

# 3.4 .

## DESIGN AND PARAMETERIZATION OF SIMULATED MULTI-TROPHIC META-COMMUNITY EXPERIMENTS: THE WATER-DEPENDENT FOREST FLOOR FOOD WEB

DOLORES RUIZ-LUPIÓN,<sup>1-2</sup> GABRIEL BARRIONUEVO,<sup>3</sup> LEOCADIO G. CASADO,<sup>3</sup>  
M. MONTSERRAT,<sup>4</sup> JOSÉ MARÍA GÓMEZ<sup>1</sup> Y JORDI MOYA LARAÑO<sup>1</sup>  
<sup>1</sup>EEZA-CSIC.  
<sup>2</sup>IMEM.  
<sup>3</sup>UAL  
<sup>4</sup>IHSM LA MAYORA-CSIC

### INTRODUCTION

Water is an essential resource in most terrestrial ecosystems, influencing the distribution and abundance of organisms at several spatial scales (Guernier *et al.*, 2004; Blankinship *et al.*, 2011; Chown and Nicolson, 2004; Gear and Schmitz, 2005; Melguizo-Ruiz *et al.*, 2012; Hawkins *et al.*, 2003). In many ecosystems water is even a limiting resource (McCluney and Sabo, 2009; Noy-Meir, 1974; Wolf and Walsberg, 1996), shaping primary productivity and favouring higher rates of litter accumulation in soils (Loustau *et al.*, 2001). Water has an important role not only in typical dry ecosystems —deserts and semiarid areas— but also in temperate forests, such as European beech *Fagus sylvatica* L. forests (Verdeny-Vilalta and Moya-Laraño, 2014). In beech forests there is an indirect water-mediated bottom-up effect of primary productivity on soil productivity (Capellesso *et al.*, 2016), which would be expressed as higher fungal growth rates in the litter, a process that affects decomposition indirectly via its effects on the food web (Lensing and Wise, 2006).

Water is often heterogeneously distributed at the micro-scale level (micro-topography) in beech forests (Herbst and Dikekkruiger, 2003; Jost *et al.*, 2004; Melguizo-Ruiz *et al.*, 2012; Schume *et al.*, 2003). This is because after rainfall ceases the differential rate of soil desiccation produces the existence of dry patches intermingled with wet patches, which can be located underneath plants, in the base of rocks or under pits formed by fallen trees, as well as at the bottom part of the slopes where water, leaf-litter and nutrients accumulate (Famiglietti *et al.*, 1998; Melguizo-Ruiz *et al.*, 2012). This spatial heterogeneity of moisture pockets may have important consequences for the dynamics, structure and persistence of food webs over time (Levins, 1968; Levins, 1969; Murdoch, 1977; Holt and Lawton, 1994; Briggs and Hoopes, 2004; Lin *et al.*, 2013; LeCraw *et al.*, 2014). During the dry period, when the water pocket distribution is more heterogeneous, soil invertebrates are attracted to wet patches to avoid water loss (Verdeny-Vilalta, 2013; Verdeny-Vilalta and Moya-Laraño, 2014). This results in higher densities of invertebrates in these moisture pockets relative to other parts of the forest

(Melguizo-Ruiz *et al.*, 2012; Verdeny-Vilalta, 2013). However, if both prey and predators are attracted to the same humid areas, a trade-off between desiccation risk and predation risk will emerge (Verdeny-Vilalta and Moya-Laraño, 2014). It is well known that larger arthropods can retain more water than small arthropods, either because of their lower surface/volume ratio or because their ability to store more water (Chown, 1993; Renault and Coray, 2004). Consequently, how litter organisms respond to moisture pockets could depend on their size, a feature that may have important consequences for the structure of food webs and the dynamics of the ecological systems. Fungivores and detritivores are attracted to patches not only with more water, but with more fungi, whereas their predators are attracted indirectly toward these patches when searching for them (Verdeny-Vilalta, 2013). In these patches predators must avoid desiccation while searching for preys. As a consequence, large predatory arthropods can contribute to the maintenance of leaf-litter community structure and the global food web stability because they can couple energy channels across space (McCann *et al.*, 2005; Rooney *et al.*, 2006).

We can envision these systems of water pockets as multi-trophic meta-communities, i. e., communities linked by dispersal and trophic interactions (Haegeman and Loureau, 2014; Holyoak *et al.*, 2005; Melián *et al.*, 2015; Pillai *et al.*, 2011; Wilson, 1992). In these meta-communities, species may form linear food chains or be otherwise embedded in complex food webs composed of a large number of species, different functional groups and genetically variable individuals (Bohan and Woodward 2013; Tamadoni-Nezhad *et al.*, 2013; Winemiller and Polis, 1996). The dynamics of these meta-communities is interesting, for example, as it has been demonstrated by empirically-informed simulations that the dispersal of individuals and the distance between resource-rich patches in heterogeneous landscapes are important drivers shaping local and regional richness (Melián *et al.*, 2015). When distances among patches vary, species diversity tend to be highest at intermediate distances, due to the coupling of different search areas displayed by preys and predators. When the islands are adjacent to each other and the space is homogeneous, because the movement among islands is not constrained, the extinction of both preys and predators, and the collapse of the entire system, is very likely. Something similar happens when the islands are far apart, because the organisms cannot move among them, a feature resulting in low colonization rates, loss of genetic diversity, and high mortality and extinction rates from severe overgrazing and strong competition in preys that are not controlled from top predators (Moya-Laraño *et al.*, 2014; Ruiz-Lupión *et al.*, unpublished data). Consequently, when habitat fragmentation occurs, either through human activity or naturally —e. g., form spatial heterogeneity of moisture pockets in leaf-litter of beech forests—, the persistence of the food web at the landscape scale will depend on the size of patches, the distances between them and the dispersal distance of the species (Harrison and Taylor, 1997; Stith *et al.*, 1996). Under these circumstances, the existence of micro-ecological corridors, conceived as geographical spaces that connect fragments of natural habitats facilitating the dispersal of species and decreasing the degree of isolation of the patches (Bennett, 1998), may be essential for the persistence of food webs.

In this work, we introduce WEAVER 2.0, a Next-Generation Individual-Based Model that describes autonomous individual organisms in complex food webs and simulates multi-trophic meta-community eco-evolutionary dynamics. This modelling platform considers a diversity of aspects that make simulations highly realistic, such as inter- and intraspecific variability, local interactions, complete life cycles, individual behaviours responding to changing environments, trait-based approaches and micro-evolution at fine spatial and temporal scale (Grimm *et al.*, 2006; Grimm *et al.*, 2017; Moya-Laraño *et al.* 2014). The

aims of this paper are: a) to present an updated version of the modelling platform WEAVER 2.0, which we have improved with several new functionalities, adding more realism to the simulations, and b) to show how to use this platform to design experiments «in silico» to explore, at the micro-scale, the effects of 1) the distances among moisture pockets; and 2) the effects of the presence of a micro-ecological corridor that vary in productivity on the ecological dynamics and persistence of a food web of beech leaf-litter (*Fagus sylvatica* L.), and the subsequent consequences for a key ecosystem process: litter decomposition.

## NEW FEATURES AND FUNCTIONALITIES OF WEAVER 2.0

Here we mention on some of the new features of the ongoing implementation of WEAVER 2.0, which is a comprehensive extension of WEAVER 1.0 (Moya-Laraño *et al.*, 2014; Bilbao-Castro *et al.*, 2015) that still allows the exploration of individual-based eco-evolutionary dynamics in multi-species food web across space but now being substantially more realistic. This framework, links genes to ecosystems through space and provides information of ecological and evolutionary dynamics at the gene, individual, population and community levels and at different spatial scales. Back in 2017, WEAVER 1.0 was the Next-Generation IBM to link biodiversity to ecosystem processes that had the highest number of biological functionalities, and thus realism (Grimm *et al.*, 2017). We are going to describe a few of the new features and functionalities implemented thus far in WEAVER 2.0.

### *Realistic implementation of time and space*

In the current version WEAVER 2.0 time elapses in day units. However, we are currently working and improving a new capability that corrects all events considering any time unit—from seconds to years—. Here, for the sake of generality we refer to each day as time step.

Relative to space, in the previous version, WEAVER 1.0, space used cells as elementary units, and animals moved distances that were measured in numbers of cells, an arbitrary unit. In this new version, space is now absolute and realistically measured in international units and in the present simulations the elementary cell unit has a volume of  $10 \times 10 \times 10 \text{ mm}^3$ . This realistic space setup allows ecosystem biomass and productivity to be incorporated in absolute terms and animals to move realistic distances in search for resources, similarly as they do in nature.

### *The abiotic environmental conditions*

To mimic rainfall events and micro-climate conditions, we can now include a Relative Humidity (RH) time series in each patch—moisture pocket or resource islands— where RH can change from day to day—step by step—, mimicking seasonal trends in soil RH. In addition, each patch has its own «hygrostat», it is similarly to a chemostat—renewal pulses of basal resources—, controls the strength and frequency of rainfall events. These events are mimicked through changes in RH in the soil and the rainfall decreases following a decay function until the next rainfall event. Similarly, to RH each patch has its own variable temperature, which is established

by means of a time series —days or steps—. By controlling the spatial autocorrelation among time series across patches one can control both the micro- and mesoclimatic conditions of the simulation and even mimic the formation of soil pockets after a rainfall even. Thus, spatial and temporal autocorrelation in abiotic conditions can now be introduced.

### *A more realistic initialization of individuals*

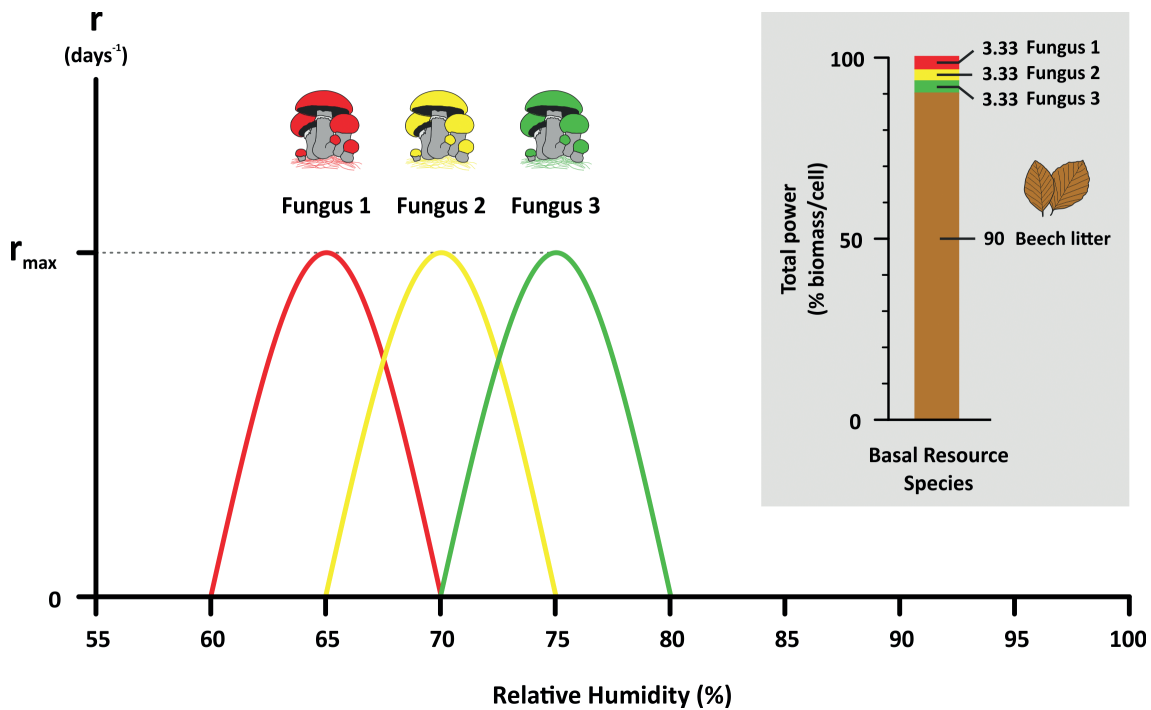
In WEAVER 1.0, to further include realism in the simulations, we initialized the density of each species and instar following mass-abundance allometric constraints (Damuth, 1981; Reuman *et al.*, 2009), using the equation  $N = 74.8M^{-0.75}$  (Schneider *et al.*, 2012), where  $N$  is the number of individuals and  $M$  is fresh body mass (mg). We assumed 69 % of water body content, based on the mean value (68,8 %) for all species of terrestrial arthropods obtained by Hadley, 1994, to calculate the number of individuals of each instar and species. Note that this approach also assumes that water body content proportions do not change with body mass (e. g., perfect isometry) and thus that on average it does not affect mass-length allometric relationships. In WEAVER 2.0, we initialize the number of individuals for each species and instar based on real abundances measured in field experiments. For example, using the data obtained of abundance of beech soil and litter meso- and macrofauna in Ruiz-Lupión *et al.* (2019a) or Melguizo-Ruiz *et al.* (2020). The reasoning behind this new type of initialization is that  $N \sim M$  relationships can be emerging properties of our simulations, rather than inputs.

### *The food web features*

#### **Basal resources**

Formerly, basal resources were the microbiota that grew in the litter, such as fungi and bacteria. In the present parameterization of WEAVER 2.0, however, since there are no bacterivores, we are not considering bacteria. Now basal resources also include litter, considered here as a year-to-year renewable resource, consumed only by detritivores. In WEAVER 1.0, in each patch, the basal resource (fungi) grew according to a conventional logistic growth function, and its dynamics followed an update of the algorithm in Moya-Laraño *et al.* (2012). Since this equation was used to merely model the dynamics of a single cell, and not that of the entire space in the simulation, and this equation generates chaotic dynamics beyond values near 2.7 for the intrinsic rate of increase  $r$  (May, 1974), we now use a recursive exponential growth model at the cell level. When fungi grow in excess of a certain carrying capacity limit value that we set for the cell, it expands to nearby cells as long as carrying capacity has not been reached in those other cells. Therefore, instead of a logistic growth curve we impose truncated exponential growth at the cell level.

As in other studies we define a total power for the system (Savage *et al.*, 2004), here assumed to be the sum of the carrying capacities for all species of basal resources. In addition, in WEAVER 2.0 the growth of basal resources depends not only on temperature but also on RH (figure 1). Moreover, the simulation can consider two different scenarios of basal resource growth: a) «non-competing species of fungi»: within a cell growth occurs until the species carrying capacity is reached and therefore grows independently of what other species are doing. The



**Figure 1.** Effect of Relative Humidity (RH) on fungi growth rate and conditions for the slowly-renewable leaf-litter resource. The peaks of the parabolic curves correspond to the maximum growth rate ( $r_{max}$ ) values of each species. In our simulations the total power of each cell (the sum of carrying capacities) is allocated 90 % to beech litter and 10 % to the 3 fungus species (i. e., 3,33 % for each). Own elaboration.

sum of all carrying capacities determine the total power of the cell; or *b*) «competing species of fungi»: grow according to their own biomass and temperature-water dependent growth rate but share a common maximum cell carrying capacity. Here, we consider the sum of the biomasses of all the fungus species in a cell, and the biomass of each species grows as long as the sum of the total biomass considering all species does not exceed the cell total power (i. e., the carrying capacity of the cell). Note that this new functionality will also produce apparent competition (*sensu* Holt, 1977) among fungus species, as differential grazing upon one fungus species will allow the non-preferred species to grow to fill the available fraction of the cell until the cell carrying capacity is reached, resulting in a negative correlation between the abundances of both species.

When fungi grow in a patch beyond saturation, mycelia colonize neighboring patches, allowing the amount of extra-grown fungi to fill these patches up to the values of either the species-specific carrying capacity —non-competitive fungi— or the cell total power —competitive fungi— of the newly colonized patch. In addition, complete competitive exclusion among basal resources will never happen, because there is a threshold value of fungus biomass below which this fungus cannot be consumed by any of the fungivorous species nor outcompeted by any of the other fungus species. This enables basal resources to recover within each of the cells, and entails a more realistic scenario, as not all parts of the basal resources are equally edible —e. g., old *vs* fresh mycelia—.

## Types of interaction between individuals

In the past version of WEAVER 1.0, the species are classified as fungivores only feeding on fungi (basal resources) —e. g., Acari Oribatida and Collembola species—, or as predators feeding on fungivorous species, which may be also cannibals and/or intraguil predators (IGP) in which case they would be trophic level omnivores —e. g., spiders and centipedes—. WEAVER 2.0 allows for a more inclusive type of omnivory, in the sense that a predator can now feed not only on other predators and on fungivores (prey), but also on fungi —basal resources—. This conforms our food webs to niche model topologies. Although the literature is not clear on this point, we have assumed that many species of Mesostigamata and Prostigmata Acari should be able to feed on these two types of resources. In the simulation, however, fungi are the least preferred and profitable food for predators.

## Selection of edible species

Now, in WEAVER 2.0, animals have coefficients that determine their preferences for, and the profitability of, each prey species. Omnivores are forced to feed on fungi only when animal prey are not available. In addition, omnivorous species can be cannibalistic, and feed on other prey and fungi, even though the latter are less preferred and less profitable. Additionally, preferences can be now weighted by relative abundances, as consumers can memorize the quantity of ingested food from each species, allowing them to switch to the resource species that becomes more abundant —i. e., predator or consumer switching— (Murdoch, 1969). This should increase the persistence of the system from ongoing frequency-dependent selection.

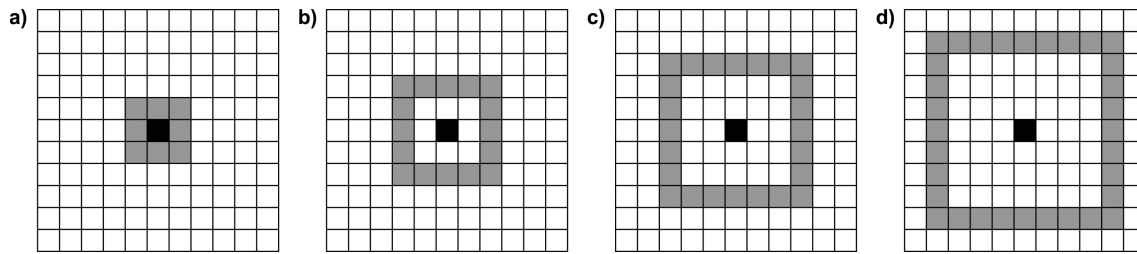
## *The searching and movement algorithm*

In WEAVER 1.0, animals moved adaptively in 3D space. In addition, they remembered the cells visited the same day and did not revisit them. Animals explore the 27 or 9 surrounding cells plus the cell where the animal is currently located in a given time in 3D or 2D simulations, respectively. At each move, fungivores switched to cells with the lowest ratio between predation threat and fungus biomass; and predators behave in a similar way, they assessed predator threat and prey availability —both fungivores and IGP-prey— and following an empirical mass ratio criterion for prey that would be fit as edible:

$$\log \frac{\text{mass Predator (mg)}}{\text{mass Prey (mg)}} \in [-1.21, 6.68] \quad [1]$$

In addition, both prey and predators could jump at a distance which was established by drawing a random number from a uniform distribution ranging between 2 and their «Search Area» trait, i. e., the maximum number of cells that the animal could visit in one day (see a detailed description of the traits below) when food availability within the 27 neighboring cells —26 surrounding cells plus the cell where the animal is currently located— was zero (Moya-Laraño *et al.*, 2014).





**Figure 2.** New algorithm for searching in WEAVER 2.0. World have  $11 \times 11 \times 1$  cells<sup>3</sup> dimensions, each cell measures  $1000 \text{ mm}^3$  ( $10 \times 10 \times 10 \text{ mm}^3$ ). In black, the cell where the animal is located and in gray, the cells assessed in one time step by one individual: *a)* circle of 8 surrounding cells to search, following the original algorithm but with the new searching criterion including the abundance of conspecifics and a new function of basal resources and predator-prey ratios; *b)* circle of 16 contiguous cells; *c)* circle of 24 contiguous cells; and *d)* final circle of 32 cells —maximum «Search Area» of that particular individual—. Cells have been used for clarity, however space is now implemented using real units. Own elaboration.

In WEAVER 2.0, the distances that the animals are allowed to travel per unit of time are still ruled by the trait «Search Area», but this time in mm not in cells, and the total distance travelled is corrected accordingly depending on whether space transitions are realized between adjacent or diagonal cells. Animals move in 3D space and they remember the cells they visited not repeating the same cell during the same day (or step). At each move, fungivore species will move to cells with fewer predators, greater fungus biomass and, if the species is gregarious (i. e., *Collembola* species), with the highest number of conspecifics up to certain density threshold when they start avoiding conspecifics. This simulates that the animals can assess the Allee effect —i. e., a positive correlation between density and individual fitness— (Allee, 1931) and behave accordingly: tending to aggregate at low densities. At very high densities, however, competition should be a problem and conspecifics avoid each other. A series of coefficients determine the relative importance of food, predators or conspecifics in affecting the behavior of each individual. Predators behave in a similar way, they assess predator threat and prey availability —both fungivorous and IGP-prey species— as well as conspecifics, including the assesment of the amount of fungus biomass if they are also omnivorous. Now, instead of a simple predator-prey size ratio to decide who eats whom, a realistic non-linear model based on forcing a normal distribution of predator-prey ratios to that observed in terrestrial invertebrates (Brose *et al.*, 2006) has been incorporated. This is now more realistic because large predators will refuse to feed on tiny preys. In addition, instead of jumps when food is scarce, WEAVER 2.0 includes the possibility of animals assessing cells farther away from neighboring cells at a touch distance. Remember that animals assess the 26 or 8 cells surrounding its cell in 3D or 2D simulations, respectively. Now, when food availability is zero, they expand the search to 66 or 16 adjoining surrounding cells in 3D or 2D simulations, respectively. If food availability is zero again, they expand the search in concentric circles (figure 2) until they reach their «Search Area» trait . Note that the animal assesses these cells at a distance, without moving to them until a prey is located. This is an especial type of algorithm that is triggered only when food nearby cannot be found.

### *The moulting algorithm*

In WEAVER 1.0, the moulting algorithm depended on the shape of the animals, and thus the decision to change to next instar was given by the mass-length allometric relationship:

$$M = aL^b \quad [2]$$

where  $M$  is the body mass in mg,  $L$  is total body length without appendages in mm,  $a$  is a scaling factor and  $b$  is an allometric factor. This equation was used to transform the mass available for moulting into the length of the animal in order to allow for growth in length to be governed by the fixed trait growth ratio. Since growth curves are not ruled by a single ratio parameter, but rather this ratio changes over time, we also included a given time as an alternative target for moulting. A ratio between the time elapsed in the prior instar and the time elapsed in the target instar was included. The ratio between the time elapsed in the target instar *vs* the time in the prior instar was established as a second rule of thumb to moulting. However, this did not impede animals from moulting at unrealistically higher rates (Moyarano *et al.*, 2014).

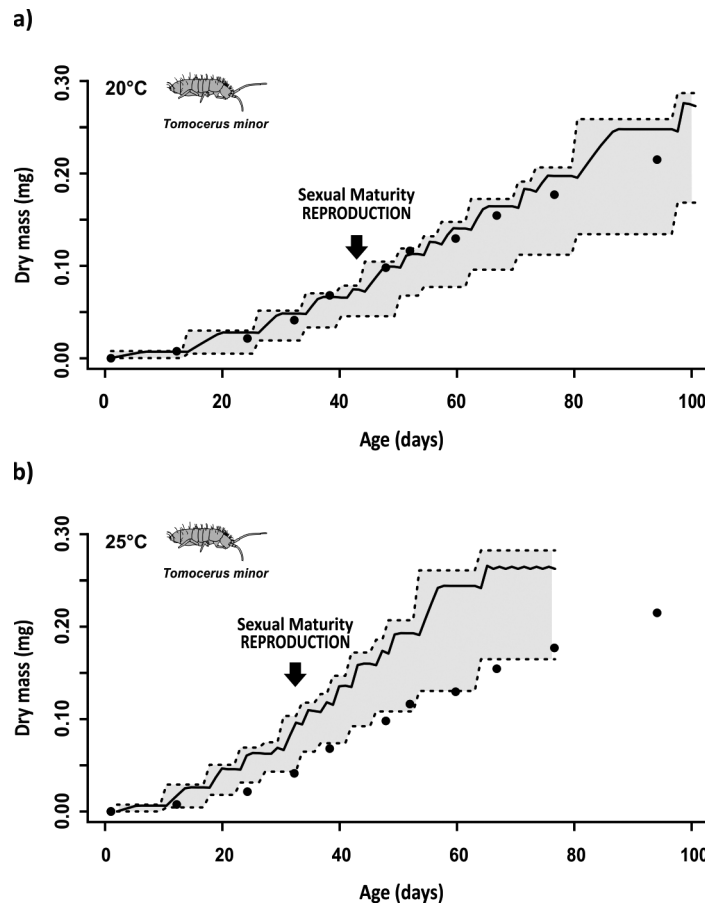
A more realistic moulting algorithm is used in WEAVER 2.0, based on published species-specific growth curves. We included the relationship between time (days) and length (mm) for each simulated species using our own database (Ruiz-Lupi3n *et al.*, 2019b) and externally we adjusted a Von Bertalanffy growth curve (Bertalanffy, 1968), where each instar includes a double time and length target that the animal should follow to moulting (figures 3a y b):

$$L_t = L_\infty (1 - e^{-k(t-t_0)}) \quad [3]$$

where  $t$  is the age at time  $t$ ,  $k$  is the growth coefficient,  $t_0$  is the extrapolated time at which the animal would have zero length,  $L_\infty$  is an asymptotic size or maximum size. After fitting a non-linear regression model we use the estimates of  $L_\infty$ ,  $k$  and  $t_0$  as parameters in the model. However, at any given body size, higher temperature leads to greater metabolic rates (Gillooly *et al.*, 2002). This effect —if uncompensated— would tend to decrease growth efficiency at higher temperatures. This leads to the prediction that species developing at higher environmental temperatures may be affected on their size at maturation. This is known as the Temperature Size Rule (TSR), which denotes the plastic response of body size to environmental temperature variation (Angilletta *et al.*, 2003, 2004). Plastic organisms are capable of allowing their body size to decrease according to environmental temperature. In more realistic growth curves, individuals mature faster and they become adults at a smaller size when temperature increases. In WEAVER 2.0 at initialization we input the growth curve at the laboratory temperature (°C) at which it was measured (figure 3a), and then using the Metabolic Theory of Ecology (MTE) and the TSR we extrapolate the curve at other temperatures (figure 3b).

As in WEAVER 1.0, we used Equation 2 to transform the length of the animal into available energy for moulting. For WEAVER 2.0 we compiled a comprehensive database of mass-length





**Figure 3.** Real and simulated growth curves in dry mass (mg) of Collembola (*Tomocerus minor*) species implemented in WEAVER 2.0, with indeterminate growth. *a*) Growth curve at 20 °C of temperature, and *b*) growth curve at 25 °C of temperature. Black points represent the real growth curve as obtained in the laboratory at 20 °C (Joosse and Veltkamp, 1970), and used to parameterize WEAVER 2.0; black lines represent the simulated growth curves and gray shadows delimited by black dashed lines show the area or biological limits within which the animal can grow from plasticity. Own elaboration.

allometric relationships (Ruiz-Lupi3n *et al.*, 2020). WEAVER 2.0 also includes the possibility for indeterminate growth; that is, individuals can remain growing after sexual maturity and first reproduction —e. g., as many Collembola species— (figure 3). In addition, it includes holometabolism or complete metamorphosis, which is a form of insect development with four life stages: egg, larva, pupa, and imago or adult. Holometabolism is a synapomorphic trait of all insects in the superorder Endopterygota. Immature stages of holometabolous insects are very different from the mature stage. For this, now we can include in the parameterization two different mass-length allometric relationships, one for larvae stages and another for the adult stage; and we can indicate the number of days that the individuals are in pupa stage during which they are not moving or feeding, and for simplicity we assume that they cannot be predated either.

## *The reproductive algorithm*

### **Quantitative genetics with realistic recombination rates**

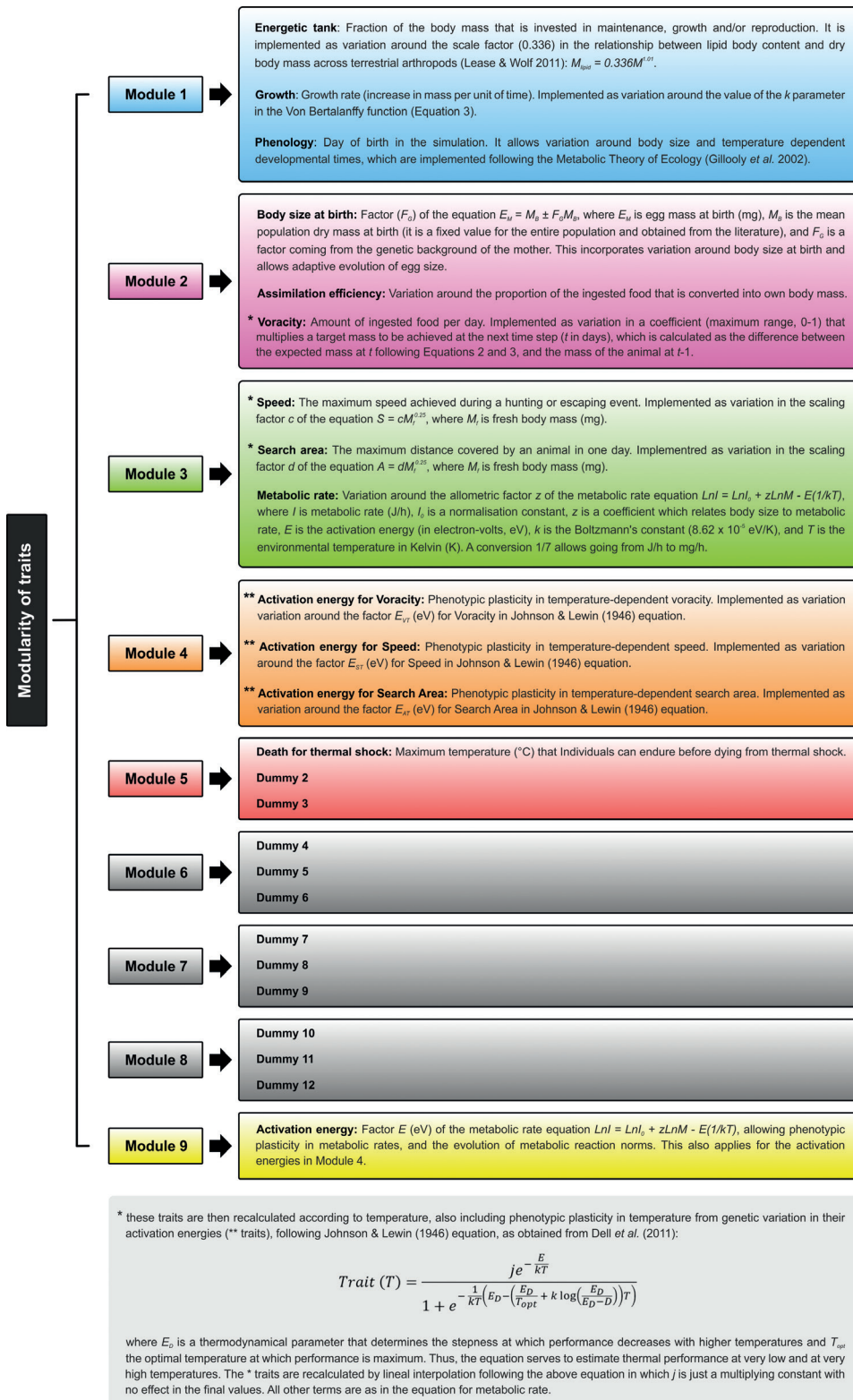
In addition to multidimensional quantitative genetics with Mendelian inheritance, we have modified the recombination and meiosis algorithms, including now the possibility for recombination and segregation. In the former version of this IBM framework, mini-AKIRA (Moya-Laraño *et al.*, 2012), the genetic correlations were induced 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. WEAVER 2.0 mimics recombination more realistically. The formerly described loci vectors (Moya-Laraño *et al.*, 2012), which are useful to induce the desired degrees of genetic correlations among traits, now termed “correlosomes” in WEAVER 1.0 (Moya-Laraño *et al.*, 2014). In WEAVER 2.0, we have substantially improved the meiosis algorithm truly reflecting the effects of recombination, which were unintentionally oversimplified in the former version.

### **Reproductive modes**

As a novelty we have included separate sexes —males and females—, and thus more realistic sexual reproduction in animals with two different sex roles, although no sexual dimorphism (e.g., in size) has been implemented so far. Also, we consider three sexual modes: *a*) diploidy, in a diploid system both males and females contribute half of their genetic material to build a  $2n$  zygote; *b*) haplodiploidy, in haplodiploids (i. e., mites) females that do not mate make gametes that produce haploid males which are the result of the female meiosis; and *c*) asexual reproduction, in the mode of asexual reproduction populations are only composed of females which produce other diploid ( $2n$ ) females identical to themselves. Future implementations should include intermediate forms of parthenogenesis, in which females have variable offspring from recombination occurring during meiosis. Asexual reproduction allows prey populations to grow very rapidly when the environment permits, and to highly influence food web dynamics. Additionally, by comparing populations identical in all parameters but in reproductive mode, one can study the advantages of sexual reproduction in species embedded in food webs.

### **Modularity of traits based on multidimensional quantitative genetics**

In WEAVER 2.0, several changes have been made relative to the implementation of traits (figure 4): *a*) «Voracity», «Speed» and «Search Area» traits are no longer the allometric factor  $b$  of the allometric equations ( $Trait = aM^b$ ), but now they represent the scaling factor  $a$ ; and *b*) the traits « $Q_{10}$  Voracity», « $Q_{10}$  Speed» and « $Q_{10}$  Search Area» have been replaced by the «activation energy» ( $E$ ) for «Voracity», «Speed» and «Search Area». In addition to the 13 traits present in WEAVER 1.0, WEAVER 2.0 includes 12 new traits scattered in 4 new 3-trait modules that we call «dummy» because they have the entire genetic machinery to work but these traits are not functional. Thus, if no further implementation is added the genes associated to these traits behave neutrally and are thus subject to genetic drift. This alone is useful to document genetic drift during simulations.



**Figure 4.** Modularity of traits based on multidimensional quantitative genetics. The traits are grouped into nine modules that are genetically independent of each other. Within each module the traits are correlated with each other, and the degree of correlation determines the degree of phenotypic integration. Own elaboration.

However, the main purpose of these genes is that an intermediate-level programmer in C++ can add new functional traits without having to deal with programming the entire genetic machinery. In this way, we have programmed the first dummy trait to become death by thermal shock. When temperature increase dramatically, individuals begin to synthesize Heat Shock Proteins (HSP) (Ritossa, 1962), a family of proteins found in all living organisms, from bacteria to humans, that are produced in response to exposure to stressful conditions, such as extreme temperatures (Matz *et al.*, 1995; Wu, 1995) or UV light (Cao *et al.*, 1999), providing variation to death from heat shock. Everything else regarding genetics is very similar as in Moya-Laraño *et al.* (2012) and Moya-Laraño *et al.* (2014).

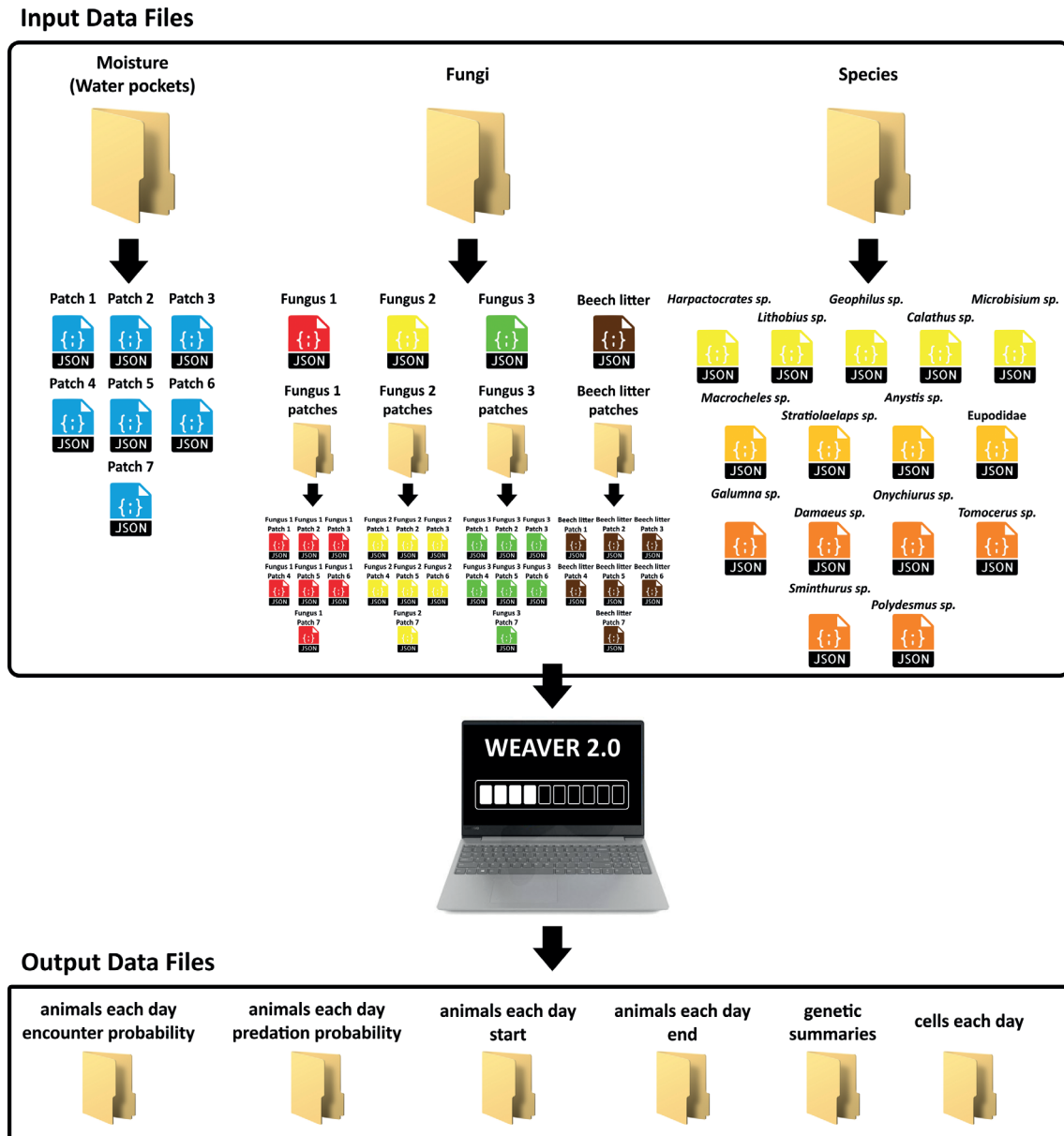
## WORKING FLOW OF WEAVER 2.0

In summary, WEAVER 2.0 has new implemented functionalities: it uses real space units (mm), temporal series of temperature and relative humidity, an initialization of individuals based on real data of abundance, syntopic basal resources with or without competition, new types of interactions between individuals and selection of edible species based on food preferences and the possibility of switching. Also, the movement, moulting and reproduction algorithms have gained in realism. Figure 5 shows the working diagram of WEAVER 2.0.

## APPLICATION TO EMPIRICAL DATA FOR SIMULATED EXPERIMENTAL DESIGN. DESCRIPTION OF THE FOOD WEB, NETWORK ANALYSIS AND NICHE MODEL NETWORKS

We used the database of growth curves (Ruiz-Lupión *et al.*, 2019b) to select the model species that are more similar to the real species or genera in the beech leaf-litter food web, and then we parameterized and implemented them in WEAVER 2.0. Central to the functioning of this version continues to be mass-length allometric relationships (see above), for which we have performed a detailed bibliographical survey. We calculated the among species means of the «log(a)» and «b» for the mass-length relationships available (Ruiz-Lupión *et al.*, 2020). The backtransformed means of scaling factors «log(a)» and the means of the allometric factors «b» are equal for juvenile and adults in ametabolous species and differs for holometabolous species. And finally, for the implementation of the species in the food web we used real abundances of meso- and mesofauna in the beech-litter soil (Moya-Laraño and Melguizo-Ruiz, unpublished data).

Using this dataset, we built an initial leaf-litter food web of the beech forest composed of 19 species belonging to four trophic levels (figures 6 y 7a). The fourth (top) trophic level is composed of 5 intraguild and cannibalistic predators: 4 large predators —a cursorial spider *Harpactocrates sp.*, 2 species of chilopoda, one Geophilomorpha *Geophilus sp.* and one Lithobiomorpha *Lithobius sp.*, and a carabid beetle *Calathus sp.*— with body length ranging between 10 and 40 mm as adults (growth curves and body size data from Murakami, 1958; Lewis, 1961; Andersson, 1990; Fisher and Vasconcellos-Neto, 2005), and a 1 medium-size predator —a pseudoscorpion *Microbisium sp.*— of about 1.5 mm in



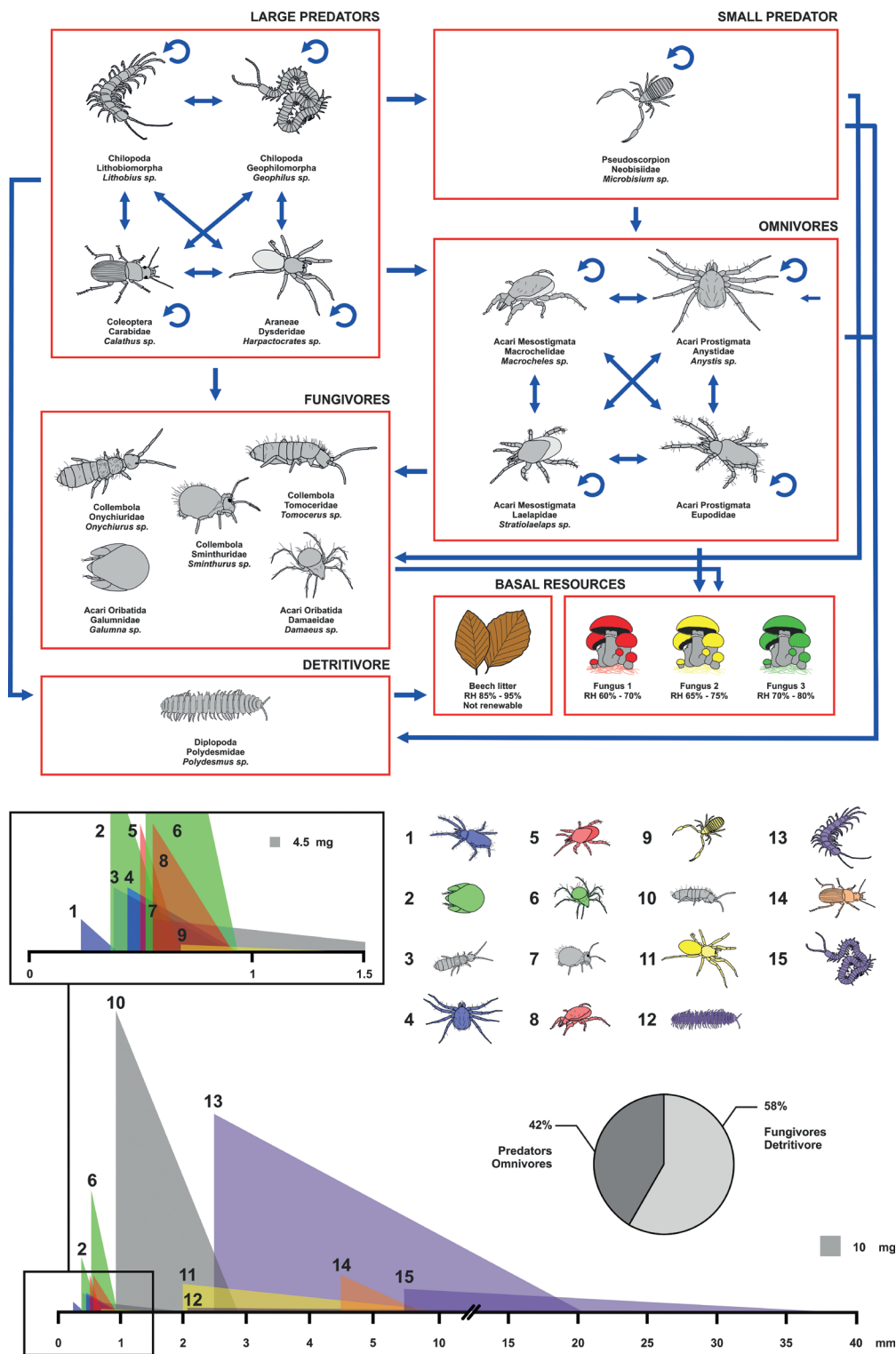
**Figure 5.** Working diagram of WEAVER 2.0. The moisture folder includes information about time series for temperature and relative humidity for each of the moisture spherical patches. The fungi folder includes all features for the fungi species and beech litter and how each of these basal resources is scattered around moisture patches. The species folder includes all features for each consumer species—developmental and growth information, mass-length allometric relationship, traits based in quantitative genetics, feeding links, food preferences and profitabilities, etc.—. Finally, we get multiple outputs—number of encounters and predation events of each individual/day, amount of food consumed, trait values and genetics throughout the simulation, cells visited of each individual/day, time and energy spent in each step of the program, etc.—. Own elaboration.

body length as adult (growth curve and body size data from Sakayori, 1989). Predators account for 39 % of the total biomass at the beginning of the simulation (figure 6). The third trophic level included 4 omnivorous species that feed on other arthropods as well as on fungi —2 Acari Mesostigmata *Macrocheles sp.* and *Stratiolaelaps sp.*, and 2 Acari Prostigmata *Anystis sp.* and Eupodidae—. These species have a length ranging between 0.3 mm and 1.0 mm and represent 3 % of the initial biomass (growth curves and body size data from Sorensen *et al.*, 1976; Cabrera *et al.*, 2005; Abou-Awad *et al.*, 2006; Mei-Fang *et al.*, 2017; Balanzategui-Guijarro, unpublished data) (figure 6). The second trophic level include 5 fungivorous species —2 Acari Oribatida *Galumna sp.* and *Damaeus sp.*, and 3 Collembola *Onychiurus sp.*, *Tomocerus sp.* and *Sminthurus sp.*— with length range of 0.3 - 4.0 mm, and accounting for 58 % of the initial biomass (growth curves and body size data from Maclagan, 1932; Sengbusch and Sengbusch, 1970; Jooose and Veltkamp, 1970; Walsh and Bolger, 1990; Balanzategui-Guijarro, unpublished data), and 1 large detritivorous species (a Diplopoda *Polydesmus sp.*) reaching 20 mm in body length but representing just 2 % of the initial biomass (growth curve and body size data from Snider, 1981) (figure 6). Finally, the first trophic level was composed of 4 basal resources, three of them syntopic fungi with different Relative Humidity optima (Fungus 1 RH Range = 60 % - 70 %; Fungus 2 RH Range = 65 % - 75 % and Fungus 3 RH Range = 70 % - 80 %) and beech leaf-litter —which is only renewable once every year - litter fall of a deciduous forest— (figure 6).

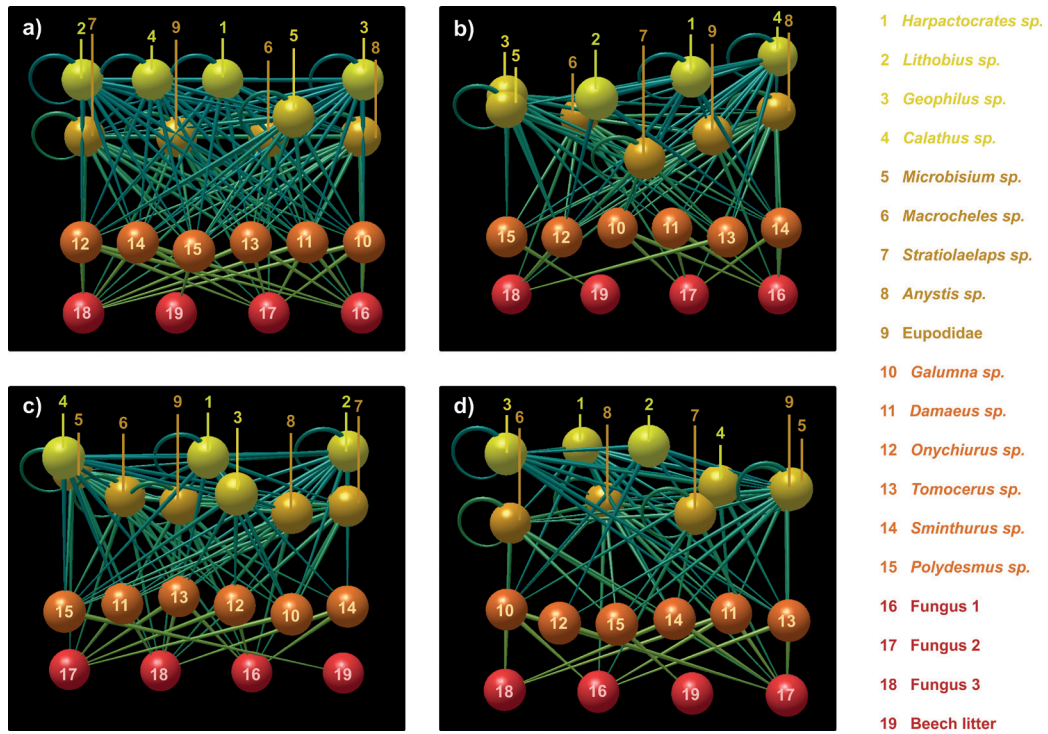
In the next step, we performed a network analysis to know the properties of the initial food web using Network3D 1.0.0.0 developed by ©Microsoft Corporation for Microsoft Research and the PEaCE Lab. To that end, we loaded data from a predation matrix that describes our food web with all possible links constrained by food level as explained above (figures 6; 7a; see table S1, Appendix). Finally, we obtained the principal features of the initial food web: 1) number of species ( $S$ ); 2) links ( $L$ ) per species ( $S$ ), calculated as  $L/S$ ; 3) connectance, calculated as  $L/S^2$ ; 4) fraction of top predators that have neither intra- nor interspecific predators (none in our study); 5) fraction of intermediate consumers that have both predators and prey (in our study all predators and omnivores); 6) fraction of basal species —fungi and beech litter—; 7) fraction of fungivorous and detritivorous species; 8) fraction of omnivorous species; 9) fraction of cannibalistic species; 10) standard deviation of generality —generality of a node is the number of species it consumes, normalized by  $L/S$ —; 11) standard deviation of vulnerability —vulnerability of a node is the number of species by which it is consumed by normalized  $L/S$ —; and 12) standard deviation of connectivity —connectivity of a node is the number of species it is connected to, be it as predator or as prey, normalized by  $2L/S$ — (table 1; Williams and Martinez, 2008).

We use the topology of the initial food web and two empirical parameters, species number ( $S$ ) and a new value of connectance (0.25 *vs* 0.40), to obtain a new food web matching the niche model. This was done by iteration of Network3D until a web with a given targeted connectance and which fitted to the niche model was obtained (Williams and Martinez, 2000). This procedure was run three times until three food webs were obtained, which were used as the replicates for simulation in WEAVER 2.0. These three food webs only differed in their topology (figures 7b, 7c y 7d; see tables S2, S3 y S4, Appendix), with all other properties being identical (table 1).





**Figure 6.** Simplified food web including meso- and macrofauna from the leaf-litter of the beech forest floor, as implemented for simulations. The blue arrows indicate who eats whom. Closed loops indicate that the species are cannibalistic. The width of the triangles delimits the minimum and maximum body length (mm) from birth to adulthood of all species and the height indicates the amount of biomass of each species and instar, based on the number of individuals collected in field surveys. Own elaboration.



**Figure 7.** Beech forest (*Fagus sylvatica* L.) leaf-litter food webs implemented for simulation in the WEAVER 2.0. *a*) Initial food web constrained by initial assumptions; *b*) niche model food web 1; *c*) niche model food web 2; and *d*) niche model food web 3. Yellow circles represent the fourth (top) trophic level —top predatory species—, yellow mustard circles represent the third trophic level —omnivorous species—, orange circles represent the second trophic level —fungivorous and detritivorous species— and red circles represent basal resources of the first trophic level —fungi and beech litter—. Rings indicate cannibalistic species. Own elaboration.

PROPERTY	INITIAL FOOD WEB	NICHE MODEL FOOD WEBS
Number of species (S)	19	19
Links per species (L)	7.80	4.50 [4.30 - 4.70]
Connectance	0.40	0.25 [0.20 - 0.30]
Fraction of Top species	0.00	0.10 [0.00 - 0.20]
Fraction of Intermediate species	0.80	0.80 [0.60 - 0.90]
Fraction of Basal species	0.20	0.20 [0.10 - 0.30]
Fraction of Fungivorous and Detritivorous species	0.30	0.10 [0.00 - 0.20]
Fraction of Omnivorous species	0.80	0.70 [0.60 - 0.80]
Fraction of Cannibalistic species	0.50	0.30 [0.10 - 0.40]
Standard deviation of generality	0.80	0.90 [0.70 - 1.10]
Standard deviation of vulnerability	0.30	0.60 [0.30 - 0.80]
Standard deviation of connectivity	0.30	0.40 [0.30 - 0.50]

**Table 1.** Network analysis of initial and niche model food webs.

## EXAMPLE OF EXPERIMENTAL DESIGN 1

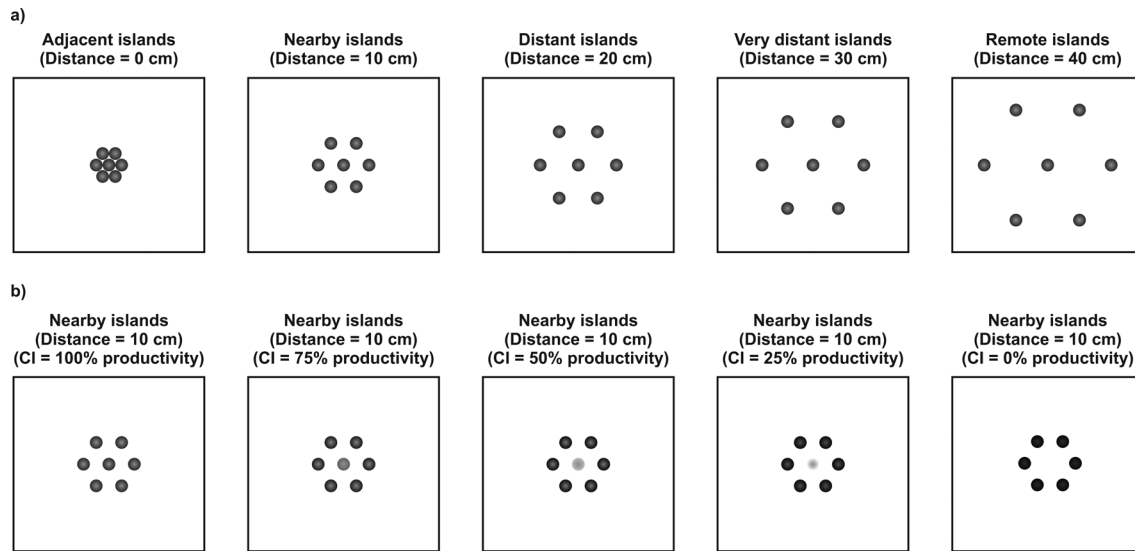
This experiment will test the effects of the distance among water pockets (resource islands) on the ecological dynamics and persistence of the implemented food webs, as well as the subsequent consequences for a main ecosystem process: litter decomposition. To incorporate a spatial component, we will simulate seven equidistant water pockets around a hexagon in which fungi will be able to grow and beech litter will be available for detritivorous species (figure 8a). These islands will be identical, with equal basal productivity (fungi and beech litter), shape (spheroids) and size (diameter = 100 mm; depth = 10 mm; volume = 419 cm<sup>3</sup>).

The space surrounding water pockets is empty, without fungi or leaf-litter, and the individuals will only use it to move between resource islands. We will establish five distance treatments (adjacent, nearby, distant, very distant and remote islands) and include seven islands at 0, 10, 20, 30 and 40 cm distances between borders, or 10, 20, 30, 40 and 50 cm between centers respectively. We will minimize edge effects by controlling the distance between the outermost islands and the border of the mesocosm in the remote island treatment by setting this distance between islands above 20 cm. The dimensions of the virtual mesocosms containing these islands will be (width × length × depth): 150 × 130 × 1 cm<sup>3</sup>, and the distance to the edge of the mesocosms will be 60, 50, 40, 30 and 20 cm, respectively (figure 8a).

Note that in WEAVER 2.0 migration depends merely on an animal's mobility that in turn depends on several state variables —e. g., fungi or prey availability, predatory threat, social behaviour, internal state and the trait searching area, among others—. Here, long distance dispersal is not considered —e. g., aerial dispersal in springtails, mites and spiders— because this would require simulating much larger ecosystems. Finally, we will evaluate the optimum distance at which greater species richness is maintained, and what is the effect of the ecological corridor (central island) in food web persistence. To evaluate top-down effects of predators and their ability to couple the global dynamics, we will estimate their dispersal distances in the simulations. We will measure the average dispersal distances of each simulated species, from birth to first reproduction, and obtain the «dispersal kernels» of each species using a normal distribution (Nathan *et al.*, 2012), which are simply probability distributions that indicate the dispersal range of the individuals of each of these simulated species.

## EXAMPLE OF EXPERIMENTAL DESIGN 2

This experiment will test the effect of variability in local productivity of a micro-ecological corridor and the effect of spatial heterogeneity in the ecological dynamics and food web persistence, as well as its consequences for litter decomposition. We will use the island configuration of experiment 1 in which we estimate the longer persistence in the food web —longer ecological dynamics without extinctions— which we will consider to be the optimal distance among islands, and we will modify the productivity of the ecological corridor —central island hereafter— keeping the system productivity constant (figure 8b). Therefore, as the productivity —fungi and beech litter— of the central island decrease, the productivity of the six outermost islands of the simulated hexagonal structure increase proportionally. We will establish five treatments based on a steady decrease in the productivity of the central island relative to the productivity of the peripheral islands.



**Figure 8.** Spatial arrangement for the «in silico» experiments. *a)* experiment 1: testing the effects of the distance among resource islands; and *b)* experiment 2: testing the effect of variability in local productivity of a micro-ecological corridor at optimal distance among islands. Blue circles represent resource islands —water pockets in the beech forest floor in which fungi is able to grow and beech litter is available for detritivorous species at sufficiently high relative humidity for the animals to settle in—. The clearer blue circles decrease (central island = CI) in productivity and the darker blue circles around the hexagon increase in productivity. The squares represent the size of the virtual mesocosm established for simulations. Own elaboration.

In decreasing order, very high productivity, high productivity, medium productivity, low productivity and zero productivity: 100 %, 75 %, 50 %, 25 % and 0 %. The productivity of each peripheral micro-island will increase proportionately in each treatment to keep the overall productivity of the system constant.

## SIMULATION RUNS

To study the effect of the distance among islands, spatial heterogeneity and variability in local productivity of a micro-ecological corridor in the ecological dynamics and persistence of the multi-trophic meta-community, we will design a bifactorial simulation experiment. In experiment 1, we will combine the three food webs and five distances among islands (figure 9a). We will run 15 combinations of treatments that will be replicated 5 times, resulting in 75 combinations. Finally, we will calculate the dispersal kernels for each species at each distance, in total 19 species and 5 spatial arrangements, we will evaluate 95 dispersal kernels.

For experiment 2, we will combine the three food webs and the five treatments of productivity using the scenario where the distance among islands will be optimal in experiment 1. Again, we will run 15 combinations, although 3 of them will take the results of the ones

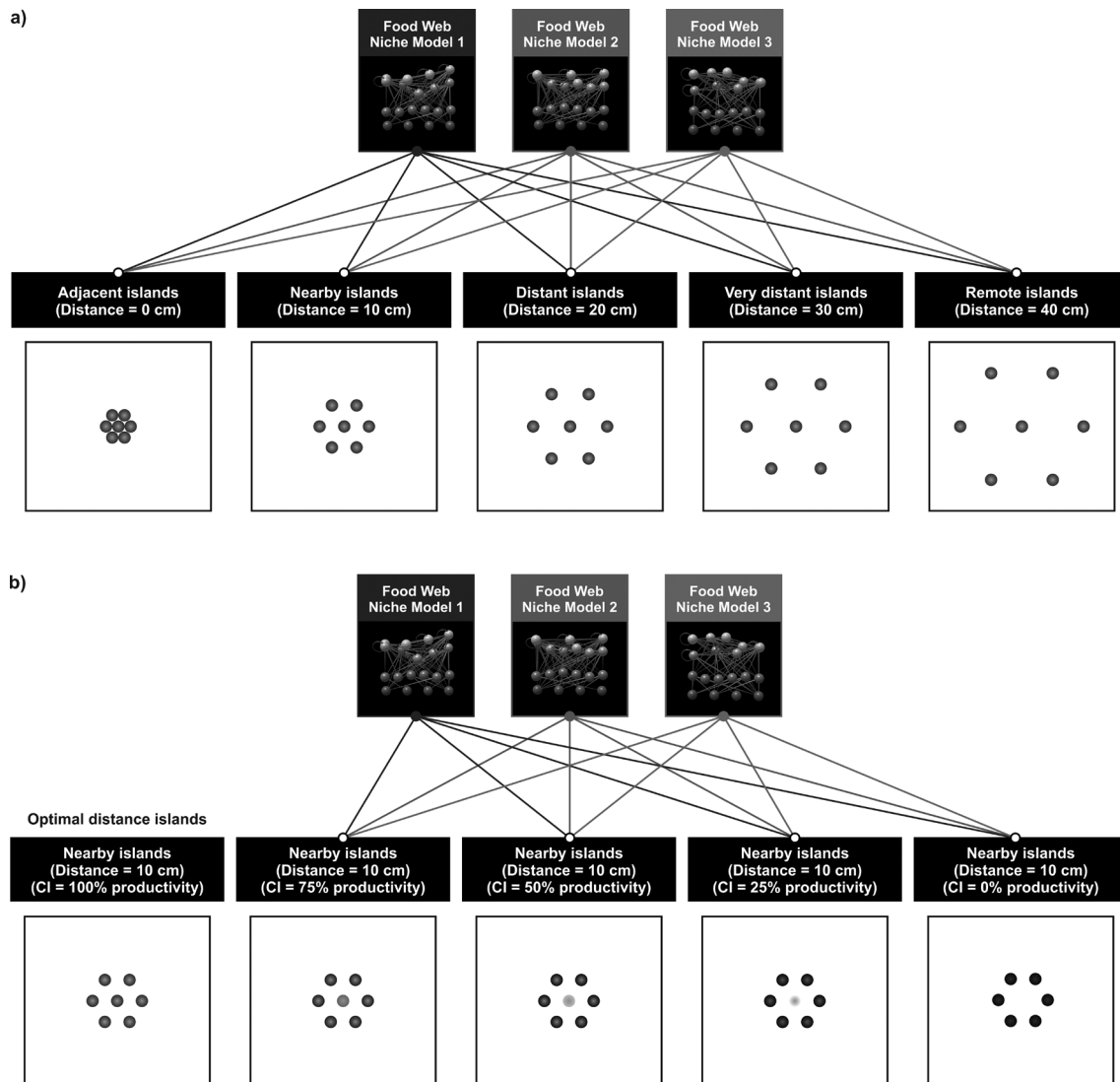


Figure 9. Set of simulations or «in silico» experiments: a) experiment 1, with a total of 75 combinations  $\times$  5 replicates; and b) experiment 2, with a total of 60 combinations  $\times$  5 replicates.

already coming from the above optimal scenario of productivity and will be replicated 5 times, resulting in a total of 60 combinations (figure 9b). All simulations will be run in a workstation (Intel® Xeon® CPU E5-2620 v4 @ 2.10 GHz, 128 GB RAM running under Ubuntu as a bash terminal in Windows 10), located in the Estación Experimental de Zonas Áridas (EEZA-CSIC).

## CONCLUSIONS

We have parameterized a set of simulations that will allow testing how the distribution and productivity of water pockets in forest floors contribute to the maintenance of an ecological network. One responsible of returning the plant residuals to the soil: the soil food web. This is but one example of parameterization and hypothesis testing to show a portion of the potentialities of WEAVER 2.0. The implementation of simulation experimental designs or experiments «in silico» is very similar to how ecologists have traditionally used the scientific method in field and laboratory experiments. An experiment aims at predicting the outcome by manipulating one or more independent variables, factors, or predictor (input) variables. The change in one or more of these independent or input variables changes the result in one or more dependent variables, also referred to as output or response variables. Simulation models often have many input variables, and determining which ones have a significant impact on the response variables of interest can be a difficult task. Thus, in these types of simulation experiments we must choose the input variables carefully, minimizing as much as possible the uncertainty in their estimates, and ensuring that the documentation of the inputs is sufficiently detailed. Finally, we can conclude that in ecological studies, IBMs are developing faster in order to perform «in silico» experiments that would be impossible to perform with traditional experimentation methods. WEAVER 2.0 is one of the most complete Next-Generation IBMs developed to date, and we hope that its potential will explode soon.

## VISION

In the past ten years our groups have been intensively working on this comprehensive Individual-Based Model called WEAVER, up to 2017, the Next-Generation IBM for studying the relationship between biodiversity and ecosystem processes with the highest number of functionalities (Grimm *et al.*, 2017). This collaboration between computer scientists and ecologists is promising and fruitful. All the new functionalities in the 2.0 version are almost now debugged, and we have parameterized food webs as disparate as soils and late Cretaceous dinosaurs, expanding 10 orders of magnitude in body sizes. Currently, we are working in parameterizing the food webs for biological pest control in crops, with which we are hoping to help reaching strategies to improve crop yield using the least amount of pesticides (Montserrat *et al.*, 2021). We envision WEAVER as a simulation laboratory in which ecological and evolutionary questions can be tested and contrasted with real systems. If we are able to make the code parallel and improve its memory allocation, supercomputing will allow expanding our questions using millions of digital organisms at once, closely resembling natural ecosystems.

## ACKNOWLEDGMENTS

We thank all the people that have been implementing, using or shown interest in mini-Akira/WEAVER in the last decade, and thanks to whom advances have been possible: Jacinto Behnadi, Matty P. Berg, José Román Bilbao Castro, Steve Brusatte, Jacintha Ellers, Oscar Franken, Àngel Galobart, Paola Laiolo, Juana López Redondo, Sara Magalhães, Josep M. Marmi, Nereida Melguizo Ruiz, Carlos Melián, Ramón Ordiales, Jennifer Rowntree, Alberto



Ruiz, Sara Sánchez Moreno, Albert G. Sellés, Diego Serrano Carnero, Timothé Van Metter, Oriol Verdeny Vilalta, Bernat Vila, Greg Wilson and David H. Wise. We additionally thank Ramón Ordiales and Alberto Ruiz who helped with the installation of the Linux virtual machine as a bash terminal in Windows 10 and for computational advice. Iñaki Balanzategui Guijarro provided mite data. Richard Williams for rendering access to the Network3D software. This work was funded by grants CGL2014-61314-EXP-R and CGL2015-66192-R from the Spanish Ministerio de Economía y Competitividad (European funds FEDER); P12-RNM-1521 from Junta de Andalucía (European funds FEDER); and PID2019-103863RB-I00 from Spanish Ministerio de Ciencia, Innovación y Universidades (European funds FEDER). D. Ruiz-Lupión enjoyed a FPU (FPU13/04933) scholarship from the Spanish Ministerio de Educación, Cultura y Deporte (MECD).

## SUMMARY

One fundamental challenge in ecology is understanding the long-term persistence and stability of complex food webs across space and time. Here, we present a preliminary multi-locus, multi-trait, multi-trophic eco-evolutionary and spatially explicit Next-Generation Individual-Based Model, WEAVER 2.0, useful for addressing this and many other matters. We highlight: 1) some of the new features and functionalities of WEAVER 2.0; 2) some examples of how to parameterize the simulations and trophic networks; 3) how to obtain more realistic food webs for simulations using the niche model; and 4) how to design scientifically sound experiments «in silico» to achieve the objectives and test hypotheses. As an example, we explain how to parameterize the model to simulate the ecological dynamics of beech (*Fagus sylvatica* L.) forest leaf-litter food webs. The food web topologies were acquired with the niche model. We evaluated how food web persistence is affected by increasing: 1) the distance between resource-rich islands —or moisture pockets—; and 2) the productivity of a central island while maintaining the global productivity of the system constant. We also discuss how the design of «in silico» experiments is comparatively similar, and follows the same procedures as the design of field and/or laboratory mesocosm experiments.

## RESUMEN

Uno de los principales desafíos de la ecología es comprender la persistencia y estabilidad a largo plazo de las complejas redes tróficas en el espacio y el tiempo. Presentamos aquí, de forma preliminar, un Modelo Basado en Individuos de nueva generación, multi-locus, multi-rasgo, multi-trófico, eco-evolutivo y espacialmente explícito WEAVER 2.0, útil para contestar esta y otras muchas preguntas. Se destacan: 1) algunas de las nuevas características y funcionalidades de WEAVER 2.0; 2) algunos ejemplos de cómo parametrizar las simulaciones y las redes tróficas; 3) cómo obtener redes tróficas más realistas para correr simulaciones utilizando el modelo de nicho; y 4) cómo diseñar experimentos científicamente sólidos «in silico» para lograr nuestros objetivos y poner nuestras hipótesis a prueba. Como ejemplo, mostramos como parametrizar este programa para simular las dinámicas ecológicas de múltiples especies incluidas en redes tróficas simplificadas de la hojarasca de los hayedos (*Fagus sylvatica* L.), con topologías obtenidas mediante el modelo de nicho. Todo ello con el fin de estudiar cómo la persistencia de la red trófica se ve afectada cuando: 1) se aumenta

la distancia entre islas ricas en recursos basales —o bolsas de humedad en el suelo—; y 2) se inducen cambios en la productividad de una isla central mientras se mantiene constante la productividad global del sistema. Finalmente, discutimos cómo el diseño de experimentos «in silico» es comparativamente similar y sigue los mismos procedimientos que el diseño de experimentos de mesocosmos de campo y/o de laboratorio.

## REFERENCES

- ABOU-AWAD, Badawi A.; EL-SAWAF, Bahira M. and ABDEL-KHALEK, Amira A. «Four new species of Eupodid mites from Egypt (Acari: Eupodoidea: Eupodidae)», *Acarologia* XLVI, 1-2 (2006), pp. 43-52.
- ALLEE, Warden C. *Animal aggregations, a study in general sociology*, Chicago, University of Chicago Press, 1931.
- ANDERSSON, Göran. «About the duration of the different stadia in the post-embryonic development of some lithobiomorphs», in A. Minelli (ed.), *Proceedings of the 7th International Congress of Myriapodology*, Leiden (The Netherlands), Brill Academic Publishers, 1990, pp. 323-335.
- ANGILLETTA JR., Michael J. and DUNHAM, Arthur E. «The temperature-size rule in ectotherms: simple evolutionary explanations may not be general», *The American Naturalist*, 162, 3 (2003): 332-342; available online: <https://doi.org/10.1086/377187> [inquiry: 23-05-2022].
- ANGILLETTA JR., Michael J.; STEURY, Todd D. and SEARS, Michael V. «Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle», *Integrative and Comparative Biology*, 44, 6 (2004); pp. 498-509; available online: <https://doi.org/10.1093/icb/44.6.498> [inquiry: 23-05-2022].
- BENNETT, Andrew F. *Linkages in the landscapes: the role of corridors and connectivity in wildlife conservation*, Gland (Switzerland) and Cambridge (UK), IUCN, 1998.
- BERTALANFFY, Ludwig V. *General system theory: foundations, development, applications*, New York, George Braziller, 1968.
- BILBAO-CASTRO, José R.; BARRIONUEVO, Gabriel; RUIZ-LUPIÓN, Dolores; CASADO, Leocadio G. and MOYA-LARAÑO, Jordi. «WEAVER. A multiagent, spatial-explicit and high-performance framework to study complex ecological networks», in J. Bajo, K. Hallenborg, P. Pawlewski, V. Botti, N. Sánchez-Pi, N. D. Duque-Méndez, F. Lopes and V. Julián (eds.), *Highlights of Practical Applications of Agents, Multi-Agent Systems, and Sustainability: The PAAMS Collection. International Workshops of PAAMS 2015*, vol. XVIII, Salamanca, Springer, 2015, pp. 139-150.
- BLANKINSHIP, Joseph C.; NIKLAUS, Pascal A. and HUNGATE, Bruce A. «A meta-analysis of responses of soil biota to global change», *Oecologia* 165 (2011), pp. 553-565; available online: <https://doi.org/10.1007/s00442-011-1909-0> [inquiry: 23-05-2022].
- BOHAN, David A. and WOODWARD, Guy. «The Potential for Network Approaches to Improve Knowledge, Understanding, and Prediction of the Structure and Functioning of Agricultural Systems», *Advances in Ecological Research* 49 (2013), pp. xiii-xviii; available online: <https://doi.org/10.1016/B978-0-12-420002-9.10000-9> [inquiry: 23-05-2022].
- BRIGGS, Cheryl J. and HOOPES, Martha F. «Stabilizing effects in spatial parasitoid-host and predator-prey models: a review», *Theoretical Population Biology* 65 (2004), pp. 299-315; available online: <https://doi.org/10.1016/j.tpb.2003.11.001> [inquiry: 23-05-2022].

- BROSE, Ulrich; JONSSON, Tomas; BERLOW, Eric L.; WARREN, Phillip; BANASEK-RICHTER, Carolin; BERSIER, Louis-Félix; BLANCHARD, Julia L.; BREY, Thomas; CARPENTER, Stephen R.; BLANDENIER, Marie-France; CUSHING, Lara; DAWAH, Hassan A.; DELL, Toni; EDWARDS, Francois; HARPER-SMITH, Sarah; JACOB, Ute; LEDGER, Mark E.; MARTINEZ, Neo D.; MEMMOTT, Jane; MINTENBECK, Katja; PINNEGAR, John K.; RALL, Björn C.; RAYNER, Thomas S.; REUMAN, Daniel C.; RUESS, Liliane; ULRICH, Werner; WILLIAMS, Richard J.; WOODWARD, Guy and COHEN, Joel E. «Consumer-resource body-size relationships in natural food webs», *Ecology* 87, 10 (2006): 2411-2417; available online: [https://doi.org/10.1890/0012-9658\(2006\)87\[2411:CBRINF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2411:CBRINF]2.0.CO;2) [inquiry: 23-05-2022].
- CABRERA, Ana R.; CLOYD, Raymond A. and ZABORSKI, Edmond R. «Development and reproduction of *Stratiolaelaps scimitus* (Acari: Laelapidae) with fungus gnat larvae (Diptera: Sciaridae), potworms (Oligochaeta: Enchytraeidae) or *Sancassania* aff. *sphaerogaster* (Acari: Acaridae) as the sole food source», *Experimental and Applied Acarology* 36 (2005), pp. 71-81; available online: <https://doi.org/10.1007/s10493-005-0242-x> [inquiry: 23-05-2022].
- CAO, Yu; OHWATARI, Nobu; MATSUMOTO, Takaaki; KOSAKA, Mitsuo; OHTSURU, Akira and YAMASHITA, Shunichi. «TGF-beta1 mediates 70-kDa heat shock protein induction due to ultraviolet irradiation in human skin fibroblasts», *Pflügers Archiv: European Journal of Physiology* 438, 3 (1999), pp. 239-344; available online: <https://doi.org/10.1007/s004240050905> [inquiry: 24-05-2022].
- CAPELLESSO, Elivane S.; SCROVONSKI, Kellin L.; ZANIN, Elisabete M.; HEPP, LUZ U.; BAYER, Cimélio and SAUSEN, Tanise L. «Effects of forest structure on litter production, soil chemical composition and litter-soil interactions», *Acta Botanica Brasílica* 30, 3 (2016), pp. 329-335; available online: <https://doi.org/10.1590/0102-33062016abb0048> [inquiry: 24-05-2022].
- CHOWN, Steven L. and NICOLSON, Sue W. «Water balance physiology», in S. L. Chown and S. W. Nicolson (eds.), *Insect physiological ecology*, New York (NY), Oxford University Press, 2004.
- CHOWN, Steven L. «Desiccation resistance in six sub-Antarctic weevils (Coleoptera: Curculionidae): humidity as an abiotic factor influencing assemblage structure», *Functional Ecology* 7 (1993), pp. 318-325.
- DAMUTH, John. «Population Density and Body Size in Mammals», *Nature* 290 (1981), pp. 699-700; available online: <https://doi.org/10.1038/290699a0> [inquiry: 24-05-2022].
- DELL, Anthony I.; PAWAR, Samraat and SAVAGE, Van M. «Systematic variation in the temperature dependence of physiological and ecological traits», *Proceedings of the National Academy of Sciences* 108, 26 (2011), pp. 10591-10596; available online: <https://doi.org/10.1073/pnas.1015178108> [inquiry: 24-05-2022].
- FAMIGLIETTI, James S.; RUDNICKI, John W. and RODELL, Matthew. «Variability in surface moisture content along a hillslope transect: Rattlesnake Hill, Texas», *Journal of Hydrology* 210 (1998), pp. 259-281; available online: [https://doi.org/10.1016/S0022-1694\(98\)00187-5](https://doi.org/10.1016/S0022-1694(98)00187-5) [inquiry: 24-05-2022].
- FISHER, Marta L. and VASCONCELLOS-NETO, João. «Development and life tables of *Loxosceles intermedia* Mello-Leitão 1934 (Araneae, Sicariidae)», *American Arachnological Society* 33, 3 (2005), pp. 758-766; available online: <https://doi.org/10.1636/S03-39.1> [inquiry: 24-05-2022].
- GREAR, Jason S. and SCHMITZ, Oswald J. «Effects of grouping behavior and predators on the spatial distribution of a forest floor arthropod», *Ecology* 86 (2005), 960e971; available online: <https://doi.org/10.1890/04-1509> [inquiry: 24-05-2022].

- GILLOOLY, James F.; CHARNOV, Eric L.; WEST, Geoffrey B.; SAVAGE, Van M. and BROWN, James H. «Effects of size and temperature on developmental time», *Nature* 417 (2002), pp. 70-73; available online: <https://doi.org/10.1038/417070a> [inquiry: 24-05-2022].
- GRIMM, Volker; AYLLÓN, Daniel and RAILSBACK, Steven F. «Next-Generation Individual-Based Models Integrate Biodiversity and Ecosystems: Yes We Can, and Yes We Must», *Ecosystems* 20 (2017), pp. 229-236; available online: <https://doi.org/10.1007/s10021-016-0071-2> [inquiry: 24-05-2022].
- GRIMM, Volker; BERGER, Uta; BASTIANSEN, Finn; ELIASSEN, Sigrunn; GINOT, Vicent; GISKE, Jarl; GOSS-CUSTARD, John; GRAND, Tamara; HEINZ, Simone K.; HUSE, Geir; HUTH, Andreas; JEPSEN, Jane U.; JØRGENSEN, Christian; MOOIJ, Wolf M.; MÜLLER, Birgit; PE'ER, Guy; PTOU, Cyril; RAILSBACK, Steven F.; ROBBINS, Andrew; ROBBINS, Martha M.; ROSSMANITH, Eva; RÜGER, Nadja; STRAND, Espen; SOUISSI, Sami; STILLMAN, Richard A.; VABØ, Rune; VISSER, Ute and DEANGELIS, Donald L. «A standard protocol for describing individual-based and anget-based models», *Ecological Modelling* 198 (2006), pp. 115-126; available online: <https://doi.org/10.1016/j.ecolmodel.2006.04.023> [inquiry: 24-05-2022].
- GUERNIER, Vanina; Hochberg, Michael E. and Guegan, Jean-François. «Ecology drives the worldwide distribution of human diseases», *Plos Biology* 2 (2004), pp. 740-746. available online: <https://doi.org/10.1371/journal.pbio.0020141> [inquiry: 24-05-2022].
- HADLEY, Neil F. *Water Relations of Terrestrial Arthropods*, London, Academic Press, 1994.
- HAEGEMAN, Bart and LOUREAU, Michel. «General relationships between consumer dispersal, resource dispersal and metacommunity diversity», *Ecology Letters* 17 (2014), pp. 175-184; available online: <https://doi.org/10.1111/ele.12214> [inquiry: 24-05-2022].
- HARRISON, Susan and TAYLOR, Andrew D. «Empirical evidence for metapopulation dynamics», in I. Hanski and M. E. Gilpin (eds.), *Metapopulation Dynamics: Ecology and Evolution*, London, Academic Press, 1997, pp. 27-42.
- HAWKINS, Bradford A.; FIELD, Richard; CORNELL, Howard V.; CURRIE, David J.; GUÉGAN, Jean-François; KAUFMAN, Dawn M.; KERR, Jeremy T.; MITTELBACH, Gary G.; OBERDORFF, Thierry; O'BRIEN, Eileen M.; PORTER, Eric E. and TURNER, John R. G. «Energy, water, and broad-scale geographic patterns of species richness», *Ecology* 84 (2003), pp. 3105-3117; available online: <https://doi.org/10.1890/03-8006> [inquiry: 24-05-2022].
- HERBST, Michael and DIEKKRUGER, Bernd. «Modelling the spatial variability of soil moisture in a micro-scale catchment and comparison with field data using geostatistics», *Physics and Chemistry of the Earth* 28 (2003), pp. 239-245; available online: [https://doi.org/10.1016/S1474-7065\(03\)00033-0](https://doi.org/10.1016/S1474-7065(03)00033-0) [inquiry: 24-05-2022].
- HOLT, Robert D. «Predation, apparent competition, and structure of prey communities», *Theoretical Population Biology* 12, 2 (1977), pp. 197-229; available online: [https://doi.org/10.1016/0040-5809\(77\)90042-9](https://doi.org/10.1016/0040-5809(77)90042-9) [inquiry: 24-05-2022].
- HOLT, Robert D. and LAWTON, John H. «The ecological consequences of shared natural enemies», *Annual Review of Ecology, Evolution, and Systematics* 25 (1994), pp. 495-520; available online: <https://doi.org/10.1146/annurev.es.25.110194.002431> [inquiry: 24-05-2022].
- HOLYOAK, Marcel; LEIBOLD, Matthew A.; MOUQUET, Nicolas; HOLT, Robert D. and HOOPES, Martha F. «Metacommunities: a framework for large scale community ecology», in M. Holyoak, M. A. Leibold and R. D. Holt (eds.), *Metacommunities: Spatial Dynamics and Ecological Communities*, Chicago, University of Chicago Press, 2005, pp. 1-31.
- JOHNSON, Frank H. and LEWIN, Isaac. «The growth rate of *E. coli* in relation to temperature, quinine and coenzyme», *Journal of Cellular Physiology* 28 (1946), pp. 47-75; available online: <https://doi.org/10.1002/jcp.1030280104> [inquiry: 24-05-2022].



- JOOSSE, Ellen N. G. and VELTKAMP, Els. «Some aspects of growth, moulting and reproduction in five species of surface dwelling Collembola», *Netherlands Journal of Zoology* 20, 3 (1970), pp. 315-328; available online: <https://doi.org/10.1163/002829670X00141> [inquiry: 24-05-2022].
- LEASE, Hilary M. and WOLF, Blair O. «Lipid content of terrestrial arthropods in relation to body size, phylogeny, ontogeny and sex», *Physiological Entomology* 36 (2011), pp. 29-38; available online: <https://doi.org/10.1111/j.1365-3032.2010.00767.x> [inquiry: 24-05-2022].
- LECRAW, Robin M.; KRATINA, Pavel and SRIVASTAVA, Diane S. «Food web complexity and stability across habitat connectivity gradients», *Oecologia* 176 (2014), pp. 903-915; available online: <http://www.jstor.org/stable/43671444> [inquiry: 24-05-2022].
- LENSING, Janet R. and WISE, David H. «Predicted climate change alters the indirect effect of predators on an ecosystem process», *Proceedings of the National Academy of Sciences of the United States of America* 103 (2006), pp. 15502-15505; available online: <https://doi.org/10.1073/pnas.0607064103> [inquiry: 24-05-2022].
- LEVINS, Richard. *Evolution in changing environments*, Princeton, Princeton University Press, 1968.
- «Some demographic and genetic consequences of environmental heterogeneity for biological control», *Bulletin of the Entomological Society of America* 15 (1969), pp. 237-240; available online: <https://doi.org/10.1093/besa/15.3.237> [inquiry: 24-05-2022].
- LEWIS, John G. E. «The life history and ecology of littoral centipede *Strigamia* (= *Scolioplanes*) *maritima* (Leach)», *Proceedings of the Zoological Society of London* 137 (1961), pp. 221-247; available online: <https://doi.org/10.1111/j.1469-7998.1961.tb05900.x> [inquiry: 24-05-2022].
- LIN, Wei-Ting; HSIEH, Chih-Hao and MIKI, Takeshi. «Difference in adaptive dispersal ability can promote species coexistence in fluctuating environments», *PLoS One* 8 (2013), e55218; available online: <https://doi.org/10.1371/journal.pone.0055218> [inquiry: 24-05-2022].
- LOUSTAU, Denis; HUNGATE, Bruce and DRAKE, Bert G. «Water, nitrogen, rising atmospheric CO<sub>2</sub>, and terrestrial productivity», in J. Roy, H. Mooney and B. Saugier (eds.), *Terrestrial global productivity*, San Diego (California), Academic Press, 2001, pp. 123-167.
- MACLAGAN, D. Stewart. «An ecological study of the “Lucerne flea” (*Sminthurus viridis*, LINN.)-I», *Bulletin of entomological research* 23, 1 (1932), pp. 101-145; available online: <https://doi.org/10.1017/S0007485300002601> [inquiry: 24-05-2022].
- MATZ, Jeannine M.; BLAKE, Michael J.; TATELMAN, Hal M.; LAVOI, Kathleen P. and HOLBROOK, Nikki J. «Characterization and regulation of cold-induced heat shock protein expression in mouse brown adipose tissue», *The American Journal of Physiology* 269 (1995), pp. 38-47; available online: <https://doi.org/10.1152/ajpregu.1995.269.1.R38> [inquiry: 24-05-2022].
- MAY, Robert M. *Stability and Complexity in Model Ecosystems*, vol. 1, Princeton Landmarks Biology, Princeton, Princeton University Press, 1974.
- MCCANN, Kevin S.; RASMUSSEN, Joseph B. and UMBANHOWAR, James. «The dynamics of spatially coupled food webs», *Ecology Letters* 8 (2005), pp. 513-523; available online: <https://doi.org/10.1111/j.1461-0248.2005.00742.x> [inquiry: 24-05-2022].
- MCCLUNEY, Kevin E. and SABO, John L. «Water availability directly determines per capita consumption at two trophic levels», *Ecology* 90 (2009), pp. 1463-1469; available online: <https://doi.org/10.1890/08-1626.1> [inquiry: 24-05-2022].

- MEI-FANG, Wen; HSIN, Chi; YING-XIAO, Lian; YU-HAO, Zheng; QING-HAI, Fan and MIN-SHENG, You. «Population characteristics of *Macrocheles glaber* (Acari: Macrochelidae) and *Stratiolaelaps scimitus* (Acari: Laelapidae) reared on a mushroom fly *Coboldia fuscipes* (Diptera: Scatopsidae)», *Insect Science* 26, 2 (2017), pp. 322-332; available online: <https://doi.org/10.1111/1744-7917.12511> [inquiry: 24-05-2022].
- MELGUIZO-RUIZ, Nereida; VERDENY-VILALTA, Oriol; ARNEDO, Miquel A. and MOYA-LARAÑO, Jordi. «Potential drivers of spatial structure of leaf-litter food webs in south-western European beech forests» *Pedobiologia* 55 (2012), pp. 311-319; available online: <https://doi.org/10.1016/j.pedobi.2012.06.003> [inquiry: 24-05-2022].
- MELIÁN, Carlos J.; KIVAN, Vlastimil; ALTERMATT, Florian; STARÝ, Petr; PELLISSIER, Loïc and DE LAENDER, Frederik. «Dispersal dynamics in food webs», *The American Naturalist*, 185, 2 (2015), pp. 157-168; available online: <https://doi.org/10.1086/679505> [inquiry: 24-05-2022].
- MONTSERRAT, Marta; SERRANO-CARNERO, Diego; TORRES-CAMPOS, Inmaculada; BOHLOOLZADEH, Mehdi; RUIZ-LUPIÓN, Dolores and MOYA-LARAÑO, Jordi. «Food web engineering: ecology and evolution to improve biological pest control», *Current Opinion in Insect Science* 47 (2021), pp. 125-135; available online: <https://doi.org/10.1016/j.cois.2021.06.006> [inquiry: 24-05-2022].
- MOYA-LARAÑO, Jordi; VERDENY-VILALTA, Oriol; ROWNTREE, Jennifer; MELGUIZO-RUIZ, Nereida; MONSERRAT, Marta and LAIOLO, Paola. «Climate change and eco-evolutionary dynamics in food webs», *Advances in Ecological Research* 47 (2012), pp. 1-80; available online: <https://doi.org/10.1016/B978-0-12-398315-2.00001-6> [inquiry: 24-05-2022].
- MOYA-LARAÑO, Jordi; BILBAO-CASTRO, José ROMÁN.; BARRIONUEVO, Gabriel; RUIZ-LUPIÓN, Dolores; CASADO, Leocadio G.; MONTSERRAT, Marta; MELIÁN, Carlos J. and MAGALHÃES, Sara. «Eco-evolutionary spatial dynamics: rapid evolution and isolation explain food web persistence», *Advances in Ecological Research* 50 (2014), pp. 75-143; available online: <https://doi.org/10.1016/B978-0-12-801374-8.00003-7> [inquiry: 24-05-2022].
- MURAKAMI, Yoshiteru. «The life history of *Bothropolys asperatus* Koch (Chilopoda, Lithobiidae)», *Zoologisches Magazin, Tokyo* 67 (1958), pp. 217-223.
- MURDOCH, Williams W. «Switching in general predators: experiments on predator specificity and stability of prey populations», *Ecological Monographs* 39, 4 (1969), pp. 335-354; available online: <https://doi.org/10.2307/1942352> [inquiry: 24-05-2022].
- «Stabilizing effects of spatial heterogeneity in predator-prey systems». *Theoretical Population Biology* 11 (1977), pp. 252-273; available online: [https://doi.org/10.1016/0040-5809\(77\)90028-4](https://doi.org/10.1016/0040-5809(77)90028-4) [inquiry: 24-05-2022].
- NATHAN, Ran; KLEIN, Etienne; ROBLEDO ARNUNCIO, Juan J. and REVILLA, Eloy. «Dispersal kernels: review», in J. Clobert, M. Baguette, T. G. Benton and J. M. Bullock (eds.), *Dispersal Ecology and Evolution*, Oxford, Oxford University Press, 2012, pp. 187-210.
- PILLAI, Pradeep; GONZALEZ, Andrew and LOREAU, Michel. «Metacommunity theory explains the emergence of food web complexity», *Proceedings of the National Academy of Sciences* 108 (2011), pp. 19293-19298; available online: <https://doi.org/10.1073/pnas.1106235108> [inquiry: 24-05-2022].
- RENAULT, David and CORAY, Yann. «Water loss of male and female *Alphitobius diaperinus* (Coleoptera: Tenebrionidae) maintained under dry conditions», *European Journal of Entomology* 101 (2004), pp. 491-494.



- REUMAN, Daniel C.; MULDER, Christian; BANASEK-RICHTER, Carolin; BLANDENIER, Marie-France C.; BREURE, Anton M.; DEN HOLLANDER, Henri; KNEITEL, Jamie M.; RAFFAELLI, Dave; WOODWARD, Guy and COHEN, Joel E. «Allometry of body size and abundance in 166 food webs», *Advances in Ecological Research* 41 (2009), pp. 1-44. available online: [https://doi.org/10.1016/S0065-2504\(09\)00401-2](https://doi.org/10.1016/S0065-2504(09)00401-2) [inquiry: 24-05-2022].
- ROFF, Derek A. *Evolutionary Quantitative Genetics*, New York, Chapman and Hall, 1997.
- ROONEY, Neil; MCCANN, Kevin; GELLNER, Gabriel and MOORE, John C. «Structural asymmetry and the stability of diverse food webs», *Nature* 442 (2006), pp. 265-269; available online: <https://doi.org/10.1038/nature04887> [inquiry: 24-05-2022].
- RUIZ-LUPIÓN, Dolores. *Una aproximación eco-evolutiva a las redes ecológicas mediante simulación*, doctoral thesis supervised by J. M. Gómez Reyes and J. Moya Laraño, Granada, Universidad de Granada, 2019; available online: <http://hdl.handle.net/10481/71852> [inquiry: 24-05-2022].
- RUIZ-LUPIÓN, Dolores; GÓMEZ REYES, José María and MOYA-LARAÑO, Jordi. «Mass-length allometry covaries with ecosystem productivity at a global scale», *Global Ecology and Biogeography* 29, 1 (2020), pp. 87-101; available online: <https://doi.org/10.1111/geb.13010> [inquiry: 24-05-2022].
- RUIZ-LUPIÓN, Dolores; PASCUAL, Jordi; MELGUISO-RUIZ, Nereida; VERDENY-VILALTA, Oriol and MOYA-LARAÑO, Jordi. «New litter trap devices outperform pitfall traps to study arthropod activity», *Insects* 10 (2019), p. 147; available online: <https://doi.org/10.3390/insects10050147> [inquiry: 24-05-2022].
- SAKAYORI, Hiroshi. «Postembryonic development of a neotenic pseudoscorpion, *Microbisium pygmaeum* (Ellingsen, 1907)», *Acta Arachnologica* 38 (1989), pp. 55-62; available online: <https://doi.org/10.2476/asjaa.38.55> [inquiry: 24-05-2022].
- SAVAGE, Van M.; GILLOOLY, James F.; BROWN, James H.; WEST, Geoffrey B. and CHARNOV, Eric L. «Effects of body size and temperature on population growth», *The American Naturalist* 163, 3 (2004), pp. 449-441; available online: <https://doi.org/10.1086/381872> [inquiry: 24-05-2022].
- SCHNEIDER, Florian D.; SCHEU, Stefan and BROSE, Ulrich. «Body mass constraints on feeding rates determine the consequences of predator loss», *Ecology Letters* 15 (2012), pp. 436-443; available online: <https://doi.org/10.1111/j.1461-0248.2012.01750.x> [inquiry: 24-05-2022].
- SCHUME, Helmut; JOST, Georg and KATZENSTEINER, Klaus. «Spatio-temporal analysis of the soil water content in a mixed Norway spruce (*Picea abies* (L.) Karst.)-European beech (*Fagus sylvatica* L.) stand», *Geoderma* 112 (2003), 273-287; available online: [https://doi.org/10.1016/S0016-7061\(02\)00311-7](https://doi.org/10.1016/S0016-7061(02)00311-7) [inquiry: 24-05-2022].
- SENGBUSCH, Howard G. and SENGBUSCH, Craig H. «Post-embryonic development of *Opia nitens* (Acarina: Oribatei)», *Journal of the New York Entomological Society*, Volume LXXVIII: 1970, pp. 207-214; available online: <https://www.jstor.org/stable/25006229> [inquiry: 24-05-2022].
- SNIDER, Richard M. «Growth and survival of *Polydesmus inconstans* (Diplopoda: Polydesmidae) at constant temperatures», *Pedobiologia* 22 (1981), pp. 345-353.
- SORENSEN, John T.; KINN, Donald N.; DOUTT, Richard L. and CATE, James R. «Biology of the mite, *Anystis agilis* (Acari: Anystidae): A California Vineyard Predator», *Annals of the Entomological Society of America* 69, 5 (1976), pp. 905-910; available online: <https://doi.org/10.1093/aesa/69.5.905> [inquiry: 24-05-2022].
- STITH, Brad M.; FITZPATRICK, John W.; WOOLFENDEN, Glen E. and PRANTY, Bill. «Classification and conservation of metapopulations: a case study of the Florida Scrub-Jay», in **D.**

- R. McCullough (ed.), *Metapopulations and Wildlife Conservation*, Washington D. C., Island Press, 1996, pp. 187-215.
- TAMADONI-NEZHAD, Alireza; MILANI, Ghazal A.; RAYBOULD, Alan; MUGGLETON, Stephen and BOHAN, David A. «Construction and validation of food webs using logic-based machine learning and text mining», *Advances in Ecological Research* 49 (2013), pp. 225-289; available online: <https://doi.org/10.1016/B978-0-12-420002-9.00004-4> [inquiry: 24-05-2022].
- VERDENY-VILALTA, Oriol and MOYA-LARAÑO, Jordi. «Seeking water while avoiding predators: moisture gradients can affect predator-prey interactions», *Animal Behaviour* 90 (2014), pp.101-108; available online: <https://doi.org/10.1016/j.anbehav.2014.01.027> [inquiry: 24-05-2022].
- WALSH, Mary I. and BOLGER, Thomas. «Effects of diet on the growth and reproduction of some Collembola in laboratory cultures», *Pedobiologia* 34 (1990), pp. 161-171.
- VERDENY-VILALTA, Oriol. *Algunas consecuencias ecológicas y evolutivas del movimiento anila para las interacciones bióticas*, doctoral thesis supervised by Jordi Moya Laraño, Granada, Universidad de Granada, 2013; available online: <http://hdl.handle.net/10481/29823> [inquiry: 24-05-2022].
- WILLIAMS, Richard J. and MARTINEZ, Neo D. «Simple rules yield complex food webs», *Nature* 404, 9 (2000), pp. 180-183; available online: <https://doi.org/10.1038/35004572> [inquiry: 24-05-2022].
- WILSON, David S. «Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection», *Ecology* 73 (1992), pp. 1984-2000; available online: <https://doi.org/10.2307/1941449> [inquiry: 24-05-2022].
- WINEMILLER, Kirk and POLIS, Gary. «Food Webs: What Can They Tell Us About the World?», in G. A. Polis and K. O. Winemiller (eds.), *Food Webs*, Boston (MA), Springer, 1996, pp. 1-22.
- WOLF, Blair O. and WALSBERG, Glenn E. «Thermal effects of radiation and wind on a small bird and implications for microsite selection», *Ecology* 77 (1996), pp. 2228-2236; available online: <https://doi.org/10.2307/2265716> [inquiry: 24-05-2022].

APPENDIX

(Supplementary Tables)

	<i>Harpactocrates sp.</i>	<i>Lithobius sp.</i>	<i>Geophilus sp.</i>	<i>Amara sp.</i>	<i>Microbisium sp.</i>	<i>Macrocheles sp.</i>	<i>Stratiolaelaps sp.</i>	<i>Anystis sp.</i>	Eupodidae	<i>Galumna sp.</i>	<i>Damaeus sp.</i>	<i>Onychiurus sp.</i>	<i>Tomocerus sp.</i>	<i>Sminthurus sp.</i>	<i>Polydesmus sp.</i>	Fungus 1	Fungus 2	Fungus 3	Beech litter
<i>Harpactocrates sp.</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
<i>Lithobius sp.</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
<i>Geophilus sp.</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
<i>Amara sp.</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
<i>Microbisium sp.</i>	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
<i>Macrocheles sp.</i>	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0
<i>Stratiolaelaps sp.</i>	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0
<i>Anystis sp.</i>	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Eupodidae	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0
<i>Galumna sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
<i>Damaeus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
<i>Onychiurus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
<i>Tomocerus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
<i>Sminthurus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
<i>Polydesmus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Fungus 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fungus 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fungus 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Beech litter	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

PREDATOR

PREY

Table S1. Predation matrix of original food web.

	<i>Harpactocrates sp.</i>	<i>Lithobius sp.</i>	<i>Geophilus sp.</i>	<i>Amara sp.</i>	<i>Microbisium sp.</i>	<i>Macrocheles sp.</i>	<i>Stratiolaelaps sp.</i>	<i>Anystis sp.</i>	Eupodidae	<i>Galumna sp.</i>	<i>Damaeus sp.</i>	<i>Onychiurus sp.</i>	<i>Tomocerus sp.</i>	<i>Sminthurus sp.</i>	<i>Polydesmus sp.</i>	Fungus 1	Fungus 2	Fungus 3	Beech litter
<i>Harpactocrates sp.</i>	1	0	0	1	1	0	1	0	1	1	0	1	0	1	0	0	0	0	0
<i>Lithobius sp.</i>	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0
<i>Geophilus sp.</i>	0	0	0	0	1	0	1	1	1	1	0	1	1	0	1	0	0	0	0
<i>Amara sp.</i>	1	0	0	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0
<i>Microbisium sp.</i>	0	0	0	0	1	1	1	0	0	0	1	1	0	1	1	0	0	0	0
<i>Macrocheles sp.</i>	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1	1	1	0
<i>Stratiolaelaps sp.</i>	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0
<i>Anystis sp.</i>	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1	1	1	0	0
Eupodidae	0	0	0	0	0	1	0	1	0	0	0	1	0	1	1	1	0	1	0
<i>Galumna sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
<i>Damaeus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
<i>Onychiurus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Tomocerus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Sminthurus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
<i>Polydesmus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Fungus 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fungus 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fungus 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Beech litter	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

PREDATOR

PREY

Table S2. Predation matrix of food web niche model 1.

	<i>Harpactocrates sp.</i>	<i>Lithobius sp.</i>	<i>Geophilus sp.</i>	<i>Amara sp.</i>	<i>Microbisium sp.</i>	<i>Macrocheles sp.</i>	<i>Stratiolaelaps sp.</i>	<i>Anystis sp.</i>	Eupodidae	<i>Galumna sp.</i>	<i>Damaeus sp.</i>	<i>Onychiurus sp.</i>	<i>Tomocerus sp.</i>	<i>Sminthurus sp.</i>	<i>Polydesmus sp.</i>	Fungus 1	Fungus 2	Fungus 3	Beech litter
<i>Harpactocrates sp.</i>	1	0	1	0	0	1	1	0	1	1	0	0	1	1	1	0	0	0	0
<i>Lithobius sp.</i>	1	0	1	0	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0
<i>Geophilus sp.</i>	1	0	0	0	0	0	0	1	0	1	0	1	1	0	1	0	0	0	0
<i>Amara sp.</i>	1	0	1	0	0	1	1	1	0	0	1	0	1	0	1	0	0	0	0
<i>Microbisium sp.</i>	0	0	0	0	1	0	1	1	1	1	1	1	0	1	1	0	1	1	0
<i>Macrocheles sp.</i>	0	0	0	0	0	1	1	1	0	0	0	1	1	0	1	1	1	1	0
<i>Stratiolaelaps sp.</i>	0	0	0	0	0	1	0	1	0	1	1	1	0	0	1	1	0	1	0
<i>Anystis sp.</i>	0	0	0	0	0	0	1	0	1	0	1	0	1	0	1	1	0	1	0
Eupodidae	0	0	0	0	0	0	1	0	1	1	1	1	1	0	0	1	0	1	0
<i>Galumna sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Damaeus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
<i>Onychiurus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
<i>Tomocerus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
<i>Sminthurus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
<i>Polydesmus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Fungus 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fungus 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fungus 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Beech litter	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

PREDATOR

PREY

Table S3. Predation matrix of food web niche model 2.



	<i>Harpactocrates sp.</i>	<i>Lithobius sp.</i>	<i>Geophilus sp.</i>	<i>Amara sp.</i>	<i>Microbisium sp.</i>	<i>Macrocheles sp.</i>	<i>Stratiolaelaps sp.</i>	<i>Anystis sp.</i>	Eupodidae	<i>Galumna sp.</i>	<i>Damaeus sp.</i>	<i>Onychiurus sp.</i>	<i>Tomocerus sp.</i>	<i>Sminthurus sp.</i>	<i>Polydesmus sp.</i>	Fungus 1	Fungus 2	Fungus 3	Beech litter
<i>Harpactocrates sp.</i>	0	1	0	1	1	1	1	1	1	1	1	0	1	1	0	0	0	0	0
<i>Lithobius sp.</i>	0	1	0	1	0	0	1	1	1	0	1	0	1	0	0	0	0	0	0
<i>Geophilus sp.</i>	0	1	0	1	1	0	1	1	1	1	0	1	0	0	0	0	0	0	0
<i>Amara sp.</i>	0	1	0	0	0	0	1	1	0	1	1	0	1	0	1	0	0	0	0
<i>Microbisium sp.</i>	0	0	0	0	1	0	1	1	0	0	0	1	0	1	1	0	0	0	0
<i>Macrocheles sp.</i>	0	0	0	0	0	1	0	1	0	1	0	0	0	1	1	0	1	1	0
<i>Stratiolaelaps sp.</i>	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	1	1	0	0
<i>Anystis sp.</i>	0	0	0	0	0	1	1	1	0	1	1	0	1	1	1	1	1	0	0
Eupodidae	0	0	0	0	0	1	1	1	1	0	1	0	1	1	1	0	1	0	0
<i>Galumna sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
<i>Damaeus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
<i>Onychiurus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Tomocerus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
<i>Sminthurus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
<i>Polydesmus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Fungus 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fungus 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fungus 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Beech litter	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

PREDATOR

PREY

Table S4. Predation matrix of food web niche model 3.