random walks (Turchin 1998), a single movement was interpreted as a change in position between the four areas of the experimental unit. Even though these activity estimates had some error; i.e. moves of animals switching positions to an immediate section and going back to the original section within a given 30’ interval would have been missed by our observation protocol, our preliminary observations showed that this was almost never the case, as once an animal started moving it was highly likely to change the section in the container thereafter. We scored a switch in container section (transition) as 1 and recorded a 0 if the animal had not changed the container section within the 30’-interval. The "rate of movement" of an individual was simply calculated as the fraction of transitions across the observation period.

Finally, we also calculated the "potential and actual encounter rates" between a predator and a prey assuming that two individuals will interact more likely if 1) they share the same area in a given 30'-interval or if 2) they switch container sections reciprocally (e.g., when the prey moves from section 1 to 2 and the predator moves from section 2 to 1 in the same 30'-interval). Since in the first experiment, predators and prey were placed individually in different experimental units, we randomly paired predators and prey for calculating their "potential encounter rates". For the second experiment, we considered that predator and prey encountered each other even though the distance between them within a section, or even the distance when they switched containers reciprocally, could be long enough to prevent an actual encounter (i.e., "actual encounter rates"). However, we would like to emphasize that the probability of encounter in these instances is relatively much higher than when animals are in separate sections or do not reciprocally switch sections. We predicted that due to anti-predatory behaviour on behalf of the prey as well as prey chasing on behalf of the predator, there would be differences between "potential" (EXP1) and "actual" (EXP2) encounter rates.

Data analyses

For the statistical analyses of mobility; i.e., location preference, rate of movement and encounter rates (both potential –EXP1- and actual –EXP2-), we used Generalized Linear Mixed Models (GLMM) with Gaussian errors and identity link functions. Water treatment and taxon identity (predator –centipede- or prey –springtail-) were included as fixed factors. In order to account for the repeated use of the same individuals among water treatments, individual identity was included as a random factor. In the analysis of the predation rate we also used GLMM but with a binomial error and logit link function. Body size (length in mm) of both predator and prey were included in the analyses when appropriate. For this analysis individual ID was also included as a random factor. Also, in all models, "date" was included as a random factor to account for changes in individual motivation as the experiments progressed (e.g., predators were starved until they were able to catch a prey in the experiments). Since we had a limited number of specimens for the experiments, we sacrificed interdispersing the predation replicates (EXP2) among the separate-container replicates of EXP1 (as it would be done in one single experiment) and performed two sequential experiments (first separate containers in EXP1, second predation in EXP2), forcing in this manner the order of the experiments as to minimize loosing springtails and ensuring the completion of EXP1 before starting EXP2. Including time as a random factor served to minimize the problem of temporal pseudo-replication of our forced experimental design and allowed comparing the results between experiments. P-values were calculated using likelihood ratio test (Zuur et al. 2009). To test whether predator-prey ratios (Brose et al. 2006) or the absolute relative sizes of predators and prey were better at predicting the probability of predation, we used the Akaike information criterion as corrected for small samples sizes (AICc) to decide among models. We tested this hypothesis because, for instance, it could be that size-dependent mobility in the different treatments could affect predator-prey encounters differently. Thus, predation success based on predator-prey ratios, which relies mostly on the ability of predators to chase and subdue prey, could be a less appropriate estimate of predation success. All the analyses were performed using the library "lme4" in the statistical software R (R development core team 2012)

Results

Experiment 1: moisture preferences, rate of movement and potential encounter rates

When individuals of each taxon, either Lithobiids or collembolans, were placed in separate experimental units we found that the water treatment affected their location preference ("treatment" $\chi^2 = 57.7$, d.f. = 2, $P < 0.0001$), and that the response did not differ between prey and predators ("treatment x taxon" $\chi^2 = 1.92$, d.f. = 2, $P = 0.383$). Thus, the wet areas of the gradient treatment tended to equally attract both groups of animals. Within the gradient treatment, we did not detect a significant negative relationship between body size and location preference ("size" $\chi^2 = 0.96$, d.f. = 1, $P = 0.326$) nor were they differences in the response of different sizes between prey and predators ("size x taxon" $\chi^2 = 2.11$, d.f. = 1, p-value = 0.146). As expected, when water was homogeneously distributed neither centipedes nor springtails showed any preferences for a particular container section; i.e., the location preference was not different from 0 (Figure 1a).

Both the water treatment ("treatment", χ^2= 19.3, d.f. = 2, P<0.001) and taxon ("taxon", χ^2= 29.3, d.f. = 2, P<0.001) affected the activity rate, although the two taxa behave differently across treatments ("treatment x taxon" χ^2= 7.4, d.f. = 2, P=0.025). The Lithobiid predators had, in general, higher activity rates than the collembolans but the difference was less in the gradient treatment (Figure 1b).

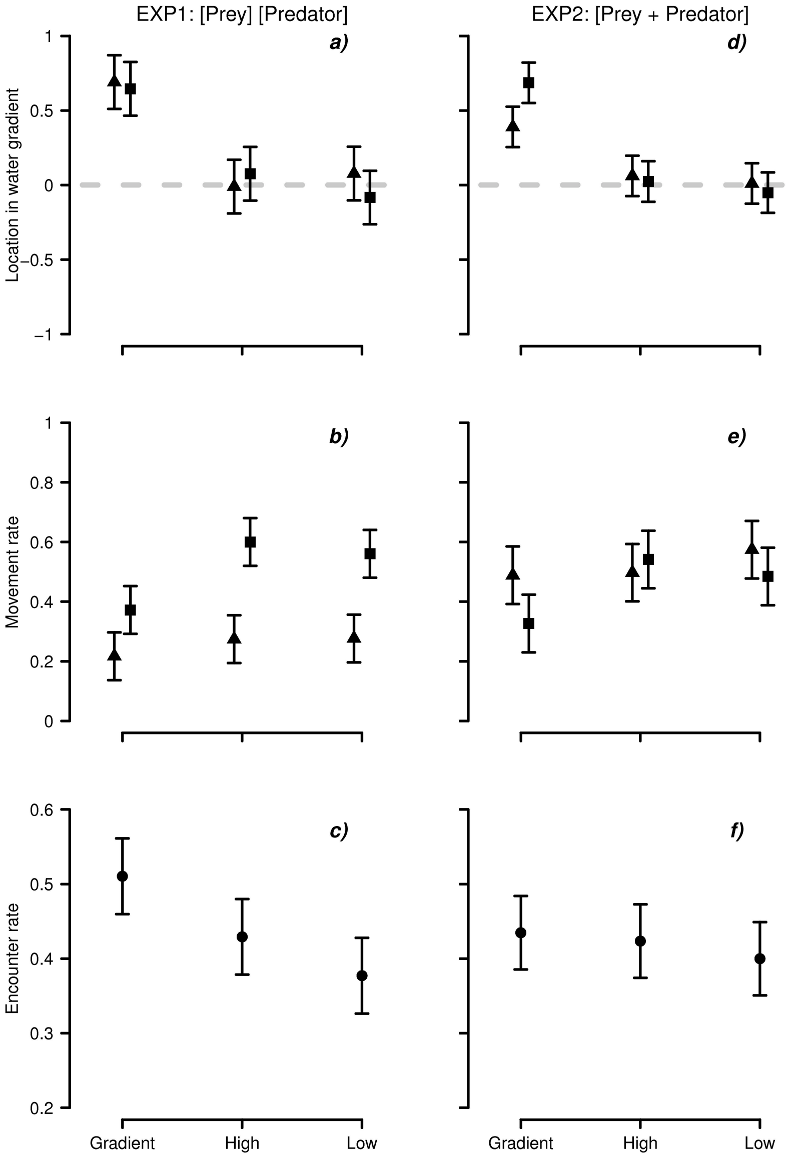

Figure 1: Response variables (Means±95%C.I.) for the first experiment (EXP1: *a*, *b* and *c* panels), in which prey and predators were in different containers, and for the second experiment

(EXP2: *d*, *e* and *f* panels), in which prey and predators were in the same container. a) and d) "location preference" in the water gradient (1 represents the wettest area in the gradient treatment and -1 the driest). The horizontal dashed line represents the mid point of the gradient (0). If the CIs do not overlap zero (the dashed horizontal grey line) we can conclude that there is a significant non-random preference for a given container section. b) and e) “rate of movement”; c) “potential” and f) “actual” encounter rates between centipedes and springtails. An encounter was considered to occur when either both animals were found in the same container section or when they crossed while moving to opposite sections of the container.

Including body size in the model showed that regardless of taxon or treatment ("treatment x taxon x size" χ^2= 2.7, d.f. = 2, P = 0.256), larger individuals moved at a higher rate ("size" in a model retaining “treatment x taxon”, estimate=0.028, χ^2= 9.0, d.f. = 1, P = 0.003). Activity rates did not significantly differ between the high and low water treatments ("high *vs*. low water treatments " χ^2= 0.2, d.f. = 1, P = 0.645, Figure 1b).

As for the potential encounter rates, we found differences among treatments ("treatment" χ^2= 13.42, d.f. = 2, p-value = 0.001). As animals were most of the time in the wettest patches, the highest potential encounter rates were found in the gradient treatment (Figure 1c). In addition, the high water treatment had slightly higher encounter rates as compared to the low water treatment, although the difference was only marginally significant ("treatment" χ^2= 3.49, d.f. = 1, P = 0.057).

Experiment 2: anti-predatory use of space, and actual encounter and predation rates

In contrast to EXP1, when prey and predators were located together in the same container, prey spent shorter time on the wet area of the gradient treatment than did predators ("treatment x taxon" χ^2= 8.50, d.f. = 2, P=0.014, Figure 1d), and the area location for springtails was significantly different between the two experiments ("experiment", χ^2= 5.3, d.f. = 1, P=0.021), indicating that prey switched the use of space when predators were present (Figure 2). This was not the case for centipedes ("experiment ", χ^2= 0.45, d.f. = 1, P=0.500).

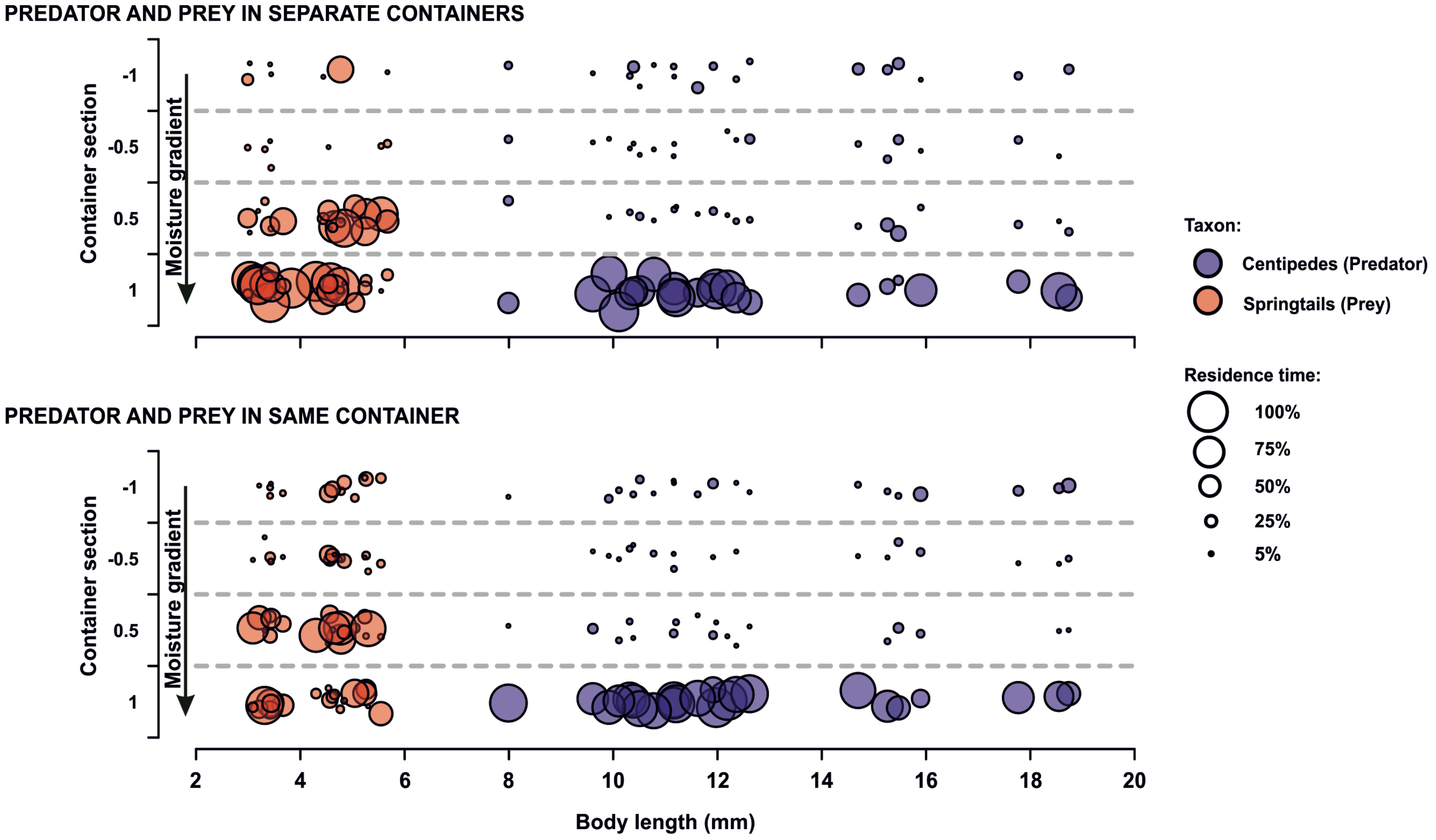

Figure 2: Patterns of space use of different-sized centipedes and springtails within the gradient treatment for EXP1 (top panel) and EXP2 (bottom panel). The diameter of the circumference indicates the proportion of time that an individual spent in each of the 4 sections within the gradient. Note how springtails (and especially larger ones) tend to avoid the wettest areas when predators are present.

Also, smaller individuals had a stronger preference for the wet area than did larger ones ("size" χ^2= 10.15, d.f. = 1, p-value = 0.001), and the pattern tended to be stronger for springtails ("size x taxon" χ^2= 3.6, d.f. = 1, p-value = 0.058; Figure 2). However, although there seems to be a clear trend in Figure 2, we did not detect significant differences between experiments for the differential patterns in location preference regarding the body size of each taxon (“experiment x size x taxon” χ^2= 0.2, d.f. = 1, p-value = 0.685).

As in experiment 1, the water treatments also affected the activity rate of each taxon differently ("treatment x taxon" χ^2= 7.8, d.f. = 2, p-value = 0.020, Figure 1e). However, the pattern was very different between experiments. Prey ("experiment" χ^2= 16.4, d.f. = 1, P < 0.001, Figure 1b,e) but not predators ("experiment" χ^2= 2.1, d.f. = 1, P = 0.149, Figure 1b,e), switched to a much higher activity in the second experiment, when springtails were exposed to predation risk (“experiment x taxon” χ^2= 46.4, d.f. = 1, P < 0.001). However, the three-way interaction was not significant, indicating no differences in these patterns across treatments ("experiment x treatment x taxon" χ^2= 0.85, d.f. = 2, P=0.655). Finally, encounter rates did not differ among treatments (treatment " χ^2= 1.54, d.f. = 2, P=0.463) nor experiments differed in how treatment determined encounter rates ("experiment x treatment " χ^2= 2.88, d.f. = 2, P=0.237). As in EXP1, considering both experiments together, larger individuals were more active ("size" in a model retaining “treatment x taxon” and “experiment x taxon” estimate=0.025, χ^2= 8.9, d.f. = 1, P=0.003). Further, regardless of body size, and perhaps because they switched to a high increase in activity in the second experiment, springtails were more active in general in the gradient treatment than were centipedes (“treatment x taxon” χ^2= 14.2, d.f. = 2, P<0.001).

Seventeen out of 41 collembolans were killed by a total of 8 centipedes. The probability of predation was positively affected by predator size ("predator size" χ^2= 11.79, d.f. = 1, P<0.001) and negatively affected by prey size ("prey size" χ^2= 6.73, d.f. = 1, P<0.01; Figure 3). Predation, however, was not affected by the water treatment ("treatment" χ^2= 0.93, d.f. = 2, P = 0.629), nor by the interaction with prey or predator body sizes (both P>0.05). Interestingly, a model including predator-prey body size ratios alone produced a worse fit (AICc=90.6) than a model including predator and prey sizes separately (AICc=80.8). Fitting a spline to the ratio model (e.g. to search for optimal body-size ratios predicting predation) did not substantially improve the fit (AICc=89.3).

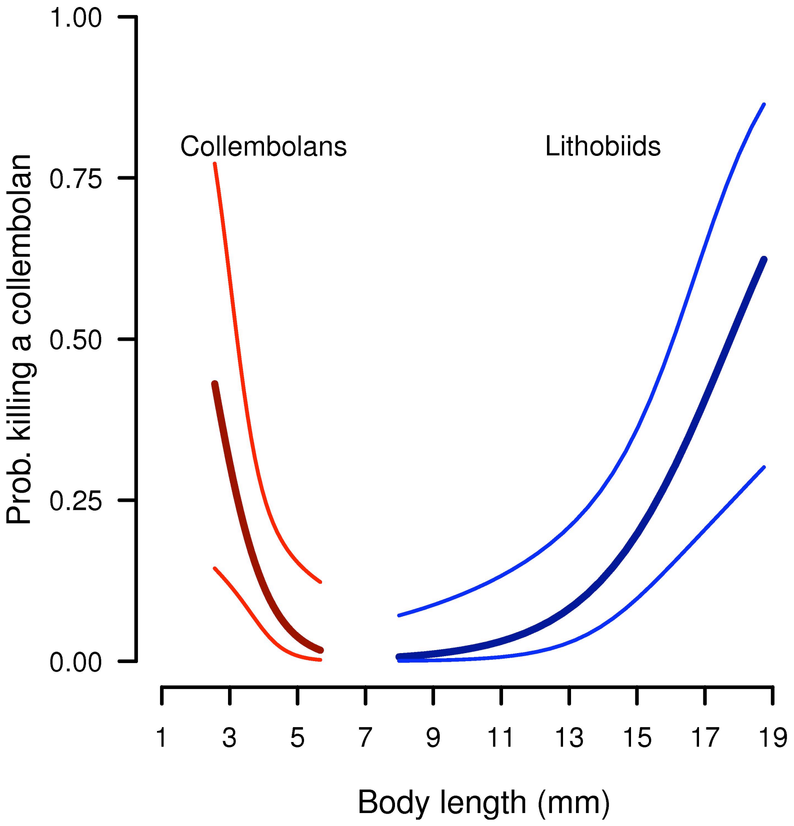

Figure 3: The probability of predation (Effects ± 95% Confidence Bands) in EXP2 depends negatively on springtail body size (in red) and positively on centipede body size (in blue). A model including the predator-prey size ratio provided a worse fit than the model including the two body sizes separately (see text).

Discussion

Our results showed that both predators and prey responded to artificial moisture gradients mimicking those found in the wild (Melguizo-Ruiz et al. 2012), and that the consequences of this behaviour can drive predator-prey interactions. First, the wettest spots in gradients, such as the ones we experimentally established, can potentially increase predator-prey encounter rates because both springtails and centipedes were attracted towards these patches. However, when predator and prey shared the same container, there was a clear tendency for prey to avoid the wettest areas, and this was more apparent in larger prey, which interestingly, can potentially resist desiccation better. This could partially explain why predation risk was lower for larger prey (Figure 3), as all prey increased their activity but larger prey tended to remain away from the wettest areas in the gradient treatment. In addition, predator and prey sizes entered in a model predicting predation resulted in a better fit than predator-prey size ratios as single predictors in a model, indicating that size-dependent mobility and anti-predatory behaviour, in addition to the ability to chase and pursue prey on behalf of relatively larger predators (predator-prey ratios alone), were relevant to predict the probability of predation. Moreover, prey moved at substantially higher rates when predators were present. These two behavioural switches in EXP2 are evidence of anti-predatory behaviour directed towards the centipedes, which could explain why predation rates were similar among treatments (EXP2) despite the potential for encounter rates is highest in the water gradient treatment (EXP1).

As soil moisture is highly spatially heterogeneous (Herbst and Diekkruger 2003, Schume et al. 2003, Jost et al. 2004), has multiple drivers (Facelli and Pickett 1991, Melguizo-Ruiz et al. 2012, Katra et al. 2007, Prieto et al. 2012), and this animal “positive hygrotaxis” has been documented in other soil systems before (Hopkin 1997b, Badejo et al. 1998, Lensing et al. 2005, Doblas-Miranda et al. 2009, Chapter 2) our findings could be extrapolated to most terrestrial ecosystems and to other soil taxa. Nevertheless, high levels of soil moisture due to flooding or heavy rain can also affect the distribution of soil invertebrates in the opposite direction, and fauna can temporally migrate towards the trunks, canopies or other suitable parts of the forest (Hopkin 1997b, Ausden et al. 2001, Adis and Junk 2002, Frouz et al. 2004, Chapter 2).

Moisture-dependent rates of activity

Contrary to what other studies found (Shultz et al. 2006), and contrary to what it has been suggested to occur across terrestrial ecosystems (Moya-Laraño 2010), in our study we found that the amount of homogeneously distributed water did not have a major direct effect on the activity nor encounter rates of individuals. This result suggests that, at least within the range of moisture that we used, springtails and centipedes do not change their movement rate as a function of relative humidity. Instead, it seems that the behavioural strategy is rather to move towards patches of increased humidity. Alternatively, the two taxa studied might need to experience water shortages for longer periods of time before they start reducing their activity to prevent desiccation.

Physiological constraints, anti-predator behaviour and predation rates

In the second part of our laboratory experiment, when both the predator and the prey were located in the same arena, we found that prey changed their movement behavior by switching to the area in which the predator was not present. Although the wet areas of the gradient treatment biased the movement of the individuals by attracting them, springtails seemed to assess the predation risk and be less attracted to wet areas, where the predators were more likely present. But importantly, this predatory avoidance behavior of prey was guided by the body size of individuals in such a way that smaller prey spent more time on wettest but dangerous sections of the gradient. This may be explained because larger individuals resist desiccation better due to their lower surface to volume ratio and the possibility to store relatively higher amounts of water in their larger bodies (Chown 1993, Renault and Coray 2004). Since smaller prey are predated at a higher rate regardless of treatment, this pattern would entail evidence for a physiological trade-off by which smaller prey suffer from higher predation risk likely because the risk of desiccation prevails. However, smaller springtails may have other means of avoiding predation.

Additionally, the springtails significantly increased their movement rate when exposed to predators and did so to a larger extend when they were located in the gradient treatment. The end result of this is that in the gradient treatment, where the expected encounter rates between predators and prey were highest, the collembolans diminished the encounter rate with the centipedes in a similar degree as in the other treatments, leading to similar predation rates across treatments. Thus, our findings suggest that when there is an aggregation of fauna due to moisture gradients, mobility may be exacerbated because encounter rates are higher due to increases in densities around wet areas (Chapter 2). However, these findings go against what the conventional wisdom and evidence on anti-predatory behaviour postulates: a decrease in prey activity with predation risk (e.g. Lima and Dill 1990, Moran and Hurd 1994, Beckerman et al. 1997, Schmitz et al. 1997, Peacor and Werner 2001, Danner and Joern 2003). Perhaps, in more realistic situations in the wild, prey do actively move seeking for a shelter and decrease their activity once safely hidden. Future experiments should also manipulate shelter availability. However, it has also been proposed that prey can adopt a risky behavior, with higher movement rates, in dangerous environments (Urban 2007a, b). By using this risky strategy prey would forage more intensively, grow faster and enter into a body size refuge that will reduce the risk of predation later in life. Nevertheless, our experiments suggested that the differential anti-predatory behaviour displayed by springtails in the gradient treatment (i.e., higher activity and settling in suboptimal patches in terms of water availability) likely served to equal predation rates to that of the other treatments, pointing to the adaptive value of this behaviour.

Predator and prey sizes *vs*. predator-prey size ratios in heterogeneous environments

We found that rather than body size ratios (e.g. Cohen et al. 1993, Brose et al. 2006, Brose et al. 2008, Petchey et al. 2008), including the body size of the prey and the predator separately in the model had better explanatory power for predicting predation rates. A model (Perssons et al. 1998) and a recent study testing it (Brose et al. 2008, see also Chapter 2) has demonstrated that even when predators and prey are allowed to freely interact in laboratory arenas, there is an optimal predator-prey body size ratio predicting predator attack rates. However, the above models do not take into consideration habitat heterogeneity and anti-predatory behaviour.

By monitoring anti-predatory behaviour in the heterogeneous environment (gradient treatment), we found that smaller prey incurred a higher predation risk in the gradient treatment as compared to other treatments and that prey moved at higher rates in this treatment. In addition, both larger prey and predators moved at higher rates, which made the probability of encounter increasing with the body size of each member of the pair. These patterns may largely explain why the body sizes of both prey and predators additively contributed to explain predation rates, and why they predicted predation rates better that predator-prey size ratios. We believe that more studies like the one we present here will help to disentangle how predator and prey body sizes and traits associated with them (Chapter 5) can influence predator-prey dynamics.

Conclusions

In conclusion, we have shown how the distribution of water in soils have the potential to affect the encounter rates between different trophic levels and alter predator-prey interactions such as the two invertebrate taxa in our study. Thus, water may not only play a central role in typically water-limited ecosystems, such as deserts and semi-arid areas, as it can also alter predator-prey interactions of invertebrates inhabiting the leaf litter of temperate deciduous forests, such as in European beech forests, were water is not as limiting. We also documented prey anti-predator behavior in terms of micro-habitat selection (guided by what it may be a trade-off between water physiological needs and predator avoidance) and increased activity, which could probably explain why predation rates were not different among water treatments. Contrary to recent predictions, we did not find that water availability *per se* increased invertebrate activity and predator-prey interactions. Water heterogeneity, instead of the absolute quantity, seems more relevant and drives encounter and activity rates. Finally, we found that perhaps due to mobility, anti-predator behaviour and size-dependent physiological constraints (smaller prey spent more time in wet and dangerous patches), including the body sizes of predators and prey separately had a better predictive power on predation rates than typical predator-prey ratios. We believe that extending this sort of studies to other ecosystems and extending them to grasp the complexity of soil food webs (Chapter 2) may help our understanding on the role of water availability in the functioning of detrital food webs and associated ecosystem processes.

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Chapter 2

Spatial heterogeneity in the availability of water and basal resources determines spatial aggregations and possibly indirect effects in soil macrofauna

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Abstract

Prolonged droughts alter not only average water availability but also the spatial heterogeneity of water in soils. Because under desiccation stress terrestrial invertebrates can behaviorally balance their water budgets by moving to wetter places, heterogeneity in water availability may strongly affect the spatial distribution of the different invertebrate groups inhabiting terrestrial ecosystems. In addition, since water availability enhances the growth of basal resources (both plants and microbiota), there is a potential indirect effect of the distribution of water on the distribution of consumers. We conducted a field experiment in a forest floor food web in which, after recreating a drought episode, we manipulated water and fungi availability in a bi-factorial design and 1) quantified the aggregative responses of prey and predators to the spatial heterogeneity of water and fungi, and in a subsequent predator removal experiment 2) estimated how a potential resource-dependent redistribution of invertebrates affected predatory mortality of different types of prey. Densities of most invertebrates (both predators and prey) were found to be highest in the moistest plots with added fungi (additive effects). Nevertheless, there was high variability of aggregative responses among different taxa, with one taxon (Pselaphognata millipedes) preferring drier patches. The combination of treatments affected predator-prey size ratios, possibly affecting predator-prey interactions. However, after including taxon as a random factor in the models the latter effect disappeared, suggesting that most predator-prey size differences in space could be assigned to taxonomy alone. Furthermore, predators and prey responded directly to water and while prey responded directly to fungi, predators responded indirectly through responding to prey aggregations around fungi. We also found possible indirect predatory effects enhancing some small prey taxa. Our results suggest that climate change may induce changes in food web structure and dynamics through changes in precipitation regimes influencing the strength and duration of predator-prey spatial aggregations.

Introduction

Species interactions are necessarily located in space. Therefore, the study of animal movement and spatial patterns in species abundances (e.g. prey and predators) provides useful information regarding the distribution of potential interactions across space, e.g. estimates of which are the species and individuals holding particular trait values (e.g. body size) which are most likely to interact (Kareiva 1990, Amarasekare 2008, Vazquez et al. 2009). Probably because most terrestrial invertebrates have gained behavioral adaptations to balance their water budgets (e.g. seeking sufficiently wet patches), water availability is one of the most important resources influencing the distribution and abundance of most soil invertebrates (Hopkin 1997, Chown and Nicolson 2004, Lensing et al. 2005, Shultz et al. 2006, Blankinship et al. 2011, Melguizo-Ruiz et al. 2012). Thus, the availability and distribution of water may be a key factor that explains the patterns of interactions in some terrestrial food webs and, given the predicted increase in the severity and frequency of draughts with global warming in some regions (IPCC 2007), this could have important implications for how climate change affects food web structure and dynamics, as well as its associated ecosystem processes.

However, while the effects of water on plant-plant interactions are well studied (Dawson 1993, Casper and Jackson 1997, Scholes and Archer 1997, Weigelt et al. 2000, Maestre et al. 2003, Maestre and Cortina 2004, Pugnaire et al. 2004, Soliveres et al. 2011), research on how water availability affects animal-animal interactions and food web dynamics is scarce. Furthermore, although most studies on the effects of water on animal interactions have been conducted on drylands or desert ecosystems (Noy-Meir 1974, McCluney and Sabo 2009, McCluney et al. 2011, González-Megías and Menéndez 2012; but see Lensing and Wise 2006, Spiller and Schoener 2008), water scarcity may be temporaly important in most terrestrial ecosystems. Moreover, an important indirect source of variation that has been usually neglected in most studies is the separate consequences of the positive correlation between water availability and productivity (Rosenzweigh 1968, Webb et al. 1983, Sala et al. 1988, Huxman et al.

2004, Iovieno and Baath 2008, Rousk and Baath 2011). Water alone may trigger aggregations of animals which seek to prevent desiccation (Chapter 1), and at the same time by enhancing productivity, water may contribute to increase animal densities by either aggregative responses of individuals around basal resources or by triggering a bottom-up numerical response (e.g. Scheu and Schaefer 1998, Chen and Wise 1999, Gruner 2004). To our knowledge, despite the potential importance of these aggregations for soil biotic interactions and ecosystem processes, the direct (via regulation of water budgets and aggregations) and indirect (via food resources) contribution of water availability to the spatial distribution of animal densities, as well as the consequences for animal-animal interactions, has not been explored so far. In order to better predict how the network of interactions may change according to water availability, these direct and indirect effects of water on terrestrial food webs need to be investigated. This is even more relevant if we want to predict the potential effects of altered precipitation patterns from climate change.

These predicted alterations in precipitation will likely affect water availability in soils, even on the top leaf-litter layer (Senevirante et al 2010). As a consequence of altered precipitation and temperature regimes, some species of plants, such as beech trees (*Fagus sylvatica*) in their southern limit of their distribution may be shifting their distribution range (Peñuelas and Boada 2003). Moreover, prolonged droughts may also lead to changes on the spatial distribution of water, which is often heterogeneous at the micro-scale level of the forest floor (Herbst and Diekkruger 2003, Schume et al. 2003, Jost et al. 2004, Katra et al. 2007). The homogenous input of water coming into the soil system from rainfall is progressively redistributed according to complex topographical elements, soil characteristics, plant composition and density, or the amount of leaf litter (Facelli and Pickett 1991, Famiglietti et al. 1998, Pockman and Small 2010, HilleRisLambers et al. 2001, Melguizo-Ruiz et al. 2012). Since some parts of the forest may dry faster than others (e.g. thick *vs*. thin leaf litter layers; Facelli and Pickett 1991; Melguizo-Ruiz et al. 2012), droughts may accelerate water heterogeneity in the soil. Therefore, as the dry period extends, the proportion of dry *vs*. wet patches will increase, and the remaining wet patches will be relegated to the areas that better retain humidity (Famiglietti et al. 1998). This environmental heterogeneity, along with the associated changes in biotic interactions, may contribute to the formation of the often observed spatial patterns of invertebrate abundances (Levings and Windsor 1984, Perfecto and Vandermeer 2008, Rietkerk and Van de Koppel 2008, Doblas-Miranda et al. 2009, Birkhofer et al. 2010, Melguizo-Ruiz et al. 2012). Due to this environmental heterogeneity, most individuals would constantly need to evaluate multiple cues and take complex decisions in order to improve their survival prospects. For instance, if predators are attracted to the wettest areas too, or use the availability of basal resources to find prey, prey individuals may be forced to exploit suboptimal areas in terms of water and food availability (see Chapter 1 for an example with water).

Alternatively, when the distribution of water and the associated energetic resources (e.g. fungi, bacteria) increment the density of both prey and predatory individuals, this may also affect the functional responses of predators; i.e., how the *per capita* consumption rates of predators change as a function of prey density (Holling 1959a). Depending on these functional responses some prey may decide to move to richer patches despite the presence of predators because the per-capita mortality could be reduced if these aggregations increase the densities above predation satiation levels (Holling 1959a). In addition, per-capita mortality could be reduced when large numbers of prey aggregate merely by predatory dilution effects (Turchin and Kareiva 1989, Vulinec 1990). However, prey aggregation may become more conspicuous and attract more predators, increasing prey per-capita mortality (Uetz and Hieber 1994, Ioannou et al. 2011). Furthermore, since there is variation in drought tolerance across species (e.g. Walter et al. 2012) and in predation risk (e.g. the largest prey have lower predation risk), different taxa and size classes should differentially respond to drought.

These patterns may have strong consequences for food web structure and dynamics. If different species or phenotypes are differently driven towards different areas, body size ratios of predators and prey could change across gradients, which may in turn affect predator attack rates (Woodward et al. 2005; Brose et al. 2006, 2008), interaction strengths (Emmerson and Raffaelli 2004, Woodward et al. 2005), and food web complexity (Petchey et al. 2008).

Additionally, taxa and phenotypes segregated in space will not have the chance to interact. Given the unanticipated outcomes resulting from these combined direct and indirect biotic effects in complex communities (Sih et al. 1985, Amarasekare 2008), anticipating the risk of a given patch may be challenging for prey.

In this article we recreated a drought episode and subsequently experimentally established heterogeneous micro-landscapes in the forest floor to quantify for the first time the extent to which experimental manipulations of water and fungi availability (mimicking the indirect effect of water on basal productivity) drive aggregative responses in invertebrate meso- and macrofauna (~>0.5mm), and whether these responses can potentially affect predator-prey interactions and food web structure. We tested whether water and fungi affected the spatial distribution of the invertebrate community as a whole, or differentially affected prey and predators, different taxa or even different size classes. Through possible changes in the spatial distribution of i) abundances, ii) taxonomic groups, or iii) body sizes food web structure could be severely modified, for instance because some prey taxa or size classes might choose to move to sub-optimal areas with fewer resources if predation risk is too high, while others may expose themselves to relatively higher predation risk. We then experimentally manipulated predator densities in aggregates to investigate if the resulting redistribution of invertebrates as driven by resource heterogeneity, changed predator-prey interactions and as a consequence prey increases survival after predator removal. This study can potentially add to our understanding of how climate change may affect ecosystem processes.

Materials and Methods

Study area

The study was conducted in a primary deciduous beech (*F. sylvatica*) forest 756 m.a.s.l. in the Natural Park of Redes (43° 14'N, 5° 18'W), in Asturias, north Spain. Beech forests are well represented in this area, and in the Natural Park they extend through > 9000ha, being the major type of forest of the Park and the deciduous forest more representative in the Cantabrian Mountains (Muñoz Sobrino 2009). A rich community of surface-dwelling and soil invertebrates lives in the leaf-litter interface of beech forests, actively contributing to the process of litter decomposition and nutrient cycling (Wise and Schaefer 1994, Schaefer and Schauermann 2009, Lavelle and Spain 2001, Schaefer et al 2009, Melguizo-Ruiz et al. 2012). The estimated annual rainfall is ~1400 mm (Ninyerola et al. 2005).

Experimental design

Initial setup

During 25 days, beginning the 15th of May 2011, we excluded rainfall from 12 1x1m plots by covering each of them with a 2x2m plastic roof, 70cm. The roof was sufficiently high as to prevent excessive dew condensing underneath. Plots were located in flat micro-sites scattered across a 1600m^2 forest area. Surprisingly, during the very first days, areas with excluded water attracted more invertebrates. This attraction towards water-excluded plots was maximal after 16 days, when a heavy rain (43.4 l/m^2 in 48h) produced a migration of arthropods into the plot (density increased by ~X2.5, not shown). After the heavy rain resumed, and once we detected that invertebrates could begin to give up the drying plots because the system started to dry up and conditions were not suitable, we fenced the 12 plots and continued the rainfall exclusion treatment for 9 days until we were sure that the litter was dry enough to produce some water stress but not too strong as to affect animal survival within the plot. This much drought (days without rainfall) is not unusual in Iberian beech forest (Ninyerola et al. 2005). Fencing was accomplished by setting an aluminium 1x1m structure 0.4m height, buried 10cm deep in the ground to prevent horizontal migration. A preliminary study showed that most of the migrations of macrofauna occurred on the horizontal rather than on the vertical axis (unpublished data).

Field Experiment 1: Water and fungi availability and micro-habitat selection among different soil taxa and size classes

In the first experiment we assessed the effects of enhanced basal resources and water on the spatial redistribution of invertebrates. Although water is likely not a resource in the sense that it can barely be limiting and promote exploitative competition for it, for simplicity we refer to both additions as resources. After the period of rainfall exclusion, we applied the treatments using a full factorial design. We divided the plots in four subplots of 0.5x0.5m and subsequently applied the full combination of treatment levels: added water and fungi (W+F+), added water (W+F-), added fungi (W-F+) and neither water nor fungi added (W-F-). The division of the plots into subplots did not prevent the invertebrates to freely move among the four areas; on the contrary it was actually intended to allow mobility and to test how animals actively choose the patch of their preference. Within each plot, the spatial configuration of treatments was randomly assigned.

Water in the W+ treatments was supplied with water from the Sigüenza natural fountain (*Fontvella®*, with the following mineral composition: HCO_3^- 300mg/l, Na^+ 4mg/l, Mg^{2+} 24mg/l, Ca^{2+} 78 mg/l) using a backpack sprayer. After the initial drying manipulations and until the end of both experiments, subplots with added water received 0.25l water/day. The added amount of water reflected approximately the collected precipitation inside the forest for a period of 26 days (the same time expand as the water exclusion manipulation, from May 15th to June 14th 2011 -i.e., 1.11 l/m^2 per day), after discounting the 4 days of heavy rain (>35 l/m^2 in 48h) during which the amount of rainfall negatively affected soil invertebrates as they started migrating towards our drying plots. Using the actual rainfall estimates within the forest prior to our study to decide the amount of water to be added for our manipulations, provided more accurate information than if we had used interpolated data from nearby weather stations (as in Ninyerola et al. 2005). For instance, the intricate relief of the Cantabrian Mountains entails high variability in mesoclimatic conditions, which largely influences the temperature and rainfall within the region. In addition, the Oceanic character of the Cantabrian weather involves that a great amount of the rain falls in drizzling form, a 10-30% of which can be lost from canopy interception and evapotranspiration (Aussenac and Boulangeat 1980). Additionally, we recorded the relative humidity within the leaf litter at 30'-

intervals using 39 *thermo*-hygrometer sensors (DS1923-Hygrochron), which were buried within the leaf-litter. Since we did not have enough sensors for all the subplots, some subplots were either not monitored at all or only temporally monitored. However, we always kept a minimum of 3 sensors per plot, systematically placing two sensors in dry and one in wet subplots (as wet subplots exhibited less variation in RH than dry plots). The sensors were placed in a metallic grid cage that had a 1cm mesh size, small enough to prevent leaves from directly touching the sensor but not too small to create an artificial microclimate. Although with only a small recorded effect, we successfully induced differences in water availability in dry *vs.* wet plots, as within the leaf litter, the dried subplots had a relative humidity (mean ± SD) of 92.05% ± 0.36 and the wet subplots of 97.47% ± 0.22 (GLMM with plot as a random factor: $\chi^2 = 51.68$; d.f. = 1; $P < 0.001$).

Subplots with fungi in the *F+* treatments received 25g of dry yeast, this being the same quantity of micro-fungi found in a Danish beech forest (Holm and Jensen 1980). Therefore, we assumed equal quantities in our forests, and doubled the amount of micro-fungi in *F+* treatments. A preliminary experiment showed that leaf-litter micro-patches with added yeast attracted more invertebrates of diverse taxa than ambient forest patches (results not shown). The added yeast treatment was applied only once at the beginning of the experiment. We carefully and homogeneously mixed the leaf-litter layer and yeast. In order to control for the potential effects of litter mixing, the litter of the subplots that received no extra-fungi was gently mixed too.

For each subplot we measured abundances and body sizes of invertebrates, before (abundance, mean ± S.E.: 491ind/m^2 ± 104.72), and 15 days after we applied the water and fungi treatments (abundance, 424.92ind/m^2 ± 57.66). In order to minimize disturbances prior to the experiment, when estimating initial abundances and before applying the treatments, only a quarter of the subplot area (0.25x0.25m) was measured. Final abundances and body size distributions were estimated by sampling the entire subplot (0.5x0.5m).

Field Experiment 2: Effects of generalist predators on prey in patches with different amounts of water and fungi after invertebrate redistribution

In the second experiment we explored the consequences of the differential redistribution of invertebrate macrofauna (prey and predators) on the mortality of prey (detritivores and fungivores) due to predatory effects from the largest predators cascading down to lower trophic levels (detritivores and fungivores), due to differences in resource availability (high *vs.* low water and/or fungi). The experiment was conducted within the same 12 plots of EXP1 and right after the first experiment concluded, using the same 5099 individuals that were alive at the end of EXP1. To prevent migration of macro- and mesofauna among bags, we used sealed organza bags (nylon bags of very fine mesh size <0.1mm). Each subplot (e.g. *W+F+*) was divided in two treatments (bags) as follows. The *"Prey + Predator"* treatment bag contained half of the prey and half of the predators found in the subplot. In the *"Prey"* treatment predators were removed and therefore the bag only contained the other half of the prey found in the subplot. Thus, averaging among treatments in the final conditions of EXP1, the initial density of invertebrates used in EXP2 was 221.5prey/m^2 ± 25.08 and 185.17predators/m^2 ± 33.19 in the *"Prey + Predator"* treatment and 225prey/m^2 ± 25.32 in the *"Prey"* treatment (N=12).

Prey individuals were randomly assigned to treatment bags, irrespective of their taxonomic affiliation. In total the experiment summed 96 bags: 12 plots x 4 subplots x 2 bags. Each organza bag contained also half of the sifted leaf-litter left over in each subplot from EXP1. The experiment was run for 15 days, after which time abundances and body sizes were again estimated, providing a density of 160 prey/m^2 ± 16.05 in the *"Prey"* treatment and of 187.83 prey/m^2 ± 20.64 and 98.17predators/m^2 ± 17.05 in the *"Prey + Predator"* treatment. In general, we successfully diminished the abundances of all predatory groups in the predator removal treatment. Predator removal efficiency (*PRE*) was computed as $PRE = \left(N_{P*} - N_P\right)/N_{P*}$, where N_P and N_{P*} are the final abundances of predators for the *"Prey"* and *"Prey + Predator"* treatments respectively. We used a GLMM to test whether predator removal efficiency depended on 'initial predator abundance' by including N_P, 'predator treatment' as well as 'water' and 'fungi' as covariates (N_{P*} was the dependent variable). Removal efficiency was higher when there were initially more predators in the subplot (GLMM: 'predator treatment' x 'initial predator abundance' $\chi^2 = 45.92$; d.f. = 1; $P < 0.0001$). The overall *PRE* across treatments was 84.5%. Note that the removal efficiency may be underestimated because when we estimated the final predator counts, the number of predators in the *"Prey + Predator"* bags could have dropped more severely due to stronger intraguild predation from predation relative overcrowding. Furthermore, the few predators that remained in "Prey" bags were 12.11% smaller than those in the "Pred + Predator" bags, although the result was not significant (p = 0.10), suggesting that removal efficiency was slightly higher for larger animals.

Sampling protocol and measured variables

In both experiments, we used the same methodology to estimate leaf-litter invertebrate abundances and individual body lengths. First, we manually sampled leaf-litter of the four subplots of a given plot. Samples were rapidly collected in order to avoid undesired migrations of individuals among treatments or down below the ground. The collected leaf litter was gently sifted 3 times through a 1.5cm-mesh sifter. The resulting material was then carefully sorted and examined twice for relatively large invertebrates (>0.5mm). Each individual found was measured to the nearest 0.5 mm and classified into broad taxonomic groups (Figure 1). Unfortunately, further detailed taxonomic classification was not accomplishable because the idiosyncrasy of the experiment required identifying the specimens alive and by sight in the field (Decaens 2010). However, while we agree that performing this type of experiments up to the genus or species level could reveal responses that likely remained cryptic to us, the method used here sufficed to uncover some relevant and previously undocumented patterns. The sampled individuals corresponded to the large range of mesofauna (>0.5mm in length) and macrofauna (>2mm), and we refer to the entire group as macrofauna for simplicity. In order to account for the shape of the different taxa, body lengths were transformed into body masses by using taxon-specific equations from the literature (Hódar 1996, Edwards and Gabriel 1998, Hodar 1998, Johnson and Strong 2000, Sabo et al. 2002, Gruner 2003, McLaughlin et al. 2010).

Individuals were also recorded as either prey or predators. In general, predators were considered as all those invertebrates that hunt and feed upon other individuals during most of their lifetime, and prey were those that mostly ingest detritus or graze on fungi or bacteria. Although the group of mites and diplurans may contain some predatory species, they were classified as prey. Mites are a diverse group of arthropods (Coleman et al. 2004) and, although most large mites were likely predators (e.g. mesostigmata), their relatively small size when compared to most macro-arthropod predators made them intermediate consumers at most. Thus, predatory mites were likely prey for most of the macro-arthropod predators in our experiment (Schneider et al. 2012). Diplurans, which were classified as prey, may also contain some predatory species. However, most diplurans found were campodeids, which feed on very small mites or collembolans (not sampled here) and fungal mycelia and detritus (Coleman et al. 2004). During both experiments we counted and measured a total of 13,341 invertebrates, which likely included a large number of animals measured more than once (EXP1 and EXP2). These invertebrates belonged to 31 broad taxonomic groups of variable abundance (Figure 1).

Statistical analyses

Abundances of both experiments were analyzed using Poisson Generalized Linear Mixed Models (GLMMs) with logarithmic link functions. Body masses were transformed to logarithms and analyzed using Gaussian GLMMs with identity link function. The model fits were computed using restricted maximum likelihood (REML).

The random factor 'plot' accounted for the non-independence of samples of subplots within a plot. For experiment 2 (estimates of Predatory effects) we also included the random factor 'subplot' for the variation within the subplots (pairs of bags coming from the same subplot), and the random factor 'bag' accounted for the shared variation within the nylon predation bags at the initial and final stages. Finally, the random factor 'sample', that is a vector of sequential numbers from 1 to number of rows, was used in the Poisson GLMMs to account for overdispersion (Bates et al. 2011) as in González-Megías and Menéndez (2012). In order to test our main hypotheses, we used a combination of inferential strategies. First, we selected the most parsimonious model among all competing models by using the Akaike information criterion corrected for small sample sizes (AICc which converges to AIC for large sample sizes) and Akaike weights (ω_i) to compare models, which based on AICc, measures the relative importance of model *i* as compared to the rest of tested models (Burnham and Anderson 2002). Once we identified a candidate model, we proceeded to calculate its estimates and standard errors as well as to test the null hypothesis of no effect of the estimate by using the likelihood ratio test (LRT) comparing models with and without the variable of interest (Bolker et al. 2009, Zuur et al. 2009).

In order to quantify how resources affect the pattern of movement of individuals and what are the consequences for prey survival, we computed five groups of models, four of which analyzed abundance and one them body size:

1. Overall community response: We tested for mobility responses towards increases in water and/or fungi on behalf of the invertebrate community as a whole. Since the analysis was performed at the community level, we did not account for the taxonomic group and instead summed up the number of invertebrates within subplots regardless of taxon. Additionally, we tested for differences in taxon richness (Fig. 1) across patches differing in resources.
2. Predator *vs.* prey responses: We analyzed the effects of water and fungi on the abundance of prey and predators. To see if both predators and prey responded either directly or indirectly to enhanced resources (e.g. predators responding to fungi through prey), the abundance of the other group (e.g. prey if we are examining predators) was included in the model as a covariate. Thus, the independent variables were 'water', 'fungi' and the abundance of the other group. The variables 'plot' and 'subplot' were included as random factors. Here we also summed up the number of predators and the number of prey in two separate variables, without considering the taxon within each functional group.
3. Responses by taxon: To test responses by taxon, we constructed a GLMM model for each of the eighteen most abundant taxonomic groups (Fig. 1) of predators and prey. In this case we did not select the best model by the AIC procedure, but instead constructed the full model 'water x fungi + initial abundances' and tested for multiplicative *vs*. additive effects of the

resource treatments. We chose the 18 most abundant taxa (Fig. 1) because we thought this was a good compromise between not loosing too much statistical power after correction for multiple tests and including the most relevant groups for analysis. In order to account for increases in type I error rates when performing multiple tests, we used the false discovery rate adjustment to correct alpha levels (Benjamini and Hochberg 1995).

4. Changes in prey numbers after predator removal: To examine changes in numbers associated with predator presence/removal and previous (from EXP1) treatment in EXP2, we performed an analysis for each of the 9 most abundant taxonomic groups of prey. During model selection we examined whether the final model contained an interaction between 'time', either initial or final abundances of animals located in the bags, and any of the fixed factors. This interaction would indicate that the fixed effect (either resources or predator presence/absence) had an impact, positive or negative, on the abundance of the focal taxon, as it would mean that abundances differently increased or decreased across treatments. Diplurans were not analyzed because despite their high initial density, their final abundances were surprisingly very low in all treatments, likely indicating that they are very sensitive to leaf-litter sifting. When calculating p-values, false discovery rate adjustments were also applied in these tests. However, the particular nature of the p-value distribution kept corrected alpha levels as 0.05.
5. *Body size*: Finally, in EXP 1 only, we examined if there was a differential response of different size classes by testing if the body size of responding prey and predators differed among treatments. The models included the logarithm of body mass as a dependent variable and 'water', 'fungi' and group ('predator-prey') as explanatory factors. Again, the variable 'plot' was used as a random factor. In addition, we ran two models, one including ‘taxon’ as a random factor and one without considering the taxonomic affiliation of each individual. This approach served to distinguish the effects of body size alone from those of taxonomy. If body size were significant despite taxonomy being included in the model this

would mean that animals of different body sizes were responding differently to the treatment, irrespective of their taxonomic affiliation (a proxy of their phylogenetic relationships). If however, we found that the body size responses disappeared after including taxon as random factor, this would mean that body sizes were responding through differences in body sizes among taxa alone, and that body size and taxa effects are indistinguishable, at least at this level of resolution (length was measured to the nearest 0.5mm).

All the analyses were computed with R ver. 2.14.2 (R Development Core Team 2012) and the libraries 'lme4' (Bates et al. 2011), 'effects' (Fox 2003) and 'aiccmodavg' (Mazerolle 2012).

Results

Field Experiment 1: Water and fungi availability and micro-habitat selection among different soil taxa and size classes

The relative abundance of the different taxa can be found in Figure 1.

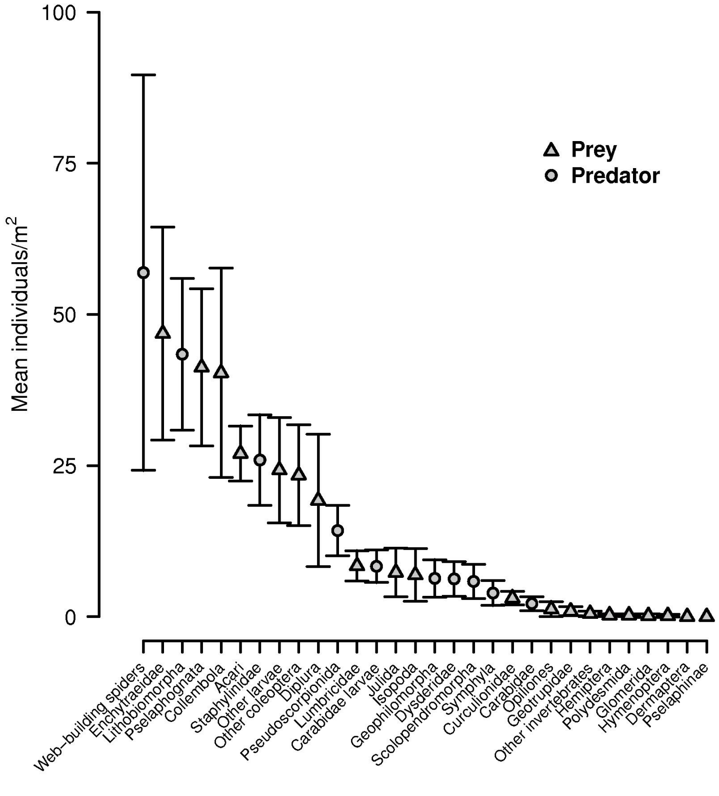


Figure 1: Rank-abundance curve (mean individuals/m^2 ± 95% C.I.) of the different taxa sampled in the leaf litter of the beech forest at the end of the first experiment. The rank-abundance curve was constructed by averaging the taxon abundances of the 12 plots, with the data from the end of EXP1. Taxonomy corresponded to the level at which animals could be identified in the field.

The model selection approach shows that the most parsimonious model explaining invertebrate abundance in the community is that which considers only additive effects of water and fungi but not the interaction (multiplicative effects) term among variables (Table 1). In general there was a net flux of individuals towards areas with more resources (Figure 2; Table 2): wet subplots contained 2.1X as many individuals as dry subplots, whereas subplots with added fungi had 1.5X more individuals than plots with no fungi added. Additionally, wet and added fungi subplots contained 1.3X ($\chi^2 = 13.55$; d.f. = 1; $P < 0.001$) and 1.2X ($\chi^2 = 4.37$; d.f. = 1; $P = 0.04$) more taxa than dry subplots and subplots without added fungi respectively.

Table 1: Model selection for predator responses using AICc criteria and associated statistics (ΔAICc and weights, ωi).

Model	D.F.	AICc	ΔAICc	ω
(1) *Community abundance*				
W + F + Ini	**6**	**189.16**	**0.00**	**0.73**
W x F + Ini	7	191.82	2.66	0.19
W + F	5	193.55	4.39	0.08
W x F	6	196.17	7.01	0.02
W + Ini	5	201.34	12.18	<0.001
(2) *Prey abundance*				
W + F + PredEnd	**6**	**153.86**	**0.00**	**0.57**
W + F + PredEnd + PreyIni	7	156.22	2.36	0.17
W + PredEnd	5	157.63	3.77	0.09
F + PredEnd + PreyIni	6	158.11	4.26	0.07
W x F + PreyIni + PredEnd	8	159.11	5.25	0.04
(3) *Predator abundance*				
W + PredIni + PreyEnd	**6**	**151.79**	**0.00**	**0.28**
W + F + PredIni + PreyEnd	**7**	**152.10**	**0.31**	**0.24**
W + F + PreyEnd	6	152.41	0.62	0.21
W + PreyEnd	5	152.55	0.76	0.19
W x F + PredIni + PreyEnd	8	154.93	3.14	0.06

(4) *Mean body mass*				
W x F x PredPrey	**10**	**23576.12**	**0.00**	**0.99**
PredPrey	4	23586.84	10.72	<0.001
F + PredPrey	5	23587.82	11.71	<0.001
W x F + PredPrey	7	23588.30	12.18	<0.001
W + PredPrey	5	23588.65	12.53	<0.001

W: water treatment, F: fungi treatment, PredEnd: final predator abundance:, PreyIni: initial prey abundance, PreyEnd: final prey abundance, PredIni: initial predator abundance, PredPrey: whether the individual is a prey or a predator. For simplification, we only represent the higher terms of the model. Thus, a model with an interaction term implicitly contains also the additive components of the interaction. Here we only present the best 5 models. The complete table with all the tested models can be found in the appendix (Table S1).

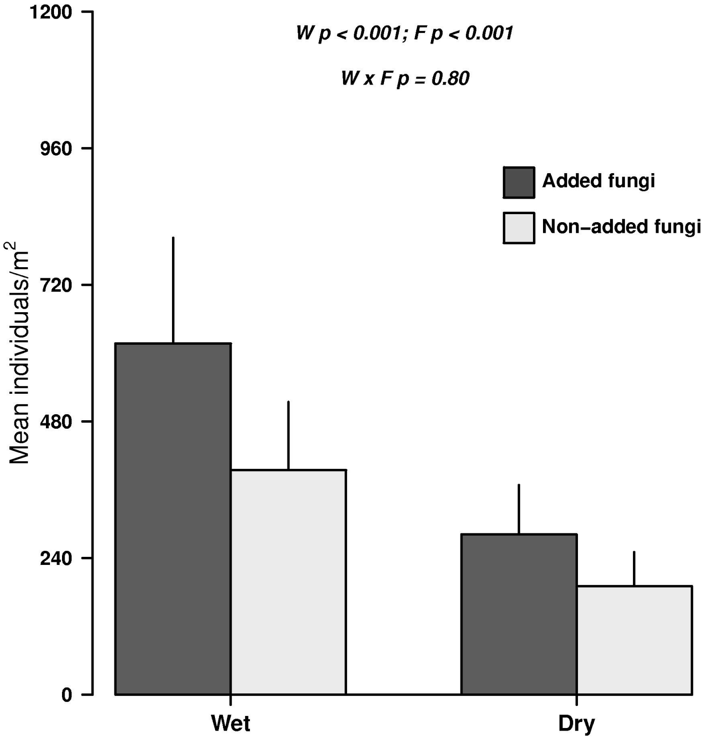


Figure 2: Experimental effects on the invertebrate community as a whole (individuals/m^2. Mean ± 95% C.I., N=12 plots). Abundance effects were back transformed into the original scale by the inverse-log link function.

Table 2: Results of the AICc candidate GLMMs models explaining abundances or body sizes.

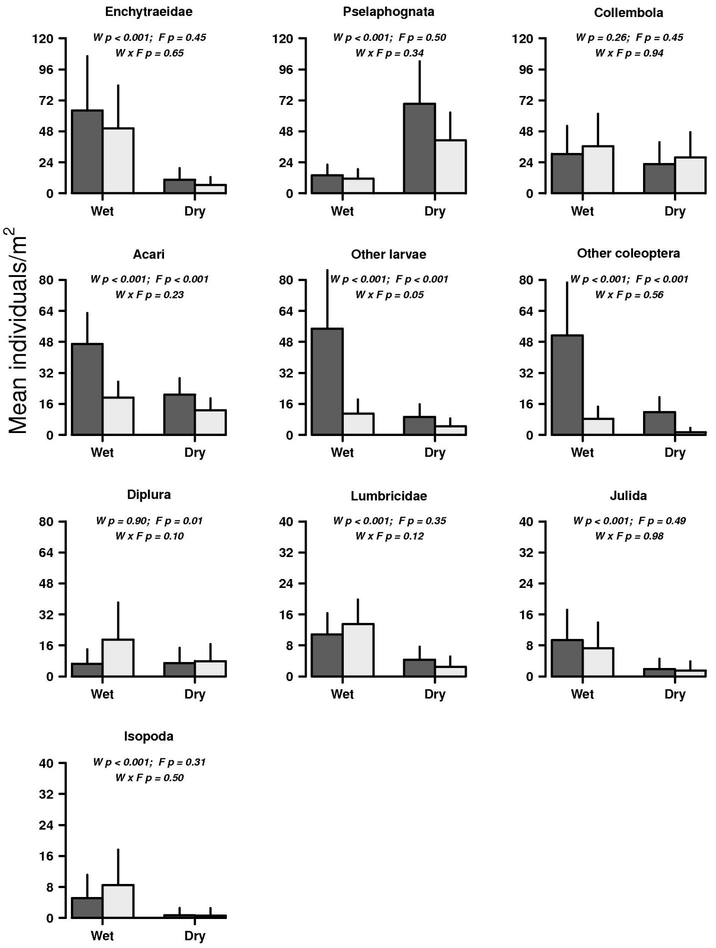
	Estimate	S.E.	X^2	d.f.	P-value
Abundance					
a) Community					
Initial	0.00	0.00	7.18	1	0.01
Water	-0.76	0.10	25.37	1	0.00
Fungi	-0.42	0.10	7.39	1	0.01
b) Prey					
Water	-0.30	0.10	19.19	1	0.00
Fungi	-0.36	0.08	10.75	1	0.00
Predators	0.01	0.00	18.26	1	0.00
c) Predator					
Initial	0.01	0.00	7.12	1	0.01
Preys	0.01	0.00	38.08	1	0.00
Water	-0.52	0.16	28.73	1	0.00
Body mass					
d) Predator/ prey					
Water	0.25	0.13	0.03	1	0.87
Fungi	0.25	0.12	1.01	1	0.31
Pred-Prey	-3.33	0.11	2470.20	1	0.00
Water x Fungi	-0.44	0.20	6.19	1	0.01
Water x Pred-Prey	-0.73	0.18	0.81	1	0.37
Fungi x Pred-Prey	-0.82	0.16	5.99	1	0.01
Water x Fungi x Pred-Prey	1.44	0.28	27.20	1	0.00

Nevertheless, prey and predators responded differently to enhanced water and fungi. The best model explaining prey abundance included both the amount of water and fungi and the final number of predators. On the other hand, the best model explaining predator included the final number of prey, the initial number of predators and the amount of water, but not the amount of fungi. The second best model for predators, which included the amount of fungi, had a very similar Akaike weight to the best model (Table 1). However, predators only seemed to respond to fungi when the number of prey was not included in the model as a covariate ($\chi^2 = 9.71$; d.f. = 1; P = 0.001), as this effect vanished when prey were included in an additional model ($\chi^2 = 2.44$; d.f. = 1; P = 0.12) in which prey had a positive and highly significant effect (Table 1). Thus, predators seemed to respond directly to water availability and indirectly to fungi through responding to prey abundances. Overall, predator and prey did not differ in their response towards water (P=0.539), strongly suggesting that both groups are driven by physiological needs.

When we analyzed the effects of resource addition on the abundances of the most abundant taxonomic groups, we found that some groups responded differently from others, and that the variability of responses ranged from attraction to, to null effects or repulsion from either water or fungi (Figure 3). The majority of responding taxa increased their densities in subplots with resource addition. However, Pselaphognata responded negatively to water addition and Diplura to fungi addition.

The amount of resources also impacted the body sizes of invertebrates that were found in each treatment, and the effects differed between prey and predators (Table 1). Although predators were always larger than prey, the difference of body masses between prey and predator was lowest in dry subplots without fungi added, and highest in wet subplots without fungi added. The other two treatment combinations had differences of body masses which laid somewhere in between these two extremes and were of similar magnitude to each other (Figure 4). However, after including taxonomic identity as a random factor, this accounted for most of the variation in body masses across treatments, and all the treatment effects vanished (Figure 5).

Prey:



Predators:

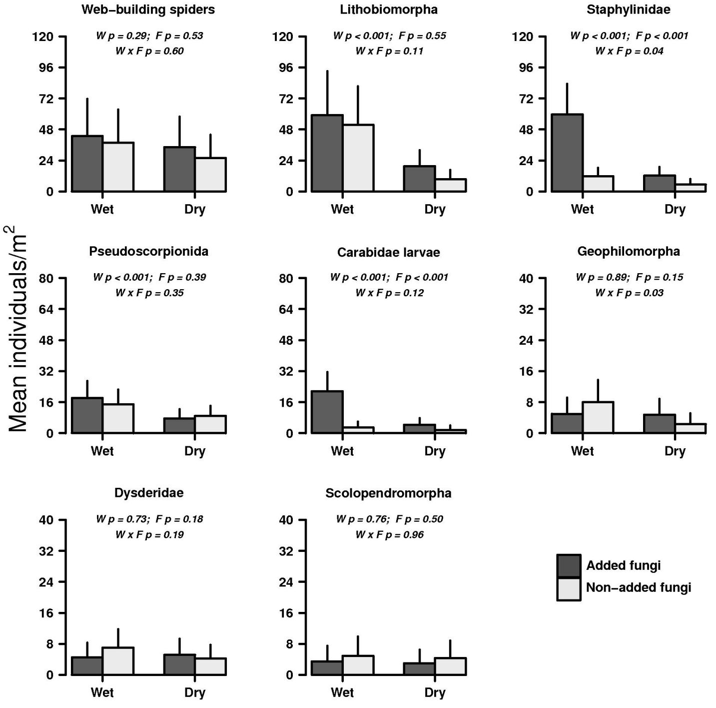


Figure 3: Experimental effects on each of the most abundant taxa (individuals/m^2. Mean ± 95% C.I., N=12 plots). Represented are the ten most abundant prey taxa (top) and the eight most abundant predator taxa (bottom). Abundance effects were back transformed into the original scale by the inverse-log link function. We used the false discovery rate adjustment for significance levels (corrected significance levels, $\alpha_W = 0.03$; $\alpha_F = 0.017$; $\alpha_{WxF} = 0.05$).

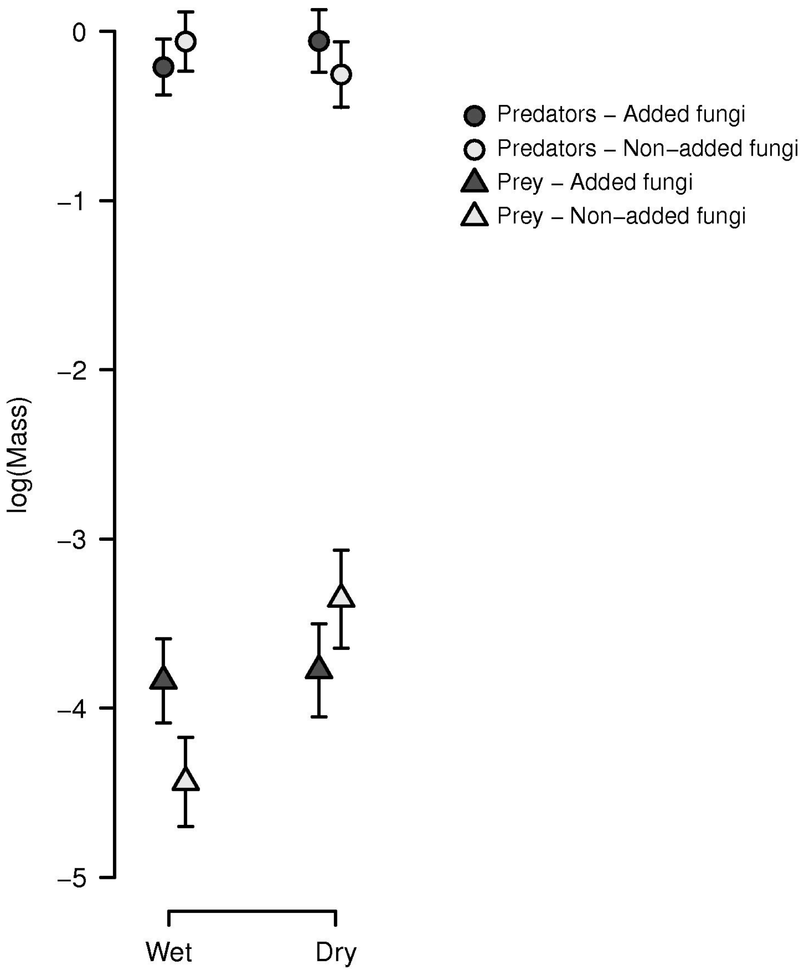


Figure 4: Experimental effects (mean ± 95% C.I.) on the log-body mass (mg) of invertebrates, suggesting differential aggregative responses of different size classes or prey and predators.

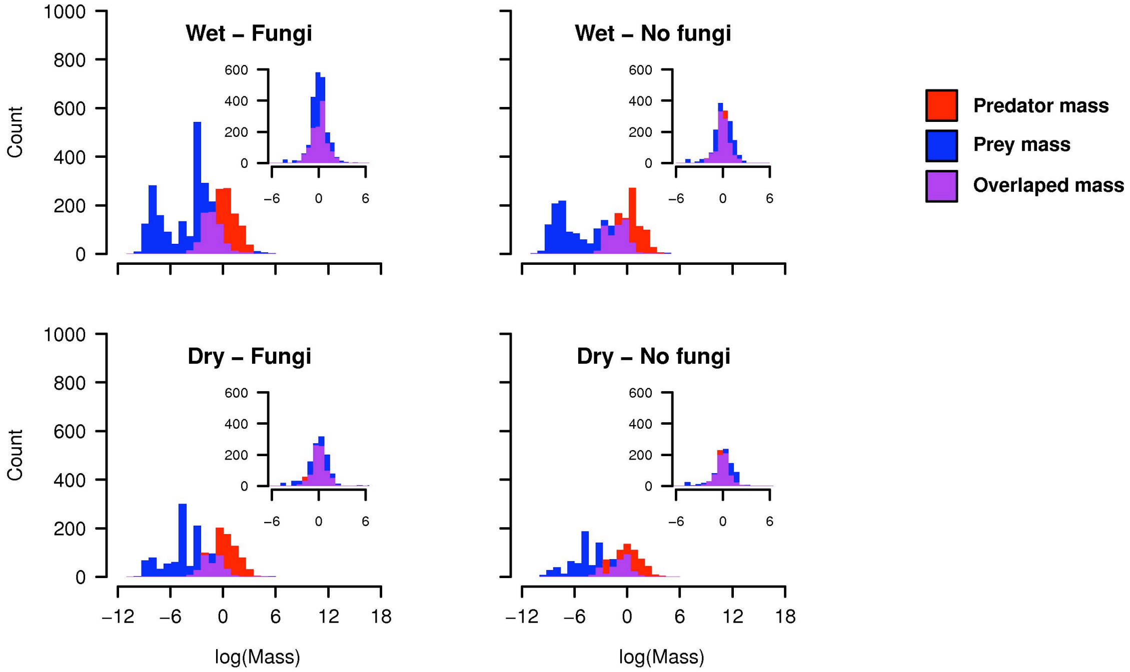


Figure 5: Frequency distribution histograms of log-body masses of prey and predators in the four treatment combinations. The smaller inset plots show the distribution of predator and prey body masses after accounting for taxonomic effects (see text).

Field Experiment 2: Effects of generalist predators on prey in patches with different amounts of water and fungi after invertebrate redistribution

We found that within the nylon bags there were substantially fewer individuals at the end (29.98ind/bag ± 2.83 on each subplot) that at the beginning (51.43ind/bag ± 4.63) of the experiment. Moreover the factor 'time', whether we measured the abundances at the beginning or at the end of the second experiment, appeared to explain the abundance of all the models of the 9 most abundant taxonomic groups of prey (Table 3). In four out of nine prey groups, the change in abundance was due to either the presence of predators, the amount of resources, or both. Only Enchytraeidae and Pselaphognata responded to the predators' removal treatment. Rather unanticipated, relative to their initial densities, there were more prey individuals in bags with predators than in the bags from which they had been removed; for Pselaphognata this was only true in plots without fungi added (Figure 6). The rest of taxonomic groups did not respond to the predator removal treatment (Table 3). Additionally, we found that the changes in abundances of some prey taxa were affected by the amount of water and/or fungi (Figure 6). Coleoptera responded to the amount of water and fungi, and Enchytraeidae, Pselaphognata and Lumbricidae responded to the amount of water only. After controlling for initial densities, Coleoptera were more abundant, even more so than at the beginning, in subplots without added water or yeast. The Clitellata (Enchytraeidae and Lumbricidae) seemed to have higher mortality in relatively dry conditions, as they had fewer individuals in these plots as compared to the initial conditions. In addition, in wet subplots Enchytraeids tended to have more individuals at the end than at the beginning. This was not the case for Pselaphognata individuals, which were relatively less abundant in wet plots at the end of the experiment, suggesting higher mortality under high humidity (Figure 6).

Table 3: Model selection results (AICc) for changes in abundance of the 9 most abundant prey taxa (a-i) in EXP2 (predator removal).

Model	DF	AICc	ΔAICc	ω
a) Enchytraeidae				
(W + Pred) x Time + F	11	530.8	0	0.37
(W x Pred + F) x Time	14	530.87	0.07	0.36
(W + F + Pred) x Time	12	532.64	1.84	0.15
(W x F + Pred) x Time	14	535	4.2	0.05
W x Time + F + Pred	10	535.42	4.63	0.04
b) Pselaphognata				
(F x Pred + W) x Time	14	338.01	0	0.86
(W + F + Pred) x Time	12	343.44	5.44	0.06
(W + Pred) x Time + F	11	344.69	6.68	0.03
(W x Pred + F) x Time	14	346.1	8.09	0.02
(W + F) x Time + Pred	11	346.78	8.77	0.01
c) Collembola				
Time	6	367.84	0	0.19
W + Time	7	368.4	0.56	0.14
F + Time	7	368.59	0.75	0.13
Pred + Time	7	368.92	1.08	0.11
W + F + Time	8	369.04	1.2	0.1
d) Acari				
W + F + Time	8	353.49	0	0.19

W + F+ Pred + Time	9	353.57	0.09	0.18
W x Time + F + Pred	10	353.91	0.43	0.15
W + F	7	355.05	1.57	0.08
W + F + Pred	8	355.12	1.63	0.08
e) Larvae				
W + F + Time	8	318.26	0	0.35
W + F	7	319.66	1.4	0.17
W + F+ Pred + Time	9	319.9	1.64	0.15
W + F + Pred	8	321.28	3.02	0.08
W + F + Pred x Time	10	321.73	3.46	0.06
f) Coleoptera				
(W + F) x Time + Pred	11	365.49	0	0.55
(W + F + Pred) x Time	12	367.13	1.64	0.24
(F x Pred + W) x Time	14	369.04	3.55	0.09
(W x F + Pred) x Time	14	369.77	4.28	0.06
(W x Pred + F) x Time	14	370.75	5.26	0.04
g) Lumbricidae				
W x Time + F + Pred	10	234.84	0	0.33
(W + F) x Time + Pred	11	236.07	1.22	0.18
(W + Pred) x Time + F	11	236.91	2.07	0.12
W + Time	7	237.38	2.53	0.09
(W + F + Pred) x Time	12	238.21	3.37	0.06
h) Julida				
W + F + Time	8	209.71	0	0.16
W + Time	7	209.81	0.1	0.16
W + F+ Pred + Time	9	209.84	0.14	0.15
W + Pred + Time	8	209.93	0.22	0.15
W + F + Pred x Time	10	210.11	0.4	0.13
i) Isopoda				
W + Time	7	173.96	0	0.41
W + F + Time	8	175.78	1.83	0.16
W + Pred + Time	8	175.81	1.86	0.16
W + F+ Pred + Time	9	177.67	3.71	0.06
W x Time + F + Pred	10	178.18	4.22	0.05

W: water, F: fungi, Pred: Predator treatment, and Time: initial or final experimental conditions. For simplification, we only represented the higher terms of the model. Thus, a model with an interaction term implicitly contains the additive components of the interaction. Here we only presented the top 5 models (see the Table S2 in the appendix for the rest of the models).

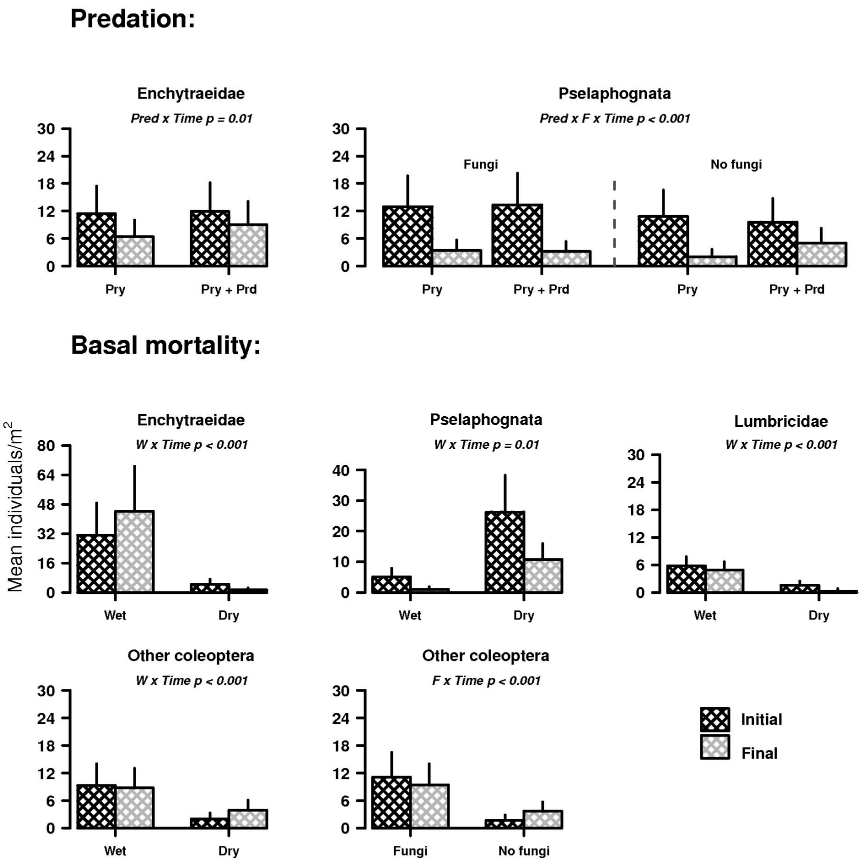


Figure 6: Predator and treatment effects on final prey densities (individuals/m^2 Mean ± 95% C.I.) by taxon. *Pred*: predator treatment, with 'Pry + Prd' (predators present), or 'Pry' (predators removed) levels; *W*: water, with 'Wet' or 'Dry' levels; *F:* fungi with 'Fungi' or 'Non-fungi' levels. Dark left columns: initial abundances; Grey right columns, final abundances. Abundance effects were back transformed into the original scale by the inverse-log link function. We used false discovery rate adjustment for significance levels (corrected significance levels, $\alpha_{PredxTime}$ = $\alpha_{PredxFungixTime}$ = α_{WxTime} = α_{FxTime} = 0.05).

Discussion

Our results revealed that spatial heterogeneity of water and basal productivity can rapidly and independently affect the movement of invertebrates within the leaf litter, and probably the associated predator-prey interactions. This occurred through non-mutually exclusive alterations in 1) the spatial redistribution of predator and prey abundances, 2) the taxonomic composition, and 3) the distribution of body masses in each of the patches. According to available theory (Holling 1959, Cattin et al. 2004, Allesina et al. 2008, Brose 2010, Vucic-Pestic et al. 2010, Schneider et al. 2012) our observed changes in resource-dependent invertebrate distribution can affect predator-prey interactions and food web dynamics. However, we detected only two prey taxa that were clearly affected in numbers from the presence of predators, and the response occurred in the opposite direction of what we initially anticipated: predator-enhanced survival. Below we discuss our findings and the ecological implications of these results.

Water- and productivity-mediated redistribution of fauna

In the first field experiment, the amount of water and yeast affected the abundance of the community of invertebrates as a whole. Higher invertebrate densities were found in patches with higher levels of water and mimicked productivity (added fungi). Since reproduction was highly unlikely to have a relevant effect in this relatively short term experiment, it is reasonably to conclude that changes in abundances were only the consequence of a biased horizontal movement towards the preferred areas of the plot. This is supported by a previous unpublished pilot experiment in the same field site and season in which we found that >80% of the migration events occurred on the horizontal rather than on the vertical direction (G. Jiménez-Navarro; N. Melguizo-Ruiz; O. Verdeny-Vilalta and J. Moya-Laraño *unpublished data*). Also, despite our poor taxonomic resolution, we found higher taxonomic richness in the wettest and fungi-enhanced subplots, which will probably affect food web structure as well as its stability (May 1974, Gross et al. 2009, Riede et al. 2010). For instance, a larger number of weak interactions is generally found in communities with more nodes, and this enhances variability in interaction strengths with a few strong and many weak interactions, which has been shown to increase food web stability (McCann 2000; but see Gross et al. 2009). Furthermore, it has been recently proposed that the detrital channel can enhance species richness and variability in interaction strengths, thus promoting stability (Rooney and McCann 2012). Our results of most taxa actively seeking basal resources as well as one of the main enhancers of basal-resource growth (i.e. water) in the detrital channel, agrees with this view.

Our data also showed that both prey and predators were attracted to the manipulated resources of our experiment. However, the attraction towards patches with higher fungi availability may have different reasons for prey than for predators. Likely because prey have a direct benefit when visiting a food-enhanced patch, a large proportion of prey taxa, most of which are either detritivorous or fungivorous, were found to be more abundant in yeast added patches. Predators also responded to the added yeast patches. However, since the fungi effect disappeared when the number of prey present in the patch was added as a covariate and prey was highly significant and positive in the model, the response of predators to fungi seems to be an indirect effect mediated by the predators responding to the number of prey. Nevertheless, because water availability is correlated with basal resources and therefore with the amount of prey, some soil predators have been found to directly follow water gradients in order to locate prey (e.g. Durou et al. 2001). Since bottom-up effects propagate through terrestrial decomposition food webs (e.g. Chen and Wise 1999), predators in detrital communities could also cue on basal resources (e.g. fungi) to locate prey. In the present study, however, since the fungi effect disappeared after controlling for prey numbers, it is likely that predators were cuing on prey rather than on fungi. As expected, if predators also seek for wet patches to avoid dehydration, the effect of water on predator densities was maintained after correcting for prey densities. We cannot dismiss, however, that predators were using the increase in water availability to prevent dehydration and find prey at the same time. However, despite what it has been found at smaller scales (Chapter 1) it seems that most prey did not avoid visiting these rich patches despite the potential risk of being eaten.

We found significant differences in predator and prey size classes preferentially moving to different resource patches. This drove differential changes in predator-prey body size ratios in different patches and therefore the potential for predator-prey interactions (Wilson 1975, Woodward et al. 2005, Brose et al. 2006). However, after including taxonomic affiliation as a random factor in the model, size effects disappeared (Fig. 5). These findings add to the debate on whether either species centred or trait-centred (e.g. body size) food webs are more appropriate to illustrate food web structure and dynamics (Raffaelli 2007, Gilljam et al. 2011, Rall et al. 2011). In our case, by measuring individuals to the next 0.5mm and transforming length to mass using published equations, body size was completely absorbed by taxonomic variance, suggesting that taxonomic and size functional approaches are exactly the same sources of variation and thus ecologically identical.

Estimated prey mortality: consequences of aggregations around water and basal resources

In our second field experiment, as migration was largely prevented by the fencing of the plots, we assumed that a reduction in abundance was due to mortality. Since the experiment only lasted for two weeks, we expected reproduction to be largely negligible. However, we discuss below unexpected increases in abundances of a few taxa which occurred during the experiment. Since predators and prey tended to aggregate in wet patches in similar relative amounts this could lead to higher predation rates just because predator-prey encounter rates could be higher. Nevertheless, as stated in the Introduction, fast satiation plateaus of predators in these aggregates with relatively high densities could also prevent these predators from inflicting sufficiently strong effects upon prey. Also, anti-predatory behaviour; e.g. prey decreasing activity when predation risk is higher (Schmitz et al. 2004) or modulating their micro-habitat use (Chapter 1), could diminish strong density impacts of predators on prey. Indeed, the analysis showed that the presence of predators influenced prey abundances of only a reduced number of prey taxa (2 out of 9) and in the opposite direction as predicted. Enchytraeidae worms and Pselaphognata millipedes decreased less in numbers in bags in which we left the predators in than in bags from which we removed the predators, suggesting that the presence of predators enhanced survival in both groups. However, in the case of Pselaphognata, the presence of predators enhanced survival only when no fungi were added. Below we discuss some possible mechanisms to explain our findings.

Several studies have found that the existence of indirect effects can often result in unexpected predator effects (Sih et al. 1985, Wootton 2002) such as the ones found here. We hypothesize that complex indirect effects may explain why the small and soft-bodied Enchytraeidae and Pselaphognata groups apparently had lower mortality when we did not remove predators from bags. First, in the case of Pselaphognata, which were enhanced by predators only if fungi were not added, it is possible that the higher mobility of other fungivorous prey in search for food under fungi limitation, exposed these other alternative prey relatively more to predation, contributing to satiate predators and enhancing the relative survival of Pselaphognata. This idea is supported by the fact that in this food web, these millepedes are perhaps one of the most slowly-moving taxa for their body size (OV, NMR and JML personal observations) and that, contrary to other prey, pselaphognata did not respond to fungi additions, likely indicating that other prey (e.g. some Coleoptera, mites, diplurans) do more actively seek for fungi.

Second, we cannot dismiss the possibility for trophic cascades mediated by IGP (trophic-level omnivory) enhancing the survival of the two responding prey taxa. Since we were not 100% successful at removing predators and we tended to miss the smaller predators, and also some of the prey groups included also very small predators (e.g. mesostigmata mites), there is the possibility that the enhanced densities of the two prey groups were the result of indirect cascading effects of the removal of the largest predators. This effect could also be due to a behavioural trophic cascade (Trait-Mediated Indirect Interaction – TMII) by reduced activity (fear) of these smaller IGP-prey in the presence of the largest predators (Brown et al. 1999, Schmitz et al. 2004, Schmitz 2008). Another possible indirect effect could be that if prey also respond decreasing their activity in the presence of predators, an increase in foraging effort and mobility on behalf of the predators could increase predator-predator encounter rates and thus IGP, further weakening the overall effect on prey.

Lastly, the amount of water and yeast also affected the change of densities in some prey taxa. Clitellata (Enchytraeidae and Lumbricidae) individuals had higher mortality in dry plots. In addition, in wet plots Enchytraeids did increase, rather than decrease their abundances relative to the initial conditions. This could be explained because water induced previously inactive individuals to end diapause or because as water means an enhancement of microbial growth, this triggered asexual reproduction by fragmentation (Christensen 1959). The group of Pselaphognata had a higher mortality on both wet and poor-yeast plots, and coleopterans seem to have slightly increased their abundances on dry and poor-yeast plots, likely due to new emergences. Therefore, after moving to seemingly preferred patches, Clitellata and Pselaphognata individuals, which seemed to actively chose wet and dry patches respectively, subsequently experienced decreased mortality, suggesting adaptive micro-habitat selection.

Potential consequences for climate change

As the severity (duration) and frequency of droughts is expected to increase within the distribution range of beech forests, so will increase the duration and frequency of similar invertebrate aggregations as the ones documented here. We mimicked a single drought episode which promoted invertebrate re-locations within the forest, modifying the opportunity for predator-prey interactions and potentially driving indirect ecological effects cascading down through the web. Since, in other temperate deciduous forests, water availability has also been documented to affect litter decomposition through modulating the strength of trophic cascades (Lensing and Wise 2006), an increase in the frequency and duration of these episodes could have strong consequences not only for the structure and dynamics of soil food webs, but also for their associated ecosystem processes.

Conclusions

Our experiments show that recreating a drought episode within the forest floor and artificially manipulating the associated spatial heterogeneity in moisture and basal resources (fungi), strongly affected the aggregative responses of soil invertebrates and potentially affected predator-prey interactions and associated indirect ecological effects. Prey of different size classes responded differently to spatial heterogeneity. However, after including taxonomic effects, taxonomy absorbed all the variance of the responses, indicating that the body size response was completely wired within taxonomy. Experimentally removing predators we found evidence for complex indirect effects which are difficult to be fully understood without further research. However, we can conclude that an increase in the frequency and duration of droughts with climate change, by increasing the frequency and duration of this predator-prey aggregates in the forest floor, will likely have long-term impacts in food web structure, dynamics and its associated ecosystem processes.

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Appendix

Table S1: Extended Table 1

Model	DF	AICc	ΔAICc	ω
(1) *Community abundance*				
W + F + Ini	6	189.16	0.00	0.73
W x F + Ini	7	191.82	2.66	0.19
W + F	5	193.55	4.39	0.08
W x F	6	196.17	7.01	0.02
W + Ini	5	201.34	12.18	<0.001
W	4	207.44	18.28	<0.001
F + Ini	5	222.23	33.07	<0.001
F	4	225.43	36.26	<0.001
Ini	4	225.63	36.47	<0.001
Intercept	3	230.43	41.27	<0.001
(2) *Prey abundance*				
W + F + PredEnd	6	153.86	0	0.57
W + F + PredEnd + PreyIni	7	156.22	2.36	0.17
W + PredEnd	5	157.63	3.77	0.09
F + PredEnd + PreyIni	6	158.11	4.26	0.07
W x F + PreyIni + PredEnd	8	159.11	5.25	0.04
PreyIni + PredEnd	5	159.42	5.56	0.04
W + PreyIni + PredEnd	6	160.24	6.38	0.02
W + F + PreyIni	6	165.38	11.52	<0.001
W + F	5	168.94	15.08	<0.001
W + PreyIni	5	177.37	23.51	<0.001
W	4	182.02	28.16	<0.001
F + PreyIni	5	192.5	38.64	<0.001
F	4	193.55	39.69	<0.001
PreyIni	4	197.35	43.49	<0.001
Intercept	3	199.61	45.75	<0.001
F + PredEnd	5	1542.84	1388.98	<0.001
PredEnd	4	2795.14	2641.28	<0.001
(3) *Predator abundance*				
W + PredIni + PreyEnd	6	151.79	0	0.28
W + F + PredIni + PreyEnd	7	152.1	0.31	0.24
W + F + PreyEnd	6	152.41	0.62	0.21
W + PreyEnd	5	152.55	0.76	0.19
W x F + PredIni + PreyEnd	8	154.93	3.14	0.06
PreyEnd	4	158.58	6.79	0.01
PredIni + PreyEnd	5	159.26	7.47	0.01

F + PreyEnd	5	160.8	9.01	<0.001
F + PredIni + PreyEnd	6	161.55	9.76	<0.001
W + F + PredIni	6	164.57	12.78	<0.001
W + F	5	165.82	14.03	<0.001
W + PredIni	5	171.66	19.87	<0.001
W	4	173.84	22.05	<0.001
F + PredIni	5	196.43	44.64	<0.001
PredIni	4	197.48	45.69	<0.001
F	4	199.47	47.68	<0.001
Intercept	3	201.34	49.55	<0.001
(4) *Mean body mass*				
W x F x PredPrey	10	23576.12	0.00	0.99
PredPrey	4	23586.84	10.72	<0.001
F + PredPrey	5	23587.82	11.71	<0.001
W x F + PredPrey	7	23588.3	12.18	<0.001
W + PredPrey	5	23588.65	12.53	<0.001
W + F + PredPrey	6	23589.61	13.49	<0.001
W + F x PredPrey	7	23591.59	15.47	<0.001
F + W x PredPrey	7	23591.59	15.48	<0.001
W + F	5	25495.31	1919.2	<0.001
F	4	25494.71	1918.6	<0.001
W	4	25493.66	1917.55	<0.001
Intercept	3	25493.1	1916.98	<0.001

Table S2: Extended Table 3

Model	DF	AICc	ΔAICc	ω
a) Enchytraeidae				
(W + Pred) x Time + F	11	530.8	0.00	0.37
(W x Pred + F) x Time	14	530.87	0.07	0.36
(W + F + Pred) x Time	12	532.64	1.84	0.15
(W x F + Pred) x Time	14	535	4.2	0.05
W x Time + F + Pred	10	535.42	4.63	0.04
(F x Pred + W) x Time	14	536.45	5.65	0.02
(W + F) x Time + Pred	11	537.26	6.46	0.01
(W x F x Pred) x Time	20	541.72	10.93	<0.001
W + F + Pred x Time	10	590.58	59.79	<0.001
(F + Pred) x Time + W	11	592.72	61.93	<0.001
W + F+ Pred + Time	9	595.48	64.68	<0.001
F x Time + W + Pred	10	597.58	66.78	<0.001
W + Pred + Time	8	597.61	66.81	<0.001
W + F + Time	8	598.66	67.86	<0.001
W + Time	7	600.81	70.02	<0.001

W + F + Pred	8	606.06	75.26	<0.001
W + Pred	7	608.21	77.42	<0.001
W + F	7	609.27	78.47	<0.001
W	6	611.44	80.65	<0.001
Pred + Time	7	649.33	118.53	<0.001
F + Pred + Time	8	650.44	119.64	<0.001
Time	6	652.64	121.84	<0.001
F + Time	7	653.73	122.93	<0.001
Pred	6	659.96	129.16	<0.001
F + Pred	7	661.04	130.25	<0.001
Intercept	5	663.29	132.5	<0.001
F	6	664.36	133.56	<0.001

b) Pselaphognata

(F x Pred + W) x Time	14	338.01	0.00	0.86
(W + F + Pred) x Time	12	343.44	5.44	0.06
(W + Pred) x Time + F	11	344.69	6.68	0.03
(W x Pred + F) x Time	14	346.1	8.09	0.02
(W + F) x Time + Pred	11	346.78	8.77	0.01
(W x F + Pred) x Time	14	347.51	9.51	0.01
W x Time + F + Pred	10	348.22	10.22	0.01
(F + Pred) x Time + W	11	348.89	10.88	<0.001
(W x F x Pred) x Time	20	349.24	11.24	<0.001
W + F + Pred x Time	10	350.06	12.06	<0.001
W + Time	7	350.82	12.82	<0.001
W + F + Time	8	352.15	14.14	<0.001
F x Time + W + Pred	10	352.34	14.33	<0.001
W + Pred + Time	8	352.37	14.36	<0.001
W + F+ Pred + Time	9	353.71	15.7	<0.001
Time	6	394.76	56.75	<0.001
Pred + Time	7	396.24	58.23	<0.001
F + Time	7	396.86	58.85	<0.001
F + Pred + Time	8	398.36	60.36	<0.001
W	6	483.32	145.31	<0.001
W + F	7	484.62	146.61	<0.001
W + Pred	7	484.84	146.83	<0.001
W + F + Pred	8	486.16	148.15	<0.001
Intercept	5	527.28	189.27	<0.001
Pred	6	528.73	190.73	<0.001
F	6	529.35	191.35	<0.001
F + Pred	7	530.83	192.83	<0.001

c) Collembola

Time	6	367.84	0.00	0.19
W + Time	7	368.4	0.56	0.14

F + Time	7	368.59	0.75	0.13
Pred + Time	7	368.92	1.08	0.11
W + F + Time	8	369.04	1.2	0.1
W + Pred + Time	8	369.5	1.66	0.08
F + Pred + Time	8	369.7	1.86	0.08
W + F+ Pred + Time	9	370.18	2.34	0.06
W x Time + F + Pred	10	371.9	4.06	0.03
W + F + Pred x Time	10	371.96	4.12	0.02
F x Time + W + Pred	10	372.4	4.56	0.02
(W + Pred) x Time + F	11	373.72	5.87	0.01
(W + F) x Time + Pred	11	374.15	6.31	0.01
(F + Pred) x Time + W	11	374.21	6.37	0.01
(W + F + Pred) x Time	12	375.99	8.15	<0.001
(F x Pred + W) x Time	14	376.85	9	<0.001
(W x Pred + F) x Time	14	379.94	12.09	<0.001
(W x F + Pred) x Time	14	380.5	12.66	<0.001
(W x F x Pred) x Time	20	388.43	20.59	<0.001
Intercept	5	441.38	73.54	<0.001
W	6	441.91	74.07	<0.001
F	6	442.1	74.26	<0.001
Pred	6	442.44	74.6	<0.001
W + F	7	442.54	74.69	<0.001
W + Pred	7	442.99	75.15	<0.001
F + Pred	7	443.2	75.35	<0.001
W + F + Pred	8	443.65	75.8	<0.001

d) Acari

W + F + Time	8	353.49	0.00	0.19
W + F+ Pred + Time	9	353.57	0.09	0.18
W x Time + F + Pred	10	353.91	0.43	0.15
W + F	7	355.05	1.57	0.08
W + F + Pred	8	355.12	1.63	0.08
F x Time + W + Pred	10	355.72	2.23	0.06
W + F + Pred x Time	10	355.8	2.31	0.06
(W + F) x Time + Pred	11	356.02	2.54	0.05
(W + Pred) x Time + F	11	356.16	2.68	0.05
(F x Pred + W) x Time	14	356.27	2.78	0.05
(F + Pred) x Time + W	11	357.97	4.48	0.02
(W + F + Pred) x Time	12	358.3	4.81	0.02
(W x F + Pred) x Time	14	359.71	6.22	0.01
(W x Pred + F) x Time	14	361.57	8.08	<0.001
F + Pred + Time	8	362.94	9.45	<0.001
F + Time	7	362.98	9.5	<0.001
(W x F x Pred) x Time	20	364.02	10.53	<0.001
F + Pred	7	364.5	11.02	<0.001
F	6	364.58	11.09	<0.001

W + Time	7	370.22	16.73	<0.001
W + Pred + Time	8	370.23	16.74	<0.001
W + Pred	7	371.8	18.31	<0.001
W	6	371.81	18.33	<0.001
Pred + Time	7	376.27	22.78	<0.001
Time	6	376.36	22.87	<0.001
Pred	6	377.86	24.37	<0.001
Intercept	5	377.97	24.49	<0.001
e) Larvae				
W + F + Time	8	318.26	0.00	0.35
W + F	7	319.66	1.4	0.17
W + F+ Pred + Time	9	319.9	1.64	0.15
W + F + Pred	8	321.28	3.02	0.08
W + F + Pred x Time	10	321.73	3.46	0.06
W x Time + F + Pred	10	321.76	3.5	0.06
F x Time + W + Pred	10	322.11	3.85	0.05
(W + Pred) x Time + F	11	323.61	5.35	0.02
(F + Pred) x Time + W	11	323.95	5.69	0.02
(W + F) x Time + Pred	11	323.97	5.7	0.02
(W + F + Pred) x Time	12	325.84	7.58	0.01
(W x F + Pred) x Time	14	326.14	7.88	0.01
(F x Pred + W) x Time	14	328.71	10.45	<0.001
(W x Pred + F) x Time	14	330.06	11.8	<0.001
(W x F x Pred) x Time	20	332.35	14.09	<0.001
W + Time	7	339.13	20.86	<0.001
W	6	340.55	22.29	<0.001
W + Pred + Time	8	340.74	22.48	<0.001
W + Pred	7	342.15	23.89	<0.001
F + Time	7	350.21	31.95	<0.001
F	6	351.63	33.37	<0.001
F + Pred + Time	8	351.83	33.57	<0.001
F + Pred	7	353.23	34.97	<0.001
Time	6	360.49	42.23	<0.001
Intercept	5	361.94	43.68	<0.001
Pred + Time	7	362.09	43.83	<0.001
Pred	6	363.51	45.25	<0.001
f) Coleoptera				
(W + F) x Time + Pred	11	365.49	0.00	0.55
(W + F + Pred) x Time	12	367.13	1.64	0.24
(F x Pred + W) x Time	14	369.04	3.55	0.09
(W x F + Pred) x Time	14	369.77	4.28	0.06
(W x Pred + F) x Time	14	370.75	5.26	0.04
F x Time + W + Pred	10	374.74	9.25	0.01
(F + Pred) x Time + W	11	376.37	10.88	<0.001

(W x F x Pred) x Time	20	377.29	11.8	<0.001
W x Time + F + Pred	10	379.49	14	<0.001
(W + Pred) x Time + F	11	380.84	15.36	<0.001
W + F + Time	8	387.7	22.21	<0.001
W + F	7	389.69	24.2	<0.001
W + F+ Pred + Time	9	389.89	24.4	<0.001
W + F + Pred x Time	10	391.21	25.72	<0.001
W + F + Pred	8	391.85	26.37	<0.001
F + Time	7	406.1	40.61	<0.001
F	6	408.12	42.63	<0.001
F + Pred + Time	8	408.26	42.77	<0.001
F + Pred	7	410.25	44.76	<0.001
W + Time	7	412.61	47.13	<0.001
W	6	414.63	49.14	<0.001
W + Pred + Time	8	414.78	49.29	<0.001
W + Pred	7	416.77	51.29	<0.001
Time	6	421.62	56.13	<0.001
Intercept	5	423.66	58.17	<0.001
Pred + Time	7	423.76	58.27	<0.001
Pred	6	425.78	60.29	<0.001

g) Lumbricidae

W x Time + F + Pred	10	234.84	0.00	0.33
(W + F) x Time + Pred	11	236.07	1.22	0.18
(W + Pred) x Time + F	11	236.91	2.07	0.12
W + Time	7	237.38	2.53	0.09
(W + F + Pred) x Time	12	238.21	3.37	0.06
W + F + Time	8	239.14	4.3	0.04
(W x F + Pred) x Time	14	239.42	4.57	0.03
W + Pred + Time	8	239.54	4.7	0.03
W	6	240.16	5.32	0.02
(F x Pred + W) x Time	14	240.19	5.34	0.02
W + F+ Pred + Time	9	241.34	6.49	0.01
(W x Pred + F) x Time	14	241.85	7	0.01
W + F	7	241.91	7.06	0.01
W + Pred	7	242.31	7.46	0.01
F x Time + W + Pred	10	242.67	7.82	0.01
W + F + Pred x Time	10	243.4	8.56	<0.001
W + F + Pred	8	244.08	9.23	<0.001
(F + Pred) x Time + W	11	244.8	9.95	<0.001
(W x F x Pred) x Time	20	247.16	12.31	<0.001
Time	6	276.16	41.32	<0.001
F + Time	7	278.17	43.33	<0.001
Pred + Time	7	278.32	43.47	<0.001
Intercept	5	278.97	44.13	<0.001
F + Pred + Time	8	280.35	45.5	<0.001

F	6	280.96	46.11	<0.001
Pred	6	281.1	46.26	<0.001
F + Pred	7	283.11	48.27	<0.001

h) Julida

W + F + Time	8	209.71	0.00	0.16
W + Time	7	209.81	0.1	0.16
W + F+ Pred + Time	9	209.84	0.14	0.15
W + Pred + Time	8	209.93	0.22	0.15
W + F + Pred x Time	10	210.11	0.4	0.13
W x Time + F + Pred	10	211.96	2.25	0.05
F x Time + W + Pred	10	212.06	2.35	0.05
(W + Pred) x Time + F	11	212.25	2.54	0.05
(F + Pred) x Time + W	11	212.35	2.64	0.04
(W + F) x Time + Pred	11	214.19	4.48	0.02
(W + F + Pred) x Time	12	214.51	4.81	0.01
W + F	7	217.32	7.61	<0.001
W + F + Pred	8	217.43	7.73	<0.001
W	6	217.44	7.74	<0.001
(W x F + Pred) x Time	14	217.51	7.8	<0.001
W + Pred	7	217.54	7.83	<0.001
(F x Pred + W) x Time	14	218.69	8.98	<0.001
(W x Pred + F) x Time	14	218.76	9.05	<0.001
Time	6	228.3	18.59	<0.001
Pred + Time	7	228.42	18.71	<0.001
F + Time	7	228.57	18.86	<0.001
F + Pred + Time	8	228.71	19	<0.001
(W x F x Pred) x Time	20	230.23	20.52	<0.001
Intercept	5	235.96	26.25	<0.001
Pred	6	236.06	26.35	<0.001
F	6	236.2	26.5	<0.001
F + Pred	7	236.32	26.61	<0.001

i) Isopoda

W + Time	7	173.96	0.00	0.41
W + F + Time	8	175.78	1.83	0.16
W + Pred + Time	8	175.81	1.86	0.16
W + F+ Pred + Time	9	177.67	3.71	0.06
W x Time + F + Pred	10	178.18	4.22	0.05
F x Time + W + Pred	10	178.4	4.44	0.04
(W + F) x Time + Pred	11	179.28	5.33	0.03
W + F + Pred x Time	10	179.58	5.62	0.02
(W + Pred) x Time + F	11	180.12	6.16	0.02
(F + Pred) x Time + W	11	180.33	6.38	0.02
(W + F + Pred) x Time	12	181.24	7.29	0.01
(W x F + Pred) x Time	14	184.29	10.33	<0.001

(W x Pred + F) x Time	14	185.62	11.67	<0.001
(F x Pred + W) x Time	14	185.8	11.85	<0.001
Time	6	190.78	16.82	<0.001
F + Time	7	192.49	18.53	<0.001
Pred + Time	7	192.61	18.66	<0.001
F + Pred + Time	8	194.35	20.39	<0.001
W	6	194.93	20.97	<0.001
W + F	7	196.74	22.78	<0.001
W + Pred	7	196.76	22.81	<0.001
(W x F x Pred) x Time	20	196.86	22.91	<0.001
W + F + Pred	8	198.59	24.64	<0.001
Intercept	5	211.78	37.82	<0.001
F	6	213.46	39.51	<0.001
Pred	6	213.59	39.63	<0.001
F + Pred	7	215.3	41.34	<0.001

Chapter 3

Foraging paths in complex environments: relative roles of architectural complexity and intrinsic stimulus strength on flies foraging for fruits

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Abstract

The perceptual abilities of animals determine to what extend the external stimuli influence the movement decisions of individuals. Moreover, most animal movements are, to some extent, determined by the architectural complexity of the environment. Yet, to date it is not well known how the strength of a stimulus impacts the geometry of animal movements in architectural complex environments. We mapped the 3D vegetation structures of apple trees and recorded the foraging paths of flies (*Rhagoletis pomonella*) foraging for fruits. We used a random walk on a graph model to obtain theoretical paths that would be expected from individuals moving in trees devoid of fruits. By comparing them with the paths of individuals that are attracted to a single fruit, we show how the architectural complexity of vegetation and the presence of a stimulus combine to influence the movement of the insect. This permitted us to quantify the sphere of attraction of a single stimulus source. The strength of attraction of the foraging resource is distance dependent. Moreover, the architecture of the vegetation determines the movement of the insect and modulates the strength of attraction of the stimulus, which as expected, was lower in denser vegetation. These results are an important step to better direct the movement of pests and improve their management.

Introduction

All animals make use of environmental information to assess the best movement patterns for locating resources, shelters or to avoid areas with predators. Yet, the perceptual range of individuals limits the spatial extent from which environmental information is obtained. Thus, the perceptual range determines the distance from which an external stimulus could impact on the animals' movement decisions (Lima and Zollner 1996, Olden et al. 2004). Examples of animals using their perceptual range for moving in geometrically complex environments include parasitic wasps searching their hosts in grass stems (Randlkofer et al. 2010), spider monkeys searching food within the forest (Boyer et al. 2006), or invertebrates moving towards water gradients in the leaf litter layer (Chapters 1, 2). Since the perceptual range is closely related with the fine-scale movement of animals, it can also influence a wide range of processes such as the redistribution of individuals, the probability to reach a given resource or the ability to respond to the presence of predators (Wiens et al. 1993, Lima and Zollner 1996).

Most of the work done in estimating the perceptual range of animals aimed to study how its range affects the detection of patches and thus the connectivity of populations in heterogeneous landscapes (Schooley and Wiens 2003, Bridgman et al. 2012). This is of importance when predicting how habitat fragmentation may limit the dispersal and the viability of populations (Lima and Zollner 1996, Flaherty et al. 2008). In principle, the species with the lowest detection range should be more susceptible to habitat fragmentation, as individuals would spend more time in the hostile matrix searching a suitable patch (Zollner 2000, Mech and Zollner 2002).

In the last decade, several studies have shown that environmental features can influence the perceptual range of animals. For example, the amount of vegetation or the wind direction may modify the visual and the olfactory detection thresholds in two species of marsupials and a cactus bug respectively (Schooley and Wiens 2003, Prevedello et al. 2011). Due to this differential perception depending on the experienced environment, Olden et al. (2004)

highlighted the importance of using context-dependent perceptual ranges to model animal movements more accurately. Nevertheless, when estimating the perceptual range of animals, ecologists have traditionally simplified the fine-scale architecture of the habitat and thus the bias that an external stimulus can introduce when animals move (Zollner 2000, Mech and Zollner 2002, Schooley and Wiens 2003, Prevedello et al. 2011). In particular, the structural geometry of the vegetation in which the animals live is of special importance because it can largely determine the movements of the animals, and, in turn, the trophic interactions (Andow and Prokrym 1990, With 1994, Casas and Djemai 2002, Gols et al. 2005). However, we are not aware of any study which tested the role of vegetation architecture on both the perceptual range and movement of animals that forage on vegetation. Thus, a complete understanding of how an external stimulus biases the movement of animals in geometrically complex environments is still out of reach.

Understanding how animals make use of environmental information in geometrically complex environments is of special importance for designing effective pest management strategies. Some farmers use different kinds of stimuli in order to disrupt the movement of the pest and make the protected resource hard to locate. Examples include the design of stimulus that mimics a resource (Foster and Harris 1997), trap crops (Hokkanen 1991, Shelton and Badenes-Perez 2006) or push-pull systems (Cook et al. 2007, Hassanali et al. 2008). However, their use is currently underexploited presumably because the method requires a good understanding on the movement behaviour of the pest (Cook et al. 2007).

In this study we investigated the relative roles of the architectural complexity of vegetation and of the strength of a foraging resource on the movement geometry of flies (*Rhagoletis pomonella*). The strength of the stimulus was estimated comparing the observed and the null probabilities of visiting the stimulus position as a function of its distance in the absence of the stimulus. To calculate the null probabilities to visit the stimulus location, we used spatially explicit graphs, a powerful methodology to model the movement of animals in topological structured environments. We further predicted that denser vegetation architectures may hinder the probability of visiting the stimulus location because individuals have more directions to follow and because denser vegetation may hamper stimulus perception. Finally, our study model enabled us to discuss pest management implications of our results to better design management methods involving a deliberate behavioural manipulation of pests.

Materials and Methods

Tree architecture

The experimental setup is detailed in Aluja et al. (1989) and Aluja (1989). Here we only provide relevant information. The three-dimensional structure of two 6-year-old apple trees planted in the field was mapped first in 1984 and again in 1985. To capture the essence of the main architecture, the trees were first divided into 14^3 imaginary 20 x 20 x 20 cm cubes. The vegetation parts that fall in any of the above cubes were then marked with a small tag containing the *[x, y, z]* coordinates of the cube. The cubes laying on the vegetative parts of the tree represent a 3D lattice in which flies moved, hereafter called *landing points*. The trees from 1984 had less landing points (tree A: 393 and B: 409 landing points) than the two older trees of 1985 (tree A: 849 and B: 684 landing points). Therefore, we hereafter refer to *sparse vegetation* architecture to mean the relatively sparse trees of 1984 and to *dense vegetation* architecture to mean the older trees (1985).

Prior to the experimental set-up we first removed all fruits from the trees and manipulated the tree architecture in order to keep it constant over the experimental period of 8 weeks and to facilitate the researcher a clear view of all the cubes in the tree. The manipulations consisted on pulling some branches and twigs and fasten them with string or nylon and on removing 40% of all leaves, without altering the total number of cubes. The direction of the pulled branches was only slightly modified from their original locations, and the removed leaves were usually those clustered around big ones. We believe that this manipulation did not alter the general tree architecture, first because the number of vegetated cubes was kept constant, and second because even if we removed some leaves to facilitate the observations, the cubes still had a large amount of landing surface area. Finally, each tree was enclosed into a 3.5 m diameter x 3.5 tall cylindrical clear screen cage. Cages were 60m apart.

Fly movements

Fly movements were recorded in the trees with and without an attractive stimulus, a wooden red sphere of 7.5 cm diam. The sphere, covered with Tarter Red Dark enamel paint (Sherwin Williams, Cleveland, Ohio, USA), mimicked the spectral reflectance curve of the red apples from the trees (Aluja 1989). We observed 4199 moves from 157 flies in trees without a sphere and 1966 moves from 93 flies in trees containing the sphere. The nature of the treatment was assigned at random. Female flies were released individually at a point situated in the central-lower vegetated part of the tree. The coordinates of the different cubes visited by the fly were recorded during a period of 20 minutes. The observation period was stopped if the predetermined time elapsed or if the fly left the tree and flew to the cage wall. If the fly was lost for more than 1 minute, we discarded those observations. Flies were obtained from infested apples collected from unsprayed orchards. Apples were kept in baskets filled with moist vermiculite. After one month, the developed puparia was collected and stored at 5°C for 6 months. When flies were needed, puparia were placed in a glass container at 24°C with 90%R.H., 16L:8D until adults emerged. Adults were held in 25cm^3 Plexiglas cages and fed with sucrose, enzymatic yeast hydrolysate and water. Finally, to ensure that all the flies were in a similar physiological state regarding fruit foraging, we allowed them to lay an egg on a host fruit before release and after the experiment. Only the individuals that laid an egg after and before the experiment were used for statistical analysis.

The null model: a random walk on graphs

We constructed a 3D random walk model in trees without stimulus (Casas and Aluja 1997), which we call the null model. The null model assumed that individuals do not have any preference of direction, and that they use the same step length distribution than the flies moving in trees without stimuli. This model allowed us to compare the moves in trees devoid of stimulus with the observed moves in trees with an attractive stimulus with high statistical power. Below we first explain how the basic random walk model works and then we develop a general random walk on a graph.

In order to calculate the next fly position from a given point we proceed in two sequential steps. First we randomly chose a step length that defines the radius of a sphere. The step length was randomly sampled from the observed step length distribution of flies moving in trees devoid of fruits. Secondly, we randomly chose one point from the sphere surface (i.e. at a distance equal to the chosen step length) and move the fly to it. The process continues until the total number of steps is reached. Hence a time step is always defined as a change in position. Since there are more available points upwards than downwards on the sphere surface, the fly will most likely move upwards. In that way the architecture of the tree itself governs the paths of the individuals and the likelihood of a landing point to be chosen. Thus, due to the heterogeneity in the amount of vegetation found in the vertical axes of the trees, this size-based sampling leads to an upwards bias, to the areas with more vegetation. This is exacerbated by the fact that flies are released in the lower part of the canopy.

Movement is thereby modelled as a random walk on a graph. Trees can be indeed represented as graph structures with landing points connected by edges. Let $\boldsymbol{M}=\boldsymbol{\pi_{ij}}$ be the matrix of transition probabilities between all the landing points, where the value $\boldsymbol{\pi_{ij}}$ describes the probability of going from landing point $\boldsymbol{i}$ to landing point $\boldsymbol{j}$. From one landing point there must be at least one connection with another one, and all the transition probabilities of one landing point must add to 1.

The transition probabilities are calculated from the distribution of observed step lengths of insects moving in trees without stimulus and from the distance matrix between the landing points. Hence, the probability that a fly will visit point j from point i is first given by the probability that the fly will move that distance. Then, because other points might be also accessible from that distance, each one will have the probability to be visited given by 1/*connectivity*. Connectivity denotes the number of points accessible from that step length. The transition probabilities $\boldsymbol{\pi_{ij}}$ are thus computed as follows:

$$\pi_{i \to j} = k\left[P\left(d_{ij}\right) \cdot c_d^{-1}\right]$$

$$k = 1 \Big/ \sum_{j=1}^{n} P\left(d_{ij}\right) \cdot c_d^{-1}$$

Where, $\boldsymbol{P(d_{ij})}$ is the probability of moving a step length equal to the distance between the point *i* and *j*, $\boldsymbol{c_d}$ the connectivity of the vertex *i* when the step length equals *d* and ***k*** is a normalization constant to make all the probabilities add up to 1.

With this formalism, we can easily obtain the n-step transition probability matrix $\boldsymbol{M^n}$, the exact probabilities of going from the landing point ***i*** to the ***j*** in exactly ***n*** steps, and also extract the probability that the fly visits the stimulus location along ***n*** steps from a given distance (*appendix 1*).

Estimation of the perception radius and intensity

A fly is assumed to be attracted to the stimulus if the observed probability to visit the location of the stimulus in the next step is higher than the expected visiting probability estimated by the null model. The radius of perception *r* is defined as the maximal distance between the fly and the stimulus at which the observed probability to visit the stimulus is higher than the null probabilities. Furthermore, the perception intensity *Δ*, analogous to the stimulus strength, measures the difference between the observed and the null probabilities to visit the stimulus within the perception radius. We define it as the difference between the areas under the two logistic curves that describe the observed and the predicted probabilities to visit the stimulus:

$$\Delta = \int_{R_0}^{R} f_{observed}\left(r\right) \, \mathrm{dr} - \int_{R_0}^{R} f_{predicted}\left(r\right) \, \mathrm{dr}$$

Where *R* is the detection radius, *R₀* the minimum distance before visiting the fruit (i.e. 1 cube) and *r* any other distance from the stimulus that lays between *R* and *R₀* (see the *appendix 2* for details). The perception intensity is a way to measure how strongly animals perceive and move towards a given stimulus, or to how strong that stimulus bias the movement of an individual. Also, by comparing two perception intensity values under different environments (e.g. dense vs. sparse canopies) one can estimate how the environment influences the perception of the stimulus.

To estimate the radius and the intensity of perception we first calculated the probability to visit the stimulus location in one step as a function of the distance to the stimulus. Using a GLM with a logistic link function we fitted logistic equations in which the distance to the stimulus was included as the independent variable, and whether or not the animal visited the stimulus location coded as 1 or 0 respectively. We then compared the fitted observed probability of visiting the location of the source of the stimulus (in situations when there was one) against the fitted probabilities in those situations were the stimulus was absent, i.e. using the fitted expected probability under the null model. If the two logistic curves were significantly different, we then calculated the perception radius from the distance at which the two curves diverged. This distance was calculated as follows: we systematically removed the data from a given distance in the logistic regression, starting from the distance of one cube and going away from the stimulus location. We tested each time whether the two curves, the observed and the expected, were statistically different. The distance at which the two curves were undistinguishable was set as the perception radius.

A fly could detect the source of stimulus from longer distances than reachable by a single step, requiring more than one step to visit it. We therefore repeated the estimation of the perception radius by calculating the probability to visit the stimulus in as many as *n* steps (*n* ranging from 1 to 5). Thus, the definition of a radius of perception does not change, but the quantification of the number of steps required to reach the stimulus is now needed.

We performed a GLM with a logistic link function to analyse the effects on the probability of visiting the stimulus location of *i*) the *stimulus* (present vs. absent), *ii*) the *distance* between the fly and the stimulus position, *iii*) the number of *steps* (from 1 to 5) and *iv*) the vegetation *architecture* (dense vs. sparse vegetation). The statistical model contained all these factors treated as additive, and the significance of the factors was calculated using the likelihood ratio test.

In the results section, the sub-index on the statistic of the likelihood ratio test (i.e. deviance) refers to these four factors.

Following the findings of (Casas and Aluja 1997), we assume an absence of correlation between successive steps and between length and direction. The step length distribution of the null model was calculated from the individuals flying in trees without stimulus.

The observed probability to visit the location of the stimulus in a single step in an tree devoid of fruits was not statistically different from the prediction of the null model following random walks (deviance χ^2= 0.14, d.f.= 1, p= 0.71), which ensures that the model is a good representation of the movements of flies in trees without stimulus.

Finally, we compared if the step lengths of individuals changed with the presence of a stimulus, and also if these steps were different from a simulated distribution of random steps. In this simulated distribution we assumed that flies randomly move between landing points and thus that the step length is given by the architecture of the vegetation itself. We performed a Poisson generalized linear mixed model (GLMM with a logarithmic link function) to test for differences among the three types of step lengths (i.e. fly moving with or without stimulus, or random steps). In the statistical model we included the step length as the dependent variable, the type of step length as fixed factor, and tree as well as the individual identity as random factors. Tukey's honestly significant difference (HSD) tests were used to compare the differences among the three step length types.

All the analysis and the developed code for the random walk model were performed with R ver. 2.15 and the libraries 'lme4' (Bates et al. 2011) and 'multcomp' (Hothorn et al. 2008).

Results

The step lengths of individuals that moved with or without a stimulus were smaller than the ones expected at random (in both cases $p<0.001$, Tukey's HSD), and the presence of a stimulus in the trees did not have an impact on the step length at all (p= 0.86, Tukey's HSD; Figure 1). However the presence of a stimulus significantly biases flies towards it (deviance$_{\text{stimulus}}$ χ^2= 2084.3, d.f.= 1, p<0.001). The shorter the distance from the stimulus, the higher the tendency of a fly to move towards it (deviance$_{\text{distance}}$ χ^2= 4990.1, d.f.= 1, p<0.001). Also, flies were more likely to reach the stimulus if they performed more steps for a given distance (deviance$_{\text{steps}}$ χ^2=422.51, d.f.=1, p<0.001, Figure 2).

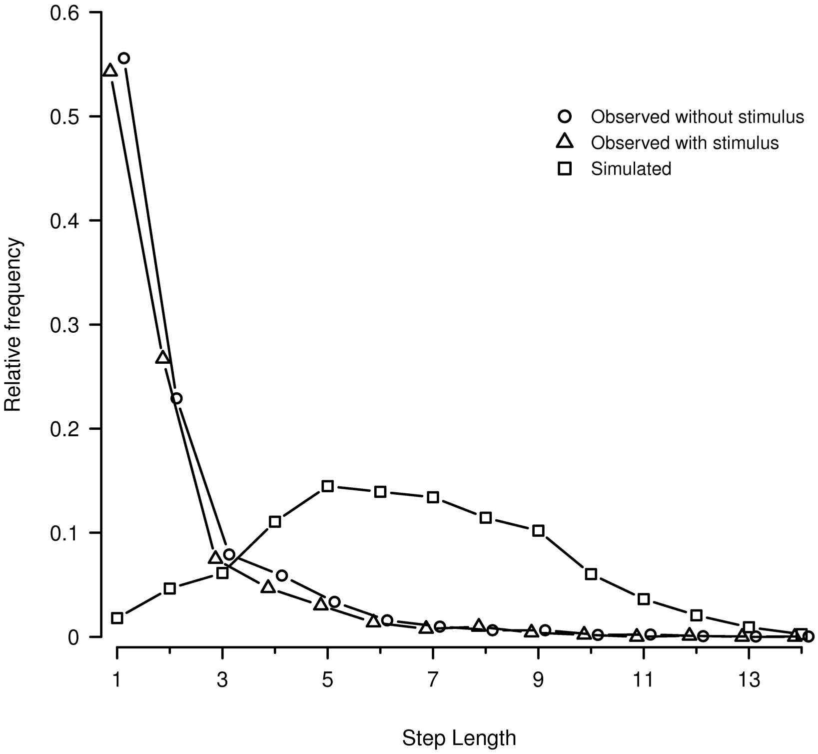

Figure 1: Relative frequencies of step length distribution. Triangles and circles correspond to observed step lengths of flies that move with or without the stimulus respectively. Squares represent the expected step lengths if flies would randomly move between the points in the vegetation.

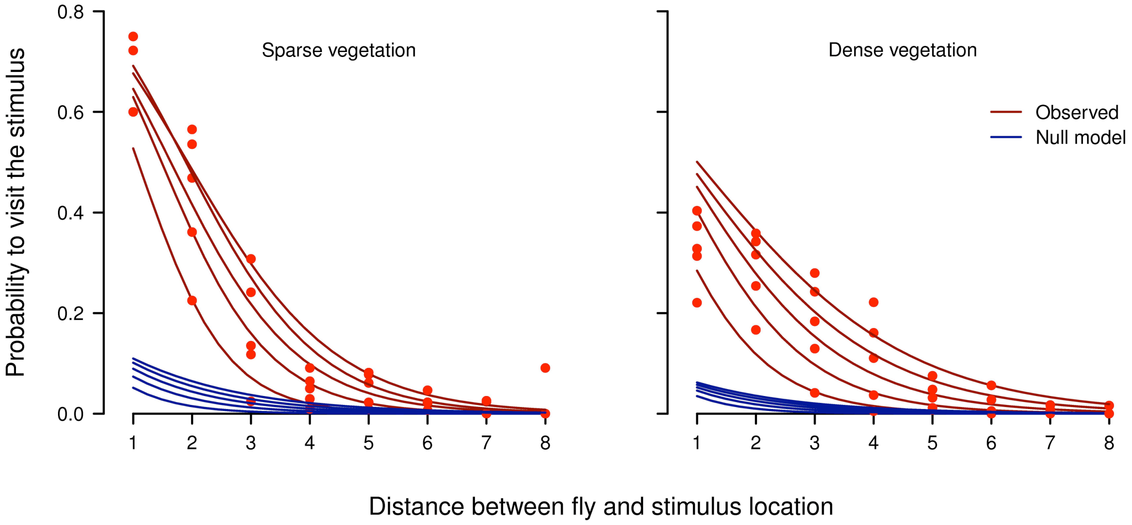

Figure 2: Probabilities to visit the stimulus source in function of its distance in sparse (left) and dense (right) vegetation. The lines are logistic fits for the visiting probabilities obtained from observed and null movement paths. The different curves represent the probabilities to visit the stimulus in the next n steps, increasing from 1 to 5 from the lower to the upper curve.

The density of the foliage affected the probability that a fly visited the stimulus position both directly and indirectly through changes in perception. First, the probability to visit the location of the stimulus source was lower in trees with higher foliage density than in trees with a sparse density of foliage ($\text{deviance}_{\text{architecture}}\ \chi^2 = 166.7$, d.f.= 1, $p<0.001$). Second, the detection radius had a mean of 80cm (4 cubes) in the high foliage density trees and 100cm (5 cubes) in the sparse foliage trees. The perception intensity was also significantly different between the tree foliage densities (deviance $\chi^2 = 0.22$, d.f.=1, $p<0.001$; see Figures 2 and 3): the flies that moved in dense trees had a lower intensity of perception (mean ± S.E.: 0.62±0.14) than the ones that moved in sparse trees (0.92±0.13). Moreover the perception intensity tended to increase with the increasing number of steps (deviance $\chi^2 = 0.73$, d.f.=1, $p<0.001$; Figure 3). A complete 3D reconstruction of the sphere of attraction in both sparse and dense vegetation architectures was constructed (Figure 4).

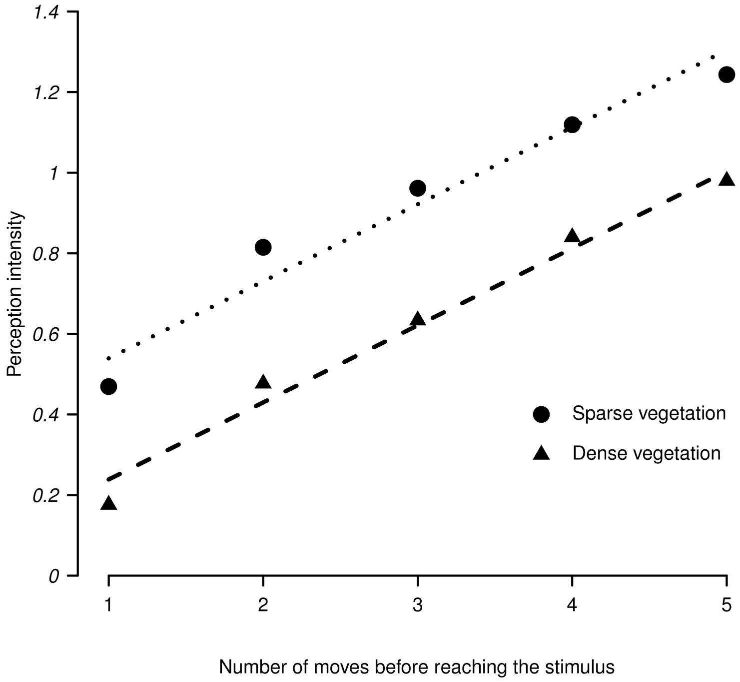

Figure 3: Intensity of the stimulus perception (see text) in dense and sparse vegetation. The dashed lines are least-squares fits.

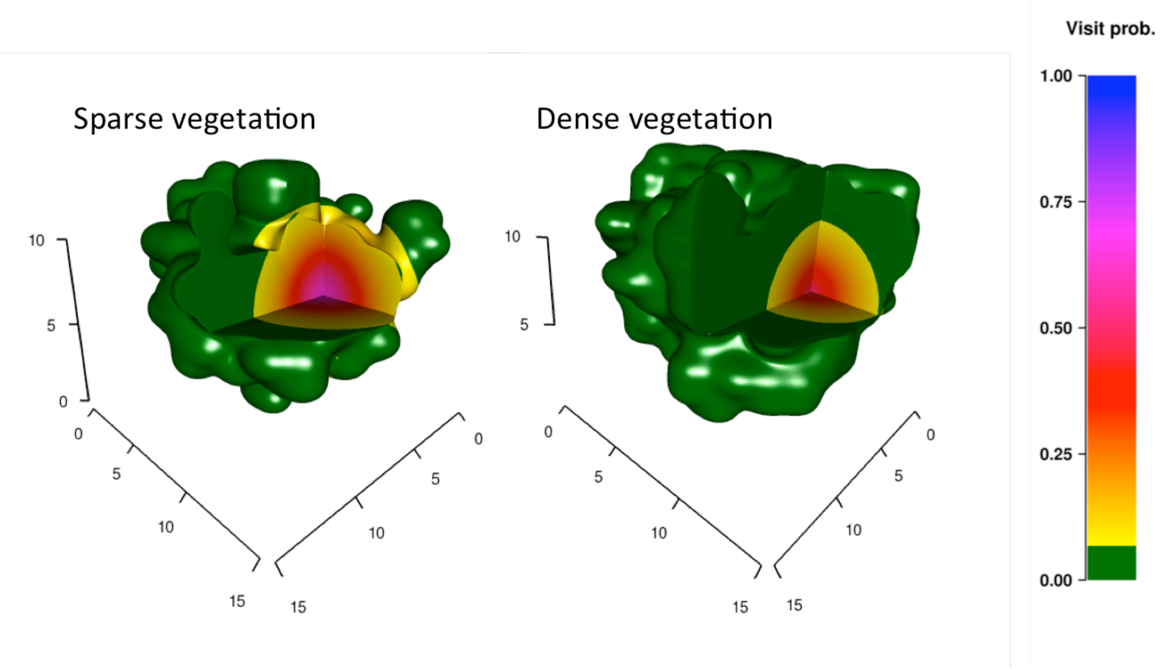

Figure 4: Probabilities to visit the stimulus position in the next 5 steps in the sparse and dense tree "A". The visiting probabilities are given by the colour bar on the right. The yellow perimeter of the sphere represents the limit of the sphere of attraction. The axes are the coordinates of the mesh of cubes (1 cube =10cm).

Discussion

Overall, our study shows the combined effects of architectural complexity and strength of attraction of a stimulus visually mimicking a feeding resource on the foraging paths of the insect *R. pomonella*. Below we discuss the importance of our findings and the ecological and pest management implications.

Vegetation architecture determines step length and overall movement

Our results showed that the individual step length distribution was the same in the presence or in the absence of the stimulus. In both cases, the observed distributions had abundant short steps and much less frequent long step lengths. This observed distribution was far from being similar to the one extracted from random movement between vegetation points. This suggests that flies did move according to a specific pattern, albeit modulated by the vegetation architecture. The most effective movement strategies to quickly locate randomly distributed resources generally use a step length distribution similar to the one observed here (Bartumeus et al. 2005), but some animals can also adjust their moves according to the density of resources (Humphries et al. 2010; Chapters 1 and 2). If flies do not change their step length distribution in the presence of a stimulus mimicking a resource, it is possible that either they do not change their movement patterns when exposed to a stimulus, or that the presence of a single stimulus is not sufficient to alter the individual searching behaviour, or that the insects use other signals, such as the colour of vegetation, to assess the amount of resources (Prokopy et al. 1998).

Moreover, the geometry of the environment strongly determined the overall insect movements and their encounter rates with the mimicking stimuli. Our null model showed that vegetation density diminished the encounter probability of the insect with different parts of the vegetation (e.g. stimulus coordinates). This is in agreement with empirical work that found that, in general, the encounter rate between individuals or between individuals and different parts of the environment decreases as the architectural complexity of the environment increases (i.e. higher vegetation connectivity) (Price et al. 1980, Andow and Prokrym 1990, Grevstad and Klepetka 1992, Casas and Djemai 2002, Randlkofer et al. 2010).

Towards a quantitative definition of a sphere of attraction

With the approach used here, we defined the sphere of attraction of a stimulus and quantified its strength on biasing the movements of individuals in complex vegetation architectures (Figure 4). The impact that any external stimulus has upon an individual depends on the animal perceptual range, which is in turn affected by the strength of the stimulus (Olden et al. 2004). Thus, the strength of attraction and the perceptual range of animals are two sides of the same coin. A change in behavior only occurred once an individual moved within the sphere of attraction. Indeed, we found a distance threshold from the stimulus, analogous to the perceptual range of animals. The probability to visit the stimulus location in the next *n* steps was much higher than the null probability to visit the same position once flies had passed this threshold distance (80cm and 100cm in dense and sparse canopies respectively). As the distance from the stimulus source decreased, its attraction increased (Green et al. 1994, Zollner and Lima 1997, Rosenthal 2007). The insect also had a higher probability to visit the stimulus location as the number of steps increased, probably indicating that individuals detected the stimulus from far away but needed multiple steps to reach it. Other approaches have been used to quantify the perceptual range of animals (Goodwin et al. 1999, Zollner and Lima 1999b). Ours is the first to quantify the distance-dependent strength of attraction, and is also the first to use a null model to quantify the probability to visit a stimulus location in its absence. We are thus in a unique position to disentangle the importance of the geometry of canopies from the intrinsic attraction power of a given stimulus source.

We also found evidence that the density of foliage negatively affected the strength of attraction of the stimulus. This could be the result of either a direct effect of vegetation or an indirect effect of a reduced perception radius. In both cases the physical properties of the environment could have changed the rates of attenuation and degradation of signals and influence stimulus detection (Endler 1992, 1993, Rosenthal 2007). Besides, it has been found that the amount of illumination can strongly influence the perceptual range of animals that use vision to obtain external information (Zollner and Lima 1999a).

Implications for pest management

Management methods involving a deliberate behavioural manipulation of pests to protect a valued resource offer an alternative to the extended use of pesticides. One method consists in using attracting traps to make the valuable resource more difficult to locate, or to reduce the pest number by attracting it to a given point from which the individuals will be easily removed (Foster and Harris 1997). For this pest management strategy to be effective, a complete quantitative analysis of the insect movement should be considered. Although we only report here the effects of a visual stimulus on the insect movement behaviour, other stimuli, such as semiochemical cues could be easily incorporated in this proposed framework.

The number of traps and their distribution are of great importance for an efficient management. By identifying the attraction radius of a stimulus as well as its influence on biasing the insect moves, we estimated in our study the optimal trap distribution within the trees in order to maximize their impact on pests. Since all individuals were released from the lower part of the canopy, we concluded that the best stimuli locations are those situated in the outer and lower part of the canopies. At large distances however, when insects are moving between canopies, the most visible parts should be those situated in the middle-upper rather than in the lower parts of the tree (e.g. Reissig 1975). Those fruits situated in the upper part of the canopy may also receive a larger amount of natural illumination facilitating visual detection (Prokopy and Owens 1983). In fact, red sphere traps situated in the upper parts of the canopies caught more flies (*R. pomonella*) than those situated in their lower parts (Reissig 1975, Drummond et al. 1984).

The power of renormalization

In a previous model (Casas and Aluja 1997), the authors implemented an explicit upwards bias to the movement of flies, i.e. a fly at a given height level had a given probability to move upwards. While the above model provided a very good fit in three out of four trees, it failed in a tree which was architecturally too different: not only was the tree smaller than the others, but it also had a different distribution of foliage. In the present study, we implemented an upwards movement rule which is analogous to a renormalization procedure (Scheaffe 1972). Flies can now choose the next location at random within a set of landing points determined by the outer surface of a sphere, the radius of which is set by the step length. Because of the tree geometry and the fact that flies start foraging from the bottom, this implies that the number of landing points is, in most cases, larger above than below (or at least than as the same height as) the fly. This proportional sampling produces a bias upwards. By this improvement, our procedure enables all trees of all shapes, irrespective of their foliage distribution or height, to be considered. This also makes much more sense, as it requires no information about the exact height level at which the flies find themselves in a tree, nor about the height of the tree in which they forage. In conclusion, our approach enables one to extract the intrinsic, distance-dependent strength of attraction of a source of stimuli as well as its modulation by the environment, being either trough its architecture or else.

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Appendix 1 - Visiting probabilities

Here we provide a sequence of simple examples to show how to calculate the probabilities of visiting specific coordinates (e.g. stimulus source) using a graph with three different coordinates.

Exactly visit a given coordinate at the *n* step

Given the matrix of transition probabilities ***M*** between all the coordinates in the graph, the n-step transition probability matrix ***Mⁿ*** give us the exact probabilities of going from the coordinate ***i*** to the ***j*** in exactly ***n*** steps.

$$M^2 = \begin{pmatrix} \pi_{11} & \pi_{12} & \pi_{13} \\ \pi_{21} & \pi_{22} & \pi_{23} \\ \pi_{31} & \pi_{32} & \pi_{33} \end{pmatrix} \times \begin{pmatrix} \pi_{11} & \pi_{12} & \pi_{13} \\ \pi_{21} & \pi_{22} & \pi_{23} \\ \pi_{31} & \pi_{32} & \pi_{33} \end{pmatrix} =$$

$$= \begin{pmatrix} \pi_{11}\pi_{11} + \pi_{12}\pi_{21} + \pi_{13}\pi_{31} & \pi_{11}\pi_{12} + \pi_{12}\pi_{22} + \pi_{13}\pi_{32} & \pi_{11}\pi_{13} + \pi_{12}\pi_{23} + \pi_{13}\pi_{33} \\ \pi_{21}\pi_{11} + \pi_{22}\pi_{21} + \pi_{23}\pi_{31} & \pi_{21}\pi_{12} + \pi_{22}\pi_{22} + \pi_{23}\pi_{32} & \pi_{21}\pi_{13} + \pi_{22}\pi_{23} + \pi_{23}\pi_{33} \\ \pi_{31}\pi_{11} + \pi_{32}\pi_{21} + \pi_{33}\pi_{31} & \pi_{31}\pi_{12} + \pi_{32}\pi_{22} + \pi_{33}\pi_{32} & \pi_{31}\pi_{13} + \pi_{32}\pi_{23} + \pi_{33}\pi_{33} \end{pmatrix}$$

The probability of exactly visit the coordinate j = 2 from the coordinate i = 1 in the second step (n=2) is the sum of all the possible combinations of moving from coordinate 1 to 2:

$$\pi^2_{1\to 2} = \pi_{11}\pi_{12} + \pi_{12}\pi_{22} + \pi_{13}\pi_{32}$$

Exactly visit a given coordinate at the *n* step, without having visited a specific coordinate

If we set the probability to visit the coordinate *S* to be =0, ***Mⁿ*** give us the exact probabilities to go from the coordinate ***i*** to the coordinate ***j*** in exactly *n* steps without visiting *S*. We say that *S* is blocked when the probability to visit the coordinate *S* is =0. In the following example we blocked the visit of the coordinate j = 3.

$$M = \begin{pmatrix} \pi_{11} & \pi_{12} & 0 \\ \pi_{21} & \pi_{22} & 0 \\ \pi_{31} & \pi_{32} & 0 \end{pmatrix}$$

Here, the probability of exactly visit the coordinate j = 2 from the coordinate i = 1 in the step n=2 without visiting the coordinate j = 3 is:

$$\pi_{1\to 2}^{2} = \pi_{11}\pi_{12} + \pi_{12}\pi_{22}$$

Visiting a given coordinate at least once during n steps of movement between two coordinates

The blocked transition probabilities (***M^n0^***) are those transition probabilities in which one coordinate (*S*) is blocked. The differences between the unblocked $\boldsymbol{M^n}$ and blocked $\boldsymbol{M^{n0}}$ transition probabilities give us the probabilities of at least have visited once the blocked coordinates when we moved from the vertex *i* to the vertex *j* in n steps.

Following our example, the probability of having visited the blocked coordinate j = 3 in the second step (n=2) when we moved from the coordinate *i*=1 to *j*=2 in n=2 steps.

$$M_S^n = M^n - M_0^n$$

$$\pi_{1\to 2}^{2} = \pi_{13}\pi_{32}$$

Visiting a given coordinate at least once during n steps of movement

To obtain the probability of visiting the blocked coordinate *S* from the coordinate *i*, after n steps of movement, we need to add all the probabilities of visiting *S* when *i* is moving to all the other coordinates.

$$V = \Pr\left(\text{i visited S}\right) = \sum_{j=1}^{k} \left(M_S^n\right)_{i,j}$$

Averaging the probabilities (*V*) of the coordinates that are at the same distance from the coordinate *S* we obtain the probability to visit *S* (e.g. stimulus source) in *n* steps from a given distance.

Appendix 2 - Perception intensity (Δ) functions

The perception intensity (*Δ*) is the difference of the area defined by two logistic functions *f(r)* that fit the observed and the null probabilities to visit the stimulus as a function of the distance to its coordinates *r*.

$$\Delta = \int_{R_0}^{R} f_{observed}(r)\ \mathrm{dr} - \int_{R_0}^{R} f_{null}(r)\ \mathrm{dr}$$

The paths of individuals that are attracted to the stimulus and the null paths obtained with the random walk model are used to obtain the observed $f_{observed}(r)$, and the null probabilities $f_{null}\ (r)$ of visiting the stimulus source respectively. The parameter *R* is the detection radius, R_0 the minimum radius distance before visiting the fruit (i.e. 1 cube) and *r* any other distance from the stimulus (between *R* and R_0). Therefore, we only integrate the area defined by the sphere of attraction. Both components of the perception intensity (*Δ*) are definite integrals of the logistic curve $f_{observed}(r)$ and $f_{null}\ (r)$, and can be calculated from the indefinite integral of the logistic function:

$$\int_{R_0}^{R} f(r)\ \mathrm{dr} = F(R) - F(R_0)$$

$$F = \int f(r)\ \mathrm{dr}$$

where the indefinite integral *F* is obtained from:

$$f(r) = \frac{1}{1 + e^{-(a+br)}}$$

$$\int f(r)\ \mathrm{dr} = \frac{\log\left(1 + e^{a+br}\right)}{b}$$

Chapter 4

Food web allometric constraints, foraging theory and foraging mode explain the evolution of egg size

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Abstract

The adaptive evolution of propagule size is linked to the variability in offspring fitness across environments of different quality. However, defining environmental quality may require accurate estimates of the selective agents acting on offspring size, which is often not feasible in comparative studies. Here, we propose that environmental quality can be described using available theory. We link food web allometric constraints (body size-abundance relationships) and foraging theory (predator-prey size ratio-dependent attack rates) to predict the evolution of egg size in predators of contrasting life histories (sit-and-wait *vs*. actively-hunting modes). Because predator abundance scales negatively with body mass and predation depends on predator-prey mass ratios, slightly increasing offspring egg mass simultaneously allows offspring to feed on more prey and escape from more predators. However, differences in mobility between sit-and-wait and actively-hunting offspring should alter their encounter rates with predators and prey. We show that after considering the fundamental egg size/number trade-off, females of actively hunting predators should invest in larger (and thus fewer) offspring relative to sit-and-wait predators. A phylogenetically-controlled analysis on 268 spider species confirms this prediction, supporting the view that the structure of ecological networks may serve to predict relevant selective pressures acting on key life history traits.

Key words: *Smith-Fretwell model, mobility, foraging theory, foraging mode, size spectra, egg size, spiders.*

Introduction

Since larger propagules may have enhanced fitness, propagule size is one of the most studied reproductive traits to date (Lack 1947, Smith and Fretwell 1974, Bernardo 1996, Fox and Czesak 2000). Investing in larger offspring may be beneficial to both parents and offspring (Smith and Fretwell 1974, Parker and Begon 1986). However, since the relationship between offspring size and fitness can change across environments, and there is a fundamental trade-off between offspring size and number given limiting resources allocated to reproduction, different environments with different selective pressures will determine different optima for offspring sizes (Parker and Begon 1986, Bernardo 1996, Fox and Czesak 2000, Roff 2002, Segers and Taborsky 2011), which could explain, for instance, why demersal fish (Duarte and Alcaraz 1989) and invertebrates with aplanktonic larvae (Marshall et al. 2012) lay larger eggs. In general, larger eggs should evolve in harsh (or low quality) environments. On the other hand, stochastic environments, i.e., those in which the mortality of hatching offspring is largely unpredictable, such as the pelagic environment, select for females that lay as many eggs and as small as possible (Duarte and Alcaraz 1989, Marshall et al. 2012, see also Morrongiello et al. 2012), and in species with indeterminate growth, this effect is stronger for species with larger asymptotic size (Christiansen and Fenchel 1979, Andersen et al. 2008).

Understanding the evolution of traits and the relationship between environment, trait and fitness is usually most feasible in micro-evolutionary studies, in which natural selection can be studied across different environments (Endler 1986). However, predicting the performance across environments is not always feasible, for instance, when testing hypotheses concerning many taxa and using the evolutionary comparative method (Felsenstein 1985, Harvey and Pagel 1991). In these cases, usually, we lack the accurate data on the selective pressures that we hypothesize that have originated the observed patterns. To support hypotheses tested using the comparative method, different modelling approaches have been used to build on hypotheses of adaptive evolution of traits and have been successful at explaining why different trait values (and under which environments) have a fitness advantage (Moya-Laraño et al. 2002, Rezende et al. 2007, Moya-Laraño et al. 2008, Ingram et al. 2012). When the focus is studying the evolution of egg size, defining the environmental quality experienced during evolutionary time by the many taxa involved in the study may be a major challenge. Simple models using the available theory could help in this task.

Food webs in particular (Thygesen et al. 2005, Andersen et al. 2008, Olesen et al. 2010, Moya-Laraño et al. 2012) and ecological networks in general (Fontaine et al. 2011, Guimaraes et al. 2011, Hagen et al. 2012), can be considered as environments in which the existing links can act as selective pressures on particular nodes (populations). Furthermore, distant nodes can act as indirect selective pressures (indirect effects) with important evolutionary consequences (Guimaraes et al. 2011, Walsh 2013). Modelling approaches focusing on the size-abundance structure (size spectra) of food webs have been recently used to explain the evolution of life history traits, including the evolution of egg size in animals with indeterminate growth (Andersen et al. 2008). Here, we use these size spectra or allometric size-abundant constraints in food webs, together with recent developments of foraging theory predicting predator-prey attack rates (Persson et al. 1998, Brose et al. 2008) to depict the distinctive environments experienced by offspring of predators that use either a sit-and-wait or an active hunting strategy (Schoener 1971). Active predators encounter food at a higher rate than sit-and-wait predators, and consequently grow faster regardless of their higher metabolic rates (Huey and Pianka 1981, Werner and Anholt 1993 and references therein). However, higher movement is also usually associated with an increase in the rate at which predators are encountered (Huey and Pianka 1981, Werner and Anholt 1993), and encounters among active predators within the same guild can lead to cannibalism and Intraguild Predation (IGP), in which, as in most predator-prey interactions (Wilson 1975, Brose et al. 2006), body size asymmetry largely determines who eats whom (Polis et al. 1989, Rypstra and Samu 2005, Wise 2006). The balance between higher predation success and higher predation risk in actively hunting animals can be determined by the relative abundance of each size class within the food web, which has been shown to be ruled by allometric constraints based on first energetic principles (Brown and Gillooly 2003, Reuman et al. 2009, Mulder et al. 2011), determining a negative relationship between abundance and body mass. Thus, slightly increasing predator offspring size, will allow offspring to avoid increasingly more predators (a size refuge, Wilson 1975, Paine 1976) and having increasingly more chances to be an IGP-predator instead of an IGP-prey. When mobility is higher (such as it is the case in actively hunting animals relative to sit-and-wait animals), the balance towards the advantage of encountering relatively more prey than predators, should favour the evolution of offspring size. However, since offspring fitness and female fitness face a conflict mediated by the offspring-size/offspring-number trade-off faced by females (Smith and Fretwell 1974), predicting whether larger eggs should evolve more likely in actively-hunting relatively to sit-and-wait predators is not straightforward.

We develop a graphical model starting up with the classic Smith-Fretwell (1974) model relating offspring size to female fitness and then assumed that the offspring of species that have evolutionarily gained either of the two contrasting foraging strategies (sit-and-wait vs. active hunting) experience very distinctive environments even within the same food web environment, just from the fact that the rate of encounters with prey and predators differs dramatically for individuals following either strategy. In order to test the predictions of the model, we then used the evolutionary comparative method and a sample of 268 spiders (Mascord 1970, Kaston 1981) to compare egg size and egg number between sit-and-wait and actively hunting spiders.

Materials and methods

The model

In order to predict the evolution of optimal egg size in animals of contrasting life histories (hunting modes), namely sit-and-wait *vs.* active - hunting generalist predators, we built a model that links the model of Smith and Fretwell (1974), originally envisioned to predict optimal propagule size, to recent developments in food web theory: a) body size-abundance allometric constraints (e.g. Reuman et al. 2009) and b) recent advances in foraging theory to describe patterns of predator-prey interactions (Brose et al. 2008, Schneider et al. 2012b). Since differences in mobility between the above two contrasting life histories involve differences in encounter rates with prey and predators, relative to active hunters, sit-and-wait predators experience environments which differ in the potential for interacting with prey and other predators (De Mas et al. 2009, Moya-Laraño et al. *in press*). The former strategy will increase the probability of finding prey (a benefit) while simultaneously increasing the probability of finding predators (a cost). We argue that the balance between these two selective pressures will shape the adaptive evolution of egg size, and that such a balance will be determined by i) the structure of the food web -e.g. allometric constraints, which set the abundance of the different body size classes of predators and prey in the network (e.g. Thygesen et al. 2005, Andersen et al. 2008) - and ii) by the shape of the relationship between attack rates and predator-prey ratios, from which maximal attack rates can be derived (Brose et al. 2008). We further incorporate in the model the fact that body size ratios may be more important for hunting prey in active hunting spiders relative to sit-and-wait spiders, for which we reanalyzed published data (Nentwig and Wissel 1986) using the evolutionary comparative method (Harvey and Pagel 1991).

The Smith-Fretwell model

The graphical model of Smith and Fretwell (1974) predicts the evolution of optimal propagule size by assuming that offspring fitness and female fitness are linked by the fundamental trade-off between propagule size and propagule number as faced by females. Even though offspring fitness could potentially continue to increase with size, the offspring of females reaches an optimum at intermediate offspring sizes where the compromise between number and quality allows maximum fitness for her. However, since the relationship between body size and fitness changes in different environments, different optimal propagule sizes should evolve in each environment (e.g. Parker and Begon 1986, Fox and Czesak 2000, Roff 2002). Here we extend this graphical modelling approach by assuming that individuals embedded in a food web will experience a very different environment depending on their own mobility, which will depend on their hunting strategy, and explore how this will determine the evolution of propagule (egg) size.

Incorporating food web allometric constraints and foraging theory

The spectrum of body sizes in populations (Damuth 1981) and in food webs (Brown and Gillooly 2003, Reuman et al. 2009, Petchey and Belgrano 2010) can be predicted by metabolic constraints, assuming that for a given portion of habitat all populations within the same trophic level absorb the same quantity of energy and that the amount of energy available for populations diminishes as trophic level increases (the Energetic Equivalence Hypothesis –EEH– with Trophic Transfer Correction –TTC– Brown and Gillooly 2003). This renders larger species (or stages) in a food web less abundant and smaller species (or stages) more abundant, following the relationship: $N=aM^{-b}$, where $b<3/4$ (where N is number of individuals and M is body mass). Since predator-prey ratios determine who eats whom, with higher ratios usually increasing the probability of predation (Brose et al. 2006), this confers to food webs a highly nested character, in which the least abundant and larger species (stages) include more of the lower trophic levels in their diets (Wilson 1975, Woodward et al. 2005). In order to test if this allometric negative relationship was found in a typical spider-centred food web, we used conventional methodology (Blackburn et al. 1992) and analyzed the data on predatory macro-fauna from the forest floor food web of Berea in Central Kentucky (US), in which >80% of the macrofauna generalist predators are spiders belonging to more than 50 genera (Moya-Laraño and Wise 2007). Specimens were measured to the nearest 0.5 mm and we then used conversion equations (Hódar 1996, 1998) to transform length to dry weight. Using a total of 1587 individuals, we found the following relationship: $N = 57.5M^{-0.49}$ (intercept, $P < 0.0001$; slope, $P=0.002$), a slope coefficient (-0.49, CIs=[-0.74,-0.26]) which agrees with the EEH with TTC, is very close to estimates for other soils (Reuman et al. 2009) and lays within the range found in forest soils (Mulder et al. 2011).

In addition, a model based on foraging theory predicts that predation rate should be maximum at intermediate predator-prey ratios (Persson et al. 1998). The model, which is strongly supported by recent findings including spiders

(Brose et al. 2008), predicts that the predation (or attack) rate (P_{ij}) of a predator of size class *i* on a prey of size class *j* is:

$$P_{ij} = P_{\max}\left[\frac{R_{ij}}{R_{\max}}\exp\left(1-\frac{R_{ij}}{R_{\max}}\right)\right]^{\gamma} \qquad (1)$$

P_{max} is the maximum predation rate, R_{ij} is the body size ratio of a predator of size class *i* and prey of size class *j*, R_{max} is the ratio at which maximum predation (P_{max}) occurs. The parameter γ is a scaling parameter which tunes how much predation rate increases or decreases with R_{ij} below or above R_{max} respectively. Below R_{max} what is most relevant about γ is that it measures how much attack rate increases with a unit increase in body mass ratios (Persson et al. 1998). In order to obtain data on γ for sit-and-wait and actively hunting spiders we reanalyzed data for 4 sit-and-wait and 4 actively-hunting spider species (Nentwig and Wissel 1986). Sit-and-wait spiders had lower γ estimates (estimate=0.35) than actively-hunting spiders (estimate = 0.54; $P<0.001$ Appendix 1), indicating that below R_{max}, a small increase in predator-prey ratios means higher predation success for AH than for SW spiders. We used the same data base in combination with the data in Brose et al. (2008) to obtain R_{max} and P_{max} for SW and AH spiders (Appendix 1).

Considering both allometric constraints and foraging theory we can predict that the absolute predation risk (PR_j) for a propagule (spiderling) of size class *j* embedded in a food web as the one described above will be:

$$PR_j = \sum_{i=1}^{k} N_i P_{ij} d \qquad (2)$$

$$d = \begin{cases} 1, & \text{if } R_{ij} \le R_{upp} \;\&\; R_{ij} \ge R_{low} \\ 0, & \text{otherwise} \end{cases}$$

where N_i is the number of predators of class size *i*, as estimated from equation $N = 57.5M^{-0.49}$. The minimum class size is the smallest spiderling (i.e. egg size), and the maximum class size is the largest predator of the forest floor food web of Berea. R_{low} and R_{upp} are respectively the minimum and maximum ratios at which predator *i* attacks prey, which constrains predation to the minimum and maximum class sizes considered in the study.

Adding the fact that mobility (ε) of the target propagule scales with body size as M^{ε} and considering relative predation risk (RPR_j) as the relative risk of predation of a propagule of size class *j* relative to the maximum predation risk suffered by any single size class (*m*), we get

$$RPR_j = \alpha M_j^{\varepsilon} \frac{PR_j}{\max\limits_{m \in [R_{low}, R_{upp}]} \left(PR_m\right)} \qquad (3)$$

where *ε* takes values between 0.17 and 0.25 (Peters 1983, Schmidt-Nielsen 1984). As we were interested in knowing how mobility (foraging mode) differently affected the evolution of propagule size, we took values of 0.25 for actively hunting animals and then tested decreasing values for sit-and-wait animals (0.25, 0.22, 0.19, 0.16). The parameter α is a constant (0.28) included to convert body mass into a proportion dimensionless mobility index which takes 1 for the maximum propagule size (that of maximum mobility) in the community, setting the upper level for encounters with predators due to the propagule own mobility.

Similarly, the predation success of different propagule sizes should vary according to the same parameters. The absolute predation success (PS_j) for a propagule of size class *j* would be:

$$PS_i = \sum_{j=1}^{l} N_j P_{ij} d$$
$$d = \begin{cases} 1, & \text{if } R_{ij} \le R_{upp} \;\&\; R_{ij} \ge R_{low} \\ 0, & \text{otherwise} \end{cases} \qquad (4)$$

Here P_{ij} and R_{ij}, refer now to the predation rate of propagule of size class *i* (IGP-predator) on propagules of size class *j* acting as IPG-prey, PS_i is the absolute predation success for a propagule of size class *i* and N_j is the number of propagules of class size *j*, calculated again from equation $N = 57.5M^{-0.49}$. The relative predation success (RPS_i) for propagule of size class *i* relative to the maximum predation success for propagule of size *n*, will be thus

$$RPS_i = \alpha M_i^{\varepsilon} \frac{PS_i}{\max\limits_{n \in [R_{low}, R_{upp}]} \left(PS_n\right)} \qquad (5)$$

However, rather than predation rate, what should benefit a predator propagule is how much biomass is accessible for predation. Considering the body size of the available propagules one can calculate the potential predation ingestion (PI_i) for propagule of size class *i* as

$$PI_i = \sum_{j=1}^{l} B_j P_{ij} d$$
$$d = \begin{cases} 1, & \text{if } R_{ij} \le R_{upp} \ \& \ R_{ij} \ge R_{low} \\ 0, & \text{otherwise} \end{cases} \qquad (6)$$

where B_j is the biomass of the IGP-prey propagule of size class *j*, calculated as the product of the number of propagules of size class *j* times the average body mass of propagules of that same size class *j* ($B_j=N_jM_j$). The potential relative predation ingestion (RPI_i) for the IPG-predator propagule of size class *i* will be thus

$$RPI_i = \alpha M_i^{\varepsilon} \frac{PI_i}{\max\limits_{q\in[R_{low},R_{upp}]} \left(PI_q\right)} \qquad (7)$$

Here, for simplicity we are assuming constant mobility of animals in the food web environment and that encounter rates depend only on the mobility of the target propagule. In reality a combination of different sizes of sit-and-wait and actively hunting predators will likely affect encounter rates differently in different food webs. Nevertheless, these differences will likely not affect the fact that encounter rates for target sit-and-wait propagules will be higher than for actively-hunting propagules.

Considering now the Smith-Fretwell model, the fitness of females (W_{fi}) if they allocate their entire clutch to propagules of size class *i* will be

$$W_{fi} \propto (1-RPR_i)RPI_i a M_i^b \qquad (8)$$

The first term explains propagule survival from predation risk in the food web environment; the second term, explains propagule success from ingested food from IGP within the same environment and the third term reflects the egg size-number fundamental trade-off faced by females (a = 3.8 assuming b=-1 as in Smith and Fretwell 1974 – and in agreement with recent meta-analyses – Hendriks and Mulder 2008). The across-species egg mass range to graph the model (0.12-2.1mg) was also obtained from the last reference.

For simplicity the model does not include the fitness effects from potential indirect effects cascading down through the web (Schneider et al. 2012b, Walsh 2013), nor considers the extra-benefits of Intraguild-Predation of alleviating competition by killing members of the same guild (Polis et al. 1989, Polis and Holt 1992). Similarly, the competitive advantage of offspring size has not been considered here. Recent work using size spectra in animals with undeterminate growth (fish) has actually demonstrated that optimal offspring size is as small as physiological constraints allow (Thygesen et al. 2005, Andersen et al. 2008). Thus, here access to shared (non-IGP) prey is assumed to be of similar magnitude across offspring sizes and we focus on the IGP advantage of offspring size.

Model results

Figure 1 shows the expected female fitness as a function of propagule size (equation 8) for both sit-and-wait and active hunting spiders. Optimal propagule size for active hunting spiders is sensitively higher than for sit-and-wait spiders, and the difference increases as the difference in mobility between these two contrasting life history strategies increases (i.e., the ε parameter). Sensitivity analyses using different food web allometric constraints or size spectra ($N = 74.8M^{-0.75}$ as in Schneider et al. 2012) and parameterization (e.g. equation 1 with parameters for carabids from Brose et al. 2008) provided qualitatively the same results (not shown). The model prediction is thus straightforward; sit-and-wait spiders should lay more and smaller eggs than actively hunting spiders. We tested both predictions using a compiled spider data set and controlling for phylogenetic relationships to ensure statistical independence.

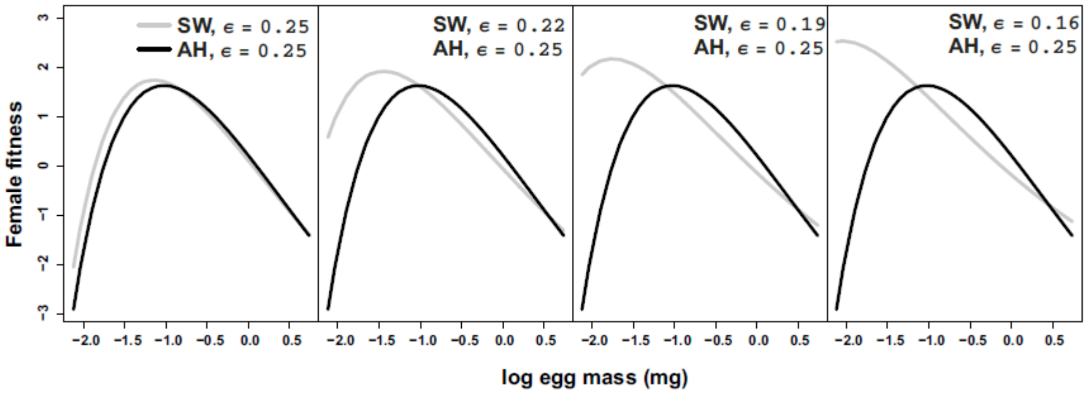

Figure 1: Model results showing optimal egg sizes for sit-and-wait (SW, in grey) and actively-hunting (AH, in black) animals. The parameter ε estimates differences in mobility between foraging modes. Note that as SW animals move relatively less than AH animals, relatively smaller eggs are favoured.

Testing the model

The data

We gathered data from literature sources of two biogeographic regions: Kaston (1981) from the nearctic region (Connecticut) and Mascord (1970) from the australasia region (Australia). Two-hundred and sixty-eight spider species from 38 families were used to gather the following data: female prosoma length and width (in mm), egg diameter (in mm) and egg number per clutch. Prosoma width and length measures were obtained by using a caliper to measure drawings (Kaston 1981) or pictures of each species (Mascord 1970, Hawkeswood 2003) to the nearest 0.01 mm. These estimates were then rescaled relative to the average body size lengths reported in the literature (Moya-Laraño et al. 2008). Unfortunately, for some of the spider species we lacked information (e.g., female size, egg size) and sample size varied between egg (n=159) and clutch (n=195) size.

Foraging mode and female body size

Using information from the literature (Kaston 1981, Prenter et al. 1997, Prenter et al. 1998, De Mas et al. 2009), we then assigned each species to each of two foraging modes: sit-and-wait (SW) or actively hunting (AH). Although this mode of classification may be a little bit imprecise, as there may be rather a continuum of foraging modes/mobilities (Uetz 1992, De Mas et al. 2009) and food availability may affect mobility and exposure to predators (Huey and Pianka 1981, Kreiter and Wise 2001, Moya-Laraño 2002, Moya-Laraño et al. 2003), it is still true that sit-and-wait spiders move at a lower rate than actively-hunting spiders.

Hagstrum (1971) proposed prosoma (or carapace) width to be the best linear estimator of spider size. However, since our analyses showed differences in body shape between AH and SW spiders (not shown) we used prosoma area (roughly approximated as the product of length and width) as the predictor of body size. We then rescaled prosoma area to the linear dimension by square-root transformation. Finally, to make the relationship between female size and egg parameters linear we transformed data to their natural logarithms.

Phylogenetically corrected statistical analysis

Because species are related phylogenetically, species data points are not statistically independent and phylogenetic distances should in principle be considered for statistical analysis (Felsenstein 1985, Harvey and Pagel 1991). We first used Mesquite 2.7 (Maddison and Maddison 2009) to assemble the phylogenetic tree (Figure S2 Appendix 2) and estimate the phylogenetic correlation structure (Paradis 2006) as a means to correct for phylogenetic dependence. The basic tree structure (from sub-order to family level) was built using the information available in Coddington (2005) and Maddison and Schulz (2007). When additional phylogenetic information was available from diverse literature sources (up to genus or species level) this was incorporated (Scharff and Coddington 1997, Griswold et al. 1998, Griswold et al. 1999, Bosselaers and Jocque 2000, Fang et al. 2000, Hormiga 2000, Hedin and Maddison 2001, Bosselaers and Jocque 2002, Levi 2002, Agnarsson 2003, Maddison and Hedin 2003, Agnarsson 2004, Arnedo et al. 2004, Benjamin 2004, Garb et al. 2004, Miller and Hormiga 2004, Coddington 2005, Agnarsson 2006, Murphy et al. 2006, Arnedo et al. 2007). Otherwise, species were incorporated in the tree as soft polytomies (Purvis and Garland 1993).

A statistical model was constructed for testing the two predictions of the model, namely that SW spiders have more and smaller eggs than AH spiders, and analyzed them by means of Phylogenetic Generalized Least Squares (PGLS) including the phylogenetic correlation structure as distance matrix. First, we investigated which of the three most common models of evolution (Brownian, Pagel or Ornstein-Uhlenbeck – Blomberg et al. 2003, Butler and King 2004) better described the evolution of the two traits: egg size and egg number, for which we used AIC. Once an appropriate evolutionary model was found, we set the minimum model to test each hypothesis and proceeded to find the most parsimonious model structure (adding interactions and/or covariates) using again the AIC criterion. Because the trees used in each analysis contain a large amount of soft polytomies (129 nodes were unsolved across the tree) we also repeated the analyses using the Martins's (1996) simulation method, which is most useful when the true phylogeny is not well known (Appendix 2).

We used R 2.11 (R Development Core Team 2012) and the packages "picante" (Kembel et al. 2010), "ape" (Paradis et al. 2004) and "nlme" (Pinheiro et al. 2012) for statistical analyses.

Results

Our analyses based on AIC showed that both traits, egg size and clutch size, followed an Ornstein-Uhlenbeck model of evolution (Table S1 Appendix 2). As predicted by the model, we found that SW spiders lay both more and smaller eggs than AH spiders. However, we detected significant "female size x foraging mode" interactions predicting both egg size (P < 0.001) and clutch size (P = 0.013). A look at the pattern (Figure 1) shows that although SW spiders lay more and smaller eggs across the entire range of female sizes, the pattern is less strong as female size increases.

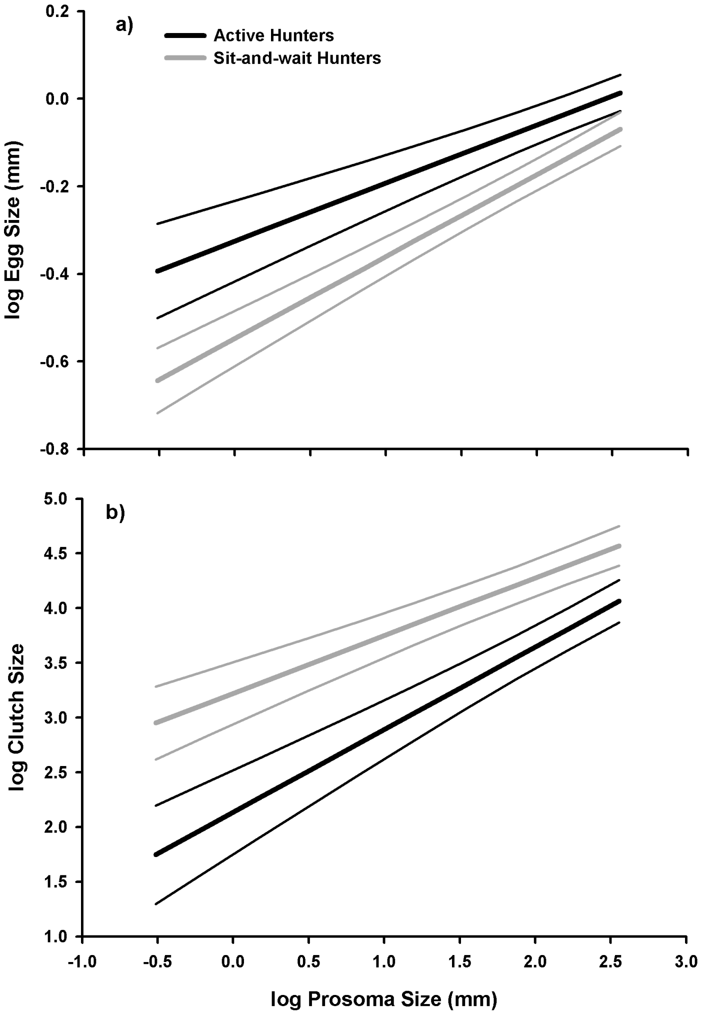

Figure 2: Effect plot of the PGLS (see Appendix S1) for the "body size x foraging mode" interaction in a) egg size model (n = 159) and b) clutch size model (n = 195). Thick lines are the partial slopes, and the thinner lines above and below the effect, the 95% confidence. The estimates are presented in table S3.

Discussion

Our results show that, as predicted by a simple graphical model integrating food web allometric constraints and foraging theory, active hunting spiders lay fewer and larger eggs than sit-and-wait spiders. The difference was consistent across female size classes despite the fact that the difference between hunting modes was less as female size increased. Therefore, for females of species of high mobility (AH), the fitness balance between having offspring that find both more IG-predators and more IG-prey, seems to be shifted toward the benefit (biomass intake from IG-prey) if offspring are born slightly larger. Due to the egg size/number fundamental trade-off, females that invest in larger offspring will necessarily lay fewer eggs, as we found in our comparative analyses. Therefore, due to differences in mobility, foraging theory and food web structure (size spectra) can explain the evolution of egg size in animals of contrasting hunting modes.

Larger eggs have been proposed to be more advantageous in harsh environments or habitats of lower quality (Bernardo 1996, Fox and Czesak 2000). However, defining past evolutionary environmental quality may be not always feasible. Here, we successfully used available food web and foraging theory to estimate environmental quality based on IGP and predicted that the more active animals should benefit more than sit-and-wait animals from laying larger offspring. In highly mobile hunting animals, e.g. wandering spiders, investing in relatively large hatchlings may be adaptive because it may enhance the offspring's hunting ability, since larger bodies (e.g. with longer and stronger legs and larger fangs) may translate into having a better ability to subdue prey (Nentwig and Wissel 1986, Marshall and Gittleman 1994, this paper). In fact, predator/prey body size ratios are central to understanding "who eats whom" in food webs (Wilson 1975, Cohen et al. 1993, Woodward et al. 2005, Brose et al. 2006). In the context of food webs and the negative size-mass relationship, a relatively large body size in a dispersing, newly-hatched actively hunting spider could mean reaching a size refuge that allow decreasing the number of potential IGP-predators, and a substantial increase in the number of available IGP-prey. The higher mobility of active hunters generally increases the encounter rates with both predators and preys (Werner and Anholt 1993 and references therein). Thus, in addition to reaching a body size refuge allowing to decrease IGpredation risk, larger offspring will have a higher chance of catching more prey and enhance their own growth rate, which could have the extra-benefit of decreasing the time exposed to predators. Hence, as demonstrated by our graphical optimality model, the net effect should be for natural selection to favour large propagule sizes. In sit-and-wait spiders, on the other hand, since predator-prey ratios may not be as relevant to catch prey or avoid predators (Nentwig and Wissel 1986), small size could be additionally favoured because higher fecundity is beneficial. Indeed, in salamanders under low predation pressure (Sih and Moore 1993) and in the extreme case in salmon hatcheries where predation rates are absent (Heath et al. 2003) higher fecundity and small egg sizes are favoured.

The question remains for why the pattern of fewer and larger eggs in actively-hunting relative to sit-and-wait spiders is less strong as female body size increases. We propose three non-mutually exclusive explanations: 1) differences in predominant dispersal mode with body size and life style, 2) the relationship between body size and viability selection is stronger in smaller species and 3) female size-egg size constraints. Spiderlings disperse by three main mechanisms, which can be combined depending on the nature of the environment and the body size of the disperser: walking, bridging and ballooning. Walking is mostly used by non-web-building spiders living on the ground. Bridging (i.e., running upside-down in own made silk bridges – Peters and Kovoor 1991, Moya-Laraño et al. 2008) is mostly used by spiders that live in tall vegetation, and is a dominant mechanism for mid-distance dispersal in sit-and-wait spiders (both web-builders and flower ambushers – Corcobado et al. 2010). Although a very large adult size is not well fitted to bridge efficiently (Rodriguez-Girones et al.

2010), a slight increase in size up to certain limit provides an advantage during bridging locomotion because legs (and thus speed) increase in length disproportionally with body size (Moya-Laraño et al. 2008). However, in both sit-and-wait and actively hunting spiders (e.g. Dean and Sterling 1985), long-distance dispersal is usually accomplished by ballooning (dragged by the wind by means of own-made silk “kites” - Bell et al. 2005) and is favoured at smaller body sizes (Dean and Sterling 1985, Roff 1991, Suter 1999). Therefore, it could be that for the small offspring of the taxa with small sit-and-wait females, ballooning is more frequent and thus a relatively small body size is favoured. In addition, since ballooning is a highly stochastic dispersal mechanism (e.g. landing on one or another habitat depends on the strength and direction of the wind), a high number of offspring would be favoured (e.g. Duarte and Alcaraz 1989). As the size of mothers, and thus that of the offspring (Hendriks and Mulder 2008) increase, bridging may become more important as a dispersal mechanism and thus larger offspring could be favoured for sit-and-wait spiders too.

A second explanation could be the higher vulnerability of smaller actively-hunting species, and more importantly the immature stages of them, which would be more susceptible to mortality than the larger ones (Roff 1992, Fox and Czesak 2000). This can be due for instance to the nested predatory nature of food webs in which larger predators tend to feed on more trophic levels and be more generalist than the smaller ones (Woodward et al. 2005). Therefore, the body size advantage of actively-hunting spiders due to their higher mobility could apply more strongly to small individuals laying larger eggs, as their hatchlings would increase their offensive and defensive capabilities. However, remarkably, a lower body size difference between the mother and the spiderling can substantially reduce the developmental time of the offspring (Fox 1994, Gillooly et al. 2002). Since the female size-offspring size follows a relationship with slope <1 (Hendriks and Mulder 2008) the highest benefit would go for the smallest species: viability selection (e.g. selection of individuals that quickly reach the reproductive stage) would favour larger offspring more likely for the small species, as for an equally small offspring size in absolute terms, the smaller species would gain a substantial higher proportion of the time needed to reach maturation than would larger species. Therefore, selection for larger offspring could be relatively stronger for small than for large actively-hunting spiders.

Finally, since offspring size can be physiologically constrained by the size of the mother (Hendriks and Mulder 2008) it could be that even if selection for offspring size is the same across actively-hunting taxa of all female sizes, the largest females are not able to build larger offspring beyond some threshold, even though this could be beneficial.

Conclusions

We found that integrating food web theory (size number allometric constraints) and foraging theory (predicting maximal attack rates) allowed us to model the environments experienced by offspring of two contrasting hunting modes. Using this modelling approach we predicted that sit-and-wait animals should lay more and smaller eggs as compared with actively-hunting spiders. This is because the second will find both more predators and prey due to their higher mobility and being larger allows both escaping predators and catching more prey. Body size ratios in sit-and-wait animals are not so important in determining predation events and selection should not favour larger propagules as much. We tested the predictions of the model and found that indeed sit-and-wait spiders lay more and smaller eggs when compared with actively-hunting spiders, but that the difference is less strong as female size increases. We propose three non-mutually explanations for this pattern. Our results suggest that the structure of ecological networks can be of great use to predict the selective pressures that are responsible for the evolution of relevant functional traits in ecological interactions.

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Appendix 1

Prey ratios and attack rates in sit-and-wait *vs*. active hunting spiders

Predator-prey ratios may differently affect to SW spiders than to AH spiders. For instance, most SW spiders hunt by using a web or by ambushing their prey, for which body size differences may not be as important to determine whether an encounter ends in predation (Nentwig and Wissel 1986). AH spiders, on the other hand, need to confront prey as they find them and body size differences may be much more important for successful subduing of prey. The parameter γ in Equation 1 (main text) measures how steep is the relationship between attack rates (or predation rates) and predator-prey ratios. The hypothesis that predator-prey ratios are more important for AH than for SW spiders predicts that a unit increase in predator-prey ratios determines higher predation rates in AH relative to SW spiders, and thus that AH have higher γ values than SW spiders.

Methods

We tested this hypothesis by reanalyzing the data by Nentwig and Wissel (1986, his Fig. 1), where he shows the percentage of prey acceptance for different spider species at different predator-prey ratios (measured as the percentage of body length of prey relative to the spider). Of the 8 spider species, 4 are SW spiders: *Tegenaria atrica, Pholcus phalangoides, Ischnothele guyanensis* and *Xysticus cristatus*; and 4 are AH spiders: *Pisaura mirabilis, Evarcha arcuata, Pardosa lugubris, Tibellus oblongus*. Experimental prey were either crickets (*Acheta domestica*) or flies (species not specified) and offered once per day. If the prey was not consumed, a smaller prey was offered the following day, if the prey was consumed, a larger prey was offered the following day. The results were presented as in Fig. S1, with the exception that error terms around the means were included (see below for details).

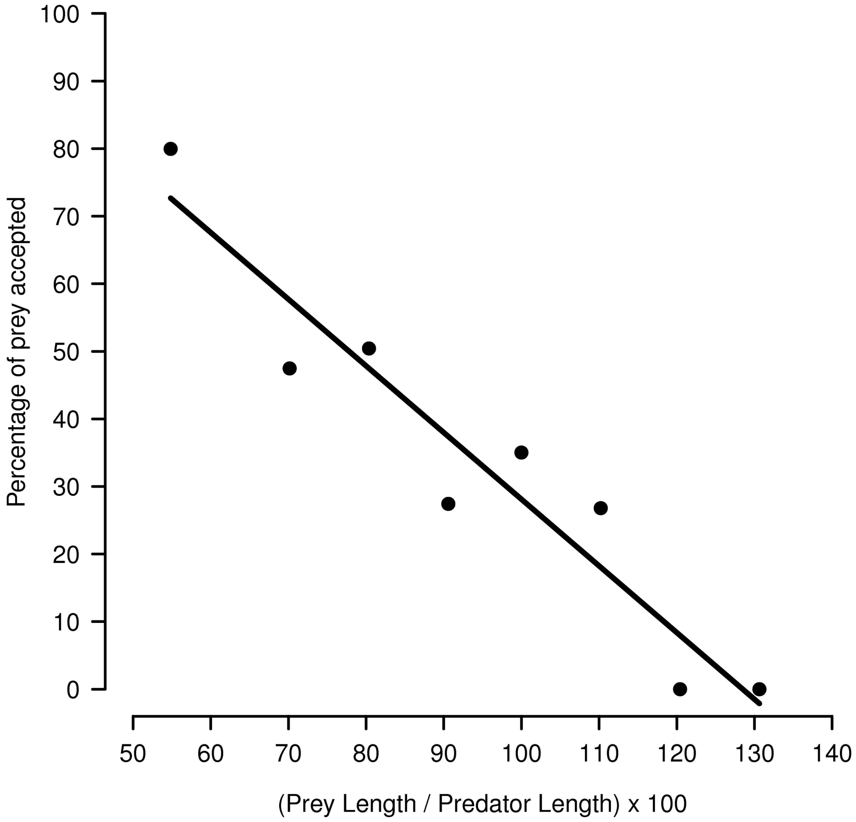

Figure S1: Example of linear adjustment for the data in Nentwig (1986, Fig. 1E *Pardosa lugubris*). Data points are means of percentages of acceptances of prey for different levels of predator-prey differences. As a first proxy of the parameter γ, we calculated the slope of the linear adjustment in these graphs. The data was extracted by measuring the graphs in Fig. 1 of Nentwig (1986) using ImageJ (Schneider et al. 2012a). These slopes were then compared between AH and SW spiders by using PGLS and the same phylogenetic sources used for testing the model in the main text.

Results and Discussion

We found that the relationship between acceptance rate and body length differences is 2X as steep for AH spiders (mean slope = -0.99) than for SW spiders (mean slope = -0.50; t_6 = 6.44, P = 0.001), concluding that an unit increase in predator prey differences determines a higher change in predation success for AH than for SW spiders. Therefore, an increase in spiderling (propagule) size can increase fitness by allowing better hunting capabilities, and this will occur to a larger degree in AH than in SW spiders.

In order to approximate the above slopes to actual γ values (eq. 1 in main text) and also obtain R_{max} and P_{max} values for SW and AH spiders, we used Hódar (1996, 1998) equations to transform prey/predator lengths into predator-prey mass ratios, which transformed the acceptance predator-prey relationship into a concave function. We fitted logarithmic models to these new functions (one for each species) and extracted the slopes, P_{max} and R_{max} values from the resulting relationships. We then averaged these estimates across SW spiders and across AH spiders and re-scaled the parameters for SW spiders by first considering the difference ratio for the three estimates relative to those for AH spiders and then assuming that the parameters published for *Pardosa* (Brose et al. 2008) were those for AH. The final parameters used in the model were those for *Pardosa* in Brose et al. (2008) for AH spiders ($\gamma = 0.54$, $P_{max} = 0.000167$ inds s^{-1} and $R_{max} = 101$) and the change of scale for SW spiders ($\gamma = 0.35$, $P_{max} = 0.000154$ inds s^{-1} and $R_{max} = 36$).

Appendix 2

Details on the Martins 1996's method

When using phylogenetic comparative methods, it is usually assumed that the phylogenetic tree is solved with very little uncertainty. However, in many taxa the phylogeny is only partially resolved as only few groups have complete phylogenies. Our spider phylogeny contains 50 soft polytomies (i.e. the topology it is not resolved), with the largest one containing 19 nodes (129 unsolved nodes in total). Therefore, we have an unknown amount of uncertainty in our statistical estimates due to the lack of phylogenetic resolution. We conducted additional analyses using a simulation method that takes into account this source of uncertainty (Losos 1994, Martins 1996). We used the procedure as follows:

We created a statistical population of 1,000 random trees in which we randomly solved the uncertainty of our trees (i.e. the polytomies) and used Grafen's (1989) branch lengths transformation as a starting point before applying any evolutionary model branch length transformation. We then estimated the same statistical parameters as in PGLS but using the simulated trees. Using joint and conditional probabilities (Martins 1996) we got p-values for the null hypothesis that the estimated regression slopes (*b*) were not differ from zero. With this procedure, one obtains a normal distribution of estimates, from which the mean represents the most accurate estimate describing the relationship between the dependent variable and the predictors.

We applied this method for 1) selecting the evolutionary models that best fitted our data; 2) selecting the most parsimonious statistical model relating traits to predictors; 3) to calculate estimates (b) and the p-values associated to them; and 4) for plotting the effects and the 95% confidence intervals of the estimates, for which we used the procedures described by Fox (2003).

Figure S2: Assembled phylogeny of the 268 spider species used to estimate the phylogenetic correlation structure for the PGLS analysis.

Table S1: Results on model selection to choose among evolutionary models. The AICs and their associated standard errors (due to the phylogenetic uncertainty – Martins 1996) are shown. The most parsimonious evolutionary model is highlighted in bold.

	Evolutionary model AIC						
Statistical models	None	Brownian		Pagel		Ornstein-Uhlenbeck	
Egg Size	-130.93	-56.11	0.11	-138.98	0.03	**-142.28**	0.03
Fecundity	421.37	495.51	0.08	400.91	0.01	**394.68**	0.04

Table S2: AIC model selection to test the predictions of our model.

	AIC	$S.E._{AIC}$
(a) Egg size - ES		
AP + FM + AP x FM	-154.73	0.04
AP + FM + AP x FM + BA	-165.37	0.03
AP + FM + AP x FM + BA + AP x BA	**-181.71**	0.03
AP + FM + AP x FM + BA + AP x BA + FM x BA	-179.91	0.03
(b) Fecundity - F		
AP + FM + AP x FM	402.35	0.04
AP + FM + BA	388.17	0.04
AP + FM + AP x FM + BA	387.97	0.04
AP + FM + AP x FM + BA + AP x BA	**380.36**	0.04
AP + FM + AP x FM + BA + AP x BA + FM x BA	381.41	0.04

The final, most parsimonious model highlighted in bold. The SEs on AIC denote variation from phylogenetic uncertainty. **ES**: Egg size; **F**: Fecundity; **AP**: Prosoma area; **FM**: Foraging mode; **BA**: Biogeographic area.

Table S3: Results of the PGLS analysis on the most parsimonious model according to AIC (Table S2). Results relevant to the test of the egg-size model are highlighted in bold.

	Estimate	SE	*t*	P value
(a) Egg size (n=159)				
Intercept	-0.25	0.07	-3.71	0.000
$_{\log}$ Area Prosoma	0.14	0.04	3.21	0.002
Foraging Mode	**-0.12**	**0.06**	**-1.98**	**0.055**
Biogeographic Area	-0.22	0.05	-4.10	0.000
$_{\log}$ Area Prosoma x Foraging Mode	**0.19**	**0.04**	**4.33**	**0.000**
$_{\log}$ Area Prosoma x Biogeographic Area	0.11	0.04	2.76	0.008
(b) Fecundity (n=195)				
Intercept	2.29	0.30	7.76	0.000
$_{\log}$ Area Prosoma	1.10	0.21	5.32	0.000
Foraging Mode	**1.09**	**0.23**	**4.75**	**0.000**
Biogeographic Area	-0.25	0.26	-0.96	0.349
$_{\log}$ Area Prosoma x Foraging Mode	**-0.45**	**0.17**	**-2.58**	**0.013**
$_{\log}$ Area Prosoma x Biogeographic Area	0.65	0.20	3.18	0.002

Chapter 5

Climate change and eco-evolutionary dynamics in food webs

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References

“*The analysis of the causes of selection is in essence a problem in ecology*” Wade and Kalisz 1990

Abstract

Past evolution determines the genetically-determined available phenotypes in populations which affect ecological dynamics in communities, shaping in turn the selective pressures that further model phenotypes. Because an increase in temperature increases metabolic rates and encounter rates, climate change may have profound eco-evolutionary effects, possibly affecting the future persistence and functioning of food webs. We introduce a semi-spatially explicit Individual-Based Model (IBM) framework to study functional eco-evolutionary dynamics in food webs. Each species embedded in the web includes 13 genetically-determined and multidimensionally-variable traits (the G matrix), four of which are flexible physiological and behavioural (personality) traits that respond to temperature. An increase in temperature and stronger correlation among traits leads to stronger trophic cascades but higher stochasticity, with higher probability of extinction for some trophic levels. A combination of the abiotic (temperature) and biotic (predators’ presence/absence) matrix of selective agents (the O matrix) generates differential selection for activation energies for metabolic rates and several instances of correlational selection (selection in one trait changes with the levels of another), suggesting how global warming might favour certain trait combinations. Our results and the future prospects of this IBM approach open new avenues for climate change research.

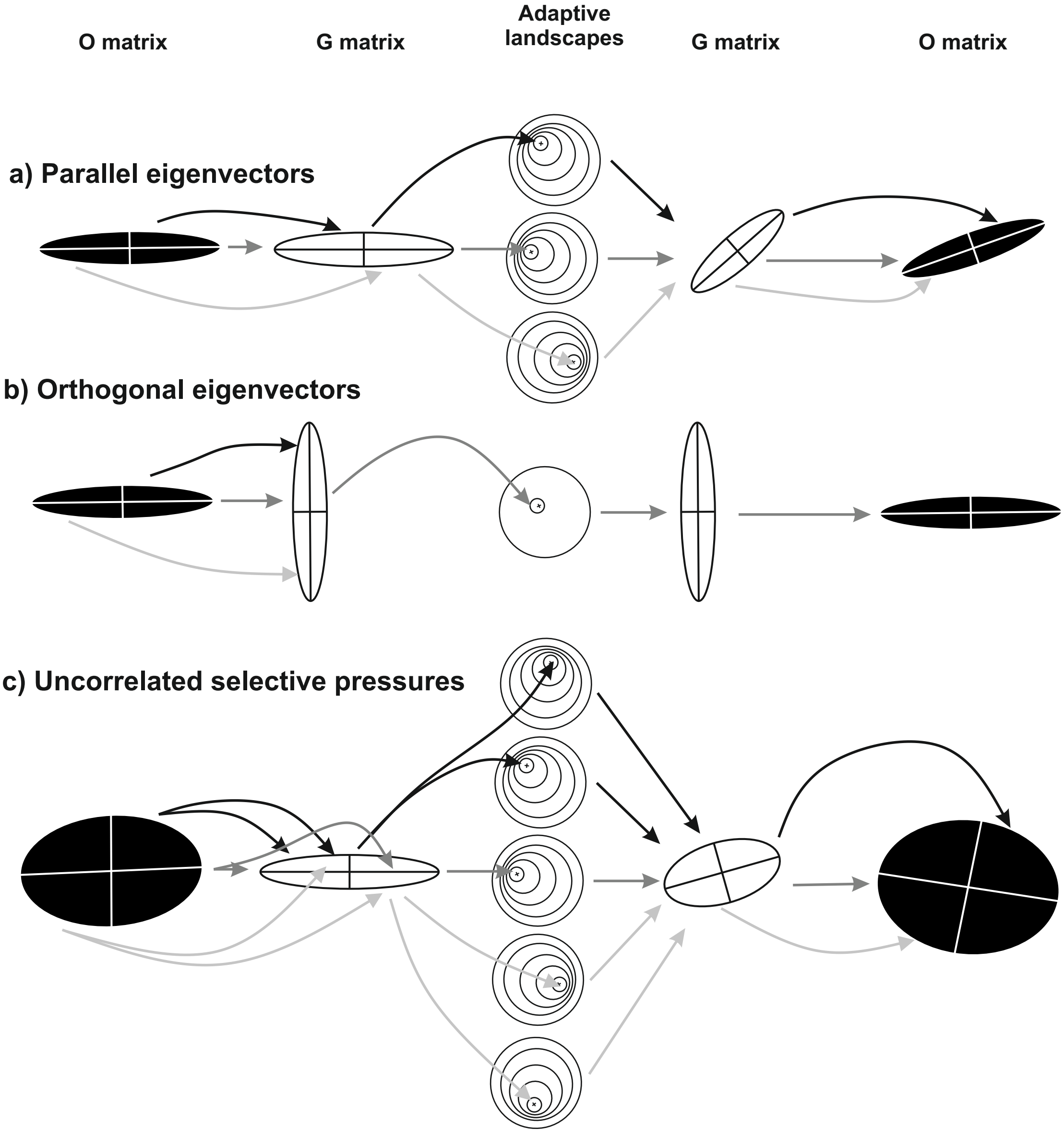
1. Introduction

There is increasing evidence that global warming generates new interactions (or alters existing ones) within food webs and other ecological networks (Tylianakis et al. 2008, Berg et al. 2010, Gilman et al. 2010). However, little is known about the consequences of climate change for eco-evolutionary dynamics and their feedbacks with ecosystem processes. In eco-evolutionary dynamics, the ecological scenario sets the background within which evolution occurs, while ongoing evolution may affect in turn ecological dynamics by changing the frequencies of phenotypes involved in ecological interactions. With global warming, the novel abiotic, temperature-driven, selective pressures may shape phenotypes, and the interaction between the latter may in turn generate new biotic conditions that alter the functioning of food webs leading to eco-evolutionary feedback loops (Woodward et al 2010). One possible path to explore these still largely unknown reciprocal effects, especially in complex ecological networks, is through computer simulations. Here we briefly review the literature on ecological interactions under climate change and introduce a new simulation framework to explore eco-evolutionary feedbacks in food webs by combining the study of O matrices (variance-covariance matrices of selective agents, MacColl 2011) with that of G matrices (variance-covariance matrices of quantitative genetic trait values, Box 1) in an Individual Based Model (IBM) which includes predators, prey and basal resources and links quantitative genes for 13 behavioural, morphological and physiological traits to an ecosystem function: trophic cascades. Following the Metabolic Theory of Ecology (MTE, Brown et al. 2004), the model also considers the direct and indirect effects of temperature on ecological interactions. We use this new framework as an example to explore how temperature and the genetic material present in populations, which originated from past evolution, can affect ecological dynamics and how the ecological background (predators plus temperature) may affect contemporary and future patterns of natural selection upon prey populations. We then discuss the consequences of our findings for understanding not only how climate change may alter eco-evolutionary dynamics and related ecosystem functions, but the consequences on adaptive evolution and diversification in spatially-structured ecological networks and the role that suits of traits (including animal personalities) play in such processes. We further discuss future applications of our approach, for instance in terms of how pest control schemes might be altered to cope with climate change by bioengineering simulated food webs. We conclude by briefly explaining how to expand our framework for contrasting eco-evolutionary neutral theories (Melián et al. 2011) with meta-community functional eco-evolutionary dynamics and the geographic mosaic of coevolution (Thompson 2005).

1.1. Climate change and ecological interactions

Climate change alters key abiotic factors, such as temperature and water availability, which in turn affect individual organisms and associated biological processes (Tylianakis et al. 2008, Berg et al. 2010, Gilman et al. 2010, Woodward et al. 2010). Warming of the climate system is unequivocal and has generated a 100-year linear trend of + 0.74 ºC, with a rise of minimum temperatures at a rate about twice as large as that of maximum temperatures (IPCC 2007). This increase has triggered a broad range of biological responses, which are well documented at individual (life cycles), population (abundance trends) and species (range shifts) levels (Walther et al. 2002, Parmesan 2006, Castle et al 2011, Minterback et al 2012). Community and ecosystem -level impacts, however, have been more difficult to quantify (but see Yvon-Durocher et al 2010a,b), as they rarely consist simply of the sum of single species responses (Kareiva et al. 1993).

Species involved in biotic interactions do not necessarily react to climate warming in a similar way, which can result in phenological mismatches or asymmetric range shifts (Schweiger et al. 2008, Olesen et a. 2010, Van der Putten el al. 2010, Walther 2010, Woodward et al. 2010). Even modest perturbations at the species level may be amplified as they ripple though the food web, and can therefore have large effects within communities (Memmott et al. 2007, Both and Visser 2001). Conversely, other seemingly large changes may be modulated and ultimately have little impact (Brown et al. 1997). Moreover, climate warming may asymmetrically affect different types of ecological interactions (such as parasitism or competition), thus disrupting the biotic regulatory forces within natural populations (Davis et al. 1998, Woodward et al 2010).



Box 1: Eco-evolutionary dynamics as represented by selective agents' (O) and genetic (G) variance-covariance matrices, and their corresponding adaptive landscapes. G matrices can be depicted by summarising the genetic variability among traits as their Principal Components (PCs). In the graph, the two main PCs of the G matrix (representing the entire genetic material of a structured population) are represented as a white ellipse (e.g. Jones et al. 2003). The length of the crossing lines (the eigenvalues) show the variance absorbed by each PC; the angles of the eigenvalues relative to a hypothetical X axis represent the eigenvectors. Similarly, the variability of those environmental factors (both biotic and abiotic) that can work as selective agents across the geographic landscape (the O matrix) can be represented by means of PCs (black ellipses). In both matrix types the shorter the relative length of the shorter eigenvalue the higher the amount of

correlation among traits. The arrows in increasingly darker grey represent different values of the selective pressures as occurring in different areas within the geographic landscape, each of which may hold a different subpopulation (i.e., selection is spatially structured). Adaptive landscapes (center) are represented by enclosed circles of diminishing size. Shorter distances between circles depict steeper landscapes (requiring stronger selection responses to reach maximum fitness). a) When both G and O traits are highly correlated (i.e. PCs are narrow ellipses) and the direction of the eigenvectors of each matrix are in the right direction, the O matrix will determine changes in the G matrix by conforming different adaptive peaks (i.e. different sets of genes or traits maximising fitness) through the geographic landscape. A change in the G matrix can in turn change the O matrix, for example when a response to selection in prey changes predator numbers or predator trait variability. The change in the O matrix will then further model the G matrix and so on. b) When both G and O traits are highly correlated and the angles of the largest eigenvalues in the G and O matrices are orthogonal (i.e. the maximum variability in the action of selection is independent on the maximum genetic variability), the effect of selection agents will only slightly change the G matrix (even a shallower adaptive peak will be difficult to climb and there will be a major lack of response to selection). Similarly, the reciprocal effect of the G matrix on the O matrix will be small. c) When there is large uncorrelated variability in selection agents and the G matrix includes highly correlated traits, diverse selective pressures can open the space for correlational selection (selection on one trait changes with the values of another trait), and the population will be able to reach diverse adaptive peaks even within the same subpopulations, thus increasing the chances for diversification. Diversification can be further enhanced by the breaking of genetic correlations under diverse sources of correlational selection (i.e. selection in one trait changes with the level of another trait), which can then further model the O matrix.

Although the documented responses vary spatially and temporally across trophic levels, some general patterns emerge (Woodward et al 2010). For instance, warming may disproportionately affect higher trophic levels, dominant competitors or specialists with obligate interactions (Voigt et al. 2003, O'Gorman et al. 2012). Moreover, climate change may facilitate pathogen and parasite outbreaks (Harvell et al. 2002) and favour competition over facilitation (Callaway et al. 2002). However, some of the detrimental effects of climate change could also be buffered by certain network properties. For example, a recent model based on the MTE shows how temperature may increase connectance, which can in turn increase food web stability (Petchey et al. 2010, Montoya and Raffaelli 2010).

The relative importance of bottom-up and top-down mechanisms in controlling population dynamics is also influenced by the climate (Meerhoff et al 2012, Jeppesen et al 2012). Temperature may change the relative importance of these forces by affecting the metabolic rate of organisms and altering their population dynamics (Brown et al. 2004, Yvon-Durocher et al. 2010). As a general rule, when temperature rises above the thermal tolerance of species and water is limiting, metabolic rate declines at all trophic levels, weakening both top-down and bottom-up effects (Hoekman 2010). When this threshold is not reached, however, effects can be multifaceted. Since warming accelerates metabolism, it may exaggerate top-down effects because faster metabolism of predators increases their growth, activity, consumption, and digestion rates (Brown et al. 2004). Nevertheless, the greater (net) metabolic requirements of higher trophic levels with respect to lower ones may render them more vulnerable to climate change (Voigt et al. 2003, Petchey et al. 1999). Warming may then exacerbate interactions among the higher trophic levels and enhance intra-guild predation, which in some instances may boost the probability of extinction of some predator species and, in turn, simplify food web structure (Barton and Schmitz 2009). Warming may also differentially affect how different traits respond to temperature (Thompson 1978, Rall et al. 2010, Englund et al. 2011, Vucic-Pestic 2011), with the balance among trait responses determining the chances of predator extinction with increased temperature.

Although in theory the loss of top predators and herbivores with elevated temperatures may increase the relative importance of bottom-up forces under novel climatic conditions, the outcome also depends on water availability (Woodward et al 2012, Ledger et al 2012), especially on arid and semiarid terrestrial systems, where productivity is strongly limited by precipitation (Holmgrem et al.2006). Empirical evidence, in fact, suggests that biotic interactions may become relatively more important in wet periods, whereas resource limitation will predominate in dry ones (Meserve et al. 2003). Temperature may also boost bottom-up forces directly, since the faster metabolism of basal trophic levels, such as autotrophs and bacterivores, increases productivity and decomposition rates respectively (Brown et al. 2004, Sagarin et al. 1999). Metabolic changes driven by warming may also indirectly affect community regulation, via its influence on population dynamics. Ectotherms at lower trophic levels, for instance, feed more at higher temperatures, thus their populations may depend more on food resources than on the control of predators as temperature rises (Chase 1996).

The anthropogenic rise in temperature has, therefore, the potential to disrupt community functioning and dynamics, and this can have important ecological and evolutionary consequences in both natural systems and in novel, human-altered or –simplified environments (Minteback et al 2012). These effects do not only affect ecological dynamics, but also evolutionary outcomes, which can trigger eco-evolutionary feedback loops (Fussmann et al. 2007, Pelletier et al. 2009).

1.2. Recent advances in eco-evolutionary dynamics and implications for climate change

Pimentel (1961, 1968) recognised early on that ecological and evolutionary processes are inextricably linked, with genetic variation being an important factor that regulates stability among interacting populations of species. More recent work has confirmed that genetic variation and evolutionary processes shape ecological communities more broadly, and that the ecological context in which populations of species operate can influence their subsequent evolution (e.g. Wade and Kalisz 1990, Odling-Smee et al. 2003, Thompson, 2005, Whitham et al. 2006, Johnson and Stinchcombe, 2007, Johnson et al. 2009, Pelletier et al. 2009, Ellers 2010, Genung et al. 2011, MacColl 2011, Schoener 2011, Smith et al. 2011).

Genotypic identity, as well as variation, can also contribute to the outcome of species interactions. We know from experiments that genetically identical individuals can respond differentially to different environments, including those that differ in temperature, resulting in genotype by environment interactions (GxE - e.g. Brakefield and Kesbeke 1997). The impact of these can extend across trophic levels and beyond trophic interactions (Rowntree et al. 2010, Johnson and Agrawal 2005) and across generations (Palkovacs and Post 2009), causing subsequent changes to the environment itself. In addition, when populations of two species interact with one another the species themselves become part of each other's environment, leading to interactions among genotypes of different species (see Tétard-Jones et al. 2007, Vale and Little 2009, Zytynska et al. 2010, Rowntree et al. 2011a for examples). Genotype by genotype (GxG) interactions between species may even lead to co-evolution. However, even without the occurrence of co-evolution, the evolutionary trajectory of one species may still depend on the genotypes of the other species encountered. Thus, a necessary preliminary step towards understanding the potential for complex eco-evolutionary dynamics to occur, particularly in the face of climate change, is the empirical documentation of GxE and among species GxG interactions.

Many of the advances made in this area have come from the use of a combined experimental-mathematical modelling approach (e.g. Yoshida et al. 2003, Becks et al. 2012). As study systems become more realistically characterised and their complexity increases as a result, the analysis and interpretation of empirical data becomes correspondingly more difficult. Hence, the development of mathematical models, and in particular individual based techniques enhanced by ever increasing computing power, are assuming ever greater importance. In particular, these types of models enable us to explore the multitrophic space around eco-evolutionary interactions in more detail and extend them to complex networks of interactions. Such approaches can thus be an important tool enabling a better understanding of the future of populations under climate change scenarios by facilitating the study of eco-evolutionary dynamics under changing abiotic conditions, e.g. temperature.

1.3. Eco-evolutionary dynamics and ecological networks

The eco-evolutionary perspective is being currently expanded to ecological networks (Olesen et al. 2010, Fontaine et al. 2011, Guimarães et al. 2011, Hagen et al. 2012) and even to ecosystem processes (Schmitz et al. 2008, Matthews et al. 2011). Importantly, indirect ecological effects imply also the action of selective agents whose effects propagate through the network, with very important implications for the persistence of the interacting species and for coevolution, which in a network context cannot be simply understood as mere pair-wise interactions of co-adapting species (Olesen et al 2010, Guimarães et al. 2011). This implies that eco-evolutionary dynamics can affect different trophic levels in different ways. In the last two decades we have witnessed important advances in the modelling of predator-prey interactions and food webs in an evolutionary context, with some studies giving a central role to adaptation (e.g. Abrams and

Matsuda 1997, Abrams 2000, Kondoh 2003, Kimbrell and Holt 2005, McKane and Drossel 2005, Loureau and Loeuille 2005, Beckerman et al. 2006, Kondoh 2007, Petchey et al. 2008, Loureau and Loeuille 2011, Heckmann et al. 2012). However, how adaptive evolution affects ecology in food webs, and *vice-versa*, has only been considered explicitly very recently (Melián et al. 2011). In an original approach, Melián et al. (2011) successfully linked the evolutionary (Kimura 1983) and the ecological (Hubbell 2001) neutral theories. By explicitly considering variability on prey diversity (or intraspecific variation in the number of prey or connectivity) the authors were able to show that variability around species nodes could explain food web structure and the convergence between ecological and evolutionary dynamics.

In contrast to neutral models, explicitly considering both natural selection acting on functional traits and functional multidimensional trait diversity acting on ecological functions is a way by which eco-evolutionary dynamics research can gain insight on how the dynamics of adaptation shape populations. It also allows us to consider how this functional change in populations might feed back to ongoing natural selection. In addition, in the context of climate change, we can perform this exercise by adding a third set of drivers, the abiotic environment, which can have potentially powerful effects on the system's dynamics. This would substantially increase our understanding of how rapid evolution occurs and its role in the convergence of ecological and evolutionary dynamics, as natural selection, allowing disproportionately fast rates of gene fixation or elimination contrasts with genetic drift, which, especially in sufficiently large populations will take far longer to fix or eliminate functional genes, the former thus offering a more likely candidate driver for the occurrence of rapid evolution for functional traits (Heath et al. 2003, Hairston et al. 2005, Carroll et al. 2007). Furthermore, by taking a functional multi-trait approach to study eco-evolutionary dynamics we could be able to, among other things:

1) Identify traits (and even allele effects) that are responsible for food web functioning - especially those that could add some effect independently of (orthogonally to) body size (Woodward et al. 2011) - and/or estimate their effect relative to other traits (alleles).

2) Identify suits of traits that respond to natural selection (e.g. Agashe et al. 2011) and document the strength of selection on them in different ecological and climate change scenarios.
3) Identify traits that act themselves as selective agents, estimate how trait mean and variation in one population affect the strength of natural selection on another, and document the impacts that climate change may have on the outcome of these interactions.
4) Identify whether the joint effect of different traits affects the above three points additively or multiplicatively.
5) In different climate change scenarios, document the fate and probability of persistence of functional alleles under eco-evolutionary dynamics in the face of both genetic drift and natural selection. Thus, this approach could serve to test whether the loss of genetically-based functional diversity could have stronger impacts than the loss of functionally redundant taxa.

As an example, here we will focus on point 2 only: the study of natural selection. However, at the ecological level, we will also consider how predator-prey-resource dynamics can change at different temperatures.

1.4. Individual-Based Models: modelling individual variation in ecology

There is little doubt that in sexually-reproducing species all individuals in the population differ from one another. These differences are in fact the core of evolutionary biology (Darwin 1859, Fisher 1930). Community ecology, on the other hand, has been classically species-mean oriented (Raffaelli 2007, but see MacArthur and Levins 1967, May and MacArthur 1972), making the implicit assumption that all individuals in a population are functionally identical. However, the realisation that individual and/or genetic variability may be important has started to appear in the ecological literature (Woodward et al 2010b, Gilljam et al 2011, Bolnick et al. 2011, Violle et al. 2012) and has even given birth to a specialised field: “community genetics”, which addresses the question of how – and to what extent - variability in genetically-based phenotypes within populations affects ecological patterns and processes (Antonovics 1992, Agrawal 2003, Rowntree et al. 2012a, Johnson et al. 2011). Among other things, phenotypic/genetic variation can affect species coexistence (Clark 2010), food web structure (Woodward et al 2010b, Moya-Laraño 2011) and some ecosystem processes and properties such as primary productivity, decomposition, resilience or the fluxes of energy and nutrients (Hughes et al. 2008, Perkins et al 2010, Bolnick et al. 2011, Reiss et al 2011).

The study of ecological networks has greatly increased in the last two decades, allowing extending our thinking and modelling approaches from considering pair-wise interactions or food chains to now consider complex networks of relationships which include tens to hundreds of species and hundreds to thousands of links (Jordano 1987, Polis 1991, Bascompte et al. 2007, Ings et al. 2009, Olesen et al. 2010, Jacob et al 2011). In food web models that explore food web structure and persistence, the typical interacting unit (or node) is the species (e.g., Cohen 1990, Caldarelli et al. 1998, Drossel et al. 2001, Solé and Montoya 2001, Williams and Martinez 2000, Cattin et al. 2004, Gross et al. 2009). Expanding the above models by including interactions at the level of the individual, which it is truly the level at which trophic interactions occur, could be a major step towards our understanding of the ecological and evolutionary processes occurring in these complex networks of interactions. Actually, averaging the properties of individuals could hide important food web attributes, and using an individual-based approach could improve our understanding and predictability power of food web structure and dynamics (Woodward et al. 2010b). Indeed, this is complemented by studies in which the role of instraspecific variability has begun to be considered also in experimental approaches which test how predator trait variation could affect predator/prey interactions and top-down control (e.g. Ingram et al. 2011). In order to include the individual perspective in food web models, one potentially useful tool is provided by the family of Individual-Based Models (IBMs).

Individual-Based Models are computer simulations in which within a given set of individuals - which may differ from each other (or not) at the beginning of the simulation - each experiences a different set of interactions and environments (e.g. DeAngelis 1980, DeAngelis and Mooij 2005, Grimm 2006). Each individual has also a set of state variables which can use the computer memory to keep records of relevant information for the history of interactions that it has experienced or for its morphological, physiological or reproductive status. These can, in turn, determine with whom subsequent interactions occur. Therefore, even if all individuals are identical at the beginning of a simulation, they typically end up being different. Actually, biotic interactions have been classically studied from a theoretical point of view using state variable models (with sets of differential equations) because they have the advantage that one can calculate equilibrium points, the conditions for stability or other properties of the model which can be useful for making generalisations (May 2001, Cantrell and Cosner 2003, Murray 2005, Schreiber et al. 2011).

The main advantage of IBMs is that they allow the explicit inclusion of multiple sources of individual variation at the beginning of a simulation; e.g., from different spatial positions to differences in genetic and/or phenotypic values for multiple traits. This is critical for assessing the role of genetics and trait variation in ecology, as well as to uncover the mechanisms which lead to one or another food web topology and/or ecosystem functioning. Such complexity could not possibly be included in systems of differential equations, especially if one aims at finding an analytical solution (cf Rossberg 2012), so IBMs provide an alternative approach.

The feedback between these models and reality, using a systems biology approach (Purdy et al. 2010), can be used to modify the IBMs and slowly approach reality in closer detail. These simulation experiments and the extraction of all the explanatory factors of the dynamics, is one of the main advantages of simulating living beings in the computer, which have been recently called synthetic lives (Solé 2012). Another advantage of IBMs is that they do not necessarily require complex mathematical formulations, so long as the model is documented in sufficient detail for its *a posteriori* replication. For this reason, there is a standard IBM protocol for ecologists building and publishing IBMs: the ODD (Overview, Design concepts and Details) which was established to develop a general and formal description of IBMs (Grimm et al. 2006). Here we are concerned about the modelling of ecological interactions, for which IBMs have been used for a large array of individual features (DeAngelis and Mooij 2005). To the best of our knowledge there is still no single IBM that considers both ecological and evolutionary dynamics, as well as a genetic quantitative background for the traits in species embedded in food webs. One necessary step for making simulated populations able to respond to natural selection is to implement the genetic background of traits in individuals.

1.5. The study of natural selection

The study of natural selection distinguishes within-generation changes, usually mediated by traits and their covariation with fitness (selection per se), from the response to selection across generations, which involves changes in gene frequencies and depends on the standing genetic variability. Therefore, to implement natural selection in functional eco-evolutionary models, the quantitative genetic basis of traits needs to be taken into account. Microevolution by natural selection based on single traits can be successfully summarised by the simple breeder's equation:

$$R = h^2 s \qquad (1)$$

where R is the response to selection, h2 is the narrow sense heritability due to the additive genetic variance (i.e., many loci each adding a small effect), and s is the selection differential, which is merely the arithmetic trait mean before selection subtracted from the mean after selection. The multidimensional (multi-trait) version of the breeder's equation includes multiple functional traits at once and explicitly controls for the fact that neither natural selection acting on each trait nor the quantitative genetic basis of each trait are independent among traits (Lande 1979):

$$\Delta \bar{z} = \mathbf{G}\boldsymbol{\beta} \qquad (2)$$

where $\Delta \bar{z}$ is a column vector which represents the change in the mean value of each trait, G is the variance-covariance genetic matrix (or G-matrix), and β is the matrix of directional selection gradients which can be thought of as coefficients of directional natural selection acting orthogonally (i.e. independently) from each other on each trait. These selection gradients can be calculated by a multiple regression analysis in which an estimate of relative fitness (e.g. the fecundity of each individual divided by the average fecundity in the population) is the dependent variable, and the standardised N(0,1) trait values the independent variables (Lande and Arnold 1983, Arnold and Wade 1984a,b). The G matrix involves negative and positive associations among traits (genetic correlations) and the extent to which traits are correlated with each other explains to what extent evolution is constrained by natural selection, as under strong correlation one trait will not be able to respond to selection without involving a response (either in the same or opposite direction) from other correlated traits (Box 1). Thus, the G matrix may be behind evolutionary trade-offs, although this is not necessarily always the case (Roff 1997, Roff and Fairbairn 2007). Importantly, G can be decomposed into its principal components, and the one with the highest eigenvalue; i.e., that which explains most of the variance, has been called the "line of least resistance" (Box 1). This is because this axis summarises the partition of the variance of correlated traits which are most susceptible to being shaped by natural selection (Schluter 1996, 2000). The amount of genetic correlation among traits is affected by linkage disequilibrium (non-random distribution of alleles across individuals) and by pleiotropic effects (i.e., genes affect more than one trait). However, as linkage disequilibrium is broken by recombination at each generation, what renders genetic correlations relatively stable is usually pleiotropy (Roff 1997). We warn that recent developments in genotype-phenotype relationships have shown that the G matrix is likely an oversimplification as a mechanism to explain phenotypic variation and trait correlations. For instance, the magnitude and direction of the G-matrix is frequently environmentally-dependent (Sgrò and Hoffmann 2004). Further, abundant hidden genetic variation, which expresses only under stressful conditions and could be linked to the evolution of phenotype robustness (Espinosa-Soto et al. 2011), has been discovered recently (Le Rouzic and Carlborg 2007, McGuigan and Sgrò 2009). Additionally, epigenetic mechanisms (e.g., changes in genome expression by nucleotide methylation), are gaining increasing prominence in the literature as alternative mechanisms of phenotypic variation (e.g. Pigliucci 2008, Greer et al. 2011).

But, how does ecology affect the magnitude and pace of adaptive evolution? The ecological causes of natural selection (Wade and Kalisz 1990) have been recently reemphasised in a new framework involving O (oikos) matrices (MacColl 2011). An O matrix is a variance-covariance matrix of environmental values that act as selective agents (Box 1). When perfectly correlated (high off-diagonal values in O), two selective agents will act in the same direction across the geographic landscape (Box 1a) and their effects on phenotypic and genetic changes may be largely indistinguishable (i.e., the action of the different selection agents will be redundant across the geographic landscape). However, when the direction of the maximum eigenvalue (the eigenvector) in the G matrix matches that of the maximum eigenvalue of selective agents (Box 1a) a response to selection and a rapid climbing of diverse adaptive peaks across the geographic landscape will occur. When the angles between these two matrices are orthogonal (Box 1b) the peak of the adaptive landscape will be shorter while more difficult to reach. A third possibility occurs (Box 1c) when selective agents have low correlation, in which case diverse angles of selection can occur differently on different parts of the trait range. This can lead, for instance, to correlational selection, which can form multiple adaptive peaks in populations, and increase the chances for diversification across the geographic landscape. The extent to which selective agents are uncorrelated will add a multidimensional character to natural selection, and if we consider that selective agents can interact with each other this will affect selection gradients (MacColl 2011). Thus, the long term changes in the G-matrix due to natural selection can be better understood if we explicitly build these O-matrices of abiotic and biotic factors that act as selective agents. It is also true, however, that the nature of the G-matrix can affect the O-matrix, especially the biotic component of the latter (Moya-Laraño 2012). For instance, indirect genetic effects (Wolf et al. 1998), by which the genotype of an individual can affect the phenotype of another (i.e. inter-individual epistasis), can trigger feedbacks that can accelerate evolution. In complex (i.e. real) ecological networks myriads of indirect genetic effects are possible, and have been recently invoked to explain whole community heritability (Shuster et al. 2006), which in itself could be considered as an estimate of the potential for the long term stability of selective agents. Therefore, to understand eco-evolutionary dynamics from an adaptive point of view, we must consider the reciprocal nature of the effects of G and O matrices (Box 1).

2. Methods

2.1. An IBM framework to study eco-evolutionary dynamics in food webs

Here, we introduce an IBM which, using the above framework in a food web context, can be used as a tool to investigate the impacts of climate change on eco-evolutionary dynamics and an associated ecosystem property: trophic cascades. In its first version, our IBM simulates cannibalistic predators (one species), shared prey (one species), and basal resources (one species) that are distributed in micro-patches of variable productivity which are distributed within a single micro-site. Both predators and prey have quantitative genetic basis for 13 traits and are able to move from micro-patch to micro-patch using a set of adaptive rules. Some traits are plastic to temperature and variation was introduced by implementing genetic variation in traits for plasticity (Figure 1, Appendix). Furthermore, the model incorporates some of the latest paradigms in predator-prey interactions, such as predator-induced stress affecting metabolic rates and assimilation efficiencies (Hawlena and Schmitz 2010a) by explicitly affecting state variables depending on the previous encounter with predators (see the Appendix). Figure 2 shows the

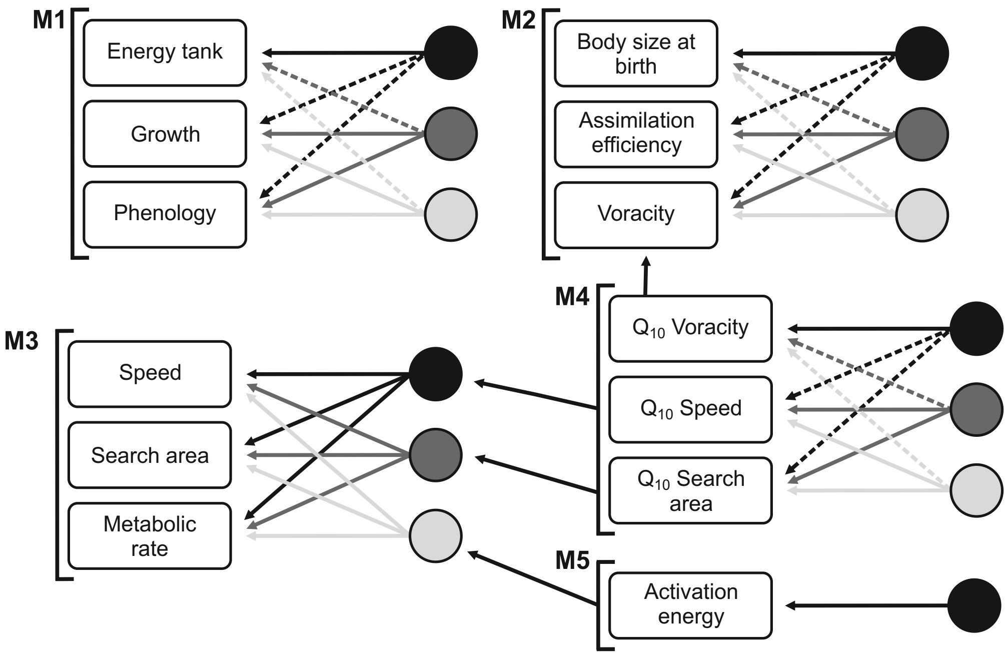


Figure 1: Quantitative genetic effects on 13 traits as implemented in the IBM (see Table 1 for a description and range of the traits). Traits are scattered in 5 modules (M1 to M5) which are genetically independent of each other. The degree of correlation among traits within the module, and thus the level of phenotypic integration across individuals, may vary among modules. The filled circles represent groups of alleles that have an effect on the traits towards which the arrows point. Plain arrows represent positive pleiotropic effects, while dashed arrows represent negative pleiotropic effects (genetic trade-offs). Modules M4 and M5 represent genetic variation for plasticity by which they epistatically affect the traits towards which they point. The epistatic effect of the pointing traits for plasticity depends on temperature and variability in these plasticity traits determines the shape and magnitude of the reaction norm of the pointed traits (see Appendix for further details).

flow diagram describing the algorithm. Although the model simulates a 3-species food chain, given that predators feed on each other there are in essence four trophic levels. In addition, the initial diversity of individuals and alleles and the great diversity of potential interactions simulates an individual-based complex food web, in which different alleles and phenotypes affect others both directly and indirectly (through the network) and both consumptively (predation) and non-consumptively (affecting searching and antipredatory behaviours). Thus, although not done here, an individual-based ecological network of interactions, as well as an allele-to-allele ecological network reflecting indirect genetic effects (Wolf et al. 1998), could be drawn by simply recording all the consumptive and non-consumptive interactions occurring during the simulation.

2.2. The aim of the simulations

Table 1 shows a list and description of traits along with the range used in the present simulations. The outputs generated by the current version of mA include enough information to document the drivers of eco-evolutionary feedbacks in detail (e.g., how the G matrix affects the O matrix and viceversa, Box 1). However, for the sake of simplicity, responses to selection across generations ($\Delta\bar{z}$ in eq 2) were not analysed here.

To explore how rising temperatures may affect eco-evolutionary dynamics in food webs, as well as how they affect associated ecosystem processes such as trophic cascades, we simulated eco-evolutionary food web dynamics for one season of 120 days at environmental temperatures of T=16ºC, 20ºC or 25ºC. We used 16ºC as the lowest temperature instead of 15ºC because this was the only way to produce inter-individual variability around Q values (Appendix). We ran 5 replicates per simulation, each of which can be interpreted as a within-season isolated micro-community where natural selection occurs locally (i.e., without migration among micro-sites) in each micro-site. Each simulation/micro-site started with 50 predators (mites) and 500 prey (collembola) which were randomly distributed in micro-patches arranged across a unidimensional micro-site (Appendix). As each simulation is a micro-site in real space, we neither need to assume nor to explore local ecological and evolutionary stabilities. The present

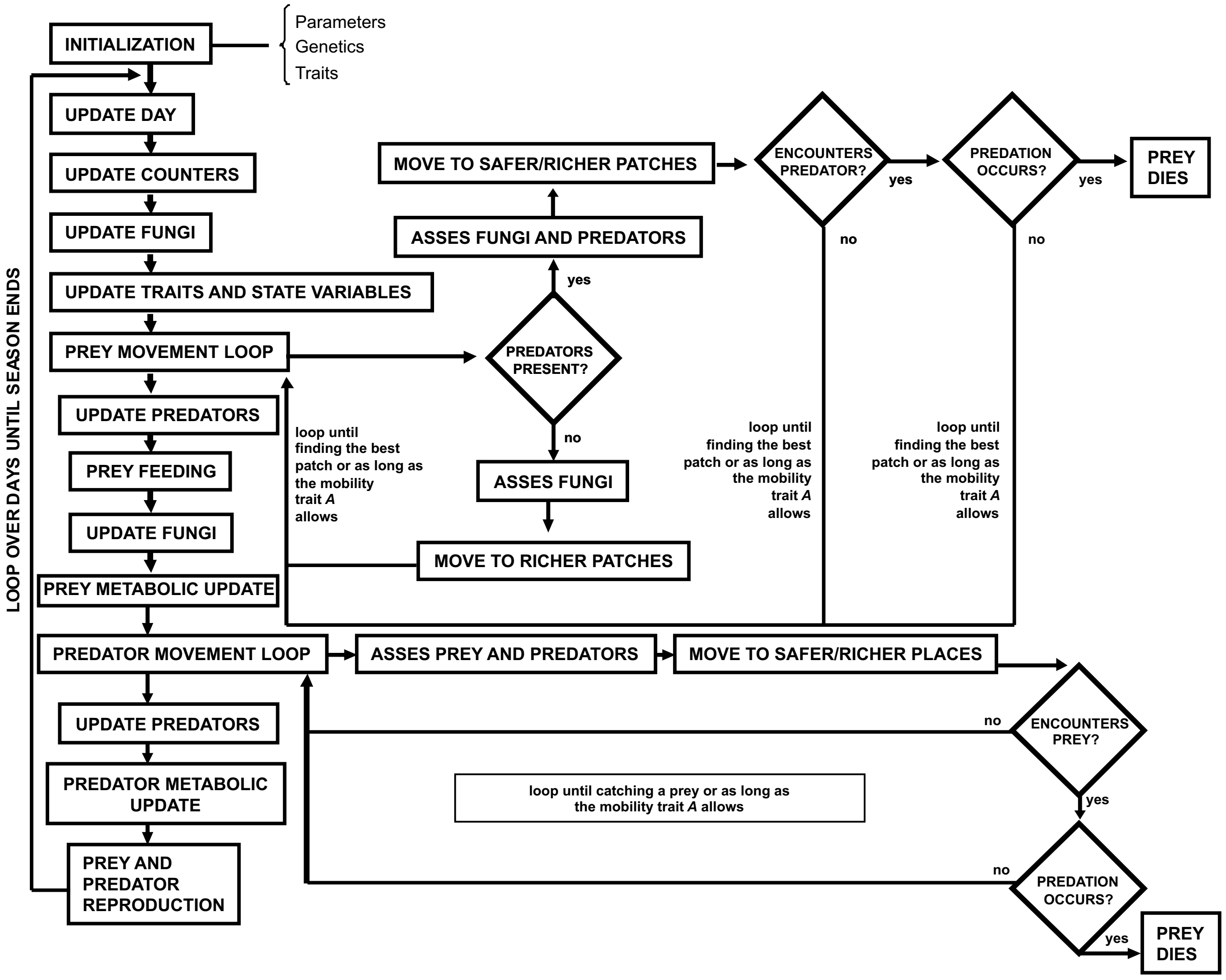


Figure 2: Flowchart of the Individual-Based Model. Each time step is one day and simulations were run for 120 days starting with 500 prey and 50 predators.

Table 1. Phenotypic modules and traits, with the trait ranges used in the simulations and the sign of the genetic correlations among traits within modules

MODULE	TRAIT NAME	ABBREVIATION/S	DESCRIPTION	Range for prey	Range for predators	r sign*
1	ENERGY TANK	tank_ini, ε_0	proportion of body mass devoted to maintenance, growth and reproduction	0.3125-0.4375	0.3125-0.4375	-,-
1	GROWTH	g	linear growth ratio from instar to instar	1.0325-1.0775	1.0575-1.1525	-,+
1	PHENOLOGY	pheno	birth date (in days)	4-8	5-9	-,+
2	BODY SIZE AT BIRTH	size_ini, B_0	fixed, structural body mass at birth (in mg)	0.00875-0.01175	0.01575-0.01875	-,-
2	ASSIMILATION EFFICIENCY	assim	proportion of ingested food that is converted to own mass	0.75-0.85	0.75-0.85	-,+
2	VORACITY	v	scaling coefficient of 0.1M^v , where M is body mass	0.625-0.675	0.625-0.675	-,+
3	SPEED	s	scaling coefficient of 4M^s , where M is body mass	0.15-0.25	0.15-0.25	+,+
3	SEARCH AREA	search_area, m	scaling coefficient of M^m , where M is body mass	0.25-0.35	0.15-0.25	+,+
3	METABOLIC RATE	met_rate, a	scaling coefficient for the mass dependence of metabolic rate	0.725-0.775	0.625-0.675	+,+
4	Q10 ON VORACITY	vorQ10	Q10 on v	2.5-3.5	2.5-3.5	-,-
4	Q10 ON SPEED	spdQ10	Q10 on s	1.75-2.25	1.75-2.25	-,+
4	Q10 ON SEARCH AREA	srchQ10	Q10 on m	1.75-2.25	1.75-2.25	-,+
5	ACTIVATION ENERGY ON METABOLIC RATE	E_{met}	Activation energy of metabolic rate (in electron-volts)	0.6-0.7	0.35-0.45	

* Sign of the additive genetic correlation with the other two traits in the module, left sign corresponds to the first acompanying trait in the module as read from top to bottom, right sign to the second

framework assumes that eco-evolutionary stability may occur at a scale across simulated communities in the different micro-sites, which we will be able to explore when migration among -micro-sites- communities is included in future versions of the model. Here we merely focus in the outcome variability and the general patterns emerging among replicates, and consider that the longer the three-species community persists (i.e.; there is biomass present for the three trophic levels) in a given micro-site, the more that particular micro-site will contribute to the overall stability of the system across the landscape. To estimate the magnitude of trophic cascades, we ran the same simulations (replicates) both with and without predators. This also allowed us to explore two biotic environments that affected selection on prey: one driven only by intraspecific competition (without predators) and another in which both competition and predation were included as selective agents acting upon prey. Therefore, we also constructed a bi-dimensional O matrix in the following bi-factorial simulation experiment, which included 5 replications of each O matrix combination: predators present at 16, 20 and 25ºC and predators absent at 16, 20 and 25ºC. The two axes of the O matrix (predators and temperature) were perfectly orthogonal (uncorrelated), thus approximating the scenario of Box 1c. In order to explore how genetic correlations and the G-matrix could constrain eco-evolutionary dynamics, we further replicated the simulations for two levels of genetically-based (or genotypic) phenotypic integration (ρ=0.1 or 0.9). The temperatures chosen were within those recorded in the beech forest leaf-litter during the summer (Melguizo-Ruiz et al. in press), where the simulated animals live (Ehnes et al. 2011). This involves temperatures that are just below optimal for most functional traits (Dell et al. 2011, Englund et al. 2011), thus we are simulating only the rising part of the unimodal relationship between temperature and trait performance. Simulating the falling part (i.e.; when trait performance decreases as temperature increases beyond a threshold) is far more challenging because heat shock proteins and water loss (Chown 2011) may need to be considered.

2.3. Statistical analyses

2.3.1 Testing for differences in selection across environments

In order to elucidate if our simulations could capture differential evolution from natural selection across environments, we tested for statistical interactions between components of the O matrix (i.e., the matrix of variance-covariance environmental components potentially acting as selective agents: predator presence/absence and temperature) and trait values (i.e., the phenotypic variance-covariance matrix before selection) on fitness. This was estimated as the probability of laying at least one egg batch (i.e., of reproducing at least once). We analysed two models, one for each G-matrix type (ρ=0.1 and ρ=0.9), and each including all the simulations for that particular G-matrix (3 temperatures x 2 predator presence/absence x 5 replicates = 30 simulations totalling 15,000 individuals, as only individuals for generation 0 were used). Despite the large sample size, the resulting number of terms in a full GLM model (binomial error and logit link function in R function “glm” within library “stats”) was too high and this could lead to collinearity problems, especially when traits were highly correlated with each other. To partially solve this problem and although collinearity may still leave important traits outside the picture, we used the “step” function in R (library “stats”), which is based on the Akaike’s Information Criterion (AIC), to remove terms of the model until a sufficiently satisfactory low AIC was attained (Moya-Laraño and Wise 2007; for an example to study selection gradients see Fernández-Montraveta and Moya-Laraño 2007). This model was then tested for the significance of the terms by running a Generalised Linear Mixed Model with simulation number included as a random factor (R library “lme4” and function “lmer”). As the identity of the simulation accounted for a negligible proportion of the variance (not shown here), we then ran Likelihood Ratio tests on the original GLMs, which allowed testing for the overall significance of interactions; i.e., across all groups/levels involved. Since our primary aim was simply to provide an example, differential directional selection across environments was visualised for only one trait. For this we used the library “effects”, which is most appropriate to depict in two-dimensional space the nature of interaction terms from complex models, even for curvilinear patterns of interactions (Fox 2003).

2.3.2 Estimating selection gradients in two contrasting environments

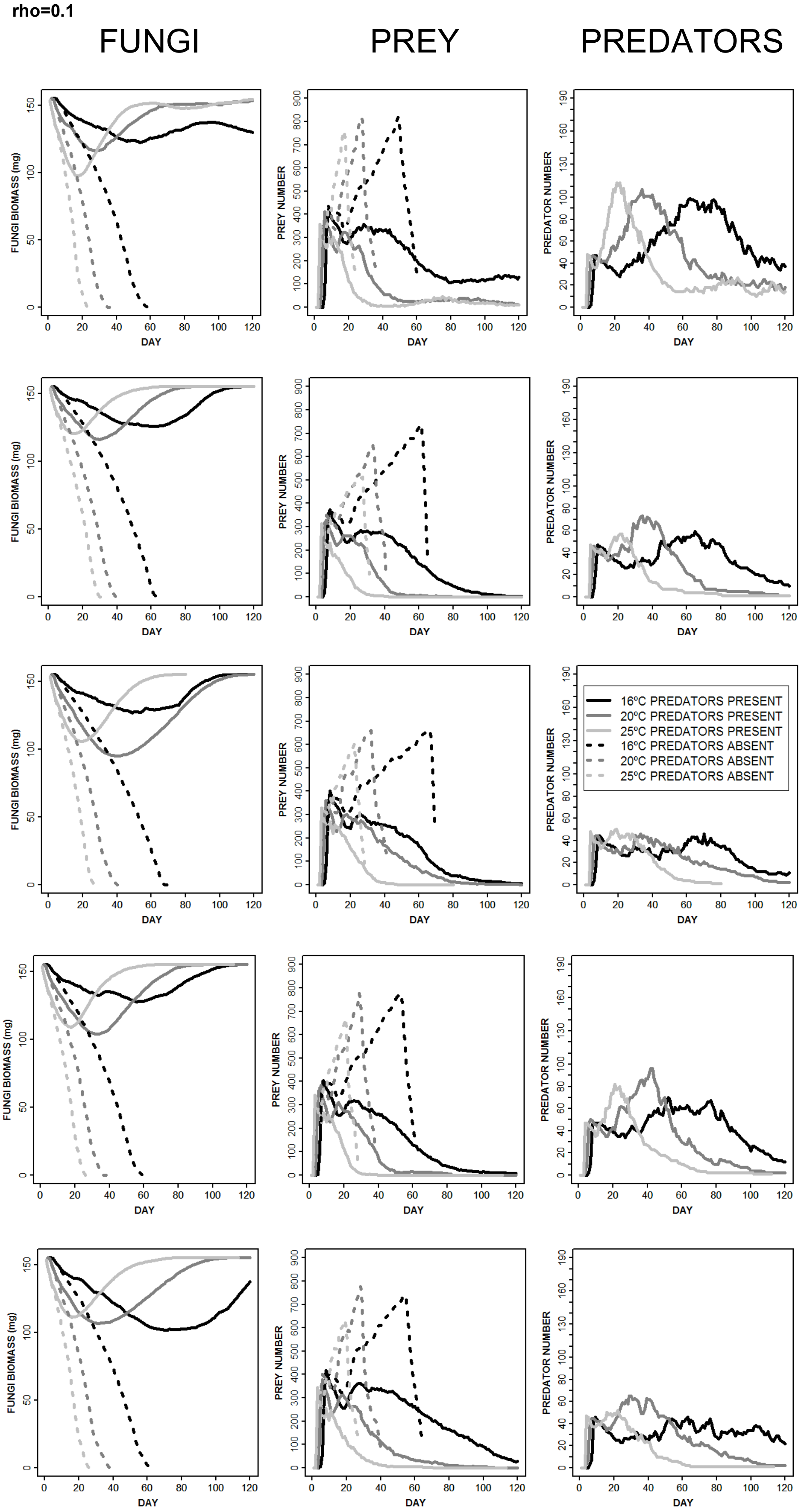
We estimated linear selection gradients (β) to test for directional selection, and non-linear selection gradients (γ) to test for stabilising, disruptive or correlational selection (Lande and Arnold 1983, Arnold and Wade 1984a,b and Phillips and Arnold 1989). In stabilising selection ($\beta>0$, $\gamma<0$), an optimal mean trait value is favoured and the tails of the distribution are selected against. In disruptive selection, the tails of the distribution are favoured and the mean is selected against ($\beta<0$, $\gamma>0$). In correlational selection, the directional selection gradient of a trait changes (whether positively or negatively) for different values of another trait (i.e., a statistical interaction). Since our purpose was to merely show how our simulation framework can be used to detect selection on new trait combinations in different environments, we analysed only the two most extreme environments among those simulated (16ºC without predators present vs. 25ºC with predators present), reflecting the least and the most stressful conditions for prey. Here we used as our relative fitness estimate the number of offspring laid by each individual (lifetime fecundity) divided by the average fecundity in the population. We ran three GLM models for each environmental combination, one to test for directional selection in all traits, another for testing for stabilising selection, for which we added quadratic terms for all traits, and another for testing for correlational selection of pairs of traits, for which we included all the possible 2-way interactions between traits. As above, for each model we selected a subset of traits and trait products by using the step algorithm and AIC (library “stats”, functions “glm” and “step”). The lowest AIC appeared for either stabilising or correlational selection. We finally combined both models into one which contained the entire set of parameters for the final correlational selection model plus the highly significant quadratic terms ($p<0.01$) of the stabilising selection model. This final model was the most parsimonious (lowest AIC) for all environmental and G-matrix combinations. Again, for visualising fitness surfaces and patterns of selection in just a few traits as an example, we used the library “effects” (Fox 2003). The output of the library “effects” are estimations of partial effects rather than fits, and thus the data points are not displayed. However, this has the advantage over conventional cubic spline techniques (Schluter 1988, Schluter and Nychka 1994) that it allows visualising complex combinations of traits and their interactions in a two-dimensional space, thus allowing easy interpretation of the type of selection. Indeed, when patterns of selection appeared to be complex (e.g. when a trait had significant interactions with other traits as well as significant quadratic terms), we applied splines (R library "splines", function "bs") to the trait and plotted their interaction with some of the other traits. Directional selection appears as a linear fit, stabilising selection is described by a hump-shaped curve (indicating maximum fitness at intermediate trait values) and disruptive selection with a U-shaped curve (indicating maximum fitness for extreme phenotypes of that particular trait).

3. Results

3.1. From Evolution to Ecology

3.1.1 Trophic cascades

We were able to successfully simulate top-down control that cascaded from predators to fungi. Predators were able to rescue fungi from extinction in all simulations (Figure 3). Without predators, prey populations grew faster and maintained fast growth for longer than when predators were present (note that the initial steep slopes correspond to the births of the 500 initial eggs and not to reproduction occurring within the simulation), and as a consequence prey overgrazed fungi and went extinct a few days later. As expected, the dynamics of overgrazing and extinction were faster at warmer temperatures and extinction of fungi and prey occurred earlier. Although either prey or predator extinction occurred in most replicates, predator presence allowed the persistence (until the end of the season at day 120) of the three-trophic interaction in a few of the replicates, particularly at cooler temperatures. The strength of trophic cascades (i.e.; the difference in fungi biomass in simulations with predators present vs. those with predators absent) tended to be higher at warmer temperatures. However, the earlier extinction of predators was more likely at warmer temperatures. In addition, the effect of temperature on trophic cascades also depended on the G-matrix (parameter ρ), with stronger genetic correlations increasing the stochasticity of the dynamics and leading, in some simulations, to predator-prey-fungi cycles. These population cycles were more apparent at warmer temperatures, likely because the amplitude of the cycles is longer at cooler temperatures and could not be detected with only 120 days of simulation.



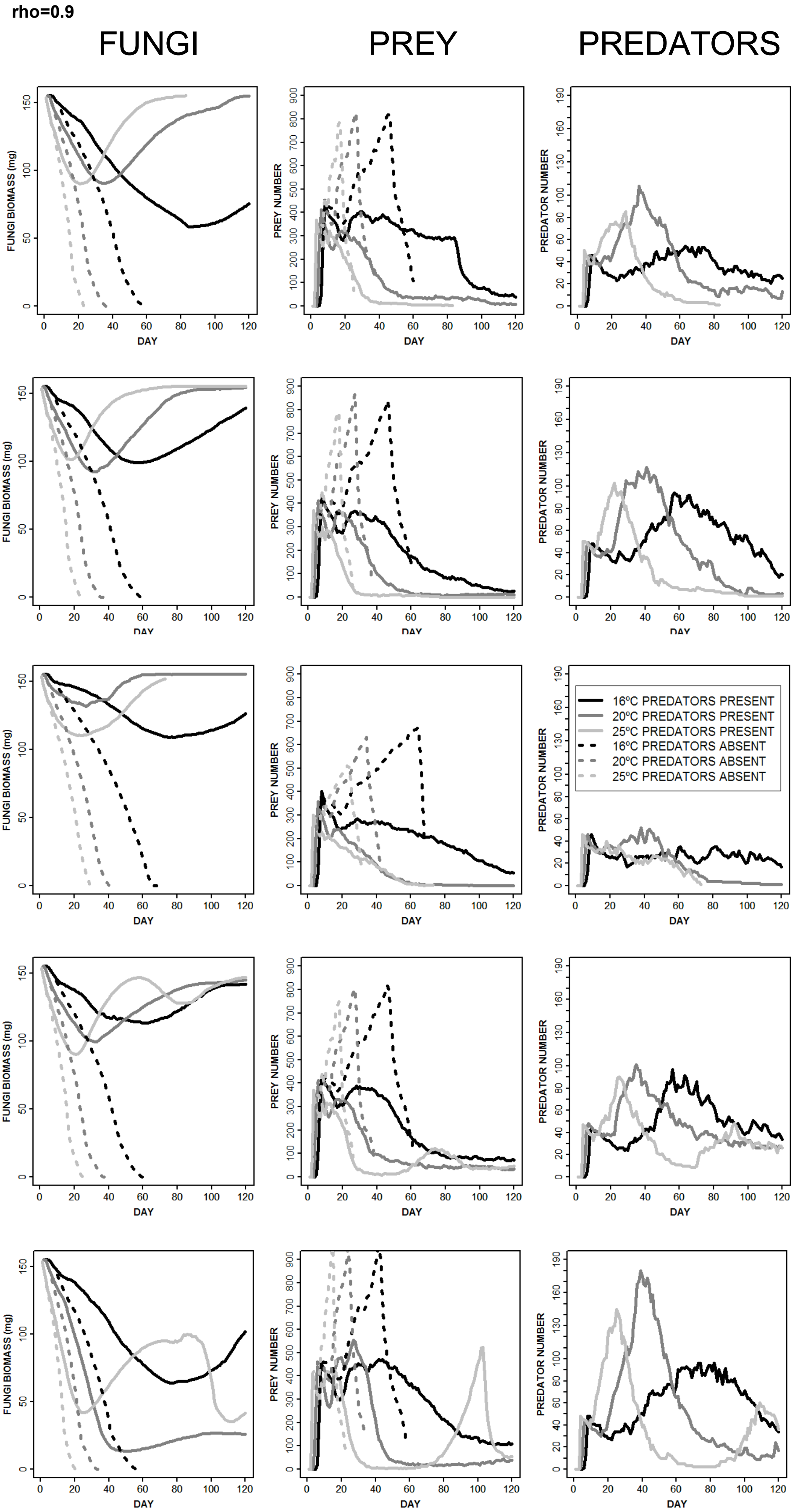
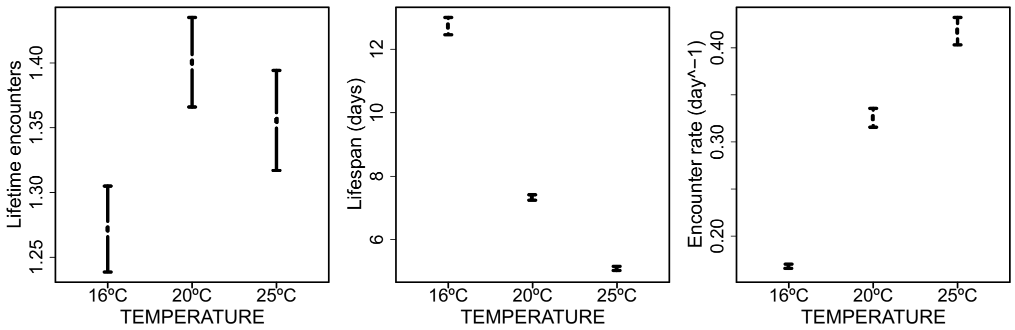

rho=0.9
FUNGI
PREY
PREDATORS
FUNGI BIOMASS (mg)
PREY NUMBER
PREDATOR NUMBER
DAY
16ºC PREDATORS PRESENT
20ºC PREDATORS PRESENT
25ºC PREDATORS PRESENT
16ºC PREDATORS ABSENT
20ºC PREDATORS ABSENT
25ºC PREDATORS ABSENT

Figure 3: Fungi (basal resource, left column), prey (middle) and predator (right column) population dynamics for the 120 days of simulation. Five replicates for each of two genetic correlation levels among the traits (ρ = 0.1, 0.9) are shown. There was a clear predator-prey-fungi cycle in the last replicate (ρ = 0.9). Simulations ran for a number of prey generations ranging from 4 to 21 and 4 to 8 predator generations. The maximum number of generations was achieved in the last replicate (ρ = 0.9) at the warmer temperature. Dynamics in fungi not leading to actual extinctions are truncated intentionally at the time predators went extinct.

a) rho=0.1



b) rho=0.9

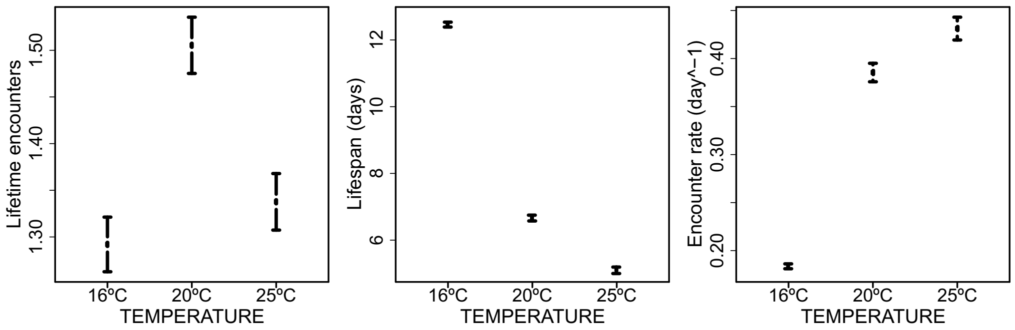


Figure 4: Lifetime number of encounters for prey (left panels), lifespan (mid panels) and encounter rates (day^{-1}, left panels) with predators for two levels of correlation among traits.

3.1.2 Encounter rates

Across replicated simulations, prey tended to encounter more predators per capita during their lifetime as temperature increased (Figure 4). However, this depended on the G-matrix as, although the relationship between temperature and encounter rates was not linear for both levels of trait correlation, there was a clearer peak with higher encounter rates at intermediate temperatures when traits were correlated (ρ=0.9). As expected, lifespan was shorter at warmer temperatures, decreasing by ca. 50% from the lowest to the highest temperatures.

After eliminating the effect of lifespan we detected a linear pattern for the effect of temperature on encounter rates (day-1), which indicates higher predation risk at higher temperatures.

From the point of view of the predator, the pattern was very similar (Figure 5), with the exception that the trend for lifetime encounters went from non-linear when traits were uncorrelated, to linear when they were correlated. Therefore, despite a trend for shorter lifespans at warmer temperatures, the number of encounters (not just the rate) was higher.

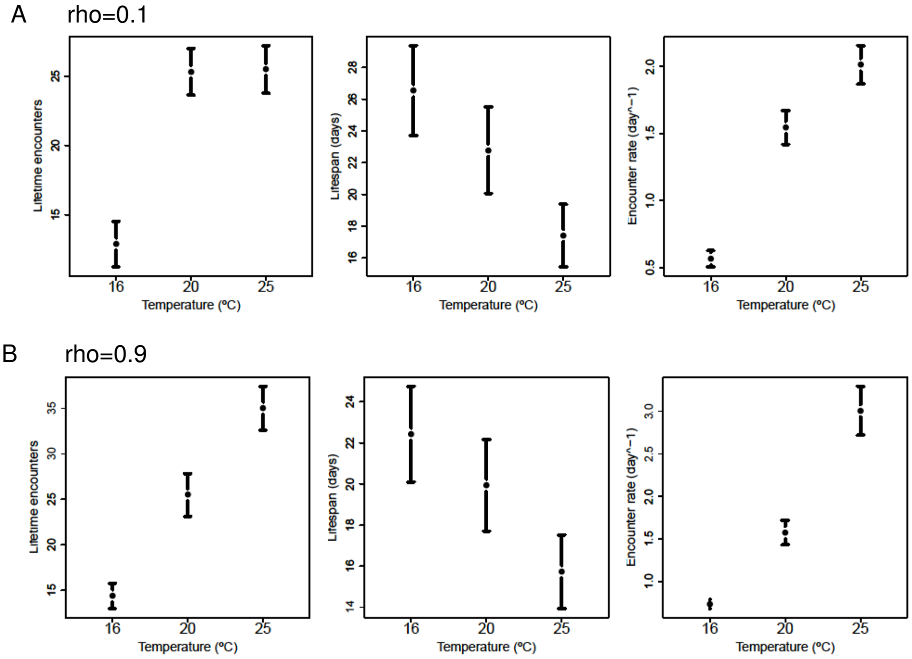


Figure 5: Lifetime number of encounters for predators (left panels), lifespan (mid panels) and encounter rates (day^{-1}, left panels) with prey for two levels of correlation among traits.

3.2. From Ecology to Evolution

3.2.1 Testing for differences in selection across environments

Differential directional selection across environments occurred in more traits (more three-way highly-significant interaction terms entered the final model) when the G-matrix was less constraining (ρ=0.1) than when traits were highly genetically correlated to each other (ρ=0.9). We detected highly significant differences in selection across the two-environment combinations for 10 traits, while only 5 were found for high correlation values (Appendix Table 1). Figure 6 shows the three-way interaction (R library "effects" – Fox 2003) for the trait growth (growth ratio). Selection for smaller growth ratios was stronger at cooler temperatures only when predators were absent.

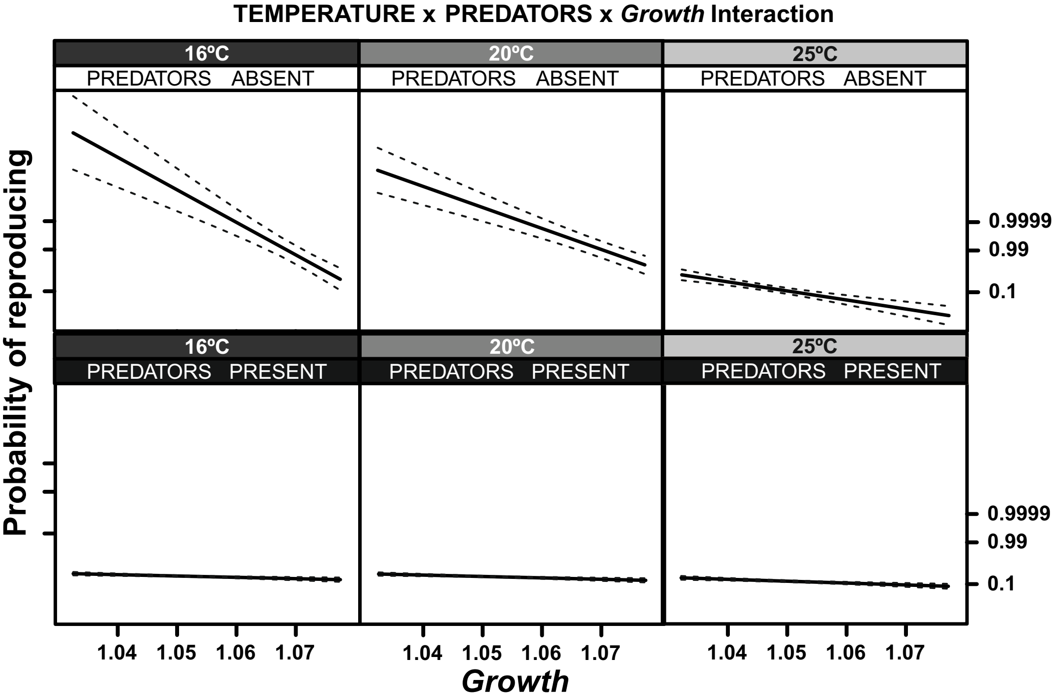


Figure 6: Environment (O matrix) x *Growth* interaction in fitness showing differences in the strength of directional selection for the trait *Growth* ratio across environments. Steeper relationships indicate stronger selection favouring smaller growth ratios.

3.2.2 Estimating selection gradients in two contrasting environments

In general, selection gradients were weak (<|0.1|, Appendix Table 2), although they were stronger (>|0.1|) when the traits were strongly correlated to each other (ρ=0.9). Strong (>|0.5|) selection gradients were also found in the activation energy for metabolic rate. When genetic correlation was strong, we also found some emerging trait combinations with sufficiently strong selection gradients (>|0.1|) for traits that were previously uncorrelated, such as for activation energies and several other functional traits (Appendix Table 2). Remarkably, in the least stressful environment (low temperatures without predators) we found only 6 examples of sufficiently strong correlational selection (>|0.1|), whereas 15 cases were found in stressful environments, at high temperatures with predators. We mention some of these trait combinations as examples: for instance, at 16ºC without predators, the plastic response for temperature-dependent mobility (srchQ10) interacted with selection on assimilation efficiency (Appendix Table 2). Visual inspection of the interaction plot (R library “effects”, Figure 7a) shows how the extreme values for both traits in combination (either both high or both low) lead to the highest relative fitness. Also, at 25ºC with predators present, phenology interacted with the temperature-dependent voracity (vorQ10, Appendix Table 2). Again, visual inspection of the interaction plot (Figure 7b), showed that early birth combined with lower plasticity for voracity or late birth with high plasticity gave the highest fitness combinations. Another example was the interaction of temperature-plasticity for searching area (srchQ10) with growth ratio (Appendix Table 2). Selection favoured the extremes, with lowest growth ratios being favoured together with low temperature-plasticity for searching area, and vice-versa (Figure 7c). In general, the combination of traits and the magnitude of the selection gradients were very different for the two environments (Appendix Table 2), suggesting a role for both abiotic (temperature) and biotic (predator presence) factors, and the interaction between them. Traits for temperature-adjusted activity were generally more frequently significant (i.e., they were more likely under selection) in the models at warmer temperatures with predators.

The strongest selection occurred on activation energy for metabolic rate, which had very strong linear terms and highly significant quadratic terms in all models. However, the sign of the quadratic term changed from negative in environments at 16ºC, with an absence of predators, to positive in environments at 25ºC with predators. The interpretation of these selection gradients is not straightforward because although the linear term was positive and the quadratic term was negative at cooler temperatures without predators, suggesting stabilising selection, both signs were positive at warmer temperatures with predators. Additionally, because this variable showed correlational selection with other variables, disentangling the nature of this complex pattern of selection required us to look deeper into the interaction terms. To do this, we applied splines to activation energies and plotted their interaction with some of the other traits. We found that selection on activation energies could be directional (linear), stabilising (hump-shaped) or disruptive (U-shaped) depending on the values of the other traits (Figure 8) and on the environment: stabilising selection was observed at cooler temperatures without predators and disruptive selection at warmer temperatures with predators. This suggested unexpectedly complex patterns of non-linear correlational selection.

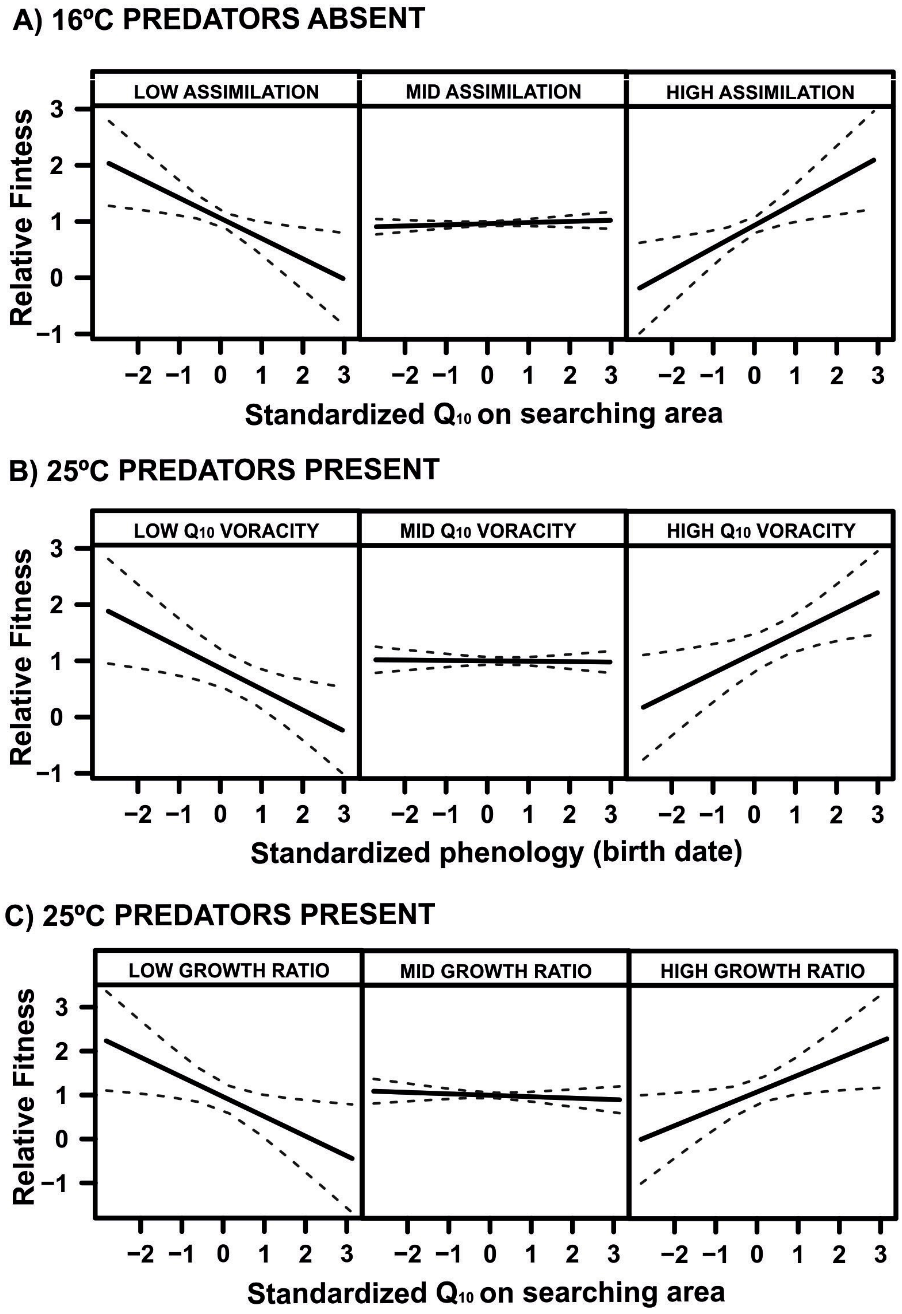
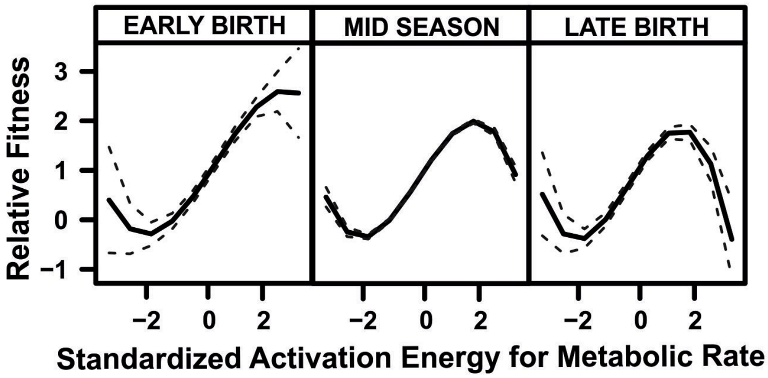
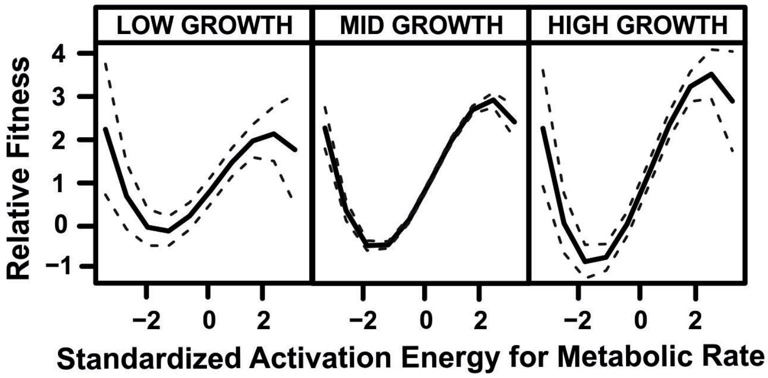


Figure 7: Examples of correlational directional selection on functional traits in two contrasting environments. a) assimilation efficiency x Q_{10} on search area at cooler temperatures with predators absent. b) Q_{10} on voracity x phenology (emergence date) at warmer temperatures with predators present. c) Growth ratio x Q_{10} on search area at warmer temperature with predators present.

A) *Phenology* at 16ºC PREDATORS ABSENT



B) *Growth* at 25ºC PREDATORS PRESENT



C) *Voracity* at 25ºC PREDATORS PRESENT

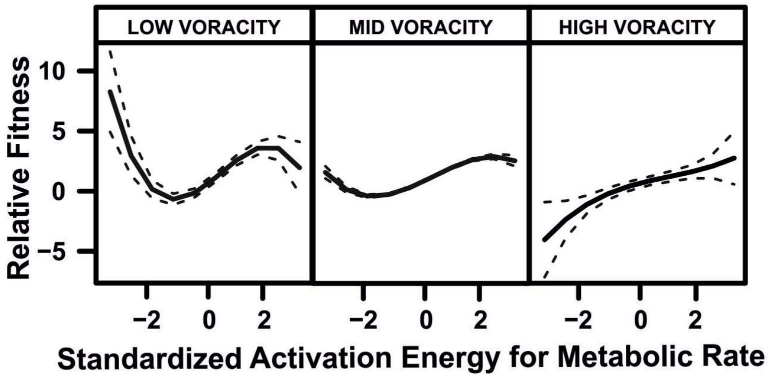


Figure 8: Complex fitness surfaces showing non-linear correlational selection for activation energies of metabolic rate in contrasting environments. a) At cooler temperatures without predators, and depending on emergence date (phenology) selection on activation energies can go from directional (early emergence, left panel) to (hump-shaped) stabilising (late emergence, right panel), b) At warmer temperatures with predators, and depending on the magnitude of the growth ratio, the depth of the disruptive selection (U-shaped) valley increases from low growth ratios (left panel) to high growth ratios (right panel) indicating an increase in the strength of disruptive selection on activation energies for metabolism with growth ratio, c) At warmer temperatures with

predators, and depending on the level of voracity, selection on activation energies can go from (U-shaped) disruptive (low voracity coefficient, left panel) to (lineal) directional (high voracity coefficient, right panel). Note that a high coefficient for voracity means lower voracity (see the Appendix).

4. Discussion

We have introduced an eco-evolutionary individual-based simulation framework that links genes to ecosystem dynamics through multiple traits that affect interactions in ecological networks. By simulating different ecological scenarios (O matrices of selective agents) and framing interactions in the context of the MTE (Brown et al. 2004), we have successfully shown how climate change can have profound effects on eco-evolutionary dynamics on trophic cascades within food webs. Evolutionary history, modelled as the degree of genetic correlation among traits, can modulate how temperature affects food web dynamics. Simulations at higher temperatures resulted in patterns that were more stochastic but that led to the earlier emergence of predator-prey-fungi cycles (and only in scenarios with high genetic correlations among traits). Our results and approach have implications for not only understanding complex eco-evolutionary dynamics and related ecosystem responses under different climate change scenarios, but also contribute to increasing our knowledge of how suites of traits evolve and how diversification rates change across climatic gradients.

Our approach can also be easily adapted to the applied sector, by using it to design adaptive pest control strategies to cope with climate change. It also opens up many exciting new prospects for future research, for instance via contrasting eco-evolutionary neutral theories (Melián et al. 2011) with meta-community functional eco-evolutionary dynamics and the geographic mosaic of coevolution.

4.1. Temperature-dependent lifetime encounters, predator-induced stress and latitudinal diversity gradients

Not surprisingly (Brown et al. 2004, Moya-Laraño 2010, Petchey et al. 2010, Dell et al. 2011) the output of the simulations showed that encounter rates between predators and prey - which were merely allowed to emerge from temperature-dependent traits rather than forced – increased with temperature. Since higher encounter rates with predators exerts more stress on prey, global warming may affect ecosystem dynamics both directly and indirectly, simply by increasing predator threat and non-consumptive effects (Hawlena and Schmitz 2010a). In addition, despite confirming the expectation that lifespan would shorten at warmer temperatures, lifetime encounters, not just encounter rates, tended to be higher at warmer temperatures. This represents the main assumption for a new hypothesis that adds to the mechanisms used to explain latitudinal diversity gradients from biotic interactions (Moya-Laraño 2010, see also Currie et al. 2004, Schemske 2002, Schemske et al. 2009, Purdy et al. 2010). According to this hypothesis, higher temperatures (and also water availability in terrestrial ecosystems) increase the frequency and diversity of interactions in the tropics, mechanisms that could enhance the maintenance of genetic variation, the evolution of phenotypic flexibility, and the occupancy of vacant niches. This combination of effects should lead to higher diversification rates and also the maintenance of high diversity in the tropics. In fact, the lifetime encounter-diversity relationship may be even more complex because the number of lifetime encounters varied differently with temperature depending on the level of genetic correlation among traits. In addition, below we show an important and previously neglected mechanism that could contribute to fuel diversification in interaction-rich environments, such as tropical habitats: correlational selection.

4.2. Correlational selection, diversification and ecosystem resilience

Ecology, in the form of abiotic (temperature) and biotic (predator presence/absence) factors (the O matrix – MacColl 2011), also affected evolution by natural selection. However, as expected (Lande 1979), these ecological effects also depended on the genetic architecture of the traits. In addition, when directional selection was considered more traits were differentially affected in different environments when they were weakly correlated among each other. Due to its implications for evolutionary responses, the long-term stability of G-matrices and its causes are an increasing focus of research activity (Jones et al. 2003: Sgrò and Hoffmann 2004, Roff and Fairbairn 2007). Thus, the initial genetic architecture, and perhaps subsequent evolution by natural selection, can affect ecological dynamics and is likely to produce important eco-evolutionary feedbacks. Furthermore, by specifically testing for correlational selection, we discovered new trait combinations that positively affected prey fitness, particularly when correlation among traits was high. Also, different trait combinations were selected at different temperatures, leading in some environments to trait interactions that provided equal fitness at opposing ends of the trait ranges (Figure 7). Since correlational selection may be a powerful source of diversification (Whitlock et al. 1995, Calsbeek and Irschick 2007), our findings may help to understand which traits contribute to diversification in different environments. This is likely to be especially pertinent when we consider the multidimensional diversifying power of biotic interactions and the room for indirect genetic effects to be manifested in ecological networks (Shuster et al. 2006, Nosil 2008, Doebeli et al. 2010, Moya-Laraño 2010, 2011, 2012).

Most importantly, by simulating all the combinations for two orthogonal axes of variation in the O matrix (temperature and predator presence/absence), we found that correlational selection was more prevalent (more cases of moderately strong selection) in biotically rich environments: i.e.; those in which prey had to deal with predators, and at higher temperatures (where encounter rates were higher), as is likely in the tropics. For correlational selection to be a source of new heritable trait combinations to accelerate diversification, however, selection pressures need to be persistent in sign and magnitude for many generations. This reflects the time needed to allow genome reorganisations to occur, as at each generation recombination breaks the linkage disequilibrium achieved by correlational selection (Sinervo and Svensson 2004, McKinnon and Pierotti 2010).

However, recent findings (Delph et al. 2010) may give a new twist to the diversification power of correlational selection and could be key to our own findings, as it appears that correlational selection can break genetic correlations when new selective pressures come into play, thus de-stabilising the G-matrix. While evolving new genetic correlations may depend on the emergence of new genetic material (e.g. pleiotropic mutations – Jones et al. 2003), genetic correlations may be broken by correlational selection acting on standing genetic variation. Although the exact mechanism is still unknown (Delph et al. 2010), it should occur at ecological timescales (Box 1c). This has important consequences for global warming because the appearance of novel selective pressures with increased temperature (Berg et al. 2010, this paper) could break otherwise stable genetic correlations and diversify the number of interactions in multidimensional space (Moya-Laraño 2011). This should increase the number of possible pathways for populations to avoid extinction and to maintain ecosystem functioning, which could be a novel mechanism for conferring ecosystem resilience, as rapid evolution after a perturbation (novel selective pressures) could increase trait multidimensionality, thus enhancing food web connectance and stability (Moya-Laraño 2011).

4.3. Contemporary evolution and the rescue of populations under climate change

That evolution by natural selection can occur at ecological timescales and that this selection can be diversifying and strong has enormous implications for climate change research. Leaving mutation rates apart, if there is enough multidimensional genetic variability in species embedded in food webs, a gradual increase in temperature from year to year could be buffered by dispersal and range shifts, as well as plastic responses and responses to natural selection from the new selective pressures imposed by warming (Berg et al. 2010, this paper). In addition, the role of correlational selection increases with temperature and interaction rates may stimulate adaptive evolution over ecological timescales. This is of central importance for food webs, as recent work (Rall et al. 2010, Vucic-Pestic et al. 2011) has shown that although predators may increase feeding performance (e.g. ingestion rates, handling time), metabolic rates do still increase at a rate that is comparatively higher. This can suppress predator survival, and may cause extinctions, as recently demonstrated experimentally (Barton and Schmitz 2009). However, even though on average predator populations would decrease in fitness with rising temperatures, correlational selection could favour those phenotypes which display a better balance between the traits involved in trophic interactions and metabolic rate, finally rescuing the population exposed to warming. That activation energies for metabolism display correlational selection with few other functional traits, and that the fitness surface for activation energies changes depending on the environment and the level of the trait with which it interacts, suggest these possibilities are worth further exploration.

4.4. Growth ratio and temperature: implications for the evolution of body size under global warming

We illustrated the joint effects of temperature and predator presence/absence upon prey with the example of the growth trait, which measures the linear increase in fixed body size between instars. While there was no clear pattern of temperature affecting growth when predators were present, selection favouring smaller growth ratios was stronger (steeper slopes) at cooler temperatures when predators were absent. This could mean that for the smallest animals, when there is no predation risk, early reproduction at lower temperatures is favoured over the benefit of having larger body sizes. This contrasts with the widespread idea that global warming (higher temperature) leads to smaller body sizes (Daufresne et al 2009, Sheridan and Bickford 2011, O'Gorman et al 2012). However, selection gradients are by definition partial effects on fitness, and when the effect of traits that are directly affected by temperature are considered via multiple regression (including complex correlational selection with activation energy for metabolic rate, Figure 8b), the net effect of selection and the overall intergenerational response to it will not necessarily favour evolving smaller body sizes at cooler temperatures. Furthermore, developmental rates are more closely dependent on temperature than are growth rates (Forster et al. 2011). Evolution can potentially target either a given body size or an age at maturation both of which can have a quantitative genetic basis and can be genetically correlated to each other (Roff 2002). For instance, artificial selection experiments show that selecting for small adult body sizes leads to shorter maturation ages (Teuschl et al. 2006). However, selection for larger body sizes, in addition to longer developmental times, lead to higher growth rates (Teuschl et al. 2006). Thus, the combination of genetic variation in several traits is what explains in turn the genetic variation of the associated growth and development rates. Therefore, since temperature affects growth and development rates, if evolution targets early development (and timing of maturation), for instance in short-lasting environments such as temporal ponds, higher temperatures will lead to adults of smaller body sizes because in that time interval metabolic constraints will allow lower net growth. However, if body size is targeted by natural selection (i.e. larger is better, for instance by enhancing fecundity), and unless compensated by other traits or if there is predatory pressure (this paper), higher temperatures and higher energetic demand will make maturation times longer for the same targeted body size, leaving population body size eventually unaffected. Distinguishing between the two contrasting targets of selection (maturation timing vs. maturation size) will involve considering moulting time (developmental rate) as an additional evolvable trait. Here, in the absence of predators our competitive environments were short lasting because populations crashed very quickly (near day 60 Fig. 3). Thus, early reproduction with smaller body sizes would have been favoured more likely in warmer environments, which lasted for shorter. However, since we did not simulate the maturation time trait per se, selection in our simulations favoured smaller growth ratios and thus smaller maturation sizes. Why selection for growth ratio was stronger in cooler environments could merely depend on the longer duration of the cool vs. the warm environment and the balance between growing more slowly, the duration of the system and selection on other traits. A close look to the patterns of the timing of reproductive events and death dates (not shown) shows that there is a stronger peak of death early in life at warmer vs. cooler temperatures when predators are not present, likely suggesting stronger selection on relevant traits other than growth rates at warmer temperatures which could explain the weaker selection in growth ratios.

4.5. Activation energy for metabolic rate: is adaptive evolution possible?

We found strong selection ($\beta > |0.7|$) for the activation energy of metabolism, but not for other traits. When the nature of this correlational selection was disentangled by plotting the fitness surfaces of activation energies for different values of other traits, we found evidence for directional, stabilising, or disruptive selection. This is despite the activation energy not being correlated with any other trait in the G-matrix. This contrasts with the empirical evidence and constraints put forward by the MTE, which suggests a value for activation energies for metabolism between 0.6 and 0.7, and high conservatism across the tree of life and different ecosystems (Brown et al. 2004, Yvon-Durocher et al 2012). Thus, although natural selection could produce different optima for activation energies far away from the 06-0.7 range, biochemical and physiological constraints seem to impede adaptive evolution. A recent study, however, has found abundant variability in activation energies for metabolism, both across and within species (Ehnes et al. 2011), so there may be more scope for adaptive evolution in metabolic activation energies than previously assumed. Artificial selection experiments in which the experimenter selects for higher or lower activation energies at different temperatures would confirm whether the evolution of adaptive activation energies is possible, which would represent a form of adaptive phenotypic plasticity.

4.6. Climate change can affect the evolution of temperature-plastic behavioural (personality) traits

At warmer temperatures with predators, temperature-plastic traits for activity (Q10 on voracity and search area) tended to show significant non-linear correlational selection gradients with other variables more often. This is consistent with the idea that temperature and plasticity play a central role in the evolution of biotic interactions (Berg et al. 2010, Dell et al. 2011). The environmentally-dependent genetic-phenotypic map that we have developed in our IBM (Figure 1 and Appendix) can be easily extended to include biotically-induced plasticity, such as inducible defences and associated trait-mediated indirect interactions (TMIIs), plastic personality traits (Dingemanse et al. 2010), responses to stress (Hawlena and Schmitz 2010a) and compensatory growth, among others.

Plastic behavioural traits were differently affected by the different environmental combinations in the O matrix. Voracity and its response to temperature (vorQ10) explained not only the amount of food eaten per unit of time, but also predation risk, as encounter rates with predators were higher for the most voracious animals (Appendix). Similarly, searching area and its dependence on temperature (srchQ10) allowed animals to find more food, but also put them at higher risk of being predated, as they visited more patches per unit of time. Therefore, as at least for prey, voracity and search area are surrogates of boldness, a composite behavioural or “personality” trait. Such traits can be important in eco-evolutionary dynamics because they may explain patterns of prey selection (Pruitt et al. 2012) and food web structure (Moya-Laraño 2011). As we found that plasticity on these traits may evolve differently at different temperatures and depending on the predator presence or absence (Appendix Table 1), climate change can affect the evolution of plasticity in animal behaviour or "personalities".

4.7. Future directions

4.7.1 Food Web Engineering: biological control, climate change and eco-evolutionary dynamics

Individual based models (IBM) linking evolutionary and food web dynamics may become essential for evaluating how climate change affects pest control. Although traditionally biological pest control has been approached from the "one pest – one natural enemy" perspective, species inhabiting agricultural systems interact with each other, forming complex food webs (Figure 9). Stronger links between certain components of the food web, or overrepresentation of certain modules (Bascompte and Stouffer 2009), can delimit smaller "subset" communities with 3 to 5 species that may be analysed and managed independently (Figure 9). Climate change, however, may alter these food webs and modules, as species interaction strength is commonly temperature-dependent (Beveridge et al. 2010, Gilman et al. 2010), and selection for heat resistance will act simultaneously on the whole community. The future of the management of agricultural systems will therefore require the understanding of the interplay between ecology and evolution at a community level (Pelletier et al. 2009), as changes in gene frequencies that translate into traits affecting the performance of natural enemies and their prey (Fussmann et al. 2007, Pelletier et al. 2009).

We can define Food Web Engineering (FWE) as an extension of biological pest control that integrates general theory in community ecology and evolutionary biology into specific agricultural systems, where communities are managed as a whole. When applying FWE for pest management, strategies will need to be designed to artificially alter those interactions with potential to influence the wider community (Figure 9). In agro-ecosystems exposed to rapid climate change, it will be necessary to determine the fitness-related environmentally driven traits that should be artificially selected in predators to maximise trophic cascades (Figure 9). Combining natural (or quasi-natural) selection experiments, in which

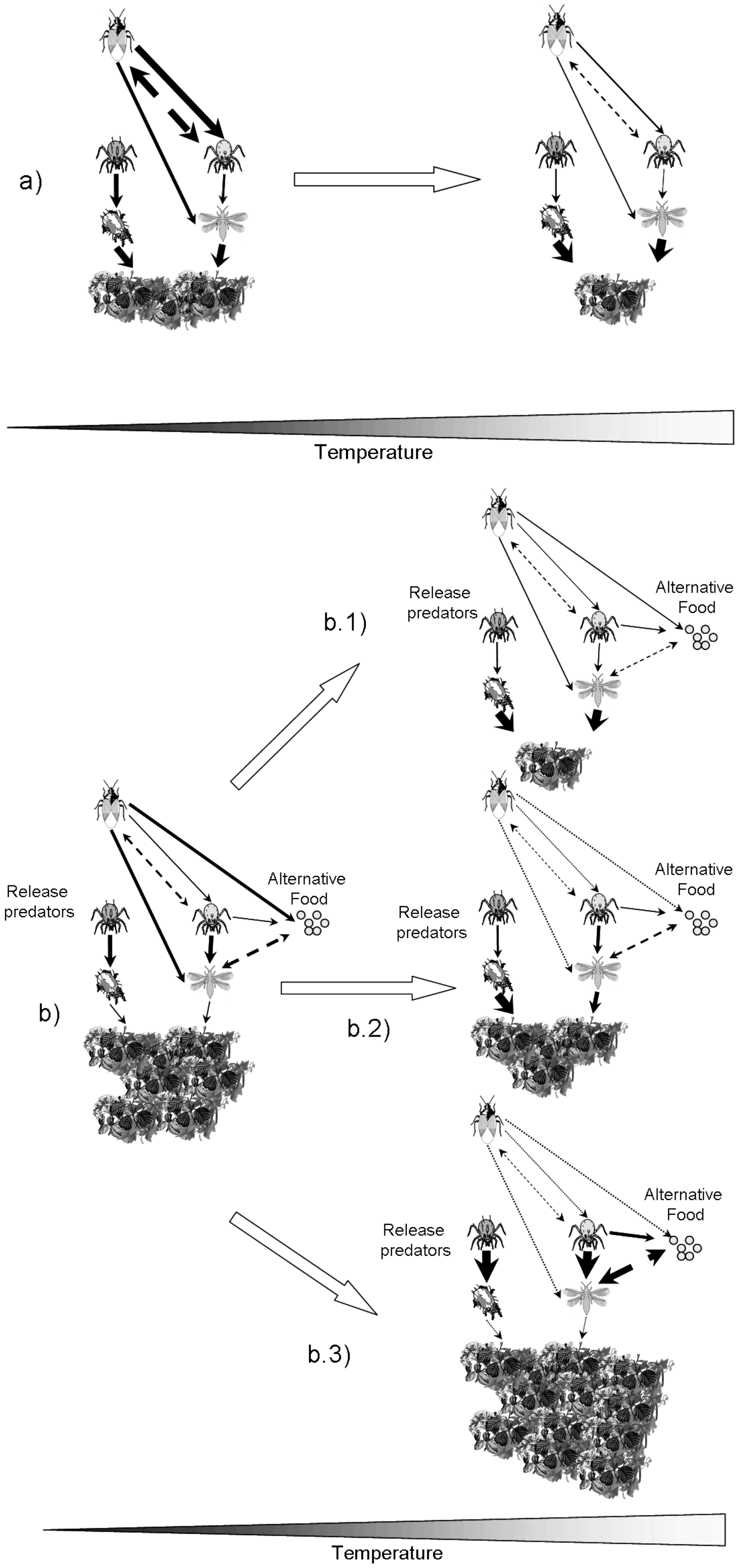


Figure 9: Temperature-dependent eco-evolutionary dynamics of a hypothetical agricultural food web. The food web is composed of two predatory mites, each one preying upon a different pest, spider mites or thrips, and a predatory bug, who is an IG-predator of one of the predatory mites,

and is the inferior competitor for the pest they share. a) non-engineered biocontrol food web under global warming. b) Three possible engineered scenarios of biocontrol under global warming. b1) Engineered food web without previous artificial selection; b2) Engineered food web with artificial selection in one direction (traits down), and only in the predatory bug, b3) Engineered food web with bidirectional artificial selection (traits up in predatory mites and down in the predatory bug). Selection and direction of the selection is designed to maximise trophic cascades. As an example, in the figure the artificial selection could have acted on predation rates and/or on reproductive conversion efficiency. Solid arrows indicate trophic interactions. Dashed arrows indicate indirect predator-predator (competition) or indirect herbivore-alternative food (apparent competition) negative interactions. The strength of the lines indicates the interaction strength.

food webs are left to evolve (Kassen 2002, Chippindale 2006, Belliure et al 2010), could be used to parameterise the whole eco-evolutionary dynamic process. IBM models could then be used to simulate the eco-evolutionary responses of communities to heat stress, as a possible basis for predicting and managing the effects of warming on pest biological control, when applying FWE to specific agricultural systems (Figure 9).

4.7.2 Neutral theories, meta-communities and the geographic mosaic of co-evolution

Our IBM models allowed the mobility of animals within each micro-site, but migration among micro-sites has not been yet implemented. Implementing migration as well as the genetic basis for dispersal and its trade-offs with other traits can expand our frame-work considerably. First, by also including neutral (non-functional) genes (not just "micro-satellites" as currently done, see Appendix), mutations and random dispersal among micro-sites, we will be able to contrast neutral eco-evolutionary dynamics (Kimura 1983, Hubbell 2001, Melián et al. 2011) with functional eco-evolutionary dynamics and eco-evolutionary meta-community dynamics. This would allow us to link community assemblages across space with micro evolution and the potential for diversification in populations with different degrees of isolation. Furthermore, by studying spatially-structured selection in complex networks, and considering random genetic and ecological drift, we should be able to disentangle the role that different traits play in the geographic mosaic of coevolution (Thompson 2005) and how continuous adaptive evolution feeds back on ecosystem functions under climate change.

One particularly important need is to increase computer capacity while maintaining simulation time reasonably short, by: 1) increasing the number of species and individuals per simulation, 2) shorten the timeframe of the simulations from days to hours or less, 3) allow more realistic 2D (or even 3D) spatial arrangements, mobility and dynamics and 4) expanding simulation time from days to years. The above can be accomplished by code parallelisation, in which different processors run different portions of the simulation at once and dynamically interchange their outputs with each other (High Performance Computing, HPC). Such a code could take advantage of hundreds of processors at once by using readily available Super-Computers, most accessible to professional researchers in the Academia, such as it is being done for solving computing-demanding phylogenies (e.g., Ayres et al. 2012).

5. Conclusions

We have introduced a new framework to explore eco-evolutionary dynamics in food webs under climate change. Our IBM approach linking genes to trophic cascades and explicitly considering the MTE is useful for documenting trophic dynamics under different warming scenarios and demonstrating how genetic constraints affect both ecological and evolutionary dynamics (i.e. the patterns of natural selection). Trophic cascades, for instance, were more important at higher temperatures and when the correlation among traits was high, but the dynamics were also more stochastic. Our simulation also revealed some important unexpected results and novel hypotheses for future testing, including how the shape of the temperature encounter relationship changes with genetic constraints. We found that the complexity of the selective environment (O matrix) can increase the chances of correlational selection, which can be a powerful mechanism fuelling diversification. We also revealed various traits that are susceptible to be of central relevance in eco-evolutionary dynamics, including behavioural “personality” traits, and that despite being highly constrained (e.g. activation energy for metabolism) there is scope for adaptive evolution. These complex patterns of potential responses to natural selection could actually serve to rescue populations of predators from extinction caused by gradual global warming. Finally, via simulating food web engineering we hope that our approach can be applied in the near future to improve pest control within the context of climate change. We also hope to extend it to compare eco-evolutionary neutral theories with meta-community eco-evolutionary dynamics and the geographic mosaic of coevolution, and the dependent ecosystem functions, when subject to climatic abiotic changes.

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Appendix

mini-AKIRA (mA, hereafter) is a semi-spatially explicit IBM implemented in the R language (R Development Core Team 2012) which aims to simulate eco-evolutionary dynamics in food webs. In its current version (1.01), mA includes a single basal resource species (fungus), a single predator species (mesostigmata mite) and one single prey species (springtail or collembolan). Increasing the number of interacting species and allowing for Intra-Guild Predation is merely a question of re-parameterisation and increasing computer time/demand. However, in the present simulations the level of complexity is already substantial because predators and prey have ontogenies, genetic and phenotypic variability for 13 traits -3 of which are temperature plasticity traits-, variable levels of genetically-based phenotypic integration (or genotypic integration) and behavioural flexibility. In addition, the rules of movement, predator-prey encounter rates and the outcome of interactions consider both environmental factors as well as environmentally-dependent state variables. Predator individuals are also able to feed on each other (cannibalism). Prey forage adaptively by searching for micro-patches with the lowest predator/resource ratio and predators also behave adaptively by searching for micro-patches with the lowest predator/prey ratio. Each loop through the program equals one day of simulated time. Fig. 1 shows the flaw diagram describing the algorithm. The present simulations were run for up to 120 simulated days and stopped when this "time" elapsed or when either the predators or the fungi went extinct. This lasted in real time ca. 48 hours when running 10 parallel sessions (replicates) in an Intel Workstation (Intel Core i7 990 Extreme Edition processor and 24GB DDR3 of RAM). A copy of the code used and the input files can be found at http://www.eeza.csic.es/eeza/documentos/mini-Akira_1.01.zip.

Space and basal resources

The model is semi-spatially explicit, with animals moving only in two alternative directions. The spatial scale is arbitrary and determined by the body size of individuals, their mobility and the productivity of the system. However, given the small body size of the animals simulated, the maximum distance between soil micro-sites in a real World scenario would be in the order of a few cms. In the present simulations, the space of each micro-site is represented by 100 micro-patches which are located in a circle, thus animals that are located in micro-patch number 100 can go to micro-patch 1 and viceversa. Productivity of the basal resource can be or can be not spatially autocorrelated. When spatial autocorrelation is included, productivity peaks at the central patch (50) and decreases linearly towards the “edges” (patches 1 and 100). In all our simulations there was spatial autocorrelation across micro-patches within the micro-site which included a gradient of carrying capacities going from 0.1 to 3mg (peak of fungi biomass production at patch 50). Thus, K increased from patch to patch in steps of 0.06mg.. In each patch, the basal resource (fungi) grows according to a conventional logistic growth function, and its dynamics is updated following the following algorithm:

$$M_t = M_{t-1} + r_T M_{t-1}\left(1 - {M_{t-1}}/{K}\right) \qquad \text{(ap1)}$$

where M_t and M_{t-1} is the total biomass of fungi in the patch at time t and time t-1, respectively; K is the carrying capacity of fungus in the patch, and r_T is the temperature-dependent intrinsic rate of increase (rearranged from Fig. 4 in Savage et al. 2004)

$$r_T = e^{b-E(1/kT)} / M_{t-1}^{1/4} \qquad \text{(ap2)}$$

where b=25.98 is a normalisation constant in the original equation (i.e., before rearrangement), and E=-0.68 is the activation energy (as calculated across organisms -Savage et al. 2004); k is Bolzmann’s constant (8.62 x $_{10}{}^{-5}$ eV/K), and T the environmental temperature in Kelvin. Here we assume that each day the total biomass of fungi (M_{t-1}) in a patch belongs to a single organism, thus r_T changes dynamically each day according to M_{t-1}. When a patch is nearly saturated (i.e. fungi grows approaching its carrying capacity), spores colonise neighbourhood patches, allowing fungi to re-settle in (neighbour) patches from which they were extinct. To ensure that simulations proceed for a number of prey and predator generations, all patches had M_0 set at 99% of K.

Predator and prey traits with quantitative genetic basis

For homogeneity in scaling functions and to speed up simulation time, all animals are <1mg as adults (thus the use of mites and springtails as predators and prey, respectively). The inclusion of more species in the future will involve substantial re-scaling and re-parameterisation. For each trait, we included evolutionary limits, beyond which the population could not evolve (assuming physical and physiological constraints) and we then established genetically-based trait variability within these limits. Thus, for each trait X we describe the limits and the range used as follows:

$$l_X = L_X + \varphi\left(\frac{U_X - L_X}{2}\right) \qquad \text{(ap3)}$$

$$u_X = U_X - \varphi\left(\frac{U_X - L_X}{2}\right) \qquad \text{(ap4)}$$

where l_x and u_x define respectively the lower and upper limits of the range used for trait X in the simulation, L_x and U_x define standard lower and upper limits for the trait and φ is a coefficient (range 0-1) which determines what proportion of the distance from the standard limits to the mid-point between them is used to calculate the final trait range (l_x, u_x). Thus, a higher φ involves lower trait variability. We forced $U_X < \mathrm{K}_X$ and $L_X > \Pi_X$, where K_X and Π_X are the uppermost and lowermost evolutionary limits for trait X, respectively. The above criteria ensured that variability was sufficiently large for new phenotypes to evolve (determined by standing genetic variation), but with thresholds far enough (L_X *and* U_X) from the evolutionary limits (Π_X and K_X). We used φ=0.5 for all simulations.

The 13 traits included in the simulations and their standard and evolutionary limits were the following:

body size at birth (size_ini, B_0): structural body mass at birth. Standard ranges (L_X,U_X): predators, 0.01425-0.02025mg; prey, 0.00725-0.01325mg. Evolutionary limits (Π_X,K_X): 0.05-0.022; which fit well within the reported body masses of springtails and mesostigmata mites (Ehnes *et al.* 2011).

energy tank at birth and after molting (tank_ini, ε_0): percentage of mass devoted to maintenance and future growth (L_X,U_X: 25-50% of body size which is added to make the total individual mass; Π_X,K_X: 0-100%). Individual body mass

(M) is thus the sum of body size and the energy tank, both of which are also state variables.

voracity (v): maximal consumption rate per day (implemented as a scaling coefficient v which makes voracity to scale with body mass as $0.1M^v$). Source: Yodzis and Innes 1992, DeRoos *unpublished notes*, which provide a fixed maximal consumption rate coefficient of 0.75; see also Englund et al. 2011 for variation around this value). For predators in the simulation, this parameter constrains the number of days in which they are actively searching for prey. If a predator catches a prey which surpasses the predator maximal consumption allowed per day, this predator will remain inactive as many days as necessary to digest this relatively large prey. L_X,U_X: 0.6-0.7; Π_X,K_X: 0.55-0.75.

speed (s): sprint speed (cm/s) when a predator (in the case of prey) or a prey (in the case of predators) is encountered and the prey tries to escape from the predator and the predator tries to catch the prey. Implemented as a scaling coefficient s which makes speed to scale with body mass as $\propto M^s$. This coefficient has been documented to vary across studies: 0.17-0.25 -Peters 1983, Schmidt-Nielsen 1984). Taking 4 as the normalisation constant ($4M^s$) we obtain sprint speeds which fall within the observed ranges from the tiniest mites (Wu et al. 2010) to the largest wandering spiders (Moya-Laraño et al. 2008a), covering a mass range of 0.03-465mg. Although collembola can escape predation by jumping (Hopkin 1997), which would certainly provide them with speeds orders of magnitude higher than the ones simulated here, we are not considering it for the sake of simplicity. L_X,U_X: 0.1-0.3; Π_X,K_X: 0.05-0.35.

metabolic rate (met_rate, a): Energy losses from metabolism follow the Metabolic Theory of Ecology (MTE, Brown et al. 2004) and recent estimates in soil fauna for the separate effects on metabolic rate of temperature, activation energy and body mass (Ehnes et al. 2011):

$$\ln I = \ln I_0 + a \ln M - E\left(\frac{1}{kT}\right) \qquad \text{(ap5)}$$

where I is metabolic rate (J/h), I_0 a normalisation constant, a a coefficient which relates body size to metabolic rate, E is the activation energy (in electron-volts eV), k the Bolzmann's constant (8.62×10^{-5} eV/K), and T the environmental temperature in Kelvin. All parameters are included as reported for mesostigamata (soil predatory mites) and for insects (collembola) (Ehnes et al. 2011). In its current version, genetic variability is included around the coefficient "*a*". L_X,U_X: predators, 0.6-0.7; prey, 0.7-0.8; Π_X,K_X: 0.55-0.85.

In addition, we also included field metabolic rates, which were calculated in an algorithm that includes environmental stress from encounters with predators (Hawlena and Schmitz 2010a) as well as on the state of voracity and amount of movement of each individual.

growth (*g*): Growth is a trait that determines how much an individual grows in each moulting event. Note that we are simulating arthropods which grow by moulting. Thus, this trait is not truly growth rate but growth ratio at moulting independently of the rate (t^{-1}) at which moulting occurs. Therefore, this trait determines how much of the available energy storage is allocated to fixed body parts in the next developmental stage (instar). Since a fraction of the energy tank at moulting should be also allocated to the post-moulting energy tank (see $\boldsymbol{\varepsilon_0}$ above), these two traits basically decide when an individual will moult. Growth is merely included as a ratio of the linear dimension of fixed (structural) body parts of the new (target) instar relative to the previous instar. We use relatively low ratios within the range of extensions of Dyar's rule for arthropod growth (Hutchinson et al. 1997). We fixed the number of instars in both predators and prey to be 4. Although some collembolans have indeterminate growth (i.e., they continue growing and moulting after maturation – Hopkin 1997) for simplicity we have not considered this trait here. L_X,U_X: predators, 1.01-1.2; prey, 1.01-1.1; Π_X,K_X: 1.01-1.2.

search area (search_area, *m*): Importantly, we distinguish between speed and mobility. Speed reflects sprint speed when trying to escape from a predator or trying to catch a prey. However, we consider mobility (search area) as how much one individual is able to move to search for resources or for safe patches. Lacking better information, the entire area covered in one day (*m*), scales with body size in a similar way as sprint speed: M^m. L_X,U_X: predators, 0.1-0.3; prey, 0.2-0.4; Π_X,K_X: 0.05-0.5. Since we set body mass to be <1mg in the entire simulation, higher *m* coefficients mean lower mobility for the same body mass. Thus, in order to include efficient predators in the simulations prey move less than predators. For translating mobility into actual search area in the simulation (see

"Space and basal resources" above), we used linear interpolation, translating the minimum M^m into moving 1 patch each day and the maximum possible (i.e., largest adult predators at the highest temperatures) into moving up to 8 patches each day.

assimilation efficiency (assim): Assimilation efficiency is merely the amount of ingested food which is converted in own body mass. Following previous work on soil fauna, we can assume to be around 0.85 (85%) (Rall et al. 2010 and references therein). L_X,U_X: 0.7-0.9; Π_X,K_X: 0-1.

phenology (pheno): Day of birth since either the beginning of the season (simulation) or since the date of oviposition. L_X,U_X: predators, 3-11; prey, 2-10; Π_X,K_X: 1-100. This trait could be also called egg developmental time, as the date of birth will depend on how fast eggs develop. In addition, for calculating the final phenological date, which will vary depending on temperature, we further included temperature-dependent developmental rates by using published equations (Gillooly et al. 2002) and calculating the average Q_{10} values across the range of body masses for our propagule sizes in the simulation, which gave $Q_{10}=2.84$).

activation energy for metabolic rate (E_{met}, E in eq. ap5): To simulate the effect of climate change on eco-evolutionary dynamics, we also included, in addition to simulations at different temperatures, variability around E, which will serve to study adaptive evolution around thermal sensitivity of metabolic rate, a form of thermal adaptation. Ranges were set around published coefficients for mesostigmata mites (predators) and springtails (Ehnes et al. 2011). L_X,U_X: predators, 0.3-0.5; prey, 0.55-0.75; Π_X,K_X: 0.3-0.75.

We further included three additional traits that represented variability in plasticity to temperature (Q_{10}) for three activity traits: voracity, speed and search area (vorQ_{10}, spdQ_{10} and srchQ_{10}, respectively). We used recent published accounts from a thorough review on temperature-dependent ecological traits in predator-prey interactions (Dell et al. 2011). For activity traits, we used Q_{10} (i.e., how many times a given trait increases for a 10ºC increase in temperature) instead of E, because we lacked information for how E and M combine to determine trait values, as it is the case for metabolic rate (I) in eq ap5 -Ehnes et al. 2011. In addition, Q_{10} values are more easily interpretable and converted to reaction norms. However, E can be easily approximated from Q_{10} by using equation 3 in Vasseur and McCann (2005). Jointly, this fourth module represents thermal plastic adaptation for mobility. For simplicity we used for simulations a maximum temperature of 25ºC in simulations, which allowed us to use trait temperature dependences below optimal (the rises in the temperature performance curve, which shows an optimum at around 25ºC – Dell et al. 2011). Although animals would ideally benefit from being more active, this could also be detrimental because the potential increase in exposure to predators (e.g. Norrdahl and Korpimäki 1998). Therefore, we expected this plasticity module to evolve differently in risky *vs*. safe environments.

Q_{10} on voracity (vorQ10): Based on data on consumption rates (Dell et al. 2011). L_X,U_X: 2-4; Π_X,K_X: 1-6.

Q_{10} on speed (spdQ10): Based on data on escaping speeds (Dell et al. 2011). L_X,U_X: 1.5-2.5; Π_X,K_X: 1-3.

Q_{10} on search area (srchQ10): Based on data on voluntary body speed (Dell et al. 2011). L_X,U_X: 1.5-2.5; Π_X,K_X: 1-3.

To estimate the effect of Q_{10} values in the simulation for all traits that involved temperature sensitivity, we used linear interpolation between the minimum and maximum temperatures used for all simulations (15-25ºC). Thus, real Q_{10} were used when a simulation was performed at 25ºC, and for simulations at intermediate temperatures we estimated the value of Q (e.g. Q_7 at 22ºC) by interpolation between the two temperatures, which assumes linearity of Q across temperatures. Since Q_{10} have a quantitative genetic basis and modify other genetically-driven traits, Q_{10} genes are epistatic in nature (i.e., the action of one gene on the phenotype is affected by the expression of Q_{10} genes). This is an epistatic view of phenotypic plasticity (Scheiner 1993, Roff 1997), as the phenotypic effect of Q_{10} genes as the environment changes (i.e., increase in temperature) is to modify the expression of other genes. Thus, this fourth module includes genes for trait plasticity to temperature variation.

Trait modularity and phenotypic integration

Phenotypic integration and phenotypic modularity explain how quantitative traits are inter-related among individuals in a population (Magwene

2001, Pigliucci 2003). Highly integrated organisms could be those in which their traits (both genetically and functionally) are strongly correlated to each other across individuals. The opposite would be to say that a highly integrated organism is an organism with low modularity, in which all traits are uncorrelated across individuals. For instance, if animals that are genetically aggressive also have high growth rates we will say that animals are phenotypically integrated for the aggressive and growth rate traits. However, if these two traits show no correlation across individuals, the animals will have low integration of these traits. A module can be defined as a set of intercorrelated traits (across individuals) which is independent of another set of intercorrelated traits, being the latter a different module. The above 13 traits were initially (i.e. before evolution at time t0) included in 5 modules, four modules with three traits each and a fifth module with a single trait (Emet). Each of the 4 three-trait modules included either all positive genetic correlations, or two negative and one positive correlation among traits, reflecting genetic trade-offs. However, we would like to stress that trait correlations are implemented as an example to introduce our eco-evolutionary framework, but that such modules do not necessarily need to be arranged in this way in nature. In the future, we need to measure trait modularity and its genetic basis in animals embedded in food webs (e.g. Santos and Cannatella 2011), and we hope that our approach encourages pursuing this line of research. Through the paper, three-trait modules will be represented by trait names and two signs, one referring to the direction of correlation with the first trait (as read from left to right) and the other referring to the correlation with the second trait. For instance, in module 1 we have: tank_ini(-,-), growth(-,+) and pheno(-,+), which means that animals which are born with more reserves invest less in growing; i.e., they grow to a smaller size and increase their growth rate, and also are born earlier (or develop faster); and thus, animals that have a higher growth ratio, do develop later. We stress that the latter pattern is also an ecological constraint, as everything else being equal, growing larger takes more time. Therefore, here the genetic constraint (negative correlation) parallels the ecological constraint. The other 3 three-trait modules were arranged as follows: Module 2, speed(+,+), met_rate(+,+), search_area(+,+); Module 3, size_ini(-,-), assim(-,+), voracity(-,+); Module 4, vorQ10(-,-), spdQ10(-

,+), srchQ10(-,+). Therefore, a negative relationship between propagule size and voracity means that larger animals tend to be proportionally more voracious beyond body size constraints, as smaller voracity coefficients mean higher voracity. Similarly, higher assimilation efficiencies positively correlated with voracity coefficients mean that the more voracious animals are the least efficient at assimilating food, reflecting a potential trade-off between voracity and assimilation efficiencies. Finally, module 4 reflects trade-offs on thermal adaptation for mobility, as plastically responding to an increase in temperature by increasing voracity trades off with increasing other mobility traits (either sprint speed or search area), therefore reflecting genetic constraints in plasticity. This allows us to first approach adaptive evolution of quantitative traits in the context of biotic interactions and climate change. However, despite previous believe, it has been recently shown that the sign and magnitude of genetic correlations can change depending on the environment, which suggests that they may constraint adaptive evolution in a lesser degree than previously thought (Sgrò and Hoffmann 2004). Once the underlying mechanisms are well understood (Roff and Fairbairn 2007, McKinnon and Pierotti 2010) this unconstrained form of plasticity integration will be easily incorporated in the present framework. However, for now we adapt the more classic view of genetic correlations and G-matrices, which have been found to be stable under climate change in at least one study (Garant et al. 2008).

Quantitative Genetics and G-matrices

To assign a quantitative genetic basis to the traits, we assumed one chromosome per trait. Thus, each individual has 13 chromosome pairs. For simplicity all animals are hermaphrodites and chromosomes are thus all autosomal. Each trait is determined by 20 loci with 10 possible alleles whose frequency is drawn from a uniform distribution. To induce genetic correlations among traits from pleiotropic effects, a number of loci were allowed to have effects on more than one trait (up to three within the same module). Stronger genetic correlations were achieved by increasing the number of loci shared by traits within a module. We defined the parameter ρ to set the number of common loci for pleiotropic effects as: ρ=SL/NL, where NL is the total number of loci involved in the trait and SL is the number of pleiotropic loci (i.e., those shared with another trait). Thus, a higher ρ value means that the trait is determined by fewer exclusive loci and by more loci that affect other traits. For instance, ρ=0.90 means that a 20-loci trait is determined by 18 (pleiotropic) loci shared with another trait and only two exclusive loci. A value of ρ=0 means that all loci are exclusive and that the trait is completely decoupled from any other trait, as it was the case for Emet. We set the parameter ρ to get an approximation of the genetic correlation (rA), thus allowing us to simulate different genetic architectures (i.e. genetic variance-covariance matrices or G-matrices). To estimate the overall phenotypic effects of alleles, each allele added a small quantity to a trait drawn from a uniform (0-1) distribution, for which we assumed exact co-dominance. Thus, regardless of allele identity, all alleles summed up to the total phenotypic value of the trait. Positive correlations between traits were induced by summing up the phenotypic values of both the exclusive and pleitropic loci which determined a given trait. Negative correlations were induced by subtracting from one the phenotypic values of the pleiotropic loci and adding the difference to the sum of the phenotypic values of exclusive loci. Then, in order to transform these arbitrary phenotypic values to ecologically meaningful phenotypic values, we used linear interpolation to change the arbitrary phenotypic scale to the ecological scale; i.e., using the ranges explained for each trait above. This procedure successfully allowed us to incorporate desirable amounts of genetically-determined phenotypic correlations among traits, which are determined by Mendelian inheritance of several genes, each with a relatively small effect, thus successfully mimicking quantitative genetics. G-matrices are thus the variance-covariance matrices of the above phenotypic values. Furthermore, since there are a number of loci which never express (i.e., in pleiotropic traits, the loci that do not express because the phenotypic value is taken from the loci in another chromosome), these loci can be used to follow the fate of neutral alleles (i.e., genetic drift) during the simulation. As in real chromosomes, the further apart neutral loci are from functional loci in the chromosome, the more neutral-like they will behave. On the other hand, loci near functional genes will be indirectly under selection just because of chances of linkage by proximity to selected genes during recombination, as it is the case for microsatellites (Martín-Gálvez et al. 2006, Stapley et al. 2010).

State variables and the environmental component of phenotypic variation

Apart from switches and counters which denote for instance the age (instar) or the state (alive, dead, reproductive) of the animal, we include phenotypic state variables such as body size (animals grow) and energy tank (energy stored for maintenance, growth or reproduction). Other traits do also change phenotypically with ontogeny and experience of individuals. Furthermore, all traits that are dependent on body size are state variables which get updated to their new value every day.

body size (B): portion of the body mass which is structural, and thus it does not include energy usable for any other function. In the case of arthropods this includes exoskeleton and muscle tissue, for instance. This parameter changes after each moult.

energy tank (ε): portion of the total body mass which is actual energy available for maintenance, growth or reproduction. This energy tank is sometimes estimated by regression methods as mass (or even density) controlled for structural body size (e.g. Jakob et al. 1996, Moya-Laraño et al. 2008b), and it is referred to as body condition. This energy tank is filled from feeding and emptied from respiration (metabolic) losses (see I above).

The above involves splitting body mass into two traits. Although it is true that overall body mass can explain predator-prey interaction links and interaction strengths to a large extent (Woodward et al. 2005, Brose et al. 2006), it is also true that the relative amount of energy stored by an ectothermic animal (or the level of satiation) can potentially determine behavioural decisions such as home range area or the frequency of hunting trips, as it has been found in spiders (Moya-Laraño et al. 1998, Kreiter and Wise 2001, Moya-Laraño et al. 2003) or attack rates, as found in mites (Zhang and Sanderson 1993, but see Baatrup et al. 2006). This is to be expected because ectothermic animals adjust their foraging mode, decreasing activity when food availability and satiation levels are high (Helfman 1990). Furthermore, in burrowing wolf spiders (*Lycosa tarantula*), escalated fights over territories end in cannibalism -which is highly costly because retaliation is very likely- if differences in fixed structural size are high enough and if the winner of the fight has low body condition (Moya-Laraño et al. 2002). Thus, although overall body mass is by no doubt the main driver in deciding the outcome of predator-prey interactions, it can still be split into two traits of contrasting outcomes, especially at low predator-prey ratios. Taking the above facts into consideration, it follows that the next two traits are also state variables that depend on condition: voracity and search area.

environmental component of voracity (voracity_tuned, *V*): each day, environmental effects add to the genetic component of voracity to determine the actual value of the trait. Relevant indirect environmental effects (e.g. the effect of temperature on metabolic rate) are those that affect overall body mass and its two components (B and ε). Fixed (structural) body size will then affect voracity following the scaling dependence of voracity on body mass. However, ε -in addition to adding to overall mass and affect voracity by scaling- will affect voracity because it reflects hunger status. Thus, individuals with filled energy tanks are less voracious than individuals with emptied tanks. Although ratios may be inappropriate to estimate condition (Raubenheimer 1995, Jasieńsky and Bazar 1999, Smith 1999), for simplicity, in order to correct for the dependence of condition to body size (i.e., larger individuals have more reserves), condition was estimated as the ratio ε/B. This value was interpolated between the maximum and minimum possible conditions (estimated from the evolutionary limits and the condition threshold preceding starvation: 0.1), and it was re-scaled between 1 and 0.1. The resulting coefficient was then multiplied by genetically-determined voracity. Furthermore, to reflect the effect that exposure to predators has on prey's anti-predator behaviour, we estimated by simulation –i.e. using *mini-Akira* with maximum temperature (25ºC) and four times as many predators- the maximum possible number of encounters with predators in a single day to be 4, and again obtained a 1-0.1 coefficient by interpolation between the lowest (0) and the highest (4) possible encounter rates with predators. This coefficient was also multiplied by genetically-driven voracity. In this way, high previous encounter rates with predators lead to lower voracities. Finally, to include the effect of temperature and the epistatic Q_{10} effects, the environmentally-driven voracity was multiplied by its Q value (vorQ10), or its interpolated estimate (Q_{VT}) if the simulated temperature was below 25ºC. Thus, the final equation determining the voracity trait (V in mg/day) for each day is:

$V = 0.1M^{v}ceQ_{VT}$ (ap6)

where v is the genetically-driven voracity coefficient, and 0.1 a normalisation constant; c is the interpolated condition coefficient, e is the interpolated coefficient for encounter rates with predators the day before, and Q_{VT} is the interpolated temperature-dependent change in voracity at temperature T.

environmental component for area searched (search_area_tuned, *A*): The maximum number of patches visited each day will depend on analogous parameters such as voracity, as animals in better condition that have found more predators the day before and at relatively lower temperatures will move less. Thus, the equation is:

$A \propto M^{m}ceQ_{AT}$ (ap7)

where m is the genetically-driven mobility scaling coefficient, and Q_{AT} is now the interpolated Q value at temperature T for search_area. Here we do not include a normalisation coefficient accompanying M, as body mass is transformed into number of patches moved per day by linear interpolation. The value of A is rounded to become an integer number of visited patches.

environmental component of speed (speed, *S*): Here we assume that the amount of energy stored interferes with running performance, as predicted by the mechanics of inverted pendulums (Moya-Laraño et al. 2008a). Therefore, the phenotypic sprint speed (S) for each day in the simulation was calculated following:

$S = 4M^{s}cQ_{ST}$ (ap8)

where s is the genetically-driven scaling coefficient for sprint speed, c is the condition interpolated coefficient, and Q_{ST} is the Q value for sprint speed at temperature T.

environmental component of assimilation efficiency (assim): Here, we incorporate recent evidence that predator-induced stress compromises the efficiency with which prey assimilate food (Trussell et al. 2006, Hawlena and Schmitz 2010a). We used the maximum reduction documented from predatory stress (76%) and interpolated this value between 0 and the maximum number of encounters with predators per day (4). Thus, animals that encounter 4 predators in one day and successfully escape from them will have a 76% reduction in assimilation efficiency for the food ingested that day, animals that experience 3 encounters will have a 57% reduction, and so on.

temperature-dependent phenology and egg developmental time (Q10pheno): As temperature affects developmental time, we used the following equation (re-arranged from Gillooly et al. 2002) to calculate an average Q_{10} value for egg developmental rate across our range of propagule masses (0.01-0.05mg):

$$t = M^{1/4} e^{\left\{\beta\left[T \,/\, \left(1+\frac{T}{273}\right)\right]+\alpha\right\}} \quad \text{(ap9)}$$

where β and α are the average slope (-0.12) and the intercept (6) of the original relationship, respectively (Fig. 1 in Gillooly et al. 2002), as calculated by least-squares regression across organisms, and M is total body mass in grams (Gillooly et al. 2002). This resulted in an average Q_{10} for developmental rate (t^{-1}) of 2.84, giving a decrease in developmental time by a factor of 0.35 for each increase of 10ºC in temperature (Q10pheno). To finally calculate birth dates, we multiplied the trait "pheno" by the above factor (for 25ºC), using linear interpolation for temperatures in the middle of the range (15-25ºC). We decided not to include the exact equation ap8 in the model because it would have lead to developmental rates being too short (less than one day for the highest temperature), thus impeding variability in birth dates. Shorter timeframes (e.g. hours instead of days) would be necessary for the inclusion of the above equation to be meaningful for such small animals. Thus, we are assuming that birth dates are not only driven by temperature and mass, but that other factors (e.g., genetic) are also important.

temperature-dependent digestion time (Q10digest): When a prey is caught by a predator and this prey is larger than the daily maximal ingestion rate for the predator, digestion will take more than one day. The number of days for digesting a prey item equals the ratio between the mass of the prey and the maximal ingestion rate. During this period, the predator is inactive and cannot encounter any other predator or prey in the simulation. Temperature-dependent digestion times are included by multiplying the number of days by a 0.25 factor at 25ºC, and interpolated between 1 and 0.25 for the range of 15-25ºC otherwise.

This shortening in digestion times with temperature have been obtained for a Q_{10} value on digestion rates of 4 (Dell et al. 2011).

In general, to include inter-individual variability around Q_x values for any of the traits, we never used T=15ºC because that would have involved Q_0 and no single value could have been interpolated. Thus, to ensure that variability values were included (e.g. for 16ºC it would be Q_1 estimated from interpolation), we always simulated temperatures above 15ºC.

Moving algorithm: adaptive movement and previous experience

As in this framework predators are allowed to engage in cannibalism, both predators and prey move from patch to patch exhibiting adaptive antipredator behavior, i.e. avoiding patches with more predators. In addition, resource availability is also considered. Thus, when choosing whether to stay in the current patch or to move to one of the two neighbour patches, animals consider the predator-to-resource ratio and choose the patch with the lowest ratio. When simulations are run without predators, prey merely move to the most productive patches. Furthermore, when resources have been depleted in both the current and neighbour cells, animals "jump" a number of cells/patches with a random direction and a number of patches which matches their mobility parameter A.

Moulting algorithm

The growth trait is a fixed value for each individual and sets the linear increment in fixed (structural) body size at each moult. Growth is a ratio between the linear structural size after moulting and the linear structural size in the previous instar. We assume that 10% of the energy and nutrients is lost at the moulting process, and that a fixed 90% is available for growth (however, different proportions are possible in arthropods -Hutchinson et al. 1997). In the simulation, an animal will moult after accumulating enough energy (ε). Therefore, moulting involves the trait "growth" (next structural size) and energy storage (next energy tank), which is genetically determined by ε_0, while considering the 90% reduction during the moulting process.

Reproductive algorithm

Once maturation is achieved (which involves reaching instar 4 in the current simulations), an individual will be able to reproduce only after accruing enough energy. The rule of energy requirements for reproduction is similar to that of moulting. However, to minimise death from starvation and ensure iteroparity (>1 egg batch during a lifetime), the necessary amount of energy for reproduction was multiplied by a factor of 1.15 for prey and 1.2 for predators and then added to the condition of the individual after the reproductive event. For simplicity, individuals are reciprocal hermaphrodites and we assume that the spatial position does not matter for finding a mate. Therefore, each day, all the reproductive individuals are assigned a mate at random, and both parts of the mating couple act as reciprocal sperm donor and receiver. Gametes are formed by inducing a single randomly-located (position 1 to 20) chiasma in each chromosome. Each newborn gets one chromosome from each parent and phenotypic values are then assigned to each individual as explained above.

Descriptions of functions or submodels according to the ODD protocol (DeAngelis et al. 2006)

crea_loci

This function generates a standard chromosome with a number of loci (20 in all of the present simulations) and alleles (10) each adding a phenotypic value from a uniform (0,1) distribution. For following their fate in the simulation and for calculating allele diversity across generations, ID codes are given to each allele. To include pleiotropic effects and genetic correlations among the three traits, the first trait in the module expresses all its genes and then the second and third traits share a number of loci with the first which depends on the parameter ρ (see main text). Which loci are pleiotropic and which are exclusive depends on the ordered position in the chromosome.

crea_module

This function assigns genetic values to each of the 3-trait modules for each individual, for which it uses the standard chromosome generated in crea_loci. Each individual gets one of the 10 uniformly distributed alleles at random for each locus and for each of the 3 chromosomes involved in the module. The phenotypic values of all these traits, which have been assigned 0-1 values in crea_loci, are summed to estimate a naïve pseudo-phenotypic value which is then transformed to ecological phenotypic values by linear interpolation.

crea_trait

It is a function like crea_module but instead of a 3-trait module creates the quantitative genetic basis for a single trait which is not genetically correlated with any other trait ($\rho = 0$), such as it is the case for Emet.

fungi_func

This is an algorithm which controls fungi growth in relation to a logistic growth function in which r depends on temperature (rT) following published equations (see main text). If carrying capacity (K) is approached, the excess in productivity (mimicking spores) goes to the neighbour cells as long as these are not also approaching K.

***prey_move* – version without predators**

This function controls the adaptive movement of prey when predators are not present in the simulation. For each individual and movement, the three cells (current, left and right) are first screened for overall fungi biomass. Then the individual moves to (or remains in) the patch with highest biomass. When resources have been depleted from the three cells, the individual performs a jump across patches in random direction and which equals the number of patches of the trait A (searched area tuned by the environment, see main text) plus 2. This last number is added to avoid negative numbers in the function.

***prey_move* – version with predators**

This function controls the adaptive movement of prey when predators are present in the simulation. For each individual and movement, the three cells (current, left and right) are first screened for overall fungi biomass and predator number. Then, values are interpolated to vary between 0 and 1 and the ratio P/Bf (predator abundance divided by fungi biomass) is used to move adaptively.

The individual moves to (or remains in) the patch with the lowest P/Bf ratio. Again, when fungi resources have been depleted from the three cells, the individual performs a jump across patches in random direction and which equals the number of patches of the trait A plus 2. During this movement, we assume that prey do not encounter any predators other than in the arrival patch. For simplicity, we assume that prey are able to assess predator abundance with perfect precision but cannot assess predator identity nor the trait values of the predators.

feed_prey

In this function, each prey individual ingests an amount of fungi from the patch in which it decides to stay after moving has ended for the day. The amount of fungi taken each day equals that of V (the voracity tuned by the environment). If there are not enough fungi to satisfy the demand, the animal takes the total amount and the fungus gets extinct from that cell.

fungi_eaten

This function merely updates the amount of fungi in each cell after all fungivores have fed. If the entire amount of fungi found in the cell approaches zero, it is considered to be extinct from that patch. However, it can be still recolonised from neighbour patches.

metab_with_growh

This is the function which controls energy losses from respiration. Additionally, this function controls when animals die from starvation, moult or reproduce and in fact contains the moulting algorithm. Furthermore, it includes the function to decide digestion time of ingested prey for predators (see main text). Basal metabolic rates and/or field metabolic rates were applied depending on the time devoted to foraging or searching activity. Assuming a trade-off between activity within a patch (e.g. foraging, searching for micro-spots with food) and activity among patches (searching for the best patch), the following function estimates the proportion of time (Pt) that an animal has been active:

$$P_t = w_A \cdot \left(\frac{W}{A_{\max}} \right) + (1 - w_A) \cdot \left(\frac{V}{V_{\max}} \right) \qquad \text{(ap10)}$$

where W is the number of patches visited, A_{max} is the maximal possible search area, V is voracity, V_{max} is the maximum possible voracity and w_a is a weighing factor which corrects for the differential energy spent in each activity. Although it is likely that moving among patches is energetically more costly, here we assume that both activities are equally expensive ($w_a = 0.5$). Because parameters for including this time budget are not available, we decided to implement this simple solution, which is still more accurate than assuming a 24-h field metabolic rate, and in addition will allow accounting for individual differences in energetic demand due to differential activity. Due to the relatively low time precision (nearest day), this is one of the few solutions for how to implement individual differences in field metabolic rates due to among-individual environmental and genetic differences in the associated traits. A_{max} and V_{max} have been calculated for the largest evolvable animal with minimum predator encounter, lowest condition and at the highest temperatures. Basal metabolic rates (I in equation ap2) are then multiplied by the proportion of time that the animal has been inactive ($1-P_t$), and field metabolic rates (which were approximated as $3I$, following Brose et al. 2008) were applied to the proportion of time active (P_t). Furthermore, the effect of predator-induced stress on metabolic rates was included by considering a recent publication which shows an increase in I of 47% when exposure to predators is maximum (Hawlena et al. 2010b). By simulation, we estimated maximal predator-prey encounter rates to be 3 day^{-1} at the highest temperature (25ºC) and for the maximum simulated predator/prey abundance ratio of 200/500. We then interpolated 0-3 predatory encounters to get the amount of induced stress to the new scale of 0-47%, and added the resulting percentage to the energetic losses.

As this function determines the energetic budget of each individual it also decides whether an individual will die from starvation. We considered that having a ε/B ratio smaller than 0.1 would cause death by starvation. To decide whether or not a non-adult animal will moult at time t, the code assesses whether 90% of the total biomass (the total available for growth minus the energy lost during moulting) of the animal is enough to meet the mass necessary to built the next instar. This is accomplished when the following condition is met:

$$0.9(B_t + \varepsilon_t) \geq g^3 B_t + \varepsilon_0 g^3 B_t \quad \text{(ap11)}$$

where B_t and ε_t are respectively structural body size and energy tank at the current time (t), g is the genetically-determined linear growth ratio and ε_0 is the energy in the tank at the beginning of each instar.

Similarly, an adult animal (i.e., in the present version, when it has reached instar 4) will lay an egg batch at time t if the following condition is met:

$$0.9(B_t + \varepsilon_t) \geq \lambda\left(g^3 B_t + \varepsilon_0 g^3 B_t\right) \quad \text{(ap12)}$$

where λ is now a coefficient (always >1, and with value 1.15 for prey and 1.2 for predators in the current simulation) which endows the individual with a safety energy margin to diminish the probability of death by starvation after reproduction has occurred. We assume that the condition to reproduce is of similar magnitude as the condition to moult -thus, the inclusion of g in the latter condition. This safety excess of energy is kept by the individual after reproduction and it is important for granting the iteroparous character of the individuals. In the current simulation, prey lay up to 2 batches and predators up to 5 batches, immediately dying afterwards.

tunea_traits* and *tunea_traits2

These functions merely apply the equations to calculate the environmental contributions to V, A, S and the stress effect on "assim" (equations ap6-ap8).

for_interaction

This function includes in an array the animals present in a cell and the necessary traits and state variables to decide interactions.

predation_prey_move

This function includes the rules to decide when a predator and a prey interact provided that a prey moves to a new patch. First, it calculates the probabilities that a prey entering a new path encounters each of the predators present in that cell (one probability for the encounter with each of the predators). Second, if encounter occurs with a given predator, it calculates the probability that predation occurs. To decide the final outcome of the interaction, these two probabilities are contrasted with a random number (0-1) drawn from a uniform distribution. The probability of encounter (Pe) for a given predator-prey pair, is calculated according to the following logistic function:

$$P_e = 1/[1+e^{-(\alpha+\beta V_{Pd}+\gamma V_{Py}+\delta V_{Pd}V_{Py}+\varepsilon B_{Pd}+\zeta B_{Py}+\eta B_{Pd}B_{Py})}] \qquad \text{(ap13)}$$

where V_{Pd} and V_{Py} are respectively the phenotypic voracities of the predator and the prey at the moment of the interaction and B_{Pd} and B_{Py} are the structural body sizes of the predator and the prey at the moment of the interaction. This equation includes the products of predator and prey traits, which are included under the assumption that the voracities (activities) and body sizes of each individual of the pair have multiplicative effects on the probability of encounter. The coefficients (α...η) are naïve coefficients (respective values from α to η: 0.01,0.01,0.01,10,0.01,0.01,10) which have been included to provide approximately equal weight to all variables depending on their range of values and to grant a sufficient expand in encounter probabilities (0.5-0.94). Lacking information for the actual effect of each trait on encounter rates, these coefficients were chosen to ensure equal weight to all traits across encounters. To decide the outcome of the encounter, P_e was then contrasted against a random 0-1 number from a uniform distribution. An encounter occurred if the former number was higher than the second. If a predator and a prey encountered each other, we then calculated the probability of predation (P_p) occurring at that encounter as:

$$P_p = 1/[1+e^{-(\alpha+\beta V_{Pd}+\gamma R_B+\delta R_S)}] \qquad \text{(ap14)}$$

where R_B and R_S are respectively the ratio in structural body sizes between the predator and the prey and the ratio between the sprint speed of the predator and the prey. Again, the coefficients used were naïve (respective values from α to δ: 0.1, 0.01, 0.01, 1). We restricted predator-prey interactions to those in which the predator was equal or larger in structural body size than the prey ($R_B \geq 1$). As all of the traits determining P_e and P_p scale with body mass, overall body mass (structural + tank) is here implicit in all traits and thus in the probability of predation.

pred_assim

This algorithm converts the ingested prey into own predator mass.

pred_move

This function controls the adaptive movement of predators. For each individual and movement, the three cells (current, left and right) are first screened for prey and for predators and the total number of each recorded. Then, these values are interpolated to vary between 0 and 1 and the ratio Pd/Py (predator abundance divided by prey abundance) is used to move adaptively. The individual moves to (or remains in) the patch with the lowest Pd/Py. When prey have been depleted from the three cells, the individual performs a jump across patches in random direction and which equals the number of patches of the trait S (searched area tuned by the environment, see main text) plus 2. This last number is added to avoid negative numbers in the function. During this movement, we assume that predators do not interact with either prey or other predators. We assume that predators have perfect assessment of prey and predator abundance but that they cannot assess predator or prey identities nor the trait values of either prey or predators.

for_interaction_x1

This function is like for_interaction but from the point of view of predators behaving as the cannibal prey, thus counts how many other predators are in a cell.

for_interaction2_x1

This function is like for_interaction but from the predator point of view behaving as predator on shared prey and as the cannibal predator.

predator_pred_move

This function is very similar to “predator_prey_move” above but here is the predator the individual that enters a new patch and potentially interacts with all the smaller (or equal in size) predators and prey.

pred_background

As, apart from themselves, predators lack other predatory species in this simulated environment, we included the predator probability of dying from predation by other, non-simulated predators (Pb), which was calculated as follows:

$$P_b = \tau\left\{1/[1+e^{-(\alpha+\beta V_{Pd}-\gamma B_{Pd}+\delta A-\varepsilon S)}]\right\} \qquad \text{(ap15)}$$

where τ is a parameter that tunes the rate of background predation to set it to reasonably values for the simulation to run for a few generations (here, τ = 0.025). This function was intended as a proxy of predation by larger predators and included all the traits that could explain predation if larger predatory species would be present. Hence, this probability depends positively on the voracity and the area searched, both of which increase the probability of encounter with predators, and negatively on body size and sprint speed, both of which decrease the probability of predation by predators. Again, the coefficients (α...ε: 0.1, 1, 0.1, 0.1, 1) are naïve, and give approximately equal weight to each trait according to its range of values. Also, to decide the outcome, P_b was compared with a random 0-1 number drawn from a uniform distribution.

repro

This function assigns mating pairs of reproductive individuals at random, calls to the function gametator and then combines the two gametes of each parent to build eggs. Because reproduction in these simulations is reciprocally hermaphroditic, both partners pass male gametes to each other. Once reproduction is granted, the number of eggs (N) laid per batch by an individual is determined by the following equations:

$$N = E_r/(B_0+\varepsilon_0 B_0) \qquad \text{(ap16)}$$

$$E_r = \varepsilon_t - \lambda\varepsilon_{\min} \qquad \text{(ap17)}$$

$$\varepsilon_{\min} = 0.1B_t \qquad \text{(ap18)}$$

where E_r is the energy available for reproduction, B_0 and $\varepsilon_0 B_0$ are respectively the genetically-determined offspring body size and energy tank at birth, ε_t is the energy tank of the individual at time t, λ is the safety coefficient (prey=1.15, predators=1.2) to diminish starvation after reproduction and ε_{min} is the minimum energy tank necessary to remain alive after reproduction, 0.1 being the ε_t/B_t ratio below which death from starvation occurs.

This function writes a record of the generation number from which the parents came, as well as the ID of the parents. Thus, and although not used in the present paper, a full pedigree of the simulation is available for later use.

Next, the function calls to the function gametator and assigns the two gametes that form the new egg and a genetic background (13 homologous chromosomes) to the offspring. After that, using the identity and recorded values of the inherited alleles, assigns naïve phenotypic values which are then translated into ecological phenotypic values by interpolation as done for initialisation (see main text). If the values surpass the phenotypically possible; i.e. they lie outside the range imposed by the evolvability limits (see main text), values are reset to the closest (KX or ΠX) limit in the range. Finally, the function assigns counters and state variables to each offspring.

gametator

This function mimics recombination for the 13 pairs of homologous chromosomes by creating a single chiasma in a random, uniformly distributed position, which differs among chromosomes, gametes and individuals.

Table 1. Results of GLMs showing trait x environment (O-matrix) interactions in fitness reflecting differences in directional selection for two levels of genetic correlation across 13 traits spread in 5 phenotypic modules. The models were selected by stepwise AIC (N=15000 individuals pooled from 5 replications of each environmental combination).

	rho=0.1			**rho=0.9**		
TRAIT/ENVIRONMENT	**LR-Chisq**	**df**	**P-value**	**LR-Chisq**	**df**	**P-value**
PREDATORS	477.8	1	<0.0001	305.9	1	<0.0001
TEMP	32.5	2	<0.0001	75.9	2	<0.0001
assim	66	1	<0.0001	38.1	1	<0.0001
met_rate	99.4	1	<0.0001	60.7	1	<0.0001
size_ini	7.4	1	0.0064	5.3	1	0.0213
tank_ini	92	1	<0.0001	15.2	1	<0.0001
voracity	192.3	1	<0.0001	56.1	1	<0.0001
pheno	2.7	1	0.1	3.8	1	0.0513
search_area	32.6	1	<0.0001			
growth	149.2	1	<0.0001	53.3	1	<0.0001
speed	0.1	1	0.8182	7.5	1	0.0062
actE_met	4749.8	1	<0.0001	5071.4	1	<0.0001
vorQ10	20	1	<0.0001	68.9	1	<0.0001
spdQ10	2.6	1	0.1059	6.8	1	0.009
srchQ10	8.4	1	0.0037	6.6	1	0.0099
PREDATORS x TEMP	32.9	2	<0.0001	74.2	2	<0.0001
PREDATORS x assim	56.3	1	<0.0001	41.6	1	<0.0001
PREDATORS x met_rate	88.5	1	<0.0001	56.1	1	<0.0001
PREDATORS x size_ini	8.2	1	0.0041			
PREDATORS x tank_ini	80.7	1	<0.0001	13.1	1	0.0003
PREDATORS x voracity	156.8	1	<0.0001	46.8	1	<0.0001
PREDATORS x pheno	2.6	1	0.1048	5.1	1	0.0237
PREDATORS x search_area	22.9	1	<0.0001			
PREDATORS x growth	123.3	1	<0.0001	46	1	<0.0001
PREDATORS x speed	0	1	0.8641	5.6	1	0.0183
PREDATORS x actE_met	1205.3	1	<0.0001	1367.9	1	<0.0001
PREDATORS x vorQ10	16.5	1	<0.0001	47.6	1	<0.0001
PREDATORS x spdQ10	4.3	1	0.0381	8.2	1	0.0041
PREDATORS x srchQ10	10	1	0.0015	5.7	1	0.0169
TEMP x assim	15	2	0.0006	14.7	2	0.0006
TEMP x met_rate	24.7	2	<0.0001	18.8	2	<0.0001
TEMP x size_ini				17.2	2	0.0002
TEMP x tank_ini	35.1	2	<0.0001	6.5	2	0.0385
TEMP x voracity	34.8	2	<0.0001			
TEMP x pheno	13	2	0.0015			
TEMP x growth	41.3	2	<0.0001	21.5	2	<0.0001
TEMP x speed	5.7	2	0.0566			
TEMP x actE_met	44.1	2	<0.0001	104	2	<0.0001
TEMP x vorQ10	12.6	2	0.0019			
TEMP x srchQ10	27.8	2	<0.0001	31.8	2	<0.0001
PREDATORS x TEMP x assim	12.5	2	0.002			
PREDATORS x TEMP x met_rate	23.8	2	<0.0001	17.8	2	0.0001
PREDATORS x TEMP x tank_ini	31.2	2	<0.0001	6.1	2	0.0477
PREDATORS x TEMP x voracity	33.2	2	<0.0001			
PREDATORS x TEMP x pheno	11	2	0.0041			
PREDATORS x TEMP x growth	42.2	2	<0.0001	21.4	2	<0.0001
PREDATORS x TEMP x speed	7.9	2	0.0193			
PREDATORS x TEMP x actE_met	44.9	2	<0.0001	106.2	2	<0.0001
PREDATORS x TEMP x vorQ10	13.4	2	0.0012			
PREDATORS x TEMP x srchQ10	19.9	2	<0.0001	34.1	2	<0.0001

Table 2. Selection gradients of prey in two contrasting environmets and for two levels of genetic correlation among traits. a) ρ=0.1 b) ρ=0.9

Table 2 a)	16ºC PREDATORS ABSENT				25ºC PREDATORS PRESENT			
	β/γ	SE	t	p-value	β/γ	SE	t	p-value
(Intercept)	1.01	0.01	70.1	<0.0001	0.82	0.03	31.6	<0.0001
actE_met	0.69	0.01	68.4	<0.0001	0.99	0.02	47.8	<0.0001
srchQ10	0.00	0.01	0.0	0.9659	0.01	0.02	0.5	0.5973
growth	-0.01	0.01	-0.9	0.3823	0.02	0.02	0.8	0.4092
assim	0.02	0.01	2.4	0.0180	0.03	0.02	1.4	0.1687
met_rate	0.02	0.01	1.9	0.0568	0.04	0.02	1.8	0.0691
size_ini	0.01	0.01	1.2	0.2301	-0.01	0.02	-0.4	0.6808
tank_ini	0.00	0.01	-0.3	0.7378	0.01	0.02	0.7	0.4750
voracity	-0.02	0.01	-1.9	0.0614	-0.04	0.02	-1.9	0.0580
pheno	0.01	0.01	1.0	0.3187	0.03	0.02	1.4	0.1604
search_area	0.01	0.01	0.6	0.5528	0.02	0.02	1.1	0.2610
speed					0.02	0.02	0.9	0.3841
vorQ10	0.02	0.01	1.7	0.0989	0.10	0.02	4.9	<0.0001
spdQ10	0.01	0.01	1.3	0.1830	0.02	0.02	0.9	0.3573
I(growth^2)	0.08	0.02	5.7	<0.0001				
I(actE_met^2)	-0.10	0.02	-6.6	<0.0001	0.38	0.04	12.2	<0.0001
actE_met x srchQ10	0.02	0.01	2.4	0.0176	0.03	0.02	1.7	0.0957
actE_met x growth	0.04	0.01	3.9	0.0001	0.08	0.02	3.6	0.0004
actE_met x met_rate	-0.02	0.01	-2.1	0.0366				
actE_met x voracity					-0.03	0.02	-1.4	0.1576
actE_met x pheno					0.04	0.02	1.7	0.0834
actE_met x vorQ10					0.07	0.02	3.2	0.0013
srchQ10 x search_area					0.05	0.02	2.4	0.0168
srchQ10 x spdQ10					-0.04	0.02	-1.9	0.0628
srchQ10 x voracity	0.02	0.01	2.4	0.0146				
growth x size_ini	0.01	0.01	0.8	0.4170				
growth x voracity	0.01	0.01	1.4	0.1583				
growth x vorQ10	-0.02	0.01	-2.1	0.0393				
assim x tank_ini	-0.02	0.01	-1.7	0.0806				
assim x met_rate					-0.03	0.02	-1.4	0.1590
assim x pheno					0.03	0.02	1.3	0.2090
assim x search_area	-0.02	0.01	-1.9	0.0623	0.03	0.02	1.3	0.2060
assim x vorQ10	0.02	0.01	2.0	0.0459				
met_rate x tank_ini	-0.02	0.01	-1.8	0.0681				
size_ini x spdQ10	-0.02	0.01	-1.6	0.1085				
size_ini x voracity					-0.03	0.02	-1.3	0.1825
size_ini x speed					0.04	0.02	1.9	0.0555
tank_ini x voracity					-0.04	0.02	-2.0	0.0480
tank_ini x pheno	-0.02	0.01	-2.0	0.0438	-0.05	0.02	-2.3	0.0227
tank_ini x vorQ10					0.04	0.02	2.1	0.0403
voracity x speed					0.04	0.02	2.0	0.0510
voracity x vorQ10					-0.04	0.02	-1.7	0.0964
voracity x spdQ10					-0.03	0.02	-1.2	0.2335
pheno x search_area	-0.02	0.01	-2.1	0.0344				

Table 2 b)	16ºC PREDATORS ABSENT				25ºC PREDATORS PRESENT			
	β/γ	SE	t	p-value	β/γ	SE	t	p-value
(Intercept)	1.00	0.02	56.9	<0.0001	0.86	0.03	25.962	<0.0001
actE_met	0.67	0.01	70.1	<0.0001	0.95	0.02	48.216	<0.0001
srchQ10	0.01	0.02	0.3	0.7441	-0.01	0.05	-0.179	0.8577
growth	0.02	0.02	1.3	0.1839	0.02	0.05	0.409	0.6826
assim	-0.03	0.02	-1.2	0.2380	0.06	0.05	1.28	0.2006
met_rate	0.05	0.02	2.5	0.0110	0.04	0.04	0.892	0.3722
size_ini	-0.03	0.02	-1.4	0.1706	0.02	0.05	0.361	0.7184
tank_ini					-0.07	0.05	-1.403	0.1607
voracity	-0.01	0.03	-0.3	0.7305	-0.08	0.05	-1.441	0.1498
pheno	0.02	0.02	1.3	0.2087	0.00	0.04	-0.041	0.9671
search_area	-0.04	0.02	-1.6	0.1200	-0.09	0.05	-1.96	0.0501
speed	0.02	0.02	1.0	0.3173	0.11	0.04	2.468	0.0136
vorQ10	-0.03	0.02	-1.1	0.2913	0.10	0.05	1.908	0.0565
spdQ10	-0.06	0.02	-2.6	0.0085	-0.02	0.05	-0.335	0.7375
I(growth^2)	0.04	0.02	1.5	0.1224				
I(actE_met^2)	-0.08	0.01	-6.1	<0.0001	0.26	0.01	9.642	<0.0001
actE_met x srchQ10	-0.05	0.02	-2.3	0.0198	-0.07	0.02	-3.458	0.0006
actE_met x growth	0.13	0.02	7.3	<0.0001	0.11	0.02	5.509	<0.0001
actE_met x assim					0.08	0.04	1.794	0.0730
actE_met x met_rate	-0.03	0.01	-2.7	0.0076				
actE_met x size_ini	-0.04	0.02	-1.9	0.0582				
actE_met x voracity	-0.06	0.02	-2.9	0.0033	-0.14	0.04	-3.121	0.0018
actE_met x pheno	-0.04	0.02	-2.2	0.0290				
actE_met x vorQ10	-0.05	0.02	-2.3	0.0237				
srchQ10 x growth	0.03	0.02	1.6	0.1044	0.14	0.06	2.337	0.0195
srchQ10 x tank_ini					0.07	0.05	1.518	0.1291
srchQ10 x assim	0.13	0.05	2.7	0.0071				
srchQ10 x voracity	-0.11	0.05	-2.2	0.0305				
srchQ10 x pheno	-0.03	0.02	-1.5	0.1403				
srchQ10 x search_area	0.05	0.02	2.2	0.0286	0.12	0.05	2.104	0.0355
srchQ10 x speed					-0.04	0.04	-1.025	0.3053
srchQ10 x spdQ10	0.01	0.01	1.7	0.0968				
growth x size_ini					0.07	0.05	1.516	0.1298
growth x search_area					0.12	0.07	1.691	0.0910
growth x speed					-0.11	0.07	-1.599	0.1101
growth x spdQ10					-0.10	0.05	-1.787	0.0741
growth x met_rate	0.01	0.01	1.4	0.1652				
growth x pheno	0.01	0.02	0.6	0.5715				
assim x met_rate	-0.02	0.02	-1.3	0.1855				
assim x size_ini	0.04	0.02	2.0	0.0455	0.02	0.01	1.406	0.1598
assim x voracity	0.05	0.02	2.2	0.0264				
assim x search_area	0.12	0.05	2.7	0.0072				
assim x tank_ini					0.12	0.05	2.275	0.0230
assim x pheno					0.07	0.04	2.015	0.0440
assim x speed	-0.07	0.04	-1.7	0.0893	-0.06	0.03	-1.734	0.0830
assim x vorQ10	0.12	0.05	2.4	0.0186				
met_rate x size_ini					0.18	0.09	1.989	0.0469
met_rate x voracity					0.17	0.09	1.923	0.0546
met_rate x pheno					0.07	0.04	1.719	0.0857
met_rate x search_area	-0.03	0.02	-1.6	0.1041				
met_rate x speed	0.03	0.02	1.6	0.1111				
met_rate x search_area					0.04	0.03	1.205	0.2284
size_ini x tank_ini					0.12	0.06	2.073	0.0383
size_ini x search_area					-0.20	0.08	-2.371	0.0178
size_ini x spdQ10					0.04	0.02	2.047	0.0407
tank_ini x pheno					-0.03	0.02	-1.808	0.0708
voracity x search_area					-0.17	0.08	-2.027	0.0428
pheno x search_area					-0.14	0.07	-1.865	0.0624
pheno x speed					0.09	0.07	1.322	0.1864
pheno x vorQ10					0.13	0.05	2.696	0.0071
pheno x spdQ10					0.11	0.05	2.07	0.0386
search_area x speed					-0.04	0.03	-1.339	0.1808
search_area x spdQ10					-0.09	0.04	-2.213	0.0270
voracity x search_area	-0.12	0.04	-2.8	0.0060				
voracity x speed	0.07	0.04	1.7	0.0979				
voracity x vorQ10	-0.10	0.05	-2.0	0.0457				
search_area x vorQ10	0.04	0.02	1.7	0.0855				

Discusión integradora

Resultados y discusión

Siguiendo con el esquema desarrollado en la Figura 1 de la Introducción, los resultados de la presente tesis doctoral muestran que factores abióticos clave, algunos afectados por el cambio climático como la disponibilidad hídrica y la temperatura, así como la arquitectura del hábitat, tienen importantes efectos sobre el movimiento de los invertebrados, pudiendo repercutir en las interacciones bióticas en general y en las interacciones tróficas en particular. Además, los resultados de la tesis demuestran que la movilidad de los animales, junto con el contexto ecológico en el que éstos se encuentran, es un factor que puede explicar la evolución de determinados rasgos fenotípicos tales como el número de huevos y su tamaño. También se ha visto como en un contexto eco-evolutivo, la evolución de determinados rasgos fenotípicos puede estar mediada por cambios en la movilidad. debida ésta a su vez a un incremento de temperatura. Esta respuesta evolutiva, en forma de variabilidad genética y su correlación entre rasgos, puede a su vez repercutir en las interacciones bióticas y tener consecuencias sobre las dinámicas de las redes tróficas. A continuación se discute la relevancia de dichos resultados.

La disponibilidad hídrica: determinante de las tasas de encuentro y las interacciones bióticas

En los capítulos 1 y 2 se ha demostrado que la distribución espacial de la disponibilidad hídrica en el suelo (capítulos 1 y 2) y la productividad basal a la que va normalmente asociada el agua -hongos- (capítulo 2), pueden afectar de manera independiente y a muy corto plazo a las redistribuciones de los invertebrados que viven en la hojarasca. En general, los invertebrados se sienten atraídos por el agua y los hongos, lo que provoca que éstas áreas tengan una riqueza de grupos taxonómicos mayor. Sin embargo, no todos los grupos taxonómicos se sienten atraídos de igual forma hacia estos dos recursos, ya sea porque distintos grupos taxonómicos tienen diferentes necesidades hídricas (Chown 1993, Renault and Coray 2004), o porque las redistribuciones de algunos grupos taxonómicos también están mediadas por la composición biótica que hay en un lugar determinado (Lima 1998, Schmitz et al. 2004, Abrams 2007, Wisz et al. *en prensa*). De hecho, en el capítulo 2 encontramos que los depredadores son atraídos por el hongo mediante un efecto indirecto, dado que dichas áreas van a contener una mayor abundancia de presas. Además, los resultados demuestran que esta atracción diferencial de los distintos grupos taxonómicos hacia ciertas partes del espacio tiene unas repercusiones sobre las distribuciones de los pesos corporales de los animales, lo que afectará a las relaciones de tamaños corporales entre depredador y presa y consecuentemente al potencial de interacción (Wilson 1975, Woodward et al. 2005, Brose et al. 2006). Todas estas redistribuciones de grupos taxonómicos y tamaños corporales pueden, según distintos estudios, tener importantes efectos sobre las interacciones depredador-presa y sobre las dinámicas de las redes tróficas (Holling 1959, Cattin et al. 2004, Allesina et al. 2008, Brose 2010, Vucic-Pestic et al. 2010, Schneider et al. 2012).

Predecir las consecuencias de las tendencias agregativas de los invertebrados en las tasas de depredación puede no ser una tarea sencilla. En el capítulo 1 encontramos que, aunque el agua distribuida en forma de gradiente podría incrementar las tasas de encuentro y por lo tanto las tasas de depredación entre un depredador y una presa, la presa se siente menos atraída por la zona mas húmeda del gradiente cuando esta zona está ocupada por un depredador, lo que parece reducir las tasas de encuentro y de depredación. Aunque la presa parece obtener un claro beneficio a corto plazo, los beneficios a largo plazo no están tan claros, dado que las perdidas de agua de la presa pueden aumentar afectando a sus funciones fisiológicas (Chown and Nicolson 2004). Numerosos estudios han analizado el compromiso entre el riesgo de depredación y la adquisición de recursos (Lima and Dill 1990, Lima 1998), sin embargo éste es el primer estudio -hasta donde sabemos- en el que la presa evaluaría la adquisición de agua. Por otra parte, en el capítulo 2 hemos observado que la presencia de depredadores sólo ha afectado significativamente a la abundancia de 2 de los 9 grupos taxonómicos de presas más abundantes en esta comunidad de descomponedores de la hojarasca. Además, los efectos han sido opuestos a los esperados, ya que la presencia de depredadores ha incrementado la abundancia de Enquitreidos y Pselafognatos. Estos resultados podrían ser explicados por los efectos indirectos que los depredadores han podido tener sobre estos dos grupos de pequeños invertebrados, ya que se ha visto que en comunidades complejas, como puede ser la que hemos estudiado, los efectos indirectos pueden llevar a que los depredadores tengan unos efectos en direcciones opuestas a las esperadas y con frecuencia difíciles de predecir (Sih et al. 1985, Wootton 2002).

En resumen, los resultados de los capítulos 1 y 2 apuntan a que rápidas alteraciones en la disponibilidad hídrica del suelo provocadas por las sequias podrían tener consecuencias sobre las interacciones bióticas, aunque muchos de estos efectos pueden ser relativamente complejos de predecir, especialmente a largo plazo.

La arquitectura de la vegetación determina los movimientos de los animales

Hasta la fecha todavía no es bien conocido el efecto combinado que tiene la arquitectura de la vegetación y la fuerza de atracción de un recurso sobre los movimientos de forrajeo de los animales. En el capítulo 3 hemos estudiado como estos dos factores determinan el movimiento del insecto *R. pomonella* forrajeando en árboles. Los resultados de este capítulo muestran que la distribución de la longitud de los pasos -la distancia entre dos posiciones- se compone de muchos pasos de longitud corta y pocos de longitud larga. En otros estudios se ha demostrado que una distribución de pasos con estas características puede maximizar la localización de recursos distribuidos de forma aleatoria para los que no se sabe cuál es su localización (Bartumeus et al. 2005, Viswanathan et al. 2008). Sin embargo, Humphries et al. (2010) demuestra que en áreas con una importante presencia de recursos, otros tipos de movimiento (ej. Browniano) mejoran su probabilidad de encuentro, aunque en nuestro caso los individuos no modificaron la distribución de pasos en presencia del recurso.

Los resultados de este capítulo también indican, tal y como otros estudios demuestran, que la fuerza de atracción del estímulo es dependiente de la distancia (Green et al. 1994, Zollner and Lima 1997, Rosenthal 2007). El movimiento de los animales es más fuertemente influenciado por el estímulo a medida que los individuos se encuentran mas cerca de su localización. También encontramos que la densidad de la vegetación afectó negativamente a la fuerza de atracción del estímulo. Probablemente, la arquitectura de la vegetación alteró la luminosidad del ambiente y por lo tanto la detección del recurso (Endler 1992, 1993, Zollner and Lima 1999). Este resultado apoya el punto de vista de que los animales tienen un radio de percepción dependiente de las condiciones del ambiente, lo que es especialmente relevante para predecir de forma mas precisa su movimiento y dispersión (Olden et al. 2004).

Evolución de rasgos mediada por la movilidad y dinámicas eco-evolutivas

Los resultados de los capítulos 4 y 5 ponen de manifiesto que la movilidad de los animales juega un importante papel en la evolución de ciertos rasgos fenotípicos. En el capítulo 4 hemos construido un modelo que predice el tamaño óptimo de propágulo (e.g. huevos) según la diferencia en movilidad de los animales. Dado que los animales mas móviles se van a encontrar con más depredadores (Huey and Pianka 1981, Werner and Anholt 1993), y que el tamaño corporal es un rasgo que determina las tasas de ataque (Wilson 1975, Brose et al. 2008), el beneficio de poner huevos de mayor tamaño en animales más móviles sería doble: tener acceso a un mayor número de presas y ser menos depredado. Este efecto se hace mas evidente si consideramos la relación negativa entre numero y tamaño de los individuos que normalmente existe en las redes tróficas (Woodward et al. 2005, Mulder et al. 2011). Las predicciones del modelo han sido validadas utilizando datos de tamaño y número de huevos de 268 especies de arañas correspondientes a distintas movilidades dadas por su modo de caza: cazadoras activas vs. sentarse-y-esperar. Además, distintos estudios apoyan la hipótesis de que en ambientes con un riesgo de depredación más elevado, las especies hacen puestas con menos huevos y de mayor tamaño (Sih and Moore 1993, Heath et al. 2003, Montserrat et al. 2007).

En el capítulo 5 hemos introducido un modelo basado en individuos que relaciona la genética con las dinámicas del ecosistema mediante múltiples rasgos que afectan las interacciones bióticas, lo que sirve para estudiar las dinámicas eco-evolutivas de las redes tróficas. Las simulaciones muestran que las tasas de encuentro entre presa y depredador se incrementan con la temperatura (Brown et al. 2004, Moya-Laraño 2010, Petchey et al. 2010, Dell et al. 2011), lo que sugiere que la temperatura puede tener unos efectos indirectos sobre el funcionamiento de los ecosistemas, ya que los depredadores podrían provocar un mayor estrés a las presas (Hawlena and Schmitz 2010). Además, aún teniendo en cuenta que la esperanza de vida decrece al aumentar la temperatura, los encuentros a lo largo de la vida de los animales incrementan con la temperatura, lo que apoya la hipótesis de que en la temperatura, junto con la disponibilidad hídrica, incrementa la diversidad de organismos porque los encuentros entre genotipos es más frecuente y por tanto diverso, lo que lleva aumentar el rango de eficacia biológica en las poblaciones y por tanto la diversidad de nichos (Moya-Laraño 2010). Los resultados también demuestran que la correlación entre 13 rasgos relacionados con las interacciones tróficas (ver capítulo 5), modula cómo la temperatura afectará las dinámicas de las redes tróficas. Por ejemplo, hemos podido ver que, cuando los rasgos de los individuos están fuertemente correlacionados, un incremento en la temperatura conlleva a que las dinámicas de poblaciones sean mas estocásticas y los ciclos depredador-presa-hongo más cortos.

Perspectivas

Aunque los resultados de los capítulos 1 y 2 sugieren que alteraciones en la disponibilidad hídrica y en los recursos basales puede tener profundas implicaciones en la estructura de la red trófica de los descomponedores de la hojarasca, es necesario investigar mas detalladamente las consecuencias de estas agregaciones sobre las interacciones bióticas (e.g. depredación). En particular, se deberían entender mejor los posibles efectos indirectos que ejercen los depredadores en ciertos grupos de presas y sobre los procesos del ecosistema (ej. la tasa de descomposición y retorno de nutrientes). Esto nos permitirá hacer predicciones acerca de cómo alteraciones en el régimen hídrico (e.g. incremento de las sequias) va a afectar a la estructura y dinámica de las redes tróficas de los descomponedores. Además, también sería interesante explorar cuales serian las consecuencias ecológicas a medio-largo plazo de las agregaciones de invertebrados, y cómo distintas distribuciones heterogéneas de agua espacialmente distribuidas en el bosque afectan a la estructura de éstas redes tróficas. Por otra parte se podría utilizar una metodología similar a la desarrollada en el capítulo 3 para diseñar experimentos de captura-recaptura con el fin de estimar la fuerza de atracción que una zona húmeda ejerce sobre distintos grupos de invertebrados. Finalmente, tal como se explica en dicho capítulo, el modelo basado en individuos (MBI) desarrollado en el capítulo 5 puede ser una herramienta eficaz para evaluar cómo el cambio climático va a afectar al control biológico de plagas, aunque para ello sería necesario acoplar el desarrollo de éste MBI a un programa experimental determinado con el fin de tener una buena calibración del modelo y así obtener buenas predicciones. Por ejemplo, predecir la cantidad de depredadores que sería necesaria, así como sus características fenotípicas, para optimizar el control de la plaga por parte de estos depredadores en un determinado contexto ecológico.

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Conclusiones

Conclusiones

1. La distribución espacial de agua y hongo del suelo altera la abundancia, la composición taxonómica y las distribuciones de tamaño corporal de invertebrados descomponedores de hojarasca. De forma general podemos decir que aquellos parches con mas humedad y hongo tienen una densidad y riqueza de invertebrados mayor.
2. La movilidad y distribución de ciertos grupos taxonómicos está mediada por el contexto biótico. Los depredadores del suelo responden indirectamente a las áreas con hongo porque son zonas con mayor densidad de presas. Por otro lado algunas presas evitan zonas húmedas y se mueven más frecuentemente cuando estas zonas contienen depredadores.
3. La presencia de depredadores incrementa la supervivencia de dos grupos de presas, lo que sugiere que complejas relaciones indirectas pueden estar actuando en la red trófica de descomponedores.
4. La arquitectura del ambiente determina el movimiento de *R. pomonella* y modula la fuerza de atracción de un estímulo, que a la vez es dependiente de la distancia. Sin embargo la presencia del estímulo no ha afectado a la distribución de la longitud de paso del insecto, que está compuesta por muchos pasos pequeños y pocos largos.
5. Las arañas mas móviles hacen puestas con menos huevos pero de mayor tamaño que las arañas menos móviles, probablemente porque en el contexto de las redes tróficas esto confiere una ventaja adaptativa.
6. Un incremento en la temperatura, acompañado de una alta correlación de rasgos que determinan las interacciones entre especies, conllevará a mayores tasas de encuentro entre presas y depredadores y a que las cascadas tróficas sean más fuertes, aunque las dinámicas serán también más estocásticas, mostrando alta variabilidad en qué nivel trófico se extingue antes.
7. Incluso una vez corregida la disminución en la esperanza de vida debida a la mayor temperatura, la tasa de encuentros que los animales tienen a lo largo de su vida es mayor a mayores temperaturas.

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