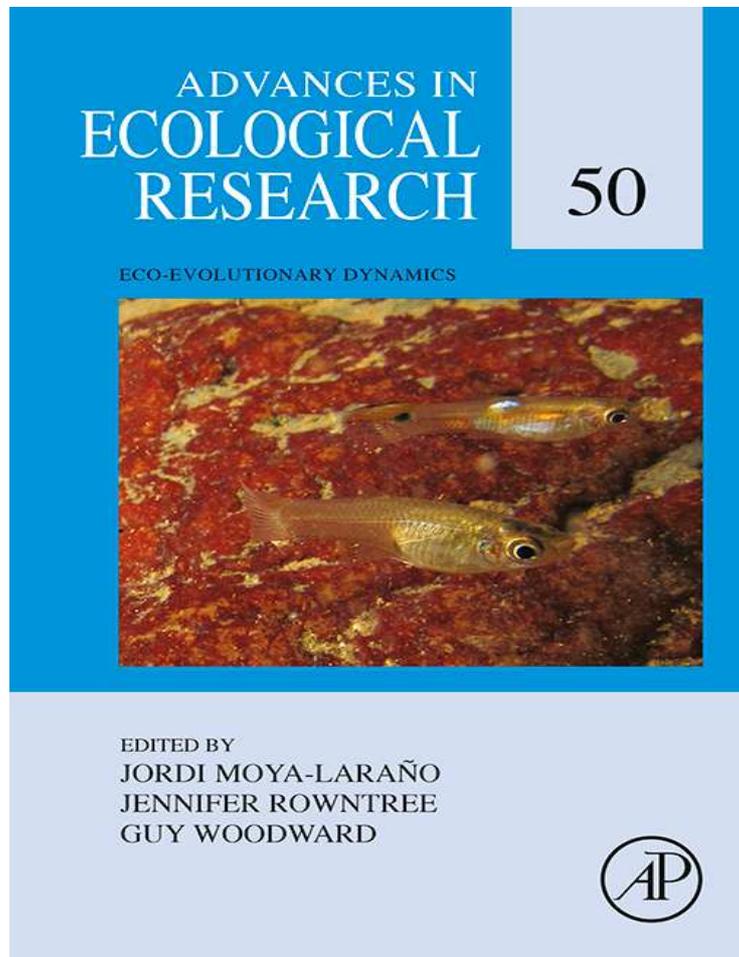


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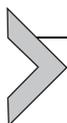
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Eco-Evolutionary Spatial Dynamics: Rapid Evolution and Isolation Explain Food Web Persistence

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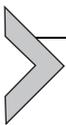
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Abstract

One of the current challenges in evolutionary ecology is understanding the long-term persistence of contemporary-evolving predator–prey interactions across space and time. To address this, we developed an extension of a multi-locus, multi-trait eco-evolutionary individual-based model that incorporates several interacting species in explicit landscapes. We simulated eco-evolutionary dynamics of multiple species food webs with different degrees of connectance across soil-moisture islands. A broad set of parameter combinations led to the local extinction of species, but some species persisted, and this was associated with (1) high connectance and omnivory and (2) ongoing evolution, due to multi-trait genetic variability of the embedded species. Furthermore, persistence was highest at intermediate island distances, likely because of a balance between predation-induced extinction (strongest at short island distances) and the coupling of island diversity by top predators, which by travelling among islands exert global top-down control of biodiversity. In the simulations with high genetic variation, we also found widespread trait evolutionary changes indicative of eco-evolutionary dynamics. We discuss how the ever-increasing computing power and high-resolution data availability will soon allow researchers to start bridging the *in vivo*–*in silico* gap.

The more ambitious plan may have more chances of success... This sounds paradoxical... [but] the paradox disappears if we look closely at a few examples... provided [these are] not based on a mere pretension but on some vision of the things beyond those immediately present.

György Pólya (1957)



1. INTRODUCTION

1.1. Food webs and eco-evolutionary dynamics

Although the notion that ecology and evolution operate at similar timescales was put forward nearly 50 years ago (Pimentel, 1968), the first use of the term eco-evolutionary dynamics dates to Savill et al. (1997). The reciprocal effect of ecology and evolution on biological interactions is central to this concept, and eco-evolutionary dynamics have mainly been studied in this context. This is illustrated by the fact that the most prominent reviews

(e.g. [Carroll et al., 2007](#); [Schoener, 2011](#)) and the seminal studies on eco-evolutionary dynamics ([Reznick et al., 1990](#); [Yoshida et al., 2003](#)) concern species interactions. At least two main factors may account for this focus on biological interactions: first, the selection pressure posed by (mainly) antagonistic interactions is very strong ([Benkman, 2013](#)), so evolutionary responses should be rapid, merging ecological and evolutionary timescales. Indeed, several studies have documented fast responses to the selection pressure posed by predators (e.g. [Orsini et al., 2012](#); [Reznick et al., 1990](#)) or parasites (e.g. [Kraaijeveld and Godfray, 1997](#); [Martins et al., 2013](#)). Second, ecological dynamics are best described for species interactions, thus providing a solid foundation for incorporating predictions of evolutionary feedbacks in ecology.

Most eco-evolutionary studies have addressed antagonistic interactions between two species ([Losos et al., 2004](#); [Palkovacs and Post, 2009](#); [Terhorst et al., 2010](#)). Beginning with Darwin's tangled bank ([Darwin, 1959](#)), however, ecologists have long been aware of the far more complex web of interactions in which individuals are embedded ([Elton, 1927](#); [Winemiller and Polis, 1996](#)). Hence, incorporating ecological networks in the framework of eco-evolutionary dynamics is a natural extension, as highlighted in a series of reviews and opinion pieces ([Agrawal et al., 2006](#); [Bolnick et al., 2011](#); [Fontaine et al., 2011](#); [Fussmann et al., 2007](#); [Olesen et al., 2010](#); [Stewart et al., 2013](#); [Thompson, 1998](#)).

Most available experimental studies of eco-evolutionary dynamics in food webs have tested how individuals with different evolutionary histories differentially affect an ecological community ([Bassar et al., 2012](#); [Chislock et al., 2013](#); [Farkas et al., 2013](#); [Harmon et al., 2009](#); [Ingram et al., 2012](#); [Lau, 2012](#); [Palkovacs and Post, 2009](#); [Urban, 2013](#); [Walsh et al., 2012](#)). For example, [Bassar et al. \(2012\)](#); see also [Travis et al., 2014](#), chapter 1 of this volume) showed that guppies that had evolved in ponds with or without predators had different effects on the prey invertebrate community. These examples show how the product of a rapid evolutionary process (i.e. organisms that have evolved in one environment or another) affect ecosystems, yet the strength and sign of prey selection (i.e. positive or negative frequency-dependent selection) remain to be tested in experiments that also account for prey abundance (see [Melian et al., 2014](#)).

Another possible way by which evolution can affect ecology on a contemporary timescale is if the evolution of the genetic composition of populations alters ecological dynamics ([Becks et al., 2010](#); [Johnson et al., 2009](#); [Rowntree et al., 2011](#); [Yoshida et al., 2003](#)). For instance,

predator–prey dynamics in genetically homogeneous prey populations changed dramatically when the prey population included two clones with different resistance properties (Yoshida et al., 2003). This led to rapid evolution of the prey population, which, in turn, affected the ecological dynamics of predator–prey cycles. A similar approach was used in host–parasite webs by Lennon and Martiny (2008), in which the introduction of viruses in a community of algae caused rapid evolution of resistance in the algal host, following a dampening of the initial effect of viruses on nutrient cycling. Similarly, Johnson et al. (2009) showed rapid evolution of plant traits and used a model to predict the impact of such changes in the arthropod community inhabiting the plants. Such an approach requires either populations with different standing genetic variations at the outset, in order to have a control for the evolutionary rate, or a strong modelling approach to generate testable predictions on the relative role of ecology and evolution in the dynamics of prey and predators.

In summary, standing genetic variation and the strength and sign of selection can alter population dynamics of species in ways that may be difficult to anticipate. One question in particular that remains to be addressed is how genetic variation at the outset of dynamics and the strength and sign of selection may affect food web structure and dynamics. Earlier results, using a modelling approach, suggested that higher genetic variability for traits contributes to food web stability by increasing connectance and variability in interaction strengths (Moya-Larano, 2011, see also Melián et al., 2011). This issue is particularly relevant in “metanetwork” food webs that are scattered in a heterogeneous space, in which local interactions will shape the outcome of each subpopulation.

1.2. Space, the next frontier

Although the literature on eco–evolutionary dynamics has been growing at an extraordinary pace, the incorporation of space has lagged behind somewhat (Urban et al., 2008), which is surprising given its prominence in other ecological and evolutionary fields (Levins, 1968). Actually, early attempts at combining ecological changes in population densities with evolutionary changes in gene frequencies have been done in the context of spatially heterogeneous environments (Levene, 1953), and some researchers have even produced spatial ecological and evolutionary data in the same study system (e.g. Singer and Thomas, 1996; Thomas et al., 1996).

Dispersal is a very powerful trait that links ecology and evolution: for instance, migration among patches changes both the density and the allele frequency of populations. In turn, both the connectivity among patches and their genetic composition can affect the sign and strength of selection for dispersal. For example, traits from rare migrants can become dominant (i.e. the advantage of the rare or negative frequency-dependent selection) or quickly go extinct in a new patch (i.e. the advantage of the common or positive-frequency-dependent selection). The role of spatial heterogeneity in eco-evolutionary dynamics has only been addressed in few experimental systems (Farkas et al., 2013; Hanski, 2011; Kerr et al., 2006; Singer and McBride, 2012), with a particularly well-documented exception being that of the Glanville fritillary butterfly, where the allele frequency in the *pgi* dispersing gene is driven by spatial heterogeneity (Hanski, 2011).

Given the links between dispersal and the dynamics of interacting populations and allele frequencies, several avenues of research are worthy of further exploration to help us understand how systems in spatially heterogeneous landscapes are shaped by eco-evolutionary dynamics.

1.3. Merging space, food webs and evolution

Recently, researchers (mainly ecologists) have focused on the study of multi-trophic metacommunities (i.e. communities linked by dispersal and trophic interactions—Haegeman and Loureau, 2014; Holyoak et al., 2005; Melian et al., 2014; Pillai et al., 2011; Wilson, 1992). The composition of such multi-trophic metacommunities reflects that of simple communities, in which species may be linked by a linear food chain or embedded in a complex food web (Bohan and Woodward, 2013; Tamadoni-Nezhad et al., 2013; Winemiller and Polis, 1996).

Spatial heterogeneity plays an important role in structuring food webs. Indeed, McCann et al. (2005) and Rooney et al. (2006) showed that the high mobility of predators can couple different food web energy channels across space and contribute to global food web stability (the “bird feeder effect”) (McCann et al., 2005; Rooney et al., 2006). Moreover, dispersal of omnivores may contribute to the robustness of the metacommunity, thereby enhancing food web complexity and species diversity (Pillai et al., 2011). None of these examples, however, considers the evolution of any of the players involved in the food web.

In a subsequent study, a mathematical model predicted that local extinction patterns in a predator-prey metacommunity had differential effects on

the evolution of dispersal in predators and prey (Pillai et al., 2012). This promising result suggests that emergent properties stem from the combination of ecology and evolution in metacommunities of two species. Hence, eco-evolutionary dynamics in metacommunities composed of more complex food webs could provide the foundation from which emergent patterns are generated. Still, both empirical and theoretical studies on this topic are conspicuously lacking (Thuiller et al., 2013; Urban et al., 2008): we aim to merge empirical observations and theory by extending food webs in heterogeneous space using invertebrate soil food webs as a model system (Moya-Laraño et al., 2012).

1.4. Soil food webs as a model system

Soil food webs are diverse systems that underpin the decomposition of organic material and nutrient recycling in terrestrial ecosystems (André et al., 2002; Decaëns, 2010; Hättenschwiler et al., 2005; Swift et al., 1979; Wardle, 2006). In recent years, both laboratory (Brose et al., 2008; Schneider et al., 2012) and field experiments (Chen and Wise, 1999; McLaughlin et al., 2010; Moya-Larano and Wise, 2007; Scheu and Schaefer, 1998; Wise and Chen, 1999) have been conducted to address relevant ecological questions related to food web theory, including how water affects decomposition processes indirectly via its effects on the food web (Lensing and Wise, 2006). Soils are highly heterogeneous ecosystems (Moore et al., 2004), with strong spatial heterogeneity in water content (Schume et al., 2003). This can drive the spatial structuring of leaf-litter food webs at micro-, local and regional scales (Melguizo-Ruiz et al., 2012). At the micro-environmental scale, water can accumulate in soil patches due to the micro-topography of the area in which the leaf litter sits (e.g. the base of slopes) or other landmarks which affect the micro-environment (e.g. underneath shrubs at the base of tree trunks). Since soil moisture affects soil fauna, by attracting them to moist areas during dry conditions (Verdeny-Vilalta and Moya-Laraño, 2014), these moisture pockets may work as islands of productivity during drought conditions. This provides an ideal scenario for studying metacommunity dynamics, using micro-environmental patches connected by migration.

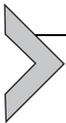
1.5. Aims: A few examples of hypothesis testing using Weaver

Here, we present Weaver, an Individual-Based Modelling computer program that aims to fill the gap between empirical observations of individual-based food webs in heterogeneous space with the theoretical

predictions coming from eco-evolutionary multi-trophic metacommunity dynamics. This program is an extension of a former simpler platform (mini-Akira, [Moya-Laraño et al., 2012](#)) which, by having greatly increased computing performance, allows the exploration of individual-based eco-evolutionary dynamics in multi-species food webs across space. This framework links genes to ecosystems through space, reaching an unprecedented level of comprehensiveness that provides insight into ecological and evolutionary dynamics at the gene, individual, population and community levels at different spatial scales. All of these can also be linked to ecosystem processes, such as top-down control of predators inducing trophic cascades affecting basal resources at different temperatures ([Moya-Laraño et al., 2012](#)), or the role of predators for maintaining biodiversity across space under different food web, island and genetic configurations. In addition, rather than being a “black box”, the present framework, and as in empirical studies, produces several detailed outputs (including gene spatio-temporal dynamics) that can be used for understanding the various mechanisms behind eco-evolutionary dynamics. The researcher can track everything that each gene and each individual has done in the simulation. As far as we know, no other framework is currently capable of providing such detail. However, although we develop some new hypotheses in [Section 4](#), here we are focused primarily on exploring food web persistence and trait evolution under different genetic and ecological scenarios: one of the great advantages is that one can perform additional simulation experiments (e.g. eliminating particular species or knocking down variability in a particular trait) to uncover the mechanisms responsible for the patterns emerging from simulations.

The overall purpose of the simulations presented here is to illustrate the usefulness of our IBM framework through a few examples, addressing some of the main open questions in the field of eco-evolutionary dynamics and ecological networks in space. We ask six questions: (1) Does connectance affect food web persistence? (2) Does standing intraspecific genetic variation alter food web persistence by triggering rapid evolution? (3) In a multi-trophic metacommunity context, how does the spatial structure (i.e. degree of spatial isolation) alter persistence and rapid evolution in food webs? (4) In all of the above scenarios, do predators inhibit prey populations in rapid evolving predator-prey systems and, if so, do predators contribute to maintain prey diversity? (5) How does standing genetic variation alter the evolutionary rate and the persistence of predator-prey systems? (6) Do traits evolve differently in prey under purely competitive environments (without predators) versus those where both predation and competition are at play?

Of course, the results derived from this approach are merely digital approximations of nature: to take full advantage of this simulation platform, the results must be tested in real systems and fed back to one each other iteratively. We propose how to integrate simulations with real systems to link, step by step, the *in vivo*–*in silico* gap, with the potential of generating an unprecedented level of understanding about how real ecosystems work. For instance, if one output is produced in nature that the simulations are not reproducing, the new estimates and parameters found in the experiment can be included in further simulations. We have included a subsection in [Section 4](#) to explain how to implement this Feedback Research Program (FRP). However, we stress again that performing studies at the digital level only, as we do here, can provide important clues and hypotheses that need to be empirically tested in future experiments.



2. MATERIALS AND METHODS

Unless stated otherwise, we here use the same approach as in the former paper ([Moya-Laraño et al., 2012](#)), in which we provided a level of detail that is beyond the scope of this chapter. We therefore refer to the reader who wants to fully grasp all the underpinnings and details of this modelling framework to the above reference. However, we have made an effort to explain the most relevant parameters necessary to follow the approach and make this article as self-explanatory as possible. When necessary, we have actually replicated some of the information in [Moya-Laraño et al. \(2012; Appendix\)](#).

We modelled 20-species beech forest soil food webs ([Melguizo-Ruiz et al., 2012](#)) with differing degrees of connectivity and genetic variation in the same 13 traits as in [Moya-Laraño et al., 2012 \(Appendix\)](#), namely: fixed body size at birth; amount of energy for maintenance and growth at birth; growth ratio; phenology (or genetically determined development time determining birth date beyond environmental constraints such as changes in temperature); searching area; voracity; sprint speed; metabolic rate; temperature plasticity for speed; voracity and searching area; and activation energy for metabolic rate. Estimates of ecological ranges for temperature-dependent traits were obtained from the literature ([Dell et al., 2011; Ehnes et al., 2011](#)). The amount of genetic trait variability is governed by the parameter φ ([Moya-Laraño et al., 2012](#)), which can be thought of as a genetic restriction parameter ranging between 0 and 1 ([Appendix](#)). Values of φ close to 0 indicate that the trait has the highest possible genetic variation (i.e. across the entire phenotypic range; [Table 3.1](#)) and

Table 3.1 Species and trait ranges included in simulations

Species ID	Class	Common name	Taxon ^a	Feeding guild	Trait ranges	
					Energy tank (%) ^b	Growth ratio
<i>(a) Webs with connectance 0.1 or 0.55</i>						
aca1	Arachnida	Mite	Mesostigmatida	Predator	0.25–0.5	1.35–1.45
aca2	Arachnida	Mite	Prostigmatida	Predator	0.25–0.5	1.35–1.45
aca3	Arachnida	Mite	Mesostigmatida	Predator	0.25–0.5	1.35–1.45
aca4	Arachnida	Mite	Prostigmatida	Predator	0.25–0.5	1.35–1.45
spd1	Arachnida	Spider	Agelenidae	Predator	0.25–0.5	1.20–1.30
spd1	Arachnida	Spider	Erigoninae	Predator	0.25–0.5	1.25–1.35
spd3	Arachnida	Spider	Dysderidae	Predator	0.25–0.5	1.15–1.25
spd4	Arachnida	Spider	Theridiidae	Predator	0.25–0.5	1.15–1.25
geo1	Chilopoda	Centipede	Geophilomorpha	Predator	0.25–0.5	1.15–1.25
lit1	Chilopoda	Centipede	Lithobiomorpha	Predator	0.25–0.5	1.15–1.25
opi1	Arachnida	Hartvestmen	Opiliona	Predator	0.25–0.5	1.15–1.25
col1	Insecta	Springtail	Collembola	Fungivore	0.25–0.5	1.25–1.35
col2	Insecta	Springtail	Collembola	Fungivore	0.25–0.5	1.35–1.45
col3	Insecta	Springtail	Collembola	Fungivore	0.25–0.5	1.15–1.25
enc1	Oligochaeta	Potworm	Enchytraeidae	Fungivore	0.25–0.5	1.35–1.45
enc2	Oligochaeta	Potworm	Enchytraeidae	Fungivore	0.25–0.5	1.25–1.35
enc3	Oligochaeta	Potworm	Enchytraeidae	Fungivore	0.25–0.5	1.25–1.35
ori1	Arachnida	Mite	Oribatida	Fungivore	0.25–0.5	1.35–1.45
ori2	Arachnida	Mite	Oribatida	Fungivore	0.25–0.5	1.15–1.25
ori3	Arachnida	Mite	Oribatida	Fungivore	0.25–0.5	1.25–1.35

Continued

Table 3.1 Species and trait ranges included in simulations—cont'd

Species ID	Trait ranges					
	Phenology (days)	Body size at birth (mg)	Assimilation efficiency	Voracity	Sprint speed	Search area
aca1	3–11	0.001–0.003	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
aca2	3–11	0.002–0.004	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
aca3	3–11	0.003–0.005	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
aca4	3–11	0.004–0.006	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
spd1	3–11	0.013–0.033	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
spd1	3–11	0.008–0.010	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
spd3	3–11	0.049–0.069	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
spd4	3–11	0.009–0.029	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
geo1	3–11	0.09–0.10	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
lit1	3–11	0.045–0.065	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
opi1	3–11	0.004–0.026	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
col1	3–11	0.001–0.003	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.3
col2	3–11	0.004–0.024	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.3
col3	3–11	0.002–0.003	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.3
enc1	3–11	0.0001–0.002	0.5–0.7	0.55–0.75	0.1–0.3	0.1–0.3
enc2	3–11	0.0001–0.002	0.5–0.7	0.55–0.75	0.1–0.3	0.1–0.3
enc3	3–11	0.001–0.003	0.5–0.7	0.55–0.75	0.1–0.3	0.1–0.3
ori1	3–11	0.003–0.005	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.3
ori2	3–11	0.0001–0.002	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.3
ori3	3–11	0.001–0.003	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.3

Species ID	Trait ranges				
	met_rate	Q10 voracity	Q10 speed	Q10 search area	Activation energy (eV)
aca1	0.6–0.8	3–4	1.5–2.5	2.0–2.5	0.33–0.42
aca2	0.6–0.8	3–4	1.5–2.5	2.0–2.5	0.36–0.46
aca3	0.6–0.8	3–4	1.5–2.5	2.0–2.5	0.33–0.42
aca4	0.6–0.8	3–4	1.5–2.5	2.0–2.5	0.36–0.46
spd1	0.5–0.7	3–4	1.5–2.5	2.0–2.5	0.65–0.75
spd1	0.5–0.7	3–4	1.5–2.5	2.0–2.5	0.65–0.75
spd3	0.5–0.7	3–4	1.5–2.5	2.0–2.5	0.65–0.75
spd4	0.5–0.7	3–4	1.5–2.5	2.0–2.5	0.65–0.75
geo1	0.46–0.66	3–4	1.5–2.5	2.0–2.5	0.75–0.85
lit1	0.45–0.65	3–4	1.5–2.5	2.0–2.5	0.75–0.85
opi1	0.46–0.76	3–4	1.5–2.5	1.5–2.5	0.65–0.75
col1	0.65–0.85	2–4	1.5–2.5	1.5–2.5	0.61–0.70
col2	0.65–0.85	2–4	1.5–2.5	1.5–2.5	0.61–0.70
col3	0.55–0.85	2–4	1.5–2.5	1.5–2.5	0.61–0.70
enc1	0.70–0.90	2–4	1.5–2.5	1.5–2.5	0.39–0.49
enc2	0.70–0.90	2–4	1.5–2.5	1.5–2.5	0.39–0.49
enc3	0.70–0.90	2–4	1.5–2.5	1.5–2.5	0.39–0.49
ori1	0.57–0.77	2–4	1.5–2.5	1.5–2.5	0.66–0.76
ori2	0.57–0.77	2–4	1.5–2.5	1.5–2.5	0.66–0.76
ori3	0.57–0.77	2–4	1.5–2.5	1.5–2.5	0.66–0.76

Continued

Table 3.1 Species and trait ranges included in simulations—cont'd

Species ID	Class	Common name	Taxon ^a	Feeding guild	Trait ranges	
					Energy tank (%) ^b	Growth ratio
<i>(b) Web with connectance 0.3</i>						
aca1	Arachnida	Mite	Mesostigmatida	Predator	0.25–0.5	1.35–1.45
aca2	Arachnida	Mite	Prostigmatida	Predator	0.25–0.5	1.35–1.45
aca3	Arachnida	Mite	Mesostigmatida	Predator	0.25–0.5	1.35–1.45
aca4	Arachnida	Mite	Prostigmatida	Predator	0.25–0.5	1.35–1.45
aca5	Arachnida	Mite	Mesostigmatida	Predator	0.25–0.5	1.35–1.45
aca6	Arachnida	Mite	Prostigmatida	Predator	0.25–0.5	1.35–1.45
spd1	Arachnida	Spider	Agelenidae	Predator	0.25–0.5	1.20–1.30
spd2	Arachnida	Spider	Erigoninae	Predator	0.25–0.5	1.25–1.35
spd3	Arachnida	Spider	Dysderidae	Predator	0.25–0.5	1.15–1.25
spd4	Arachnida	Spider	Theridiidae	Predator	0.25–0.5	1.15–1.25
spd5	Arachnida	Spider	Dysderidae	Predator	0.25–0.5	1.15–1.25
spd6	Arachnida	Spider	Erigoninae	Predator	0.25–0.5	1.15–1.25
geo1	Chilopoda	Centipede	Geophilomorpha	Predator	0.25–0.5	1.15–1.25
geo2	Chilopoda	Centipede	Geophilomorpha	Predator	0.25–0.5	1.15–1.25
lit1	Chilopoda	Centipede	Lithobiomorpha	Predator	0.25–0.5	1.15–1.25
lit2	Chilopoda	Centipede	Lithobiomorpha	Predator	0.25–0.5	1.15–1.25
col1	Insecta	Springtail	Collembola	Fungivore	0.25–0.5	1.25–1.35
col2	Insecta	Springtail	Collembola	Fungivore	0.25–0.5	1.35–1.45
enc1	Oligochaeta	Potworm	Enchytraeidae	Fungivore	0.25–0.5	1.35–1.45
ori1	Arachnida	Mite	Oribatida	Fungivore	0.25–0.5	1.35–1.45

Species ID	Trait ranges					
	Phenology (days)	Body size at birth (mg)	Assimilation efficiency	Voracity	Sprint speed	Search area
aca1	3–11	0.001–0.003	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
aca2	3–11	0.002–0.004	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
aca3	3–11	0.003–0.005	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
aca4	3–11	0.004–0.006	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
aca5	3–11	0.0028–0.0035	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
aca6	3–11	0.002–0.003	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
spd1	3–11	0.013–0.033	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
spd2	3–11	0.008–0.010	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
spd3	3–11	0.049–0.069	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
spd4	3–11	0.009–0.029	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
spd5	3–11	0.06–0.08	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
spd6	3–11	0.0035–0.0045	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
geo1	3–11	0.09–0.10	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
geo2	3–11	0.05–0.07	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
lit1	3–11	0.045–0.065	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
lit2	3–11	0.040–0.050	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.4
col1	3–11	0.001–0.003	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.3
col2	3–11	0.004–0.024	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.3
enc1	3–11	0.0001–0.002	0.5–0.7	0.55–0.75	0.1–0.3	0.1–0.3
ori1	3–11	0.003–0.005	0.7–0.9	0.55–0.75	0.1–0.3	0.1–0.3

Continued

Table 3.1 Species and trait ranges included in simulations—cont'd

Species ID	Trait ranges				
	Metabolic rate	Q10 voracity	Q10 speed	Q10 search area	Activation energy (eV)
aca1	0.6–0.8	3–4	1.5–2.5	2.0–2.5	0.33–0.42
aca2	0.6–0.8	3–4	1.5–2.5	2.0–2.5	0.36–0.46
aca3	0.6–0.8	3–4	1.5–2.5	2.0–2.5	0.33–0.42
aca4	0.6–0.8	3–4	1.5–2.5	2.0–2.5	0.36–0.46
aca5	0.6–0.8	3–4	1.5–2.5	2.0–2.5	0.33–0.42
aca6	0.6–0.8	3–4	1.5–2.5	2.0–2.5	0.36–0.46
spd1	0.5–0.7	3–4	1.5–2.5	2.0–2.5	0.45–0.55
spd2	0.5–0.7	3–4	1.5–2.5	2.0–2.5	0.45–0.55
spd3	0.5–0.7	3–4	1.5–2.5	2.0–2.5	0.45–0.55
spd4	0.5–0.7	3–4	1.5–2.5	2.0–2.5	0.45–0.55
spd5	0.5–0.7	3–4	1.5–2.5	2.0–2.5	0.45–0.55
spd6	0.5–0.7	3–4	1.5–2.5	2.0–2.5	0.45–0.55
geo1	0.46–0.66	3–4	1.5–2.5	2.0–2.5	0.45–0.55
geo2	0.46–0.66	3–4	1.5–2.5	2.0–2.5	0.45–0.55
lit1	0.45–0.65	3–4	1.5–2.5	2.0–2.5	0.45–0.55
lit2	0.45–0.65	3–4	1.5–2.5	2.0–2.5	0.45–0.55
col1	0.65–0.85	2–4	1.5–2.5	1.5–2.5	0.61–0.70
col2	0.65–0.85	2–4	1.5–2.5	1.5–2.5	0.61–0.70
enc1	0.70–0.90	2–4	1.5–2.5	1.5–2.5	0.39–0.49
ori1	0.57–0.77	2–4	1.5–2.5	1.5–2.5	0.66–0.76

^aTaxonomic level specification differs depending on the group.

^bTrait definitions: energy tank, percentage of body size devoted to maintenance and growth at birth; growth ratio, ratio between two instar body lengths; phenology, time between egg laying and birth; body size at birth, mass of the structural body size; assimilation efficiency, percentage of ingested food converted to own mass; voracity, sprint speed, search area, and metabolic rates are mass scaling coefficients for ingested mass, maximum speed, number of cells travelled per day, and metabolic rates, respectively; Q10s and activation energy for metabolic rate denote genetic variability in temperature plasticity for the same four traits (further information can be found in Moya-Laraño et al., 2012 and in Appendix).

a value of 1 means that all animals are genetically identical for that particular trait. For simplicity, we used the same value for all traits and did not play for different amounts of genetic variation in different traits. $\varphi = 0.99$ means that animals are almost genetically identical; hence, adaptation cannot occur from standing genetic variation. In the absence of genetic correlation among traits (Moya-Laraño et al., 2012), $\varphi = 0.01$ means that genetic constraints are minimal, so evolution can occur rapidly and in any direction. To narrow down the questions to be answered, we ran all simulations without genetic correlation among traits (Moya-Laraño et al., 2012). We therefore compared scenarios in which all species had maximum genetic variation in all traits ($\varphi = 0.01$) against others in which genetic variability was restricted to a minimum ($\varphi = 0.99$; Appendix).

One important feature of Weaver is that it can restrict which species are able to feed on each other by including a vector of edible species, allowing initializing simulations with particular food web structures. To manipulate connectance and to simulate realistic food webs, we used the program Network3D to build two random 20-species webs restricted to the niche model (Williams and Martinez, 2000): one with relatively low connectance (0.1) and another with relatively high connectance (0.3). To fit in the animals from the beech forest food web, top predators were assigned to the largest species (harvestmen, spiders and centipedes), intermediate size predators to predators of the smallest size (Mesostigmata and Prostigmata mites) and the smallest sizes to fungivores, namely, springtails (Collembola), oribatid mites (Oribatida) and enchytraeid worms (Clitellata). Within each taxon, we chose a diversity of offspring and adult body sizes to generate across-species diversity. The ranges of the other traits were similar among species, with the exception of that of enchytraeids. Indeed, due to their high starvation resistance, likely coming from their low activation energies for metabolic rates (Ehnes et al., 2011; see Appendix), this group grew to disproportionately large numbers in our simulations as compared to other fungivore species. We believe that some additional constraints, such as their low desiccation resistance (Lindberg et al., 2002; Maraldo et al., 2008), which is not yet incorporated in our framework, may make populations of these worms growing at lower rates in the wild despite their relatively low energy expenditure to activate metabolism. We thus decided to compensate this by decreasing their assimilation efficiencies relative to other taxa (Table 3.1). In addition, to further test the effect of connectivity on food web persistence, we simulated a hypergeneralist food web, in which all predators were able to feed on all the species, including themselves (connectance = 0.55; Fig. 3.1).

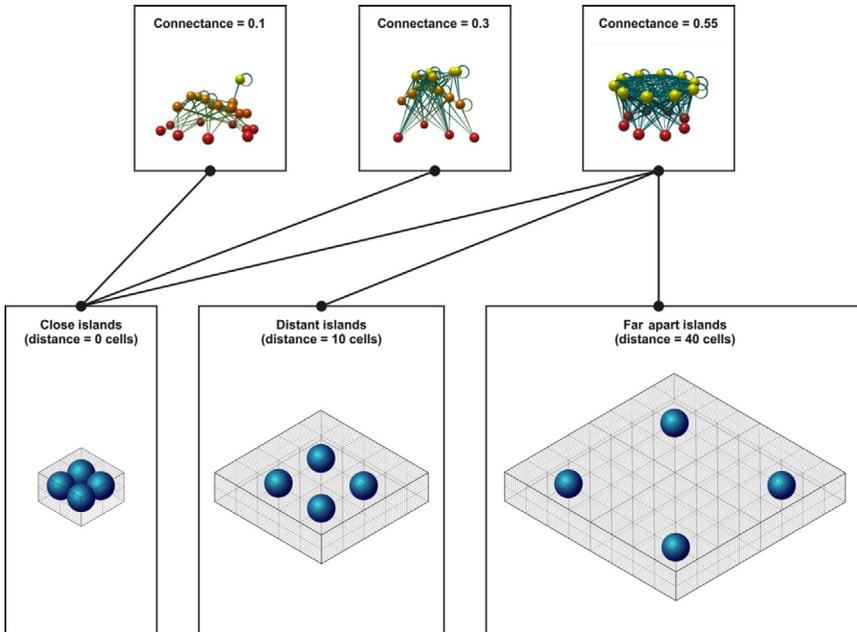


Figure 3.1 Food web and metacommunity structures included in the simulations. The joining segments indicate which food web structures were tested under which metacommunity spatial structures. The spheres in the lower panel correspond to micro-islands of moisture (moisture pockets) in the forest floor.

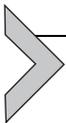
Food webs with connectance 0.1 and 0.55 had the exact same species: 11 species of predators and 9 species of fungivores. To allow its fitting to the niche model, the food web with intermediate connectance (0.3) necessarily included a different number of predators (16) and fungivores (4; Fig. 3.1 and Table 3.1). Hence, we created our hypergeneralist web by allowing all predators in the original niche model food web with connectance 0.1 to feed on all other prey and predators, therefore manipulating the latter to have a connectance of 0.55. Food web structure was built taken into account animals only, and for simplicity, we included in all webs a single fungus species upon which all fungivores fed. A simple basal resource makes these webs somehow unrealistic. However, given that we did not explicitly include trade-offs between traits in the simulations (see Section 4) nor resource-dependent assimilation efficiencies, both of which could explain the coexistence of different fungivore species, having different species of fungi or just one was functionally equivalent. As highly connected webs

were the most persistent, the remaining simulations were performed using these hypergeneralist webs.

To incorporate a spatial component, we simulated a four-micro-island scenario mimicking water (moisture) pockets in the forest floor (e.g. Melguizo-Ruiz et al., 2012) in which fungi were able to grow (Fig. 3.1). The space surrounding these islands was drier (initialized at 0% RH), thus not allowing fungi to grow. Since animals did not sense water, nor did water directly affect them, this 0% RH had effect only on fungi (i.e. it could have been any number below that which allowed fungus growth in this scenario, <85% see Appendix). Therefore, the four micro-islands had equal basal productivity. These micro-islands were spheres of 5-cell (patch) units of radius (see Appendix) and were either close to each other (distance among centres 10 cells, distance among borders 0 cells) or at a distance (10- or 40-cell distance among borders). The dimensions of the Worlds containing these islands were (depth \times width \times length) $10 \times 20 \times 20$, $10 \times 50 \times 50$ or $10 \times 80 \times 80$ cells, respectively. For the two last scenarios, in which islands were far apart, we minimized edge effects by allowing a 10-cell space around islands. Note that this is a generous edge which matches the distance between islands in the simulations at intermediate distances. Since so far migration in Weaver depends merely on an animal's mobility which in turn depends on several state variables (e.g. fungi or prey availability, predatory threat, internal stage—condition ϵ —and the trait searching area), here we did not consider long-distant dispersal (e.g. aerial dispersal in springtails and spiders).

To include additional realism in the simulations, we initialized the density of each species and instar following mass–abundance allometric constraints (Reuman et al., 2009), for which we used the equation $N = 74.8M^{-0.75}$ as in Schneider et al. (2012). As in other equations (see Appendix), we assumed 70% of water body content to calculate the number of individuals of each instar and species. To accommodate the output coming from the above allometric equation to our simulation, we applied the above equation to all instars and species and the absolute resulting number was then divided by the total number of individuals, therefore obtaining a fraction for each species and instar. To calculate the absolute number of each species and instar in the simulation, we then multiplied this fraction by the total number of individuals at initialization (i.e. the community size, which was set at 20,000) and rounded the resulting number. We tested the effect of predators on prey density and diversity (like in keystone predation—Paine, 1966) by running simulations with all species in the food web and comparing these with simulations in which predators were excluded, i.e., with fungivores only.

Because these simulations have a strong stochastic component, to assess the consistency of the results, we ran five replicates of each simulation. The deterministic effects were sufficiently strong as to allow enough statistical power to test the main hypotheses. However, as the main patterns are summarized in the statistical analyses, we only display a few of the dynamics as examples. All statistical analyses were performed in R (R development core team 2014). The main hypotheses stated above were tested using general linear models (GLMs) on all replicates, with proportion of prey, predators and all species remaining at the end as dependent variables. When necessary, we ran log-likelihood ratio tests to unravel potential differences among groups and post hoc Tukey tests to compare pairs of groups (package “multcomp”). All simulations were run for 200 days. For one of the parameter combinations that showed the strongest signs of stability, we ran one additional simulation for 500 days for two reasons: (1) to determine how many and which species would remain (long-term persistence) and to draw the final (persistent) web with species-to-species interaction strengths and (2) to explore trait evolutionary dynamics, for which we measured the change in constitutive traits (i.e. those genetically determined as opposed to plastic or environmentally determined traits) through time by fitting splines in a GLM (R library “splines”) in which time (day) was the independent variable and the constitutive trait value the dependent variable. The results of the simulations were then plotted with 95% confidence bands using the library “effects” (Fox, 2003) in R. We further explored trait evolution in one of the fungivore species that persisted until the end in one of the webs (predators present), as well as in simulations that involved competition only. The purpose of this analysis was to explore whether trait evolution differed in a purely competitive environment relative to one in which both predation and competition occurred: we predicted that traits associated with competition or anti-predatory behaviour would evolve differently.



3. RESULTS

3.1. Connectance and food web persistence

An example of the dynamics can be found in Fig. 3.2. Connectance increased the proportion of species remaining at the end of the simulation by $1.7\times$. An example of the dynamics can be found in Fig. 3.2 (GLM, $b=0.34$, $t_{14}=2.66$, $P=0.0197$; Fig. 3.3). This effect was stronger and highly significant for predators (GLM, $b=1.02$, $t_{14}=6.79$, $P<0.0001$;

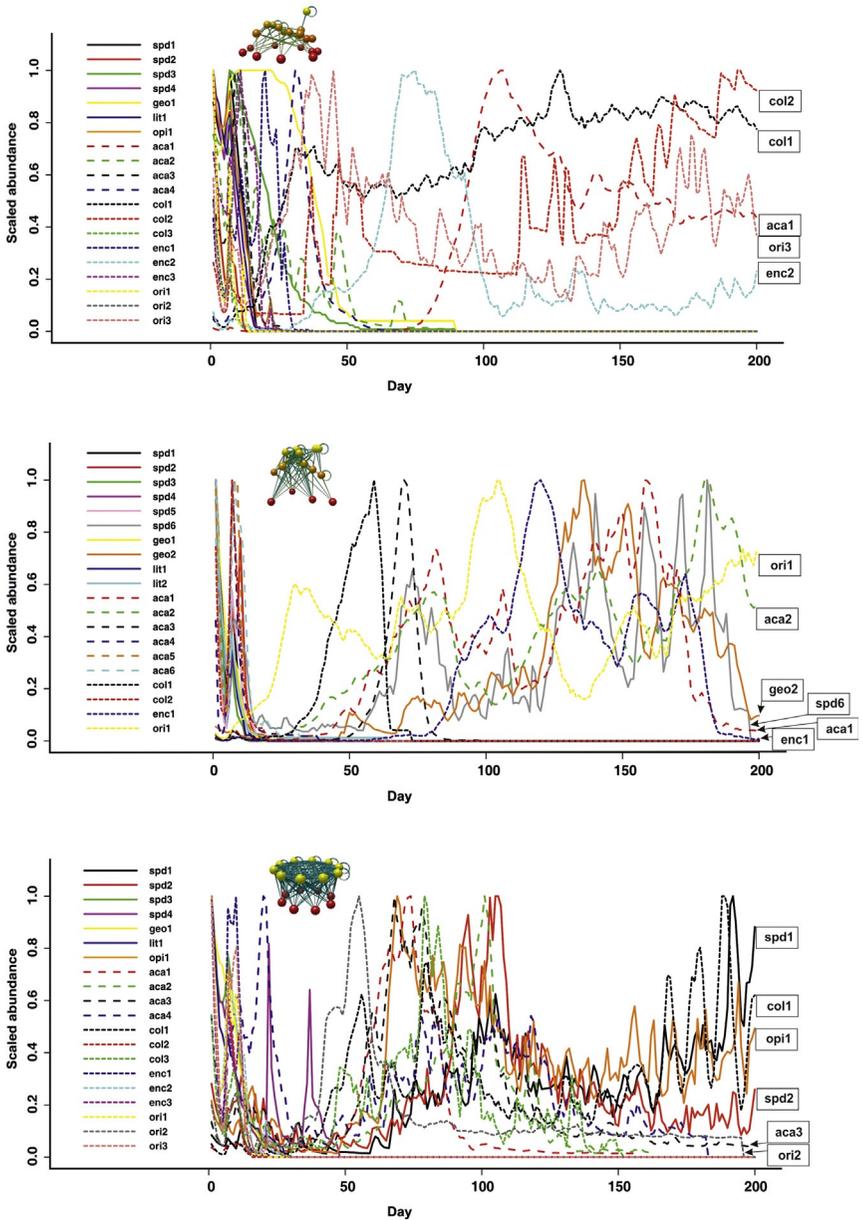


Figure 3.2 Dynamics of the population of each species (starting with 20 species) during 200 days, when the connectance of the food web was low (0.1, upper panel), relatively high (0.3, middle panel) or very high (0.55, lower panel). Figures depict one replicate out of the five ran per simulation. Abundances of each species (Y-axis) are shown scaled at 0–1. Dotted lines correspond to fungivores (oribatid mites, springtails and potworms), dashed lines to small predators (predatory mites) and solid lines to large predators (spiders, opilionids and centipedes). The codes on the right facilitate the identification of extant species in B/W printings. Names in the legend correspond to those in Table 3.1.

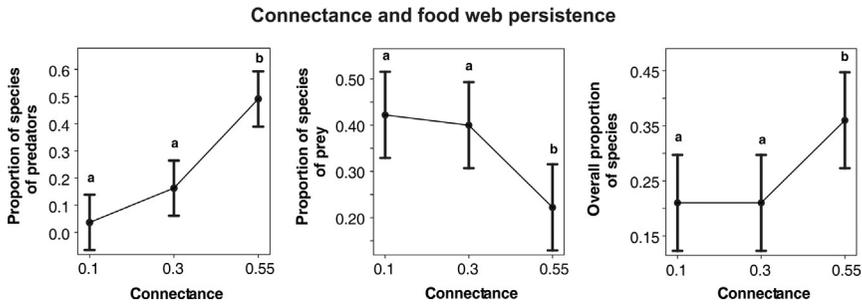


Figure 3.3 Proportion of predator (left panel), prey (central panel), and overall (right panel) species remaining at the end of the simulations ($N=5$) when the connectance of the food web was low (0.1), relatively high (0.3) or very high (0.55). Values are least-squares means \pm SE. Letters on top of bars denote significant differences among groups (<0.05).

Fig. 3.3). However, increasing connectance increased the extinction rate for prey (GLM, $b = -0.46$, $t_{14} = -3.32$, $P = 0.006$; Fig. 3.3). Note however that the trends are not linear, as the webs with connectance 0.1 and 0.3 are similar to each other (post hoc “Tukey” test, $P > 0.13$ for both comparisons) and they both significantly differ from the web with connectance 0.55 (both $P < 0.025$).

3.2. Genetic variation and food web persistence

High genetic variation allowed the persistence of $3.6 \times$ more species than either no genetic variation at all, or an intermediate level. An example of the dynamics can be found in Fig. 3.4 (prey, GLM, $b = 0.06$, $t_{14} = 3.17$, $P = 0.007$; predators, GLM, $b = 0.23$, $t_{14} = 5.54$, $P < 0.0001$; overall, GLM, $b = 0.15$, $t_{14} = 5.3$, $P = 0.0001$; Fig. 3.5). However, some patterns are clearly non-linear, and allowing the highest variability was only significantly different for prey between the two extremes (highest vs. lowest, post hoc “Tukey” test, $P = 0.006$, remaining comparisons $P > 0.15$), being the two lowest levels of genetic variation not significantly different for the proportion of predators that persisted ($P = 0.662$) and both significantly lower than the scenario with high genetic variation (both P s < 0.0001). The pattern for overall diversity was similar to that of the predators (comparison between the two lowest levels, $P = 0.443$; comparison between each of the two lowest levels vs. high genetic variation, both $P < 0.0001$).

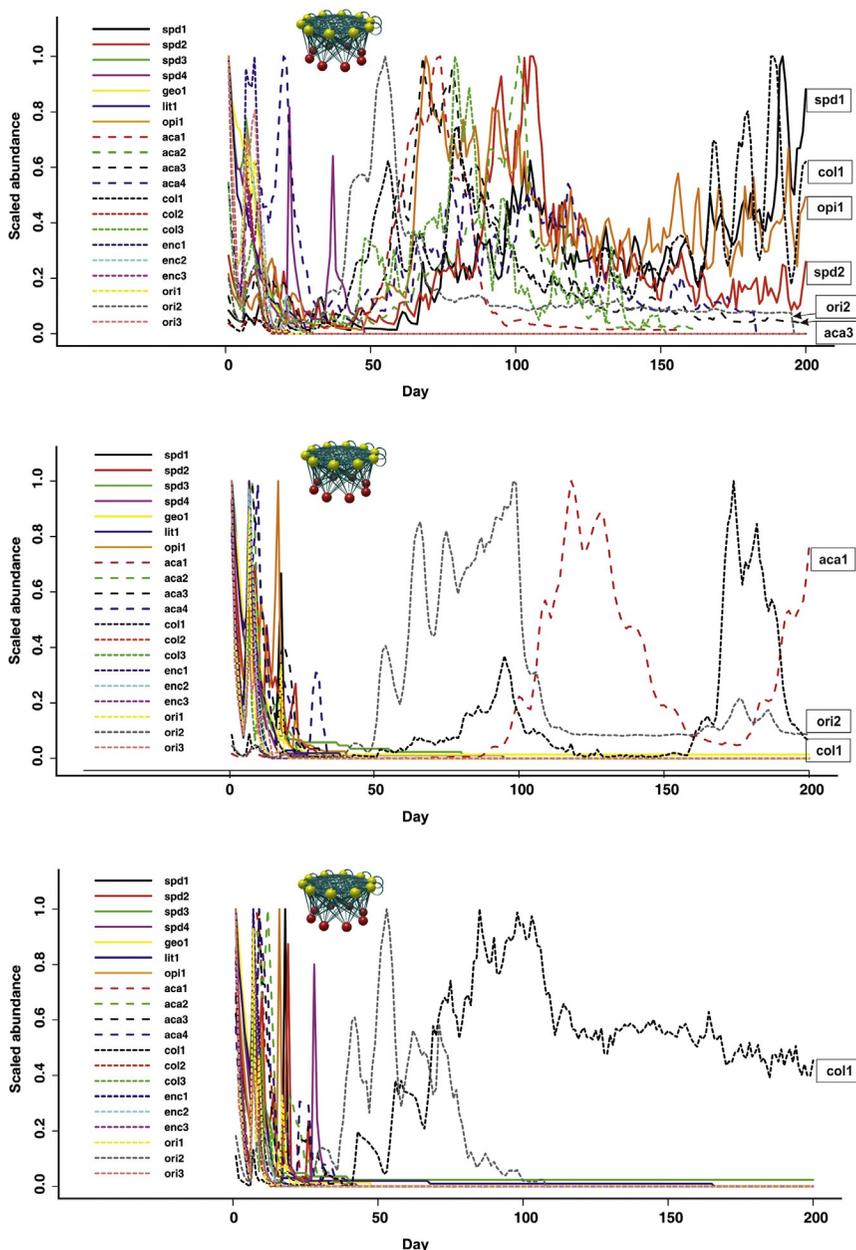


Figure 3.4 Dynamics of the population of each species during 200 days when the connectance of the food web was very high (0.55), and trait genetic variation was either high ($\varphi = 0.01$, superior panel), medium ($\varphi = 0.49$, middle panel) or almost zero ($\varphi = 0.99$, inferior panel). Figures depict one replicate out of the five ran per simulation. Abundances of each species (Y-axis) are shown scaled at 0–1. Dotted lines correspond to fungivores (oribatid mites, springtails and potworms), dashed lines to small predators (predatory mites) and solid lines to large predators (spiders, opilionids and centipedes). The codes on the right facilitate the identification of extant species in B/W printings. Names in the legend correspond to those in [Table 3.1](#).

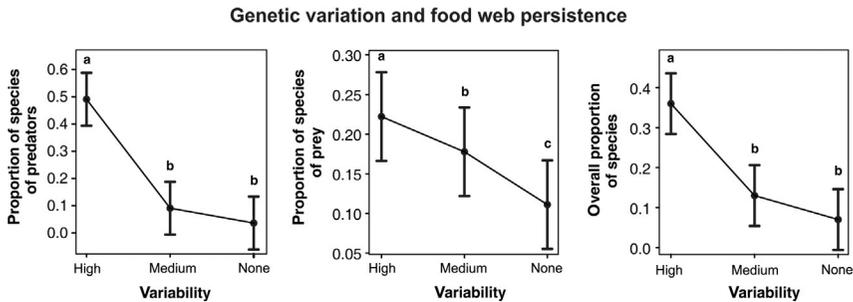


Figure 3.5 Proportion of predator (left panel), prey (central panel) and overall (right panel) species remaining at the end of the simulations ($N=5$) when genetic variation in the species embedded in the food web was high ($\varphi=0.01$), intermediate ($\varphi=0.49$), or almost zero ($\varphi=0.99$). Values are least-squares means \pm SE. Letters on top of bars denote significant differences among groups (<0.05).

3.3. Island distance and food web persistence

The overall proportion of species was between $2.6 \times$ and $3.5 \times$ more persistent in islands that were contiguous to each other or at relatively shorter distances (minimum distance 10 cells), respectively, than when they were farther apart (40 cells). An example of the dynamics can be found in Fig. 3.6. In addition, the proportion of prey species was $2\text{--}2.5 \times$ more persistent at intermediate distances. The three models were highly significant (all $P < 0.0001$; Fig. 3.7). Post hoc comparisons revealed no differences between the shortest and longest distances in the proportion of prey species that remained (Tukey test, $P = 0.750$). However, the proportion of species remaining was significantly higher at intermediate distances when compared with the shortest ($P < 0.0001$) or longest ($P < 0.0001$) distances. Predator species, on the other hand, persisted equally well at the shortest and intermediate distances ($P = 0.969$) and a $4.5 \times$ higher proportion of predators persisted at these two shorter distances relatively to the longest distances (both $P_s < 0.0001$). The pattern of overall diversity also showed the highest persistence of species at intermediate distances, with only the comparison between shortest and intermediate distances being marginally significant ($P = 0.065$), being the other two comparisons highly significant (both $P_s < 0.0001$). A total 50% of species remained at the end of the simulation at intermediate distances.

3.4. Predator top-down control on prey diversity

Overall, the presence of predators resulted in high extinction rates on prey. An example of the dynamics (Fig. 3.8) reveals that the presence of predators

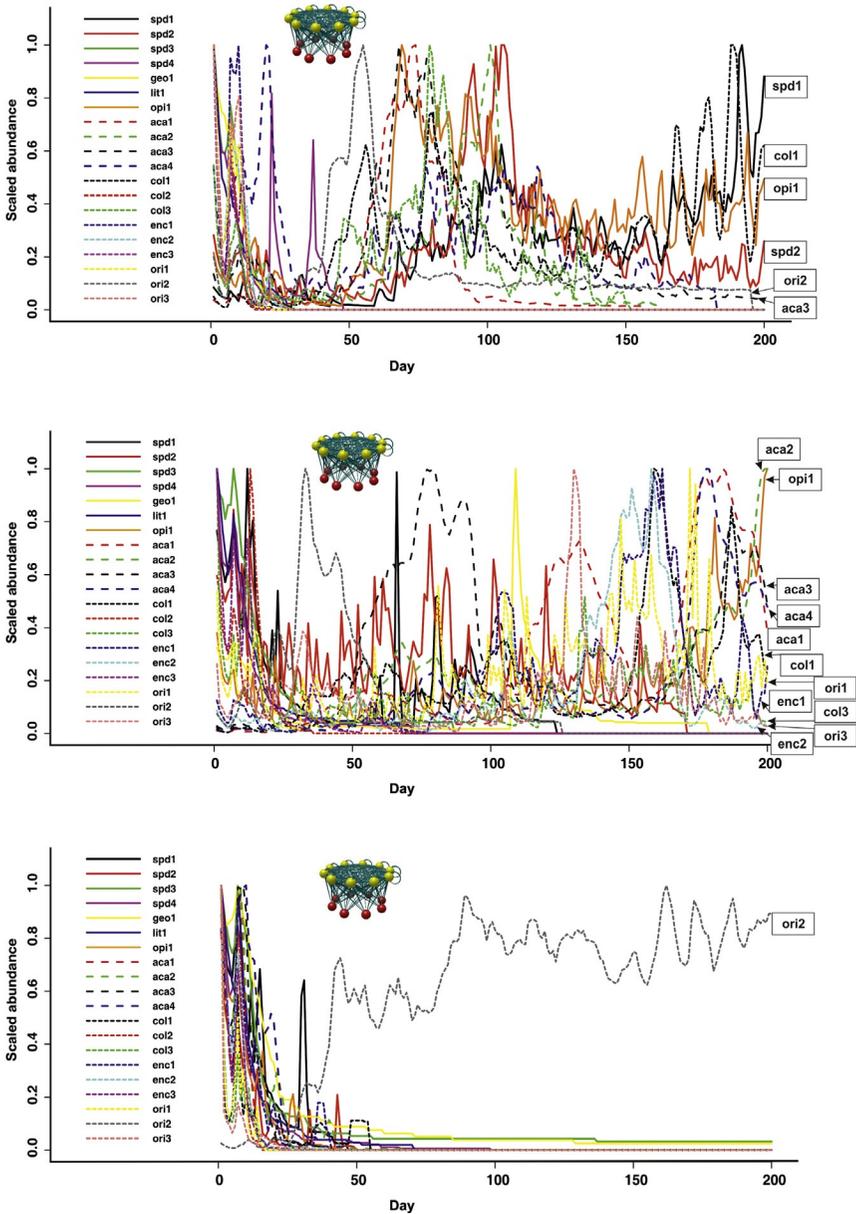


Figure 3.6 Dynamics of the population of each species (starting with 20 species) during 200 days when the connectance of the food web was very high (0.55), but islands were at different distances from each other (0 cells—superior panel; 10 cells—middle; or 40 cells—inferior panel). Figures depict one replicate out of the five ran per simulation. Abundances of each species (Y-axis) are shown scaled at 0–1. Dotted lines correspond to fungivores (oribatid mites, springtails and potworms), dashed lines correspond to small predators (predatory mites) and solid lines correspond to large predators (spiders, opilionids and centipedes). The codes on the right facilitate the identification of extant species in B/W printings. Names in the legend correspond to those in Table 3.1.

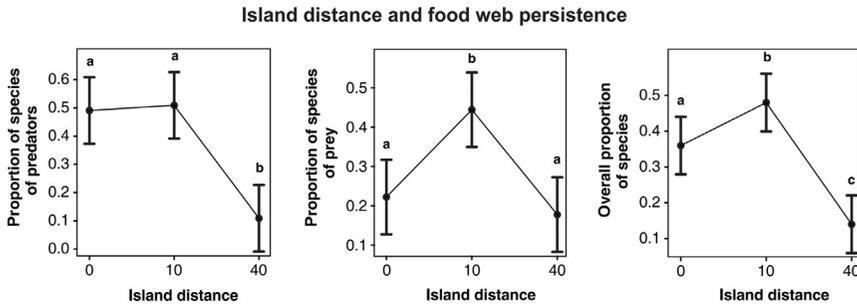


Figure 3.7 Proportion of predator (left panel), prey (central panel) and overall (right panel) species remaining at the end of the simulations ($N=5$) when islands were contiguous to each other (distance=0) or when they were separated by a minimum distance of either 10 or 40 cells. Values are least-squares means \pm SE. Letters on top of bars denote significant differences among groups (<0.05).

results in the extinction of two species of potworms (upper panel) that would have made it to the end in a competitive environment (lower panel). Conversely, in the presence of predators, a species of springtail (col1) and another of oribatid mite (ori2) persisted a pattern that never occurred in the absence of predators (not shown). In the islands located at the shortest distances (i.e. contiguous to each other), predators had a strong negative effect on prey species, diminishing the proportion of species that remained at the end of the simulation by 40% (Fig. 3.9, 0 distance), especially after longer periods, when only two species of enchytraeids persisted in the presence of predators (lower panel of Fig. 3.8). In addition, comparing the effect according to island distance reveals that, at intermediate distances, the proportion of prey species that is maintained does not differ between environments with or without predators (GLM, distance*predator presence, $\chi^2=21.6$; $P<0.0001$; Fig. 3.9 see also Fig. 3.7 Tukey test on predator effect at intermediate distances, $P=1$). Therefore, predators had a strong effect on the extinction rate of prey species, but this was contingent upon the spatial composition of the food web. In particular, predators showed a strong stabilizing effect at intermediate island distances, in which half the prey species remained until the end of the simulation. Moreover, more importantly, predators affected the identity of the species that remained.

3.5. Multi-trophic spatio-temporal dynamics during a 500-day simulation

We ran one of the most stable scenarios (highly connected web, high genetic variability islands at intermediate distances) for a longer period of time

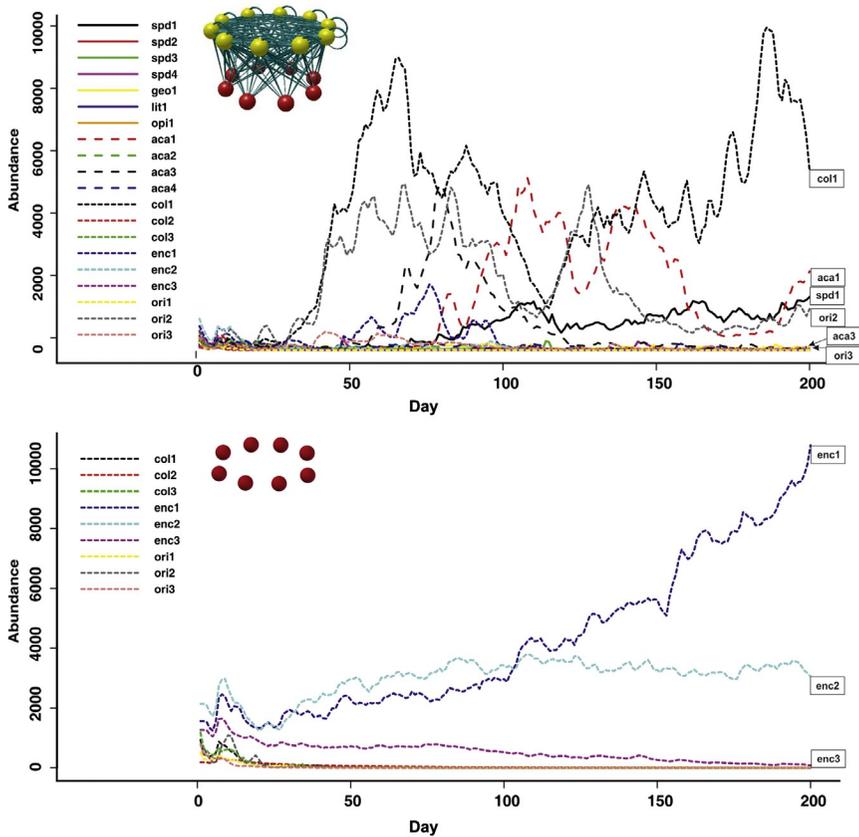


Figure 3.8 Dynamics of the population of each species during 200 days when the connectance of the food web was very high (0.55), in the presence (upper panel) or absence (lower panel) of predators. Figures depict one replicate out of the five ran per simulation. Dotted lines correspond to fungivores (oribatid mites, springtails and potworms), dashed lines correspond to small predators (predatory mites), and solid lines correspond to large predators (spiders, opilionids and centipedes). The codes on the right facilitate the identification of extant species in B/W printings. Names in the legend correspond to those in [Table 3.1](#).

(500 days) and found that out of 20 species, 5 persisted (4 species of predators and 1 prey; [Fig. 3.10](#)), and there was a steady increase in abundance of the top predator (the centipede *lit1*). The spatial dynamics for these five species were highly complex and showed some emergent patterns. First, large predators (centipedes and opilionids) were highly mobile relative to fungivores and small predators. Second, the first snapshot (day 58) showed an emerging spatial segregation among the two species of predatory mites, which occupied different islands, and also for the shared prey (springtail), which was

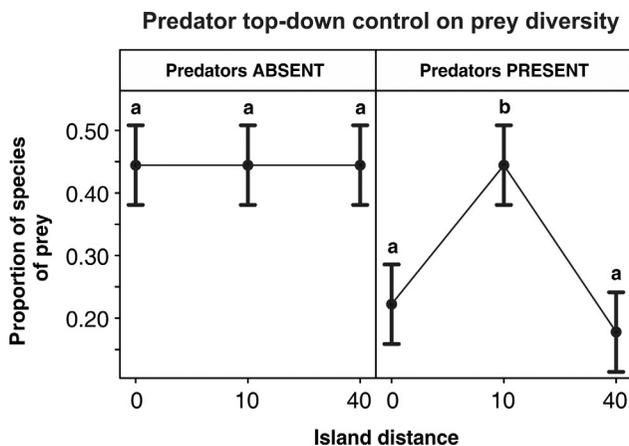


Figure 3.9 Proportion of prey species remaining at the end of the simulations ($N=5$) at three different distances between islands, and in the absence (left panel) or presence (right panel) of predators. Values are least-squares means \pm SE. Letters on top of bars denote significant differences among groups (<0.05).

present mostly in one island only. Third, at day 256, prey populations had gone extinct in three of the islands, and almost all individuals (predators and prey) were concentrated in the one island in which numbers of shared prey were still large. In subsequent days, the peak of prey populations occurred in different islands and then went extinct in the originally highly populated island: thus spatial dynamics had a very strong influence on the patterns of extinction and persistence.

During the above simulation, we also recorded all the foraging interactions and built the persistent subweb with interaction strengths, defined in two ways: (a) the proportion of individuals of each species eaten by each predator species (predator perspective, red arrows) and (b) the proportion of individuals of each species that is eaten by each predator species (prey perspective, blue arrows). This subweb (Fig. 3.11) was fairly independent of the remaining web (i.e. that including all of the extinct species) as the interaction strengths both within (cannibalism) and among these five species were much higher. The centipede was the top predator, as it interacted more strongly by feeding on all other species than vice versa. Most predators fed heavily on the shared prey. Cannibalism among predator populations was in general very strong and the smaller predator species (mites) interacted much less strongly among each other than with themselves: in general, intraguild predation (IGP) was weaker than cannibalism.

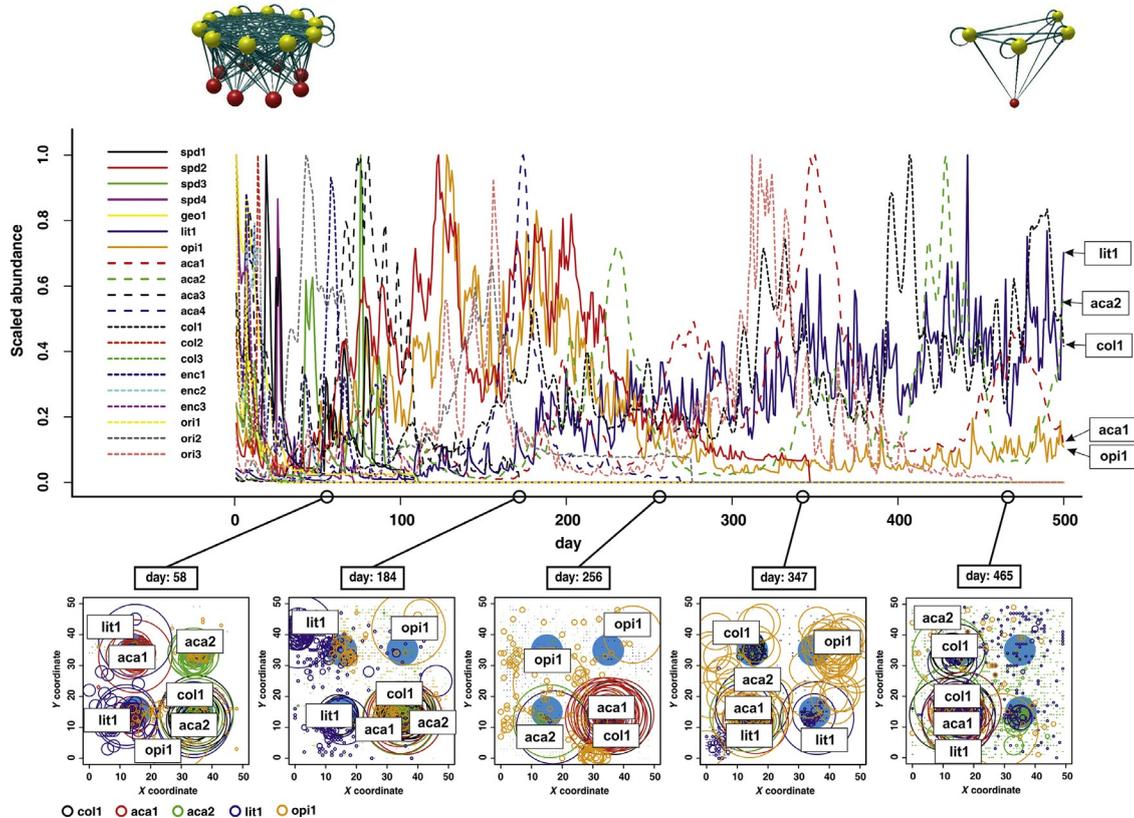


Figure 3.10 Dynamics of the most stable scenario (i.e. highly connected web, with high genetic variability and with islands at intermediate distances, solid blue (grey in the print version) circles in the bottom panels) over 500 days, when five species (four species of predators and 1 prey) persisted until the end of the simulation (superior panel). The inferior panel shows the snapshots of the spatial dynamics occurring for these five species during these 500 days. The size of the circles of equal colour correspond to the abundance of one species in that particular patch, relative to the abundance of that same species in other patches. In total, this simulation experiment included 8,891,887 individuals. The codes on the right facilitate the identification of extant species in B/W printings. Similarly, the codes within spatial snapshots facilitate the interpretation of animal mobility in B/W printings. Names in the legend correspond to those in [Table 3.1](#).

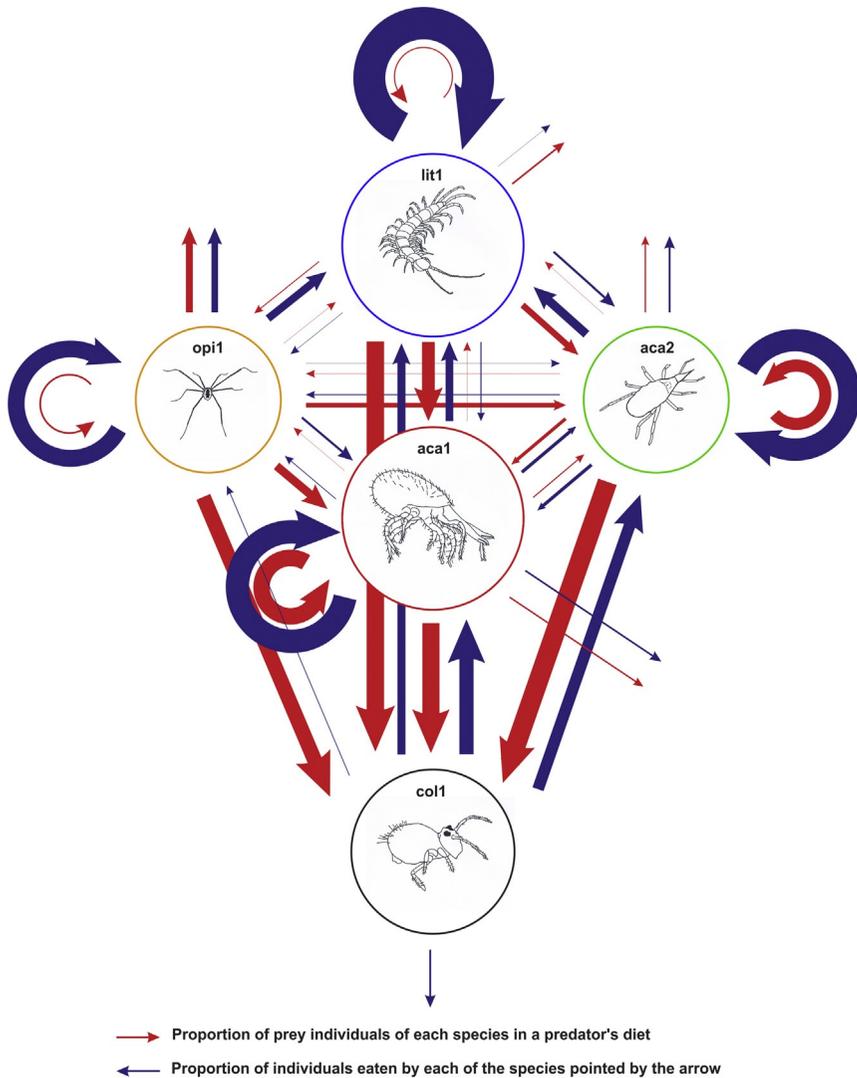


Figure 3.11 Interaction strengths of a persistent web after 500 days of simulation (population and spatial dynamics in Fig. 3.10). The red (grey in the print version) arrows departing from a species denote the proportion of individuals of each species killed and consumed by that particular species. The blue (black in the print version) arrows departing from a species denote the proportion of individuals of that particular species that have been killed and consumed by the species to which the arrow is pointing. Therefore, red (grey in the print version) arrows denote the direction of predation (who eats whom) and blue (black in the print version) arrows the direction of the energy flux.

3.6. Relatively long-term micro-evolution (500 days) in a persistent web

Figure 3.12 shows the evolutionary dynamics for 14 traits associated to the 5-species food web, which persisted for 500 days (Fig. 3.10). Unless their biological relationships were established otherwise, the traits displayed in Fig. 3.12 will be discussed in turn from top to bottom. Evolution was widespread across species and traits, with some of the latter showing clear oscillation through the course of the ecological dynamics. The first apparent outcome is that the evolution of offspring mass is largely driven by the evolution of mass allocated to maintenance, growth and reproduction and not by the fixed (structural) body size of offspring (compare three top panels in Fig. 3.12). Evolution of offspring mass also differed across taxa, with some evolving larger offspring, others smaller offspring and the mesostigmata mite (*aca1*) showing significant oscillations but without a significant change at the endpoint. In addition, fixed body size evolved to a smaller size in the smallest animals (mites and springtails) and showed either no changes (*opi1*) or oscillation of trait values (*lit1*) without evolution.

The growth rates of the two small predatory mites showed opposite patterns, with one (mesostigmata) increasing and the other (prostigmata) decreasing. Springtails (the only fungivore) decreased in growth ratio. Within large predators, one did not evolve in growth ratio, whereas the other increased (*lit1*). Phenology, or egg developmental time, showed the opposite pattern in a mite species (*aca1*) and the shared prey (the springtail *col1*), and either oscillated or did not evolve at all in the remaining three predators. As expected, assimilation efficiency generally increased over time.

Some traits have both a purely additive effect and an epistatic component (phenotypic plasticity; Appendix), the latter consisting of genes of additive effect that tune the additive component of the trait value according to environmental temperature (Q_{10} ; Moya-Laraño et al., 2012). Since both the purely additive and the epistatic component have effects on the final trait, we discuss them together. Voracity, which determines animal foraging activity within a patch, increased consistently (both the additive and the epistatic component) in only the mesostigmatid mite (*aca1*). In the other three species, either the two components evolved in opposite directions or only one of the components evolved. Sprint speed evolved to a higher value in all animals and for both the additive and the epistatic component. However, the evolutionary response was lowest for the shared prey.

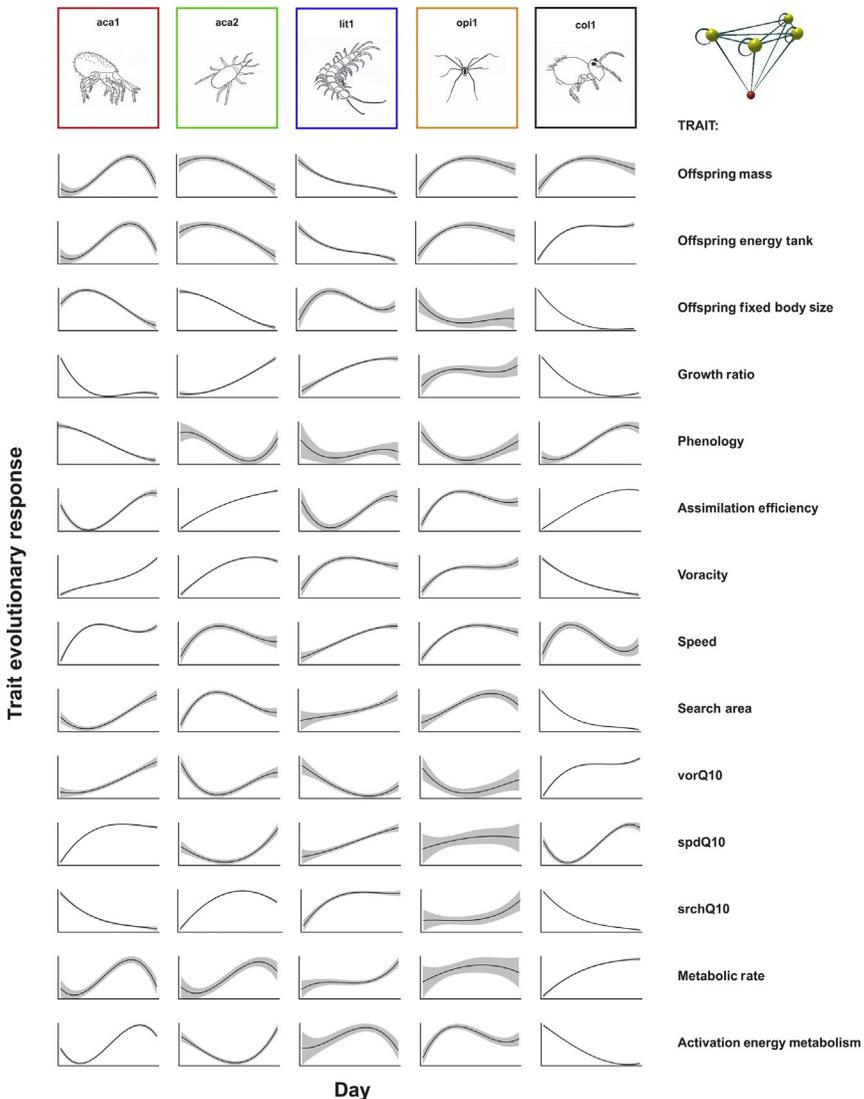


Figure 3.12 Evolution of 14 traits in the 5 species that remained in the food web after 500 days. From left to right: a mesostigmatid mite (aca1), a prostigmatid mite (aca2), a lithobiomorph centipede (lit1), an opilionid (opi1) and a collembolan (col1). The diagram in the upper right corner depicts the structure of the food web (but see Fig. 3.11). In all panels, the X-axis represents time, whereas the Y-axis represents trait values. Areas in grey correspond to 95% confidence bands, calculated across individuals. Trait definitions can be found in Table 3.1, the Appendix and in Moya-Laraño et al. (2012). The maximum number of generations attained by each population was aca1 = 58; aca2 = 39; col1 = 52; lit1 = 12; and opi1 = 14.

Search area, which determines animal foraging activity among patches, evolved consistently in both components (additive and epistatic) only for the shared prey (decrease) and for the top predator (increase). The other three species of predators showed opposite patterns of evolution for the additive and epistatic effects (*aca1*) or very weak oscillatory evolution in one of them (*aca2*) or no evolution at all (*opi1*). Finally, although there was significant evolution and oscillations on metabolic rates, the only strong response was for the shared prey in which the two components of metabolic rate, the scaling coefficient and the activation energy, evolved in opposite directions.

3.7. Evolutionary dynamics of potworms in the presence and absence of predators

In the simulations with high connectance (i.e. 0.55), the potworm *enc2* was the only species that consistently persisted until day 200, both with and without predators. Moreover, in a purely competitive environment, it became the co-dominant species together with another potworm (Fig. 3.13). We took advantage of this persistence in both environments to test for differences in the response to selection in *enc2* between the two ecological scenarios. In a purely competitive environment, selection favoured the investment in offspring with higher energy budgets (energy tanks) and smaller fixed size, whereas these traits did not significantly evolve in the presence of predators (Fig. 3.13). Surprisingly, in the absence of predators voracity evolved to a lower value and metabolic rate to a higher value. Also, temperature-dependent plasticity of sprint speed, which is only functional under the threat of predation, evolved to a higher value. Finally, activation energy for metabolic rate evolved to a lower value. In contrast, only traits directly related to predatory avoidance (i.e. speed and temperature-dependent plasticity for speed) clearly evolved to a higher value in the presence of predators. The other traits showed either no significant response (e.g. activation energy for metabolic rate) or an oscillating response, ending up in a trait value that did not differ from the initial one (e.g. voracity and search area).

3.8. Results summary

Our simulations showed some relevant patterns that will hopefully entail a step change in our understanding of eco-evolutionary dynamics in complex systems. We found that highly connected webs, with widespread trophic omnivory, suffered far less from extinction than less-connected webs.

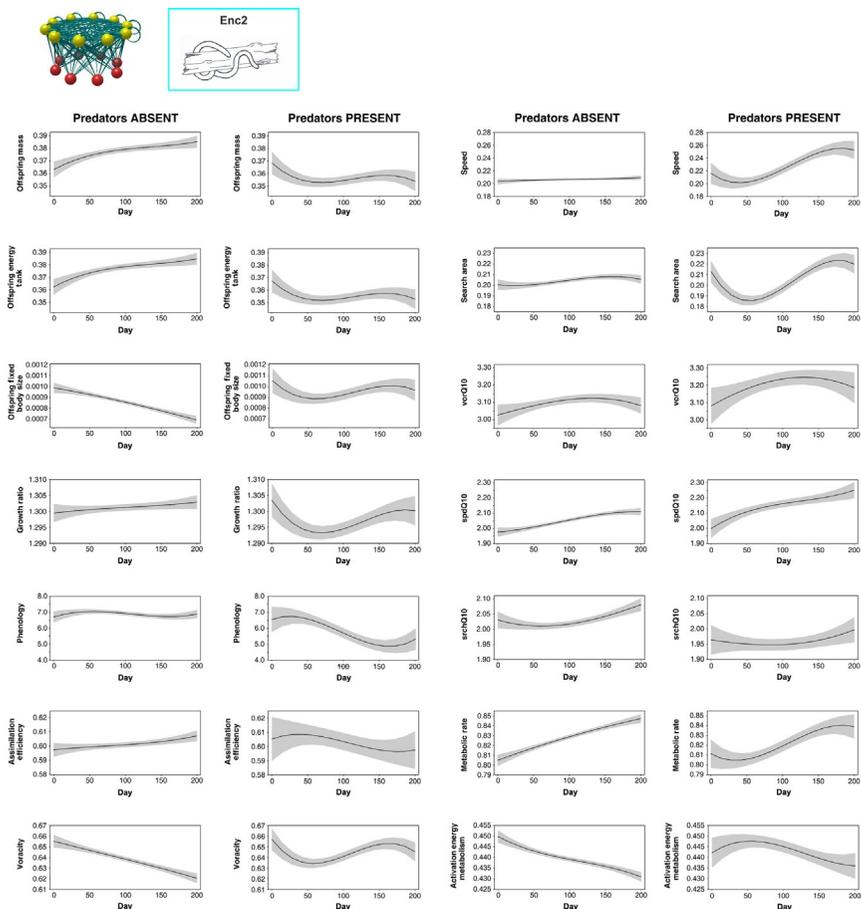


Figure 3.13 Evolution of traits in a fungivorous potworm species under two ecological scenarios: “predators absent”, in which only competitive interactions are present and “predators present” in which species engage in both competition and predation. In all panels, the X-axis represents time, whereas the Y-axis represents trait values. Areas in grey correspond to 95% confidence bands, calculated across individuals.

Nevertheless, this effect differed between predators and prey, with fewer prey and more predators remaining in connected webs. Moreover, decreasing genetic variability reduced the proportion of surviving species by 72%. However, while the effect on prey was a reduction to 50%, predators suffered a much dramatic reduction, decreasing by 87% when genetic variation was reduced by half.

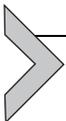
Furthermore, we found relevant patterns of metacommunity dynamics as the distance among four islands of identical basal productivity also

explained species persistence in a highly connected food web. At intermediate distances, the proportion of prey species that persisted until the end were $2\text{--}2.5\times$ higher than when islands were either close to each other or farther apart. For predators, both when islands were close to each other and at intermediate distance, the proportion of species that remained was $4.5\times$ higher than when the islands were further apart. Overall, we found the highest diversity at intermediate distances, slightly less when islands were close to each other and much lower diversity (higher rate of extinction) when islands were further apart.

We also found that in highly connected webs with widespread omnivory and high trait genetic variation, predators had a strong top-down effect on prey diversity, tending to increase the extinction rates of prey when islands were either close to each other or at the longest distances, and greatly increasing prey diversity at intermediate distances. In addition, when the amount of prey that remained in a purely competitive environment was similar to that remaining in an environment in which both competition and predation were at play, the identity of the species tended to be different, indicating that predators modified community composition.

The 500-day simulations revealed strong spatial patterns, with clear migration-extinction dynamics typical of metacommunities and spatio-temporal segregation of species, all of which could have contributed to the overall stability of this five-species food web.

Finally, we found evidence for widespread trait evolution when high genetic variation was involved. Trait evolution differed between top predators and the rest of other predators, and also between predators and fungivores. In addition, trait evolution also differed for fungivores in a purely competitive environment when compared with the same species in an environment involving predation plus competition. Remarkably, depending on the trophic level, some traits were selected up, others down and others oscillated.



4. DISCUSSION

4.1. Ecological dynamics

Our findings that (a) highly connected webs with widespread omnivory were less prone to extinction and (b) the simulation in the long run (500 days) ended up with five species that were only weakly dependent on the extinct species, agree with the view that higher connectance and intermediately strong omnivory is stabilizing (McCann, 2000; McCann and Hastings,

1997; Solé and Montoya, 2001). It is intriguing, however, that interactions were fairly strong, while stable food webs usually have many weak and a few strong interactions (McCann et al., 1998). This apparent paradox could be explained by the high cannibalistic rates, as like in some natural food webs (e.g. Woodward and Hildrew, 2002), our persistent web was maintained with a strong degree of cannibalism (Fig. 3.11). Recent findings show that both cannibalism and anti-predatory behaviour directed towards conspecifics contribute to stabilize food webs (Rudolf, 2007a,b): the highly cannibalistic web depicted in Fig. 3.11 is in line with these predictions.

A previous very simple simulation exercise (Moya-Larano, 2011) suggested that higher trait variability would lead to higher connectance and higher variability in interaction strengths, with many weak and a few strong interactions, all of which could lead to food web stability (see above). However, the latter study did not consider the fact that higher genetic trait variability could also promote rapid or contemporary evolution with ecological time (i.e. during population dynamics). Here, genetic variation on 13 traits strongly promoted food web persistence, as the most persistent webs were those in which populations had high genetic variation. Moreover, we found widespread rapid trait evolution in the five persistent species embedded in the food web. Therefore, we can tentatively conclude that genetic variation, through its effects on contemporary evolution, is also an important factor contributing to the food web stability debate.

Genetic variability may promote stability by (a) enhancing contemporary evolution as shown here or (b) leading to a high diversity of interactions in the species embedded in the food webs, therefore increasing connectance, omnivory and a variable distribution of interaction strengths (Moya-Larano, 2011; see also Steiner and Masse, 2013). Distinguishing among these two drivers of stability is important and we propose that this is feasible in a platform such as Weaver.

Our finding that at intermediate micro-island distances, food webs are more persistent can be explained by a strong top-down extinction effect of IGP predators on prey and on each other at the closest distances (i.e. spatially compressed food webs; McCann et al., 2005), predator coupling of the four islands at intermediate distances and lack of coupling of the global dynamics at longer distances, leading to strong extinction rates in each of the four islands. These results are consistent with the predictions of recent models (McCann et al., 2005; Rooney et al., 2006, 2008) in which adaptive search and rapid responses arising from highly mobile (top) predators moving towards patches where prey are available help to stabilize the system. The

high mobility displayed by top predator populations during the long-term 500-day dynamics supports this view (Fig. 3.10). Our findings confirm these models and add to other models of spatial dynamics in metacommunities involving more than one trophic level (Abrams, 2007; Amarasekare, 2008a, 2010; Koelle and Vandermeer, 2005). Note however that the effect found was only detected in highly connected webs with high genetic variation, meaning that other previously unexplored relevant ecological variables may interact with predator coupling to stabilize metacommunities.

Predators changed the identity of the dominant prey species, driving the strongest competitors to extinction, and in islands located at intermediate distances, they actually enhanced prey diversity. Therefore, our heuristic approach adds novel information for the link between keystone predation and metacommunity dynamics (Amarasekare, 2008b; Paine, 1966), in more complex systems.

4.2. Evolutionary dynamics: Relatively long-term micro-evolution (500 days) in a persistent web

Our simulations revealed that allocation of energy into offspring (offspring energy storage) had a stronger impact on the evolution of offspring mass than did structural body size at birth. This is very relevant because, given a fundamental egg-number/egg-size trade-off (Fox and Czesak, 2000), female energy allocation in offspring with materials providing starvation resistance (e.g. energy tanks) may be more important than allocation in structural body size, even though the latter provides an advantage during predator–prey interactions. This could be translated into an egg-number/starvation resistance trade-off. We found that evolution resulted in lighter offspring in two predator species and in heavier offspring in another predator species and in the shared prey (springtail). However, in another predator species, no evolutionary changes occurred in this trait. Hence, very different strategies evolved, with no clear taxonomic or trophic-level pattern. Given the egg-number/egg-size trade-off, the evolution of heavier offspring was necessarily accompanied by the concomitant evolution of lower fecundities. Therefore, selection could be targeting fecundity or egg mass in each case: further simulations and experiments could be conducted to distinguish between these two possibilities.

Despite their disadvantage in predator–prey encounters with most predators, the smaller animals (springtails and mites) evolved towards smaller offspring sizes. Possibly, in structurally smaller offspring, the overall amount of energy necessary to reach adulthood is lower and faster to accrue, and

therefore viability selection (selection to reach the adult stage and reproduce) may favour smaller fixed body sizes. However, this explanation was not supported by our results, as for each of the three small species, the individuals with structurally smaller offspring matured later: no explanation for this pattern is immediately obvious, however, and further simulations and output analyses are needed.

Much variation was also found in the evolution of growth ratio. Clearly, the evolution of shorter growth ratios can be favoured again by faster egg-to-adult developmental times, increasing viability selection, as it occurred in the fungivore (springtail) and in the mesostigmatid mite. The prostigmatid mite and the top predator (a lithobiomorph centipede) evolved higher growth ratios, which should provide an advantage during predator–prey encounters. Moreover, larger adult sizes are associated with higher reproductive investments, and therefore increased fecundity. This is consistent with the fact that these two species evolved lighter offspring, suggesting that, for these two predator species, investing in offspring number rather than survival is a better strategy.

Phenology (or egg developmental time) evolved in the opposite directions in the shared prey (longer) and in one of its predators (shorter), which likely uncoupled their phenologies, allowing prey to diminish predation from at least this species. As no constraint was imposed on assimilation efficiency, all animals evolved towards higher values for this trait.

Remarkably, traits associated with animal “personalities” (Carter et al., 2013; Wolf et al., 2007), e.g., voracity (related to aggression and within patch activity) and search area (related to boldness and activity among patches) showed patterns consistent with the balance between the need to find food and the level of predation risk affecting each species. The shared prey (springtails) was the only species that most consistently evolved lower searching areas and voracities with only one of the four activity-related traits (Q_{10} on voracity) evolving to higher values. Given the amount of predation threat upon this species (Fig. 3.11), the evolution of a cautious personality might be expected. On the other hand, predators tended to evolve at least two activity-related traits to a higher value, consistent with their lower predation risk.

Searching area is also a dispersal trait, and our results are consistent with those of Pillai et al. (2012) who found that in a metacommunity under strong predation extinction pressure during predator–prey dynamics, predators evolved higher dispersal rates, and their prey evolved to lower dispersal rates. This similarity of results, stemming from two very different modelling

approaches, provides some degree of robustness and increases confidence in our simulation approach. The intermediate degrees in the evolution of dispersal of the remaining predators can thus be understood by the differing degrees of predation risk and extinction.

The evolution of higher sprint speed was most consistent in the four predator species than in the shared prey, for which only the Q_{10} for speed evolved. In predators engaged in IGP, sprint speed is subject to two selection pressures: catching prey and escaping from predators. In contrast, in the shared prey, selection on this trait stems from predation avoidance only. Hence, selection pressure for sprint speed may be lower in prey than in IG prey. This hypothesis can be tested in real food webs. The prediction would be that after controlling for phylogenetic effects (Harvey and Pagel, 1991), the degree to which predators are involved in interactions with other predators (e.g. cannibalism or IGP either as predators or as prey) should correlate positively with their sprint speeds relatively to their body sizes and to prey of similar size.

The evolution of traits related to metabolic rates (scaling mass coefficient and activation energies) showed either oscillations or no consistent pattern between the scaling coefficient and activation energies. In other words, if higher energy expenditures would have evolved, both the scaling coefficient and activation energies should have been higher (see Appendix for an explanation). However, in none of the species did both coefficients evolve consistently. Therefore, deriving any mechanistic explanations for these patterns is not possible at this moment. These results, however, are consistent with previous findings that showed that activation energies for metabolic rates can evolve (Moya-Laraño et al., 2012).

The fact that a few traits oscillated during the time period of our simulations is consistent with the idea that during population dynamics, selective pressures change, probably due to changes in population numbers of the different species embedded in the food web, and to patterns of space use, which also show their own emerging dynamics (Fig. 3.10).

4.3. Evolutionary dynamics of potworms in the presence and absence of predators

In general, responses to selection were more linear in the competitive environment than in the predation environment, reflecting the higher complexity of selective pressures in the latter environment. In a purely competitive environment, potworms (*enc2*) evolved to produce smaller offspring (structural size) with a high energy storage (energy tank). The latter may provide a

competitive advantage by preventing death from starvation, and smaller structural offspring sizes will result in smaller adult sizes (given a fixed growth ratio and amount of energy) and shorter developmental times. Therefore, the overall effect arising from the opposing evolution of the two size traits could be to increase offspring viability. However, when predation is present, investing in a higher number of larger (e.g. larger fixed size) offspring may decrease predation risk (a size refugia—Paine, 1976; Wilson, 1975). Also, given the fundamental trade-off between offspring mass and number (Fox and Czesak, 2000), which is implicit in the model (as offspring mass and number are allocated according to the energy available for reproduction in the mother), investing in more offspring also means investing in lower energy budgets. Therefore, the counterbalancing selective pressures of competition and predation might explain why neither fixed offspring size nor the offspring energy budget evolved in the environment in which predators were present.

The fact that a competitive environment selected for lower voracity is puzzling. One possible explanation is that genetic drift, rather than selection, produced these evolutionary patterns. We have not yet incorporated non-functional traits in the simulations, which will allow controlling for random genetic drift. However, it is unlikely that the robust evolutionary patterns that we found, such as that for metabolic rates, arose from drift alone in so few (< 7) generations and in a pattern that was consistent across replicated simulations (not shown). Thus, these results must be seen as emerging patterns of responses to selection coming from a complex system, which are difficult to grasp from a reductionist viewpoint. For instance, we know that in Weaver—and likely in the real world—voracity and basal metabolic rates feedback on one another: animals that genetically spend more energy (higher basal metabolic rates) will as a consequence have lower energy storages, which will prompt them to be more active and voracious regardless of their constitutive (i.e. genetically determined) activity and voracity traits, leading to higher energy intake which may or may not translate into higher competitive ability depending on other traits, such as assimilation efficiencies. Similarly, animals with lower voracities will maintain lower energy tanks, which will make them more active searching for suitable patches.

Curiously, temperature-dependent sprint speeds evolved to higher values in the competitive environment, in the absence of predation. The evolution of body mass (at all stages) largely depends on how body mass constrains other traits (e.g. voracity, search area, metabolic rates or speed). Hence, selection targeting one of these traits can indirectly affect others,

via the covarying effect on body mass, even in the absence of genetic correlations, as was the case here. Nevertheless, the only two traits that showed a positive response to selection were fixed body size at birth and activation energy for metabolic rate, which cannot directly explain the evolution on sprint speed.

In general, when predators were present, trait evolution was weaker and oscillating, likely explained by the higher complexity of selective pressures in the presence of predators. These oscillatory evolutionary trait dynamics in more complex environments could be the result of fluctuating selection due to fluctuating selective pressures during ecological dynamics (e.g. numbers of the different species of predators changing through time) or even co-evolution (e.g. rapid evolution in predator traits acting as dynamical selective pressures on prey traits). Future simulation experiments including different food web structures and diversity of predators should reveal if there is a positive association between trait oscillations and the diversity of selective pressures. Moreover, more simulations are needed to identify consistent evolutionary patterns in webs with or without predators. One way to test this is by playing with the dimensionality of selective agents, that is, the O matrix (MacColl, 2011; Moya-Laraño, 2012).

4.4. Future directions

We found exceptionally fast dynamics, with all animals growing and reproducing at rates that are much higher than in natural soil food webs (Coleman et al., 2004). *Lithobiomorpha* centipedes, for instance, usually take more than 1 year to mature (Lewis, 1981), which would have yielded only 1.5 generations instead of the documented 12 generations. Our models are therefore still very far from reproducing the pace of soil interactions. There are various ways that the Weaver platform could be altered in subsequent incarnations to make its constituent animals more realistic. First, we need to add periods of inactivity before moulting or during egg guarding (e.g. Geophilomorpha; Lewis, 1981). Second, the standard metabolic rates as documented by Ehnes et al. (2011) need to be accompanied by the possibility of decreasing metabolic rates to survive starvation periods, a pattern that is widespread, for instance, in spiders (Anderson, 1970, 1974; Schmalhofer, 2011), and could be linked to discontinuous gas exchange occurring during resource shortage (Chown, 2011). Allowing for a decrease in metabolic rates during starvation will allow having more realistic foraging patterns and slow down the dynamics.

Although we have simulated food webs across space, we have not included many of the typical drivers of coexistence in metacommunities, such as colonization–competition and competition–predation trade-offs, which can be parameterized by manipulating trait range values (e.g. assimilation efficiencies and searching areas, for instance). In addition, Weaver allows the inclusion of multiple genetic correlations and genetic trade-offs (antagonistic pleiotropy), which we have not exploited in this chapter (but see [Moya-Laraño et al., 2012, 2013](#)). Exploring food web persistence across space in the presence of multiple trade-offs, both ecological and evolutionary, will open new avenues of research to help us understand the eco-evolutionary stability of these complex systems. However, the problem remains of determining how realistic are the results produced *in silico*. Next, we describe how to validate this framework by continuous feedback with real systems.

4.4.1 The quest for eco-evolutionary patterns: An FRP using global optimization algorithms and approximate Bayesian computation

Ideally, to test the reliability of models one has to always confront the model results with real data (e.g., [Boit et al., 2012](#); [Hudson and Reuman, 2014](#)). In order to ensure that Weaver is simulating realistic scenarios, our outputs should include eco-evolutionary patterns that reproduce the empirical observations of real food webs, including patterns of stability. For example, given ecological and evolutionary empirical data, what can we tell about the mechanisms that best reproduce those data? In the previous sections and in [the Appendix](#), we have described the different components and parameters of the simulations, as well as some relevant results. Here, we briefly describe some advanced methods to compare our model predictions with the empirical data using approximate Bayesian computation (ABC), and also global optimization algorithms to produce digitally-stable webs that can be then compared with real data.

Our preliminary simulations showed that some species persisted more than others and that some traits changed monotonically (evolved) through the entire simulation, while others oscillated. Indeed, stability of the entire system (i.e. 20 species interacting with each other following a niche model food web structure) was not reached in any of the simulations: neither ecological (population dynamics) nor evolutionary (trait dynamics) dynamics showed signs of stability. Instead, a variable number of species went to extinction before the end of each simulation. Stability could be reached given the large number of parameters involved, but here we just used a small combination of them. Actually, each simulation included 20 animal species * 13 parameters + 20 animal species * 13 trait ranges + 1 World

configuration * 4 parameters + 1 fungus species * 3 parameters, which gives 268 parameters and 260 trait ranges one could work with in order to search for more realistic eco-evolutionary food webs. Exploring in full all these parameter combinations would be extremely labour intensive, and many of them would be likely to be meaningless anyway (e.g. too far apart a combination of values from the real World to begin with): so, we need a more efficient way to refine the approach.

With the aim to address several main research questions, e.g., what drives stability, distinguish neutral from non-neutral scenarios, how does the evolution of adaptive traits affects food web structure, how does evolution affect food web-associated ecosystem process, etc., we propose a working protocol, which consists in a three-step iterative strategy or FRP:

1. Identify the data used to parameterize the model ecosystem as either internal (e.g. data coming for the same or very similar ecosystems) or external to the system (data or parameters extrapolated from other systems). In the absence of internal and external data to parameterize the model for some specific parameter values, in the Bayesian framework, our *a priori* data would be drawn from a uniform distribution (Beaumont, 2010; Grelaud et al., 2009).
2. Search for eco-evolutionary patterns by iteratively running models with different combinations of parameters. In this iterative process, set the internal parameters to the real (estimated) values and manipulate the external parameters. The predictions can then be compared with empirical observations. This is done by computing the distance between the empirical and simulated data for each parameter combination (Grelaud et al., 2009; Sunnaker et al., 2013).
3. Once a stable eco-evolutionary web has been reached, pick some of the parameter values and outputs found by the system and check if they apply to your system (e.g. check if animal fecundities in the outputs are within those measured in some of the animals of your food web). If this is not the case, either feed the newly measured parameters to Weaver setting them as internal or implement new algorithms (e.g. criteria for reproducing or different coefficients in the deterministic encounter probabilities—Eq. A6) and repeat step (2). In summary, this last step requires selecting the parameter combination that best matches the empirical observations. This can be done by setting a threshold to generate a *posterior* distribution, with all the parameter combinations being sufficiently similar to the empirical observations (i.e. those that are far from reality are discarded; Melian et al., 2011, 2014).

As an example of what type of data would be considered internal or external, animal body lengths that came from accurate measures in field experiments would be clearly internal. However, as these length data were then transformed to body masses using equations from other systems and assuming 70% of water body content as estimated in a different system (see [Appendix](#)), the latter would then be considered external parameters. As another example, basal metabolic rates came from published data on animals coming from similar soil systems ([Ehnes et al., 2011](#)) and were therefore considered as internal. Given the body lengths and metabolic rates as internal and external data, respectively, additional assumptions to include in the model are, for instance, the fitness consequences of body length and metabolic rate for each individual. In the neutral scenario, each individual would have the same fitness irrespective of its body length and metabolic rate. But, how can one meet the neutrality assumptions when these traits are actually functional and lead to different fitnesses across individuals? We propose that neutral eco-evolutionary dynamics, which could be used as null models to contrast the occurrence of niche-oriented dynamics and adaptive evolutionary dynamics, can be reproduced by randomizing reproductive events not only across individuals but also across species. This would require running two simulations in parallel, starting with the exact same individuals, one randomizing reproductive events (neutral) and another letting the adaptive evolution of traits drive the dynamics (functional).

Importantly, the above protocol can be applied to model assumptions and parameters. For instance, [Moya-Laraño et al. \(2013\)](#) simulated situations in which prey were able to assess predator threat before entering a patch and others in which predator threat could not be assessed by prey. They found that system stability involving sit-and-wait predators could only be achieved if prey were not aware about predator presence when entering a new patch. Many other biological assumptions could be tested by generating predictions and comparing them with empirical observations.

Combining parameters and algorithms in an iterative process would not be done completely at random, as this would be also almost unfeasible even for highly optimized parallel code running in high-performance computers. Instead, global optimization algorithms ([Floudas and Pardalos, 2009](#)) should be used. Next, we review these algorithms and discuss which ones would be more appropriate to accomplish step (2).

Biological systems may contain several parameters that underlie biological, evolutionary and ecological processes. Given such complexity, finding the minimal number of mechanisms (or parameters) that best predict the

empirical data is challenging. Global optimization algorithms, the most popular of which in ecology and evolution are “genetic algorithms” (Hamblin, 2013), fit this purpose. The first problem we face is to explore efficiently the highly dimensional parameter space in our model. In general terms, we have to optimize the search by giving a nonempty closed (searching domain) set S and a function f , to find the minimal value f^* and all the points $x^* \in S$ such that $f^* = f(x^*) \leq f(x)$ for all $x \in S$, or show that no such a point exists. The problem to solve can be written as

$$\begin{aligned} \min f(x) \\ \text{s.t. } x \in S \end{aligned} \tag{3.1}$$

The purpose of global optimization is to find the global minimum value f^* and the set of global minimizer points $X^* = \{x^* \in S | f(x^*) = f^*\}$. The conversion of a maximization problem to a minimization one is straightforward ($\max\{f(x) | x \in S\} = -\min\{-f(x) | x \in S\}$).

Problem (1) can be classified depending on the dimension of x (e.g. number of parameters and rules), its type (discrete, continuous or mixed), the type of f (linear, quadratic or non-linear) and how the search domain S is defined (constrained or unconstrained).

When any local minimum of **problem (1)** is also a global minimum (e.g. in linear—[Linear programming FAQ](#)—or convex programming—[Boyd and Vandenberghe, 2009](#)), local optimization methods can find the optimum easily. However, in many problems, this is not the case ([Nonlinear programming FAQ, 2013](#)). The field of global optimization and ABC are devoted to the latter, i.e. those problems of type (1) which can have several local optima apart from the global optimum ([Beaumont, 2010](#)).

The algorithms to solve these problems can be classified into different ways. A typical classification distinguishes between deterministic or stochastic methods. Stochastic methods (for instance, tabu search, genetic algorithms or simulated annealing; [Talbi, 2009](#)) apply some random factors in the local phase to converge to a solution and in the global phase to avoid getting trapped in local optima. Although these methods can find the global optimum, they can only guarantee it when the number of iterations tends to infinity. In deterministic methods (such as outer approximation, Lipschitzian optimization or branch and bound—[Scholz, 2011](#)), no random factors are included. Some of them converge to the global optimum under certain conditions, but when the algorithm is stopped after a finite number of iterations, the accuracy of the solution may not be known with exactness.

A better classification of the algorithms, based on the degree of rigour with which they find the global optimum, is the following (Markót et al., 2006): *incomplete methods*, which may become stuck in a local optimum; *asymptotically complete methods*, which reach a global optimizer with probability one if allowed to run infinitely long, but have no means of knowing when a global minimizer has been found; *complete methods*, which reach a global optimizer with certainty (assuming exact computations and infinitely long run), but knowing after a finite time that an approximate global optimizer has been found; and finally *rigorous methods*, which reach the global optimizers with certainty within a given tolerance even in the presence of rounding errors.

According to the previous classification, rigorous methods, like the *interval branch-and-bound* algorithm (Markót et al., 2006), are desirable. However, although they reach the global solution with the desired precision, execution time increases exponentially with the dimension of the problem. Additionally, they usually need the formulation of the objective function. In summary, regardless of the methods used, the global optimum may be extremely costly to find for highly dimensional ecosystems. Thus, obtaining a Bayesian posterior distribution with the parameter values that best approximate to the empirical observations may be a useful way to decrease the number of parameter candidates to infer the mechanisms explaining the observed patterns (step 3). For example, we may obtain the number of parameters and their values to characterize the distribution of trait values or phenotypes and predation coefficients that best approximate to the empirical observations.

The Weaver algorithm can be considered a model with a large set of *a priori* parameter values and biological mechanisms. One of the desirable goals of Weaver would be to determine the feasible input parameter values to obtain the output values that best approximate to the empirical observations. Depending on the research question, output values to optimize could be the distribution of traits or phenotypes, species richness and diversity or ecosystem productivity through time.

Given the high dimensionality involved in Weaver, the optimization approach, together with ABC methods, is a candidate in this FRP protocol for inferring with higher accuracy the mechanisms that shape diversity patterns in ecological and evolutionary systems.

4.4.2 Engineering food webs for pest control

The present eco-evolutionary framework could be used successfully to help engineering food webs for effective pest control (Moya-Laraño et al., 2012).

The increasing social demand for pesticide residue-free agricultural products and recent transgovernmental policies that explicitly demand sustainability in agriculture is pushing the productive sector worldwide to put agricultural methods for improving pest control while avoiding environmental impacts (Bale et al., 2008; OJEU, 2009). As a consequence, over the last 10 years, the percentage of the World's cultivated land using biological control to fight pests has increased, and the identity of the species of natural enemies involved has suffered an ecologically rational switch, as more indigenous than exotic species are being used as biocontrol agents (van Lenteren, 2012). This tendency is expected to continue in the future because biological control will be a key feature of sustainable crop production.

When untreated with chemicals, agricultural systems typically hold multiple plant-inhabiting species, which interact with each other forming complex food webs. For example, in a typical Mediterranean greenhouse, different herbivore species listed as pest organisms (aphids, spider mites, trips, caterpillars) and several species of natural enemies (phytoseiid mites, predatory bugs, lady beetles, parasitoid wasps) can coexist, all interacting directly (i.e. predation) and indirectly (competition, apparent competition) mechanisms (Messelink et al., 2012). Furthermore, the landscape in which agriculture takes place is commonly surrounded by margins and natural and semi-natural habitats that can provide source populations of natural enemies, as well as act as a reservoir for pest species (Winkler, 2005), expanding the network of agricultural interacting species beyond the actual space occupied by crops. Finally, biotic (predation, competition) and abiotic (e.g. heat stress) selective pressures acting simultaneously on whole agricultural communities may induce rapid evolutionary responses that can be key drivers in the dynamics of populations (i.e. eco-evolutionary dynamics; Fussmann et al., 2007; Pelletier et al., 2009). Hence, to develop a sustainable agriculture with robust predictive power, pest management will need to take into account both the effects of complex interactive networks and complex architectural landscapes (Bohan et al., 2013), and rapid evolutionary responses (Loeuille et al., 2013), on the dynamics and structure of agricultural communities.

Moya-Laraño et al. (2012) coined the concept of Food Web Engineering (FWE, hereafter) as an extension of biological pest control that integrates community ecology and evolutionary biology into the management of agricultural systems. The idea is to unravel how specific community modules in agricultural systems can be manipulated so that top-down pest control is maximized. The approach implicitly requires prior knowledge on which species form the community, how they interact and which traits are relevant for interactions within and among species and with the environment, and

the IBM platform presented here (Weaver) is a suitable tool to address this. Through simulations of the dynamics of specific communities by using different ranges (variability) and assumptions on the genetic determination of traits (number of loci, allele values, pleiotropic effects), different scenarios of pest control, as well as optimal solutions and conditions for stability, can be determined. Using a systems biology approach to connect the IBM and the real world could help to uncover those traits that should be selected in natural enemies to maximize trophic cascades.

The potential of Weaver in FWE is illustrated in the results presented here, which provide useful general guidelines of potential relevance to the development of more sustainable agriculture. On the one hand, simulations show that the higher the connectance in the food web, the higher the persistence of predators, hence herbivore top-down control, will be. Moreover, generalist predators are those that persist more often in our food web, thereby ensuring long-term prey control. These results support the idea that the presence of multiple generalist predators can effectively control pest populations (Faria et al., 2008; Messelink et al., 2012), contradicting the traditional view that they are less effective than specialist predators (Symondson et al., 2002; van Lenteren and Woets, 1988). However, our results also show that persistence of generalist predators in intermediate-highly connected food webs is strongly dependent on genetic trait variability. This implies that increasing predator diversity by releasing several species that are commercially available might not be appropriate. Mass-reared populations are expected to have low genetic variability because they originally started from a relatively small number of individuals, and because populations may have experienced several bottlenecks caused by the rearing methods. Instead, conservation strategies aimed at promoting naturally occurring populations of natural enemies (e.g. manipulation and recreation of the habitats they live in, adding alternative food sources to the habitat, etc.) may be a more appropriate approach.

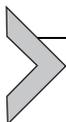
The IBM platform Weaver also offers the possibility to mimic dynamics at a metacommunity level by increasing the distance between patches (islands). A key result of the simulations is that increasing such distance reduces the persistence of predators and decreases the stability of the systems. Therefore, persistence of generalist predators could be increased by introducing islands of diversity, i.e., non-crop plant species harbouring alternative food/prey, amidst the cropping area. There is evidence that densities of herbivorous pests and natural enemies within agricultural fields are influenced by the features of the surrounding landscape (Nicholls and

Altieri, 2007), enlightening the importance of considering the spatial layout when designing future agro-ecosystems.

In conclusion, we have shown how our heuristic IBM approach is useful to test eco-evolutionary hypotheses *in silico*. We found that connectance, rapid evolution occurring contemporarily to the ecological dynamics, as well as island distance, affected food web persistence. Moreover, depending on which of these scenarios is at play, we show that predators can exert a strong effect on prey diversity. In addition, we documented diverse evolutionary responses across the different trophic levels of the food web and for up to 14 functional traits. Although these *in silico* systems may still be far from fully realistic, we propose an FRP protocol by which we hope to fill the *in silico*–*in vivo* gap. We also envisage that this research protocol can also be successfully incorporated in FWE to improve biological pest control in a changing and increasingly spatially fragmented world.

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APPENDIX

A.1. Weaver—An IBM platform to simulate eco-evolutionary dynamics in food webs

Weaver is the C++ porting of the former R code mini-Akira (Moya-Laraño et al., 2012), which has been additionally extended to 2D and 3D space. This porting means a great improvement in computer performance, in part due to algorithm optimization and in part due to the higher performance of C++ relative to R. For instance, each simulation set in Moya-Laraño et al. (2013) took about 48 h of execution in mini-Akira, which became 10 s for Weaver run in the exact same machine (17,280 times faster!). This improvement in speed has allowed us to increase the number of species and to work with more complex food webs (20 species and 20,000 individuals at initialization). Access to the executable program as well as an explanation of the

input and output files can be found here (www.eeza.csic.es/foodweb). In addition, some other changes in the former R code, as well as a different application, can be found in the material of [Moya-Laraño et al. \(2013\)](#), also available in the above site. Updates on the code and potential encountered bugs will also be reported there.

A.2. Space and basal resources—2D and 3D and a chemostat

Weaver's spatio-temporal domain is currently conceived as a portion of soil where animal interactions will occur and in which many parameters can be manipulated. Currently this includes soil moisture and temperature. A future version will include carbon, nitrogen and phosphorous, mimicking decomposing leaf litter. Computationally, space has been modelled as a set of discrete, squared, contiguous, spatial cells or voxels. Cell size can be arbitrarily chosen by the user which yields high flexibility and adaptability for different animal sizes and movement characteristics. Reducing voxel size while increasing their number will lead to much higher spatio-temporal resolution while reducing computational performance as the amount of processing needs increases consistently. Each voxel has its own values for different parameters like moisture and fungus content and based on macro- and micro-climatic conditions and resource consumption, these values will fluctuate as the simulation proceeds.

Weaver initializes the cells (voxels) that will form the simulation domain as a 3D array with width, depth and height dimensions. This creates a data structure that will hold the living individuals and basal resources. Each individual, whether a fungus or an animal (and even plants in future releases), is initialized based on user-provided parameters: genetic trait variability, genetic correlation among traits, species identity and a series of parameters that aim at both providing realism and allowing simulation functionality. As such parameters are commonly defined as a range of possible values, each individual is initialized following a random initialization process and can be considered unique. Upon initialization, each individual is randomly located into one of the existing cells. Once soil, fungi and animals are initialized, simulation starts until one or more of the stopping conditions are satisfied (e.g. number of days).

Spatial patchiness is of extreme importance to mimic metapopulation and metacommunity dynamics, as well as divergent evolution within distant islands. Related to this, the user has major control over some aspects of soil initialization such as moisture and fungus geometric distribution. For

instance, one can set a homogeneous moisture value that will be the same for all cells in the world or set fungus availability at random among cells. More complex initialization can also be carried out. The user can instruct the program to create as many patches (spheric or gaussian shaped) as needed and to select or to randomize the different parameters that define them, such as relative humidity, fungus biomass, radius of the patch (spheric patches) and sigma of the gaussian distribution (gaussian patches). Finally, these structures can be mixed, to create very complex basal resource spatial distributions. In the case that many structures affect the same voxel, the highest value (e.g. moisture) is retained for that particular voxel.

In the present version, fungi grow within the cell based on the level of relative humidity present in that cell (C–N–P will be implemented in future releases). In the absence of fungivores, fungus growth is governed by the same equations as in the former version of the framework (equations A1 and A2 in Moya-Laraño et al., 2012). Water availability affects only fungi thus far. In future versions of Weaver, animals will also have water tanks as state variables and water availability will change dynamically through space and time. All simulations presented here were run at constant 87.5% relative humidity and with a single basal resource (fungus species) that grew optimally at this humidity with a species-specific rate (i.e. r_T in equation A1 of Moya-Laraño et al., 2012 is maximum at 87.5% RH; $r_T = 0.017$, growth range, RH = 85–90%, $r_T = 0–0.017$). In the future, other fungus species differing in optimal RHs will be incorporated. However, in the current version, this possibility was not included because water availability does not change with time yet.

A.2.1 Chemostat

Preliminary behaviour of a set of simulations (11 species of predators, 9 species of prey and 4 of fungi, see main text) showed that basal resources would always go to extinction within less than 40 days. Since we were primarily interested in investigating eco-evolutionary dynamics of predator–prey interactions, and since pulses of basal resources have been shown to strongly contribute to community stability (Roelke et al., 2003), we incorporated in the simulator a chemostat that provided pulses of basal resources either at a certain (constant) frequency (days⁻¹) or when resources were close to depletion within a pre-established threshold. The former type of pulse mimics, for instance, rainy days allowing bursts of fungi growth, being by far the most realistic case. The second type can be used to allow predator–prey dynamics to go on for longer periods of time when one is interested in exploring the

evolution of certain traits. In this chapter, we only present results using the most realistic frequency-based pulsing chemostat. However, to enhance the duration of the simulation, we set the chemostat at a refilling rate of 100%/day.

A.3. Phenotypic ranges with quantitative genetic variation

The following is a simplified description of how genetics are implemented in our approach (further details in [Moya-Laraño et al., 2012](#)). Each trait is determined by a couple of vectors which include an arrangement of loci with values varying between 0 and 1. To establish the trait value for each individual, the values across loci are added and the result interpolated between the phenotypic ranges of the trait ([Table 3.1](#)). For each trait, we established evolutionary limits, beyond which the population cannot evolve (assuming physical and physiological constraints), and therefore, the genetically based trait variability is determined within these limits. Thus, for each trait X , we describe the limits and the phenotypic range used as follows:

$$l_X = L_X + \varphi \left(\frac{U_X - L_X}{2} \right) \quad (\text{A1})$$

$$u_X = U_X - \varphi \left(\frac{U_X - L_X}{2} \right) \quad (\text{A2})$$

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 ([Table 3.1](#)) and φ is a coefficient (range 0–1) which determines what proportion of the distance from the standard limits to the midpoint between them is used to calculate the final trait range (l_X , u_X). Thus, a higher φ involves lower trait variability. We forced $U_X < K_X$ 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 ensure 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 $\varphi = 0.01$ or 0.99 for simulations with high or low genetic variability, respectively.

A.4. Animal traits

We refer to the reader to our repository (www.eeza.csic.es/foodweb) to learn about all the input parameters and evolutionary limits used for each trait and species. The 13 traits (or 14 if consider total body size, e.g., B

+ ε_0 below) included in the present simulations were the following (see ranges in Table 3.1):

body size at birth (*size_ini*, B_0): structural body mass at birth.

energy tank at birth and after moulting (*tank_ini*, ε_0): percentage of mass devoted to maintenance and future growth and reproduction. 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 $0.1M^f$). Source: Yodzis and Innes (1992) and A. M. DeRoos (unpublished notes), which provide a fixed maximal consumption rate coefficient of 0.75; see also Englund et al. (2012) for variation around this value. This trait does not just constrain how much food an animal can consume per day but also affects predation risk, as the more voracious animals expend more time foraging. Thus, the probability of encounter with predators (P_p in Eq. A10) depends, among other things, on this trait. Hence, animals that are genetically highly voracious are more exposed to predation risk, which is consistent with what we know from animal personalities and behavioural syndromes (Sih et al., 2004) and does therefore include them explicitly in the framework.

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 $\propto M^f$. This coefficient has been documented to vary across studies: 0.17–0.25 (Peters, 1983; Schmidt-Nielsen, 1984). Taking 4 as the normalization constant ($4M^f$), we obtain sprint speeds which fall within the observed ranges from the tiniest mites to the largest wandering spiders, covering a mass range of 0.03–465 mg.

metabolic rate (*met_rate*, a): Energy losses from metabolism follow the metabolic theory of ecology (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):

$$\ln I = \ln I_0 + a \ln M - E \left(\frac{1}{kT} \right) \quad (\text{A3})$$

where I is metabolic rate (J/h), I_0 is a normalization constant, a is a coefficient which relates body size to metabolic rate, E is the activation energy (in eV), k is the Boltzmann's constant (8.62×10^{-5} eV/K) and

T is the environmental temperature in Kelvin. All parameters are included as reported for each animal soil group (Ehnes et al., 2011). Genetic variability was included and modelled around the coefficient “ a ”.

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, 2010) as well as on the state of voracity and amount of movement of each individual (Eq. A7).

growth (g): Growth is a trait that determines how much an individual grows in each moulting event. Note that we are simulating invertebrates 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 also be allocated to the post-moulting energy tank, 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. In Section A.7, we describe how the algorithm for growth has been improved in Weaver.

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 1 day (m), scales with body size in a similar way as sprint speed: M^m . Differently than in mini-Akira (Moya-Laraño et al., 2012), for translating mobility into actual search area in the simulation, we have derived scaling constants for Weaver (see Section A6).

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).

phenology (pheno): Day of birth since either the beginning of the season (simulation) or since the date of oviposition. This trait can be also called egg developmental time, as the date of birth will depend on how fast eggs develop beyond what is dictated by temperature and other

environmental constraints. Thus, 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. A3): To further control the effect of temperature 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 in Table 3.1 were set around published coefficients in Ehnes et al. (2011).

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 10°C 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. (A3) (Ehnes et al., 2011). In addition, Q_{10} values are more easily interpretable and converted to reaction norms. Together, these three traits represent thermal plastic adaptation for mobility. For simplicity, we ran all simulations at 18°C .

Q_{10} on voracity ($vorQ_{10}$): Based on data on consumption rates (Dell et al., 2011).

Q_{10} on speed ($spdQ_{10}$): Based on data on escaping speeds (Dell et al., 2011).

Q_{10} on search area ($srchQ_{10}$): Based on data on voluntary body speed (Dell et al., 2011).

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 ($15\text{--}25^\circ\text{C}$). Thus, real Q_{10} would be used if a simulation was performed at 25°C , and for simulations at intermediate temperatures, we estimated the value of Q (e.g. Q_3 at 18°C) 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 (Roff, 1997; Scheiner, 1993), 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.

A.5. Predator and prey quantitative genetics with more realistic recombination rates

In the former version of this IBM framework (Moya-Laraño et al., 2012), the authors successfully induced genetic correlations from pleiotropic effects by including all loci that affected the same traits in arrays which were called chromosomes. This was unrealistic because genetic correlations occur by both pleiotropic effects of quantitative genes and from linkage disequilibrium (Roff, 1997), and we only considered the former. In linkage disequilibrium, loci that are close to each other in the chromosome tend to stay together for several generations (linkage), the number of which depends on their relative distance in the chromosome and on the recombination rate. Since linkage disequilibrium has its own evolutionary importance (e.g. in genetic drift) and can be driven by many mechanisms, such as selection and non-random mating (Falconer and MacKay, 2006), we decided to improve our modelling of quantitative genetics by better mimicking true recombination. The formerly described loci vectors (Moya-Laraño et al., 2012), which are useful to induce the desired degrees of genetic correlations among traits, we now term “correlosomes”. In the current version of the algorithm, we include more realistic recombination rates by randomly permuting the position of each locus across the genome before cross-over. These random positions are established at the beginning of each simulation and are kept constant throughout for all animals. After cross-over, and before the new egg is built, the position of the loci is returned back to the correlosome position, which will allow assigning phenotypes to the newborns by keeping the original degree of genetic correlation (ρ parameter in Moya-Laraño et al., 2012). Note that the previous claim (Moya-Laraño, 2012) that non-expressing alleles in correlosomes could be taken as microsatellite markers depending on the distance to expressing alleles still holds. However, now these alleles, as functional alleles do, will recombine in random positions and their position to functional alleles will be also random, a much more realistic situation.

A.6. New adjustments in all mass-dependent equations and plastic traits

A.6.1 Water body content

In the former version of this framework, the authors did not explicitly model water body content (Moya-Laraño et al., 2012). Although water content is still static in the present version, as a prelude of a future version in which water loss will drive individual behaviour as well (e.g. Verdeny-Vilalta and Moya-Laraño, 2014), here we modelled all animals as having 70% of their body mass in water form (following Sabo et al., 2002).

A.6.2 Adjustment of scaling constants in mass- and temperature-dependent equations

In Moya-Laraño et al. (2012), the authors modelled animals that were smaller than 1 mg at maturation, which allowed all non-linear equations to behave consistently (e.g. larger animals had always higher speeds than smaller animals). In order to accommodate larger animals and to be sure that scaling was realistic, we used here linear interpolation to predict scaling constants (intercepts) from scaling coefficients (slopes). To estimate voracity, speed and search area of each animal (V , A and S in equations A6, A7 and A8 of Moya-Laraño et al., 2012, respectively), we estimated the intercepts (note that former equation A7—Eq. A5—now includes a scaling constant) by linear interpolation in which each constitutive trait assigned to each animal (the scaling coefficients v , m and s to obtain V , A and S , respectively) was linearly interpolated from the scale of the evolutionary limits (Π_X and K_X) to a final scale. This ensured that, for the smallest and largest animals, V , A and S were always higher for larger animals. We observed a high rate of starvation and a low rate of mobility depending on the coefficients of body condition (c) and rates of encounters with predators (e) in the former equations A6 and A7 (Moya-Laraño et al., 2012). To enhance survival and mobility, in what are now Eqs. (A4) and (A5), the term $c \cdot e$ has been changed to $(c + e)/2$. This gives equal weight to condition and anti-predator behaviour in determining animal voracity and mobility and does not penalize voracity and mobility as strongly when animals are well fed and have encountered many predators (e.g. low c and e values). Future data across a few animal taxa should determine how the internal state of the animal (c) and anti-predatory behaviour (e) interact to determine the levels of animal activity. Therefore, the new equations are as follows:

$$V = f_V M^v [(c + e)/2] Q_{VT} \quad (\text{A4})$$

$$A = f_A M^m [(c + e)/2] Q_{AT} \quad (\text{A5})$$

$$S = f_S M^s c Q_{ST} \quad (\text{A6})$$

where the f_s are the interpolated scaling constants (ranges f_V : 0.05–0.15, f_A : 1–12.85, f_S : 1–7). All other terms discussed in [Moya-Laraño et al. \(2012\)](#). To improve basal metabolic rate estimates, we took advantage of the strong correlation occurring between $\ln I_0$ and E across nine taxa of soil organisms in the data of [Ehnes et al. \(2011; equation A3\)](#) and used linear regression ($\ln I_0 = -7.29 + 43.97E$; $R^2 = 0.99$; $P < 0.0001$; $N = 9$) to predict basal metabolic losses for individuals genetically differing in the scaling coefficient (a) and activation energies for metabolic rates (E). This approach ensured that animals with higher E expended more energy for a given environmental temperature (more energy was needed to activate their metabolism) and greatly improved survival from starvation in the simulations.

A.6.3 Field metabolic rates

Field metabolic rates can be obtained by multiplying basal metabolic rates by a value of 2.5–3 ([Brose et al., 2008](#); [Yodzis and Innes, 1992](#)). In order to make sense of individual variation, we used a more dynamic approach of assigning the multiplying coefficient of field metabolic rates (3) only to the fraction of time (P_t) that animals were really active ([Moya-Laraño, 2012](#)):

$$P_t = w_A \left(\frac{W}{A_{\max}} \right) + (1 - w_A) \left(\frac{V}{V_{\max}} \right) \quad (\text{A7})$$

where w_A determines how much weight is given to activity among patches (W) or within patches (V), and A_{\max} and V_{\max} are maximum searching area and voracities in the community (i.e. for the largest animals with lowest condition, lowest previous encounter rates with predators and at the highest temperature $T = 25$ °C), respectively. In the current version, A_{\max} and V_{\max} values have been calculated for each species. This implies that the offspring of the largest species has a survival bonus, as they will spend relatively much lower energy from moving around than the offspring of the smallest species, which will be closer to their maximum. We decided to pursue this strategy for now because, due to the initialization following allometric mass–abundance scaling, too few of the large predators were included in the simulations, which were therefore highly subjected to stochasticity and went rapidly extinct. This procedure ensured that large predators persisted more. In a future parallelized code, which will allow initializations with >100.000

individuals, each individual will have its own A_{\max} and V_{\max} , which will in turn depend on its own traits, a much more realistic situation.

A.7. Moulting algorithm

An improvement relative to the former moulting algorithm is that now the shape of the animals, and thus the length–mass allometric relationship, is taken into account to decide when the next instar should be achieved:

$$M = aL^b \quad (\text{A8})$$

We obtained most of the a and b coefficients from published accounts (Edwards and Gabriel, 1998; Gruner, 2003; Hodar, 1996), and for enchytraeids (Clitellata), we used unpublished estimates ($a=0.0039$, $b=2.53$; O. Verdeny-Vilalta et al., unpublished data). In all equations, body length is measured in mm and mass in mg. Now, the mass available for moulting (i.e. 90% of the state variable energy tank, ε) is transformed into the length of the animal (by rearranging Eq. A5) in order to allow for length growth to be governed by the trait growth ratio. Once an individual moults, the original equation (A5) is applied to estimate the body mass of the instar. The mass allocated to ε is a fixed proportion of the fixed body mass (i.e. the B trait) which is the same proportion as that given at birth (i.e. the ε_0 trait).

In the current version, the number of instars was species specific and was calculated by first estimating egg mass for each species by fitting the following adult–offspring allometric relationship: offspring mass = $0.03 * \text{adult mass}^{0.5}$, which was calculated by visually fitting the intercept for the invertebrate relationship presented in figure 3.3 of Hendriks and Mulder (2008). We then obtained adult masses from a unpublished data set on individual lengths across four beech forests (J. Moya-Laraño et al., unpublished data) to which we applied Eq. (A5) and the same coefficients as in our simulations. Finally, we applied the moulting algorithm described above to the offspring of each species, for which we included the same growth ratio (mid-point of the range) used in our simulations. By iteration of this algorithm, we calculated the number of instars which matched the targeted adult body size and this result was used as the total number of instars for each simulated species.

Since growth curves are not ruled by a single ratio parameter, as they usually have a sigmoid shape, we allowed animals to also plastically moult by including time as an alternative for moulting. We included a couple of state variables which were time elapsed in the prior instar and time elapsed in the present instar. The ratio between time in present and time in past

instars was established as a second rule of thumb to moult with whatever amount of resources the animal could have accumulated to that point, forcing a moulting event which does not follow the growth ratio. This provides some realism to growth curves as arthropods are generally phenotypically plastic in developmental time (Nylin and Gotthard, 1998). If an individual has not moulted due to its growth ratio trait by the time determined by this ratio, the animal proceeds to moult. Ratios used in simulations were 0.8, 0.9 and 1.5 for large predators, small predators and fungivores, respectively. This difference was necessary to enhance maturation in predators, which were larger on average than prey.

A.8. Reproductive algorithm

In addition to the changes in recombination explained above, we simplified the criterion for reproduction. Now we calculated the biomass available for reproduction as 90% of the energy tank (ϵ) and when this value was twice as large as the weight of the fixed body mass of the adult individual, the animal was able to lay an egg batch. In future versions, this criterion should be changed to a species-specific mode of reproduction criterion, allowing for continuous egg laying (as many mites do) and also laying large batches at once (as spiders). Note that this is not merely a distinction between iteroparity or semelparity, as iteroparous animals can still lay either one egg at each reproductive event or an entire clutch. What is relevant for the dynamics is how much energy an individual needs to accrue before a reproductive event occurs. Continuing with this simple criterion for reproduction, and as in the former version, each prey individual was allowed to lay up to two batches before dying and predators up to 5. The number of batches and the number of eggs per batch, which are closely associated to the mode for reproduction, should be adjusted in the future in a species-specific basis.

In the former version of this IBM mate search was not necessary because we assumed that animals would encounter a mate with 100% probability as long as there was one present in the population. Since space is now relatively much larger (albeit still in arbitrary units, i.e. 4000 vs. 100 cells), we have implemented a momentary solution in which once an individual enters the reproductive state it starts searching for patches with mates (moving preferentially to patches with more reproductive individuals of their own species) and will be allowed to move up to 1000 steps per day. These individuals are both invulnerable to predation and do not expend energy during searching. This simplification had to be added to enhance mating encounters

and improve ecological dynamics. However, once mate attractants are successfully implemented, future versions should also include the cost of mate search (e.g. predation risk and energy expenditure).

A.9. Restricting and controlling attack rates

Within a given patch (or cell), the probability that a predator finds a prey and vice versa as well as the probability that predation occurs upon an encounter depends on probabilities drawn at random from a uniform distribution which are contrasted with deterministic probabilities that come from the animal traits involved (equations A13 and A14 in [Moya-Laraño et al., 2012](#)). The logistic relationship between the traits of the two animals involved in a potential encounter or predation event and the deterministic probability dependent on a set of coefficients ($\alpha \dots \eta$ for encounters and $\alpha \dots \delta$ for predation. . . δ) which determined the relative importance of each predator and prey trait would take in either encounters or predation. These coefficients were called naïve coefficients because they are not based on real data. In the future, they should either be estimated from real data or be the subject of sensitivity analysis, in particular if we want to make strong inferences about the evolution of certain traits. To facilitate the task of simulating the effects of different values for these coefficients, we estimated by simulation means and standard deviations for all traits and trait combinations (e.g. predator by prey mass interaction) which allowed standardizing these traits and their combinations as if following a standard normal distribution. This ensured that all traits and combinations had identical units in the equations, which allowed the naïve coefficients to have identical weight on the final probabilities regardless of the units of measurement of the traits involved. The final equations are thus:

$$P_e = \frac{1}{\left[1 + e^{-\left(\alpha + \beta V'_{P_d} + \gamma V'_{P_y} + \delta (V_{P_d} V_{P_y})' + \epsilon B'_{P_d} + \zeta B'_{P_y} + \eta (B_{P_d} B_{P_y})' \right)} \right]} \quad (\text{A9})$$

$$P_p = \frac{1}{\left[1 + e^{-\left(\alpha + \beta V'_{P_d} + \gamma R'_B + \delta R'_S \right)} \right]} \quad (\text{A10})$$

where the $'$ s refer to the fact that the variables (or their products) were standardized. Traits are voracities (V) of the predator or attacking individual in IGP and cannibalism (P_d) or prey or attacked individual (P_y), B is structural body mass and R_B and R_S are structural body size and speed ratios, respectively. More details can be found in [Moya-Laraño et al. \(2012\)](#). The naïve

coefficients used in the present simulation were for encounter probabilities ($\alpha \dots \eta$): 1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1; and for predation probabilities given an encounter ($\alpha \dots \delta$): 1, 0.1, 0.1, 0.1. Therefore, we assumed that all variables (and thus all traits) had equal weight in deciding an interaction outcome.

One of the problems of the above equations is that predator–prey interactions are ruled by traits and naïve coefficients and therefore attack rates could be overlay too high or excessively low to ensure any ecological dynamics. We added an additional control, which could be used for controlling attack rates upon each species. This was accomplished by restricting the range of those P -values randomly obtained from a uniform distribution which were to be contrasted against P_e and P_p to decide the outcome of interactions (i.e. an encounter occurs if $P_e > \text{random } P\text{-value}$). We first obtained the distribution of values by running a simulation and then established the following ranges of random P -values for large and small predators, and prey, respectively (webs with connectance 0.1 or 0.55): *encounters*, 0.337–0.342, 0.337–0.340, 0.337–0.3394; *predation*, 0.606–0.623, 0.606–0.617, 0.606–0.6149. For the web with connectance 0.3 (which had different species), the values were, respectively: *encounters*, 0.337–0.3375, 0.337–0.338, 0.337–0.339; *predation*, 0.607–0.612, 0.607–0.614, 0.607–0.617. This ensured that large predators (and especially the juvenile stages) suffered less from IGP. Again, this simulation strategy allowed large predators to stay longer in the simulations, as otherwise extinction occurred too rapidly. For the same reason (improving large predator survival), and since small predators already had a predation pressure coming from higher trophic levels, all background mortalities (Moya-Laraño et al., 2012) were set to zero. Although we do not know what defensive traits allow the offspring of large predators to reach maturation, it is obvious that without these improvements, we were not able to mimic the survival of juveniles in large predatory species. This in itself opens an interesting question to investigate (a) whether the offspring of large predators have improved survival over other predators of the same size and (b) which traits may be involved in this differential survival.

To further control attack rates and make them more realistic, we allowed encounters and predation events only within the following range of log body mass ratios: -1.21 to 6.68 , as data on 800 induced predator–prey encounters among individuals of a beech forest food web have shown that predation never occurs beyond these thresholds (J. Moya-Laraño et al., unpublished data).

In addition, we relaxed the 1-day one-prey criterion to allow larger predators to feed in a more realistic way. Now all predators can search and feed on several prey per day as long as the ingested body mass does not surpass that of their voracity (V) or as long as the number of visited patches in 1 day does not surpass that of the individual trait area searched (A). Since now food ingestion is at its maximum (V), we assumed that all food could be handled and digested in 1 day and set all digestion times (regardless of temperature) to zero. Therefore, all predators that rested alive were ready to hunt again the following day regardless of how much they had ingested the day before. Once we improve the capabilities of our framework, we will be able to establish simulations with time steps of hours or minutes, when real handling and digestion times will be appropriately included.

A.10. Adaptive animal movement

Animals move adaptively in 3D space similarly as they did in 1D mini-Akira (Moya-Laraño et al., 2012) with the plus that they now remember the cells they visited within the same day as not to repeat the same cell in a given day. This was implemented as to make predators to move more naturally, as once interactions (encounters plus predation) have been unsuccessfully attempted with all individuals in a patch, the predator should assess the patch as unsuitable for hunting prey. Although Weaver now implements the possibility of animals assessing cells farther away from neighbouring cells, all simulations in this paper assume that animals can only assess the 26 cells that immediate surround the cell in which the animal is located in a given time. At each move, fungivores will move to cells with the lowest ratio between predation threat and fungus biomass with the additional improvement that fungivores assess only the species to which they are linked according to the food web structure established at the beginning of the simulation (see main text) and within the predatory threshold imposed by the limits of log mass ratios (-1.21 to 6.68). Predators behave in a similar way: they assess predator threat and prey availability (both fungivores and IGP prey) considering only those species with which they are linked according to food web structure and following the log mass ratio criterion.

In addition, as in mini-Akira, both prey and predators can perform jumps so as to clear out from the areas in which edible items have been depleted. To accommodate these jumps to a 3D environment, when food availability within the 27 neighbouring cells (26 surrounding cells plus the cell where the animal is currently located) is zero, the animal will perform a jump at

a distance which is established by drawing a random number from a uniform distribution which ranges between 2 and its search area trait (A). This animal then evaluates the new area and can either perform another jump or just stay put if food is available. At each jump, the animal evaluates how many cells are within its jump value (in the 3D directions) and if an edge (wall) of the world is at a shorter distance than the projected jump, the direction pointing towards that edge is immediately discarded from the universe of possible directions towards which a jump can be performed. This same edge procedure takes place at normal moves (e.g. when only one step is performed at a time).

To prevent animals from getting stuck in an area, they track the cells they have visited each day and they do not go back to those cells within the same day. Therefore, each cell is assessed by each predator only once per day and if after having attempted to catch prey in a cell, additional prey need to be caught that day to meet the voracity demands (see above), these will be sought in a different cell. This process applies also when the animals jump, so they do not jump back to an already visited cell in the very same day, encouraging them to move through new areas. As in [Moya-Laraño et al. \(2012\)](#), the number of maximum steps an animal can attempt each day equals its search area trait (A). However, now each displacement (either a simple step or a jump) adds only a single step unit to W for estimating field metabolic rates in Eq. (A4) (A10 in [Moya-Laraño et al., 2012](#)).

A.11. Computational demand and requirements

Computationally, Weaver can be highly demanding in terms of both memory and CPU needs. Memory will be impacted by the number of individuals living in the world at a given time and cells comprising the soil structure. This should be taken into account by the user when running potentially large simulations. For example, a simulation running for 200 days with 9 species or fungivores and 11 species of predators (community size = 20,000 individuals), such as that presented here, may take only about 1 h but more than 18 GB of memory and store more than 100 GB of information, including the genetics of all organisms, the predator–prey interactions at the species level, the daily reports on trait and state variable values for each alive animal (including spatial location), the constitutive traits to document evolutionary dynamics and the number of animals for each state and instar for each day. Therefore, the program outputs will require vast amounts of hard disk to store all the information needed (which is also customizable), especially if

binary snapshots are stored at each simulation step to graphically visualize water and fungus levels, animal population densities, etc.

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