Climate Change and Eco-Evolutionary Dynamics in Food Webs

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Contents

Abstract

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

Past evolution determines the genetically determined available phenotypes in populations which affect ecological dynamics in communities, shaping in turn the selective pressures that further model phenotypes. Because an increase in temperature increases metabolic rates and encounter rates, climate change may have profound eco-evolutionary effects, possibly affecting the future persistence and functioning of food webs. We introduce a semi-spatially explicit individual-based model (IBM) framework to study functional eco-evolutionary dynamics in food webs. Each species embedded in the web includes 13 genetically determined and multidimensionally variable traits (the G matrix), 4 of which are flexible physiological and behavioural (personality) traits that respond to temperature. An increase in temperature and stronger correlation among traits leads to stronger trophic cascades but higher stochasticity, with higher probability of extinction for some trophic levels. A combination of the abiotic (temperature) and biotic (predators' presence/absence) matrix of selective agents (the O matrix) generates differential selection for activation energies for metabolic rates and several instances of correlational selection (selection in one trait changes with the levels of another), suggesting how global warming might favour certain trait combinations. Our results and the future prospects of this IBM approach open new avenues for climate change research.

1. INTRODUCTION

There is increasing evidence that global warming generates new interactions (or alters existing ones) within food webs and other ecological networks (Berg et al., 2010; Gilman et al., 2010; Tylianakis et al., 2008). However, little is known about the consequences of climate change for eco-evolutionary dynamics and their feedbacks with ecosystem processes. In eco-evolutionary dynamics, the ecological scenario sets the background within which evolution occurs, while ongoing evolution may affect in turn ecological dynamics by changing the frequencies of phenotypes involved in ecological interactions. With global warming, the novel

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

1.1. Climate change and ecological interactions

Climate change alters key abiotic factors, such as temperature and water availability, which in turn affect individual organisms and associated biological processes (Berg et al., 2010; Gilman et al., 2010; Tylianakis et al., 2008;

BOX 1

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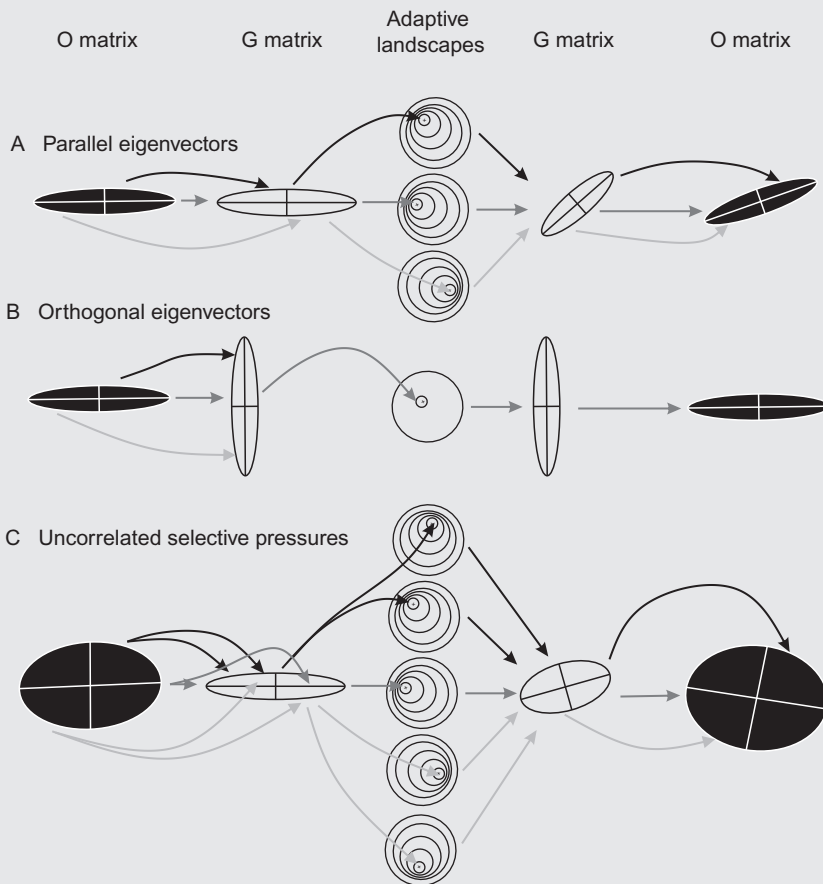
BOX 1   cont'd

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

Woodward et al., 2010a; Möllmann and Dieckmann 2012). Warming of the climate system is unequivocal and has generated a 100-year linear trend of $+0.74\,°C$, with a rise of minimum temperatures at a rate about twice as large as that of maximum temperatures (IPCC, 2007). This increase has triggered a broad range of biological responses, which are well documented at individual (life cycles), population (abundance trends) and species (range shifts) levels (Castle et al., 2011; Mintenback et al., 2012; Parmesan, 2006; Walther et al., 2002). Community- and ecosystem-level impacts, however, have been more difficult to quantify (but see Yvon-Durocher et al., 2010a, b), as they rarely consist simply of the sum of single species responses (Kareiva et al., 1993).

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

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

The relative importance of bottom-up and top-down mechanisms in controlling population dynamics is also influenced by the climate (Jeppesen et al., 2012; Meerhoff et al., 2012). Temperature may change the relative importance of these forces by affecting the metabolic rate of organisms and altering their population dynamics (Brown et al., 2004; Yvon-Durocher et al., 2010a,b). As a general rule, when temperature rises above the thermal tolerance of species and water is limiting, metabolic rate declines at all trophic levels, weakening both top-down and bottom-up effects (Hoekman, 2010). When this threshold is not reached, however, effects can be multifaceted. As warming accelerates metabolism, it may exaggerate top-down effects because faster metabolism of predators increases their growth, activity, consumption, and digestion rates (Brown et al., 2004). Nevertheless, the greater (net) metabolic requirements of higher trophic levels with respect to lower ones may render them more vulnerable to climate change (Petchey et al., 1999; Voigt et al., 2003). Warming may then exacerbate interactions among the higher trophic levels and enhance intra-guild predation, which in some instances may boost the

probability of extinction of some predator species and, in turn, simplify food web structure (Barton and Schmitz, 2009). Warming may also differentially affect how different traits respond to temperature (Englund et al., 2011; Rall et al., 2010; Thompson, 1978; Vucic-Pestic et al., 2011; Peck et al. 2012), with the balance among trait responses determining the chances of predator extinction with increased temperature.

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

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

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

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

et al., 2003; Pelletier et al., 2009; Schoener, 2011; Smith et al., 2011; Thompson, 2005; Wade and Kalisz, 1990; Whitham et al., 2006).

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

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

1.3. Eco-evolutionary dynamics and ecological networks

The eco-evolutionary perspective is being currently expanded to ecological networks (Fontaine et al., 2011; Guimarães et al., 2011; Hagen et al., 2012; Olesen et al., 2010) and even to ecosystem processes (Matthews et al., 2011;

Schmitz et al., 2008). Importantly, indirect ecological effects imply also the action of selective agents whose effects propagate through the network, with very important implications for the persistence of the interacting species and for coevolution, which in a network context cannot be simply understood as mere pair-wise interactions of co-adapting species (Guimarães et al., 2011; Olesen et al., 2010). This implies that eco-evolutionary dynamics can affect different trophic levels in different ways. In the past two decades, we have witnessed important advances in the modelling of predator–prey interactions and food webs in an evolutionary context, with some studies giving a central role to adaptation (e.g. Abrams, 2000; Abrams and Matsuda, 1997; Beckerman et al., 2006; Heckmann et al., 2012; Kimbrell and Holt, 2005; Kondoh, 2003, 2007; McKane and Drossel, 2005; Loeuille and Loreau, 2005; Loeuille and Loreau 2010; Petchey et al., 2008; Bell, 2007; Ellers et al., 2011). However, how adaptive evolution affects ecology in food webs, and vice versa, has only been considered explicitly very recently (Melián et al., 2011). In an original approach, Melián et al. (2011) successfully linked the evolutionary (Kimura, 1983) and the ecological (Hubbell, 2001) neutral theories. By explicitly considering variability on prey diversity (or intraspecific variation in the number of prey or connectivity), the authors were able to show that variability around species nodes could explain food web structure and the convergence between ecological and evolutionary dynamics.

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

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

2. Identify suits of traits that respond to natural selection (e.g. Agashe et al., 2011) and document the strength of selection on them in different ecological and climate change scenarios.

3. Identify traits that act themselves as selective agents, estimate how trait mean and variation in one population affect the strength of natural selection on another and document the impacts that climate change may have on the outcome of these interactions.

4. Identify whether the joint effect of different traits affects the above three points additively or multiplicatively.

5. In different climate change scenarios, document the fate and probability of persistence of functional alleles under eco-evolutionary dynamics in the face of both genetic drift and natural selection. Thus, this approach could serve to test whether the loss of genetically based functional diversity could have stronger impacts than the loss of functionally redundant taxa.

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

1.4. Individual-based models: modelling individual variation in ecology

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

ecosystem processes and properties such as primary productivity, decomposition, resilience or the fluxes of energy and nutrients (Bolnick et al., 2011; Hughes et al., 2008; Perkins et al., 2010; Reiss et al., 2011).

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

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

of the model which can be useful for making generalisations (Cantrell and Cosner, 2003; May, 2001; Murray, 2005; Schreiber et al., 2011).

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

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

1.5. The study of natural selection

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

$$R = h^2 s \qquad [1]$$

where R is the response to selection, h^2 is the narrow sense heritability due to the additive genetic variance (i.e. many loci each adding a small effect) and s is the selection differential, which is merely the arithmetic trait mean before selection substracted from the mean after selection. The multidimensional (multi-trait) version of the breeder's equation includes multiple functional traits at once and explicitly controls for the fact that neither natural selection acting on each trait nor the quantitative genetic basis of each trait is independent among traits (Lande, 1979):

$$\Delta \bar{z} = G\beta \qquad [2]$$

where $\Delta\bar{z}$ is a column vector which represents the change in the mean value of each trait, G is the variance–covariance genetic matrix (or G matrix), and β is the matrix of directional selection gradients which can be thought of as coefficients of directional natural selection acting orthogonally (i.e. independently) from each other on each trait. These selection gradients can be calculated by a multiple regression analysis in which an estimate of relative fitness (e.g. the fecundity of each individual divided by the average fecundity in the population) is the dependent variable, and the standardised $N(0,1)$ trait values the independent variables (Arnold and Wade, 1984a,b; Lande and Arnold, 1983). The G matrix involves negative and positive associations among traits (genetic correlations) and the extent to which traits are correlated with each other explains to what extent evolution is constrained by natural selection, as under strong correlation one trait will not be able to respond to selection without involving a response (either in the same or in the opposite direction) from other correlated traits (Box 1). Thus, the G matrix may be behind evolutionary trade–offs, although this is not necessarily always the case (Roff, 1997; Roff and Fairbairn, 2007). Importantly, G can be decomposed into its principal components, and the one with the highest eigenvalue, that is, that which explains most of the variance, has been called the "line of least resistance" (Box 1). This is because this axis summarises the partition of the variance of correlated traits which are most susceptible to being shaped by natural selection (Schluter, 1996, 2000). The amount of genetic correlation among traits is affected by linkage disequilibrium (non-random distribution of alleles across individuals) and by pleiotropic effects (i.e. genes affect more than one trait). However, as linkage disequilibrium is broken by recombination at each generation, what renders genetic correlations relatively stable is usually pleiotropy (Roff, 1997). We warn

that recent developments in genotype–phenotype relationships have shown that the G matrix is likely an oversimplification as a mechanism to explain phenotypic variation and trait correlations. For instance, the magnitude and direction of the G-matrix is frequently environmentally dependent (Sgró and Hoffmann, 2004). Further, abundant hidden genetic variation, which expresses only under stressful conditions and could be linked to the evolution of phenotype robustness (Espinosa-Soto et al., 2011), has been discovered recently (Le Rouzic and Carlborg, 2008; McGuigan and Sgró, 2009). Additionally, epigenetic mechanisms (e.g. changes in genome expression by nucleotide methylation) are gaining increasing prominence in the literature as alternative mechanisms of phenotypic variation (e.g. Greer et al., 2011; Pigliucci, 2008).

But, how does ecology affect the magnitude and pace of adaptive evolution? The ecological causes of natural selection (Wade and Kalisz, 1990) have been recently reemphasised in a new framework involving O (*oikos*) matrices (MacColl, 2011). An O matrix is a variance-covariance matrix of environmental values that act as selective agents (Box 1). When perfectly correlated (high off-diagonal values in O), two selective agents will act in the same direction across the geographic landscape (Box 1a), and their effects on phenotypic and genetic changes may be largely indistinguishable (i.e. the action of the different selection agents will be redundant across the geographic landscape). However, when the direction of the maximum eigenvalue (the eigenvector) in the G matrix matches that of the maximum eigenvalue of selective agents (Box 1a), a response to selection and a rapid climbing of diverse adaptive peaks across the geographic landscape will occur. When the angles between these two matrices are orthogonal (Box 1b), the peak of the adaptive landscape will be shorter while more difficult to reach. A third possibility occurs (Box 1c) when selective agents have low correlation, in which case diverse angles of selection can occur differently on different parts of the trait range. This can lead, for instance, to correlational selection, which can form multiple adaptive peaks in populations, and increase the chances for diversification across the geographic landscape. The extent to which selective agents are uncorrelated will add a multidimensional character to natural selection, and if we consider that selective agents can interact with each other this will affect selection gradients (MacColl, 2011). Thus, the long-term changes in the G-matrix due to natural selection can be better understood if we explicitly build these O-matrices of abiotic and biotic factors that act as selective agents. It is also true, however, that the nature of the G-matrix can affect the O-matrix,

especially the biotic component of the latter (Moya-Laraño, 2012). For instance, indirect genetic effects (Wolf et al., 1998), by which the genotype of an individual can affect the phenotype of another (i.e. inter-individual epistasis), can trigger feedbacks that can accelerate evolution. In complex (i.e. real) ecological networks, myriads of indirect genetic effects are possible and have been recently invoked to explain whole community heritability (Shuster et al., 2006), which in itself could be considered as an estimate of the potential for the long-term stability of selective agents. Therefore, to understand eco-evolutionary dynamics from an adaptive point of view, we must consider the reciprocal nature of the effects of G and O matrices (Box 1).

2. METHODS

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

Here, we introduce an IBM which, using the above framework in a food web context, can be used as a tool to investigate the impacts of climate change on eco-evolutionary dynamics and an associated ecosystem property: trophic cascades. In its first version, our IBM simulates cannibalistic predators (one species), shared prey (one species), and basal resources (one species) that are distributed in micro-patches of variable productivity which are distributed within a single micro-site. Both predators and prey have quantitative genetic basis for 13 traits and are able to move from micro-patch to micro-patch using a set of adaptive rules. Some traits are plastic to temperature and variation was introduced by implementing genetic variation in traits for plasticity (Fig. 1, Appendix). Furthermore, the model incorporates some of the latest paradigms in predator–prey interactions, such as predator-induced stress affecting metabolic rates and assimilation efficiencies (Hawlena and Schmitz, 2010a) by explicitly affecting state variables depending on the previous encounter with predators (see the Appendix). Figure 2 shows the flow diagram describing the algorithm. Although the model simulates a 3-species food chain, given that predators feed on each other, there are in essence four trophic levels. In addition, the initial diversity of individuals and alleles and the great diversity of potential interactions simulate an individual-based complex food web, in which different alleles and phenotypes affect others both directly and indirectly (through the network) and both consumptively (predation) and non-consumptively (affecting searching and antipredatory behaviours). Thus, although not done here, an individual-based ecological network of interactions, as well as an
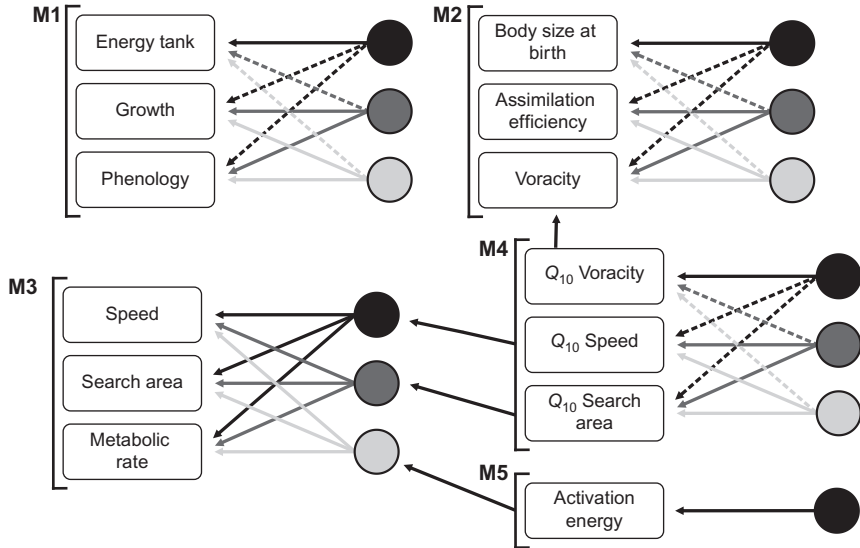
Figure 1 Quantitative genetic effects on 13 traits as implemented in the IBM (see Table 1 for a description and range of the traits). Traits are scattered in five modules (M1–M5) which are genetically independent of each other. The degree of correlation among traits within the module, and thus the level of phenotypic integration across individuals, may vary among modules. The filled circles represent groups of alleles that have an effect on the traits towards which the arrows point. Plain arrows represent positive pleiotropic effects, while dashed arrows represent negative pleiotropic effects (genetic trade-offs). Modules M4 and M5 represent genetic variation for plasticity by which they epistatically affect the traits towards which they point. The epistatic effect of the pointing traits for plasticity depends on temperature and variability in these plasticity traits determines the shape and magnitude of the reaction norm of the pointed traits (see Appendix for further details).

allele-to-allele ecological network reflecting indirect genetic effects (Wolf et al., 1998), could be drawn by simply recording all the consumptive and non-consumptive interactions occurring during the simulation.

2.2. The aim of the simulations

Table 1 shows a list and description of traits along with the range used in the present simulations. The outputs generated by the current version of *mini-AKIRA* (*mA*) include enough information to document the drivers of eco-evolutionary feedbacks in detail (e.g. how the G matrix affects the O matrix and vice versa, Box 1). However, for the sake of simplicity, responses to selection across generations ($\Delta \bar{z}$ in (Eq. 2)) were not analysed here.
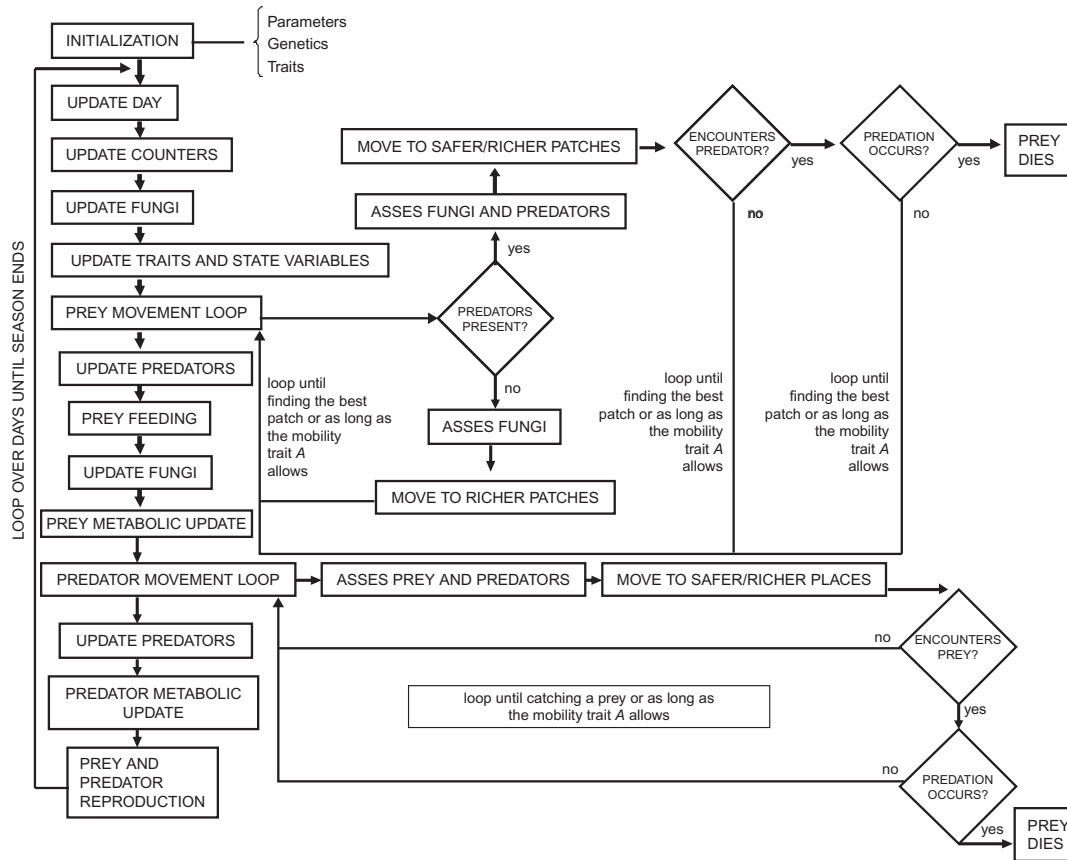
Figure 2 Flowchart of the individual-based model. Each time step is one day and simulations were run for 120 days starting with 500 prey and 50 predators.

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

Module	Trait name	Abbreviations	Description	Range for prey	Range for predators	r sign[a]
1	Energy tank	tank_ini, ε_0	Proportion of body mass devoted to maintenance, growth and reproduction	0.3125–0.4375	0.3125–0.4375	−,−
1	Growth	g	Linear growth ratio from instar to instar	1.0325–1.0775	1.0575–1.1525	−,+
1	Phenology	pheno	Birth date (in days)	4–8	5–9	−,+
2	Body size at birth	size_ini, B_0	Fixed, structural body mass at birth (in mg)	0.00875–0.01175	0.01575–0.01875	−,−
2	Assimilation efficiency	assim	Proportion of ingested food that is converted to own mass	0.75–0.85	0.75–0.85	−,+
2	Voracity	V	Scaling coefficient of 0.1 M ^V, where M is body mass	0.625–0.675	0.625–0.675	−,+
3	Speed	S	Scaling coefficient of 4 M ^S, where M is body mass	0.15–0.25	0.15–0.25	+,+
3	Search area	search_area, m	Scaling coefficient of M ^m, where M is body mass	0.25–0.35	0.15–0.25	+,+
3	Metabolic rate	met_rate, a	Scaling coefficient for the mass dependence of metabolic rate	0.725–0.775	0.625–0.675	+,+
4	Q10 on voracity	vorQ10	Q10 on V	2.5–3.5	2.5–3.5	−,−
4	Q10 on speed	spdQ10	Q10 on S	1.75–2.25	1.75–2.25	−,+
4	Q10 on search area	srchQ10	Q10 on m	1.75–2.25	1.75–2.25	−,+
5	Activation energy on metabolic rate	E_{met}	Activation energy of metabolic rate (in electron-volts)	0.6–0.7	0.35–0.45	

[a]Sign of the additive genetic correlation with the other two traits in the module, left sign corresponds to the first accompanying trait in the module as read from top to bottom, right sign to the second.

To explore how rising temperatures may affect eco-evolutionary dynamics in food webs, as well as how they affect associated ecosystem processes such as trophic cascades, we simulated eco–evolutionary food web dynamics for one season of 120 days at environmental temperatures of $T = 16$, 20 or 25 °C. We used 16 °C as the lowest temperature instead of 15 °C because this was the only way to produce inter-individual variability around Q values (Appendix). We ran five replicates per simulation, each of which can be interpreted as a within-season isolated micro-community where natural selection occurs locally (i.e. without migration among micro-sites) in each micro-site. Each simulation/micro-site started with 50 predators (mites) and 500 prey (collembola) which were randomly distributed in micro-patches arranged across a unidimensional micro-site (Appendix). As each simulation is a micro-site in real space, we need to neither assume nor explore local ecological and evolutionary stabilities. The present framework assumes that eco-evolutionary stability may occur at a scale across simulated communities in the different micro-sites, which we will be able to explore when migration among –micro-sites- communities is included in future versions of the model. Here, we merely focus in the outcome variability and the general patterns emerging among replicates and consider that the longer the three-species community persists (i.e. there is biomass present for the three trophic levels) in a given micro-site, the more that particular micro-site will contribute to the overall stability of the system across the landscape. To estimate the magnitude of trophic cascades, we ran the same simulations (replicates) both with and without predators. This also allowed us to explore two biotic environments that affected selection on prey: one driven only by intraspecific competition (without predators) and another in which both competition and predation were included as selective agents acting upon prey. Therefore, we also constructed a bi-dimensional O matrix in the following bi-factorial simulation experiment, which included 5 replications of each O matrix combination: predators present at 16, 20 and 25 °C and predators absent at 16, 20 and 25 °C. The two axes of the O matrix (predators and temperature) were perfectly orthogonal (uncorrelated), thus approximating the scenario of Box 1c. In order to explore how genetic correlations and the G-matrix could constrain eco-evolutionary dynamics, we further replicated the simulations for two levels of genetically based (or genotypic) phenotypic integration ($\rho = 0.1$ or 0.9). The temperatures chosen were within those recorded in the beech forest leaf-litter during the summer (Melguizo-Ruiz et al. 2012 *in press*), where the simulated animals live (Ehnes et al., 2011). This involves

temperatures that are just below optimal for most functional traits (Dell et al., 2011; Englund et al., 2012), thus we are simulating only the rising part of the unimodal relationship between temperature and trait performance. Simulating the falling part (i.e. when trait performance decreases as temperature increases beyond a threshold) is far more challenging because heat shock proteins and water loss (Chown, 2011) may need to be considered.

2.3. Statistical analyses

2.3.1 Testing for differences in selection across environments

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

"effects", which is most appropriate to depict in two-dimensional space the nature of interaction terms from complex models, even for curvilinear patterns of interactions (Fox, 2003).

2.3.2 Estimating selection gradients in two contrasting environments

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

dimensional space, thus allowing easy interpretation of the type of selection. Indeed, when patterns of selection appeared to be complex (e.g. when a trait had significant interactions with other traits as well as significant quadratic terms), we applied splines (R library "splines", function "bs") to the trait and plotted their interaction with some of the other traits. Directional selection appears as a linear fit, stabilising selection is described by a hump-shaped curve (indicating maximum fitness at intermediate trait values) and disruptive selection with a U-shaped curve (indicating maximum fitness for extreme phenotypes of that particular trait).
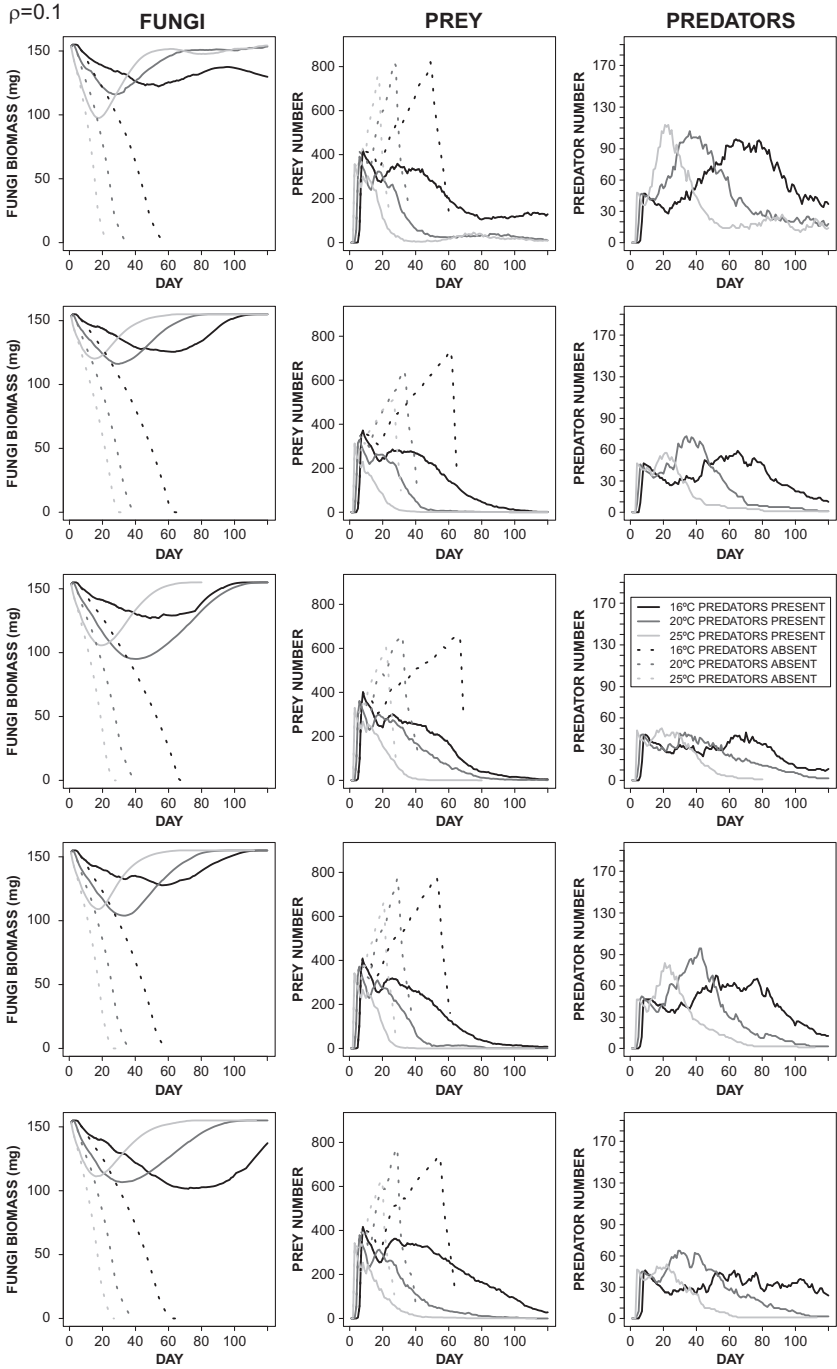
3. RESULTS

3.1. From evolution to ecology

3.1.1 Trophic cascades

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

ρ=0.1

FUNGI — FUNGI BIOMASS (mg) vs DAY

PREY — PREY NUMBER vs DAY

PREDATORS — PREDATOR NUMBER vs DAY

Legend:
16ºC PREDATORS PRESENT
20ºC PREDATORS PRESENT
25ºC PREDATORS PRESENT
16ºC PREDATORS ABSENT
20ºC PREDATORS ABSENT
25ºC PREDATORS ABSENT
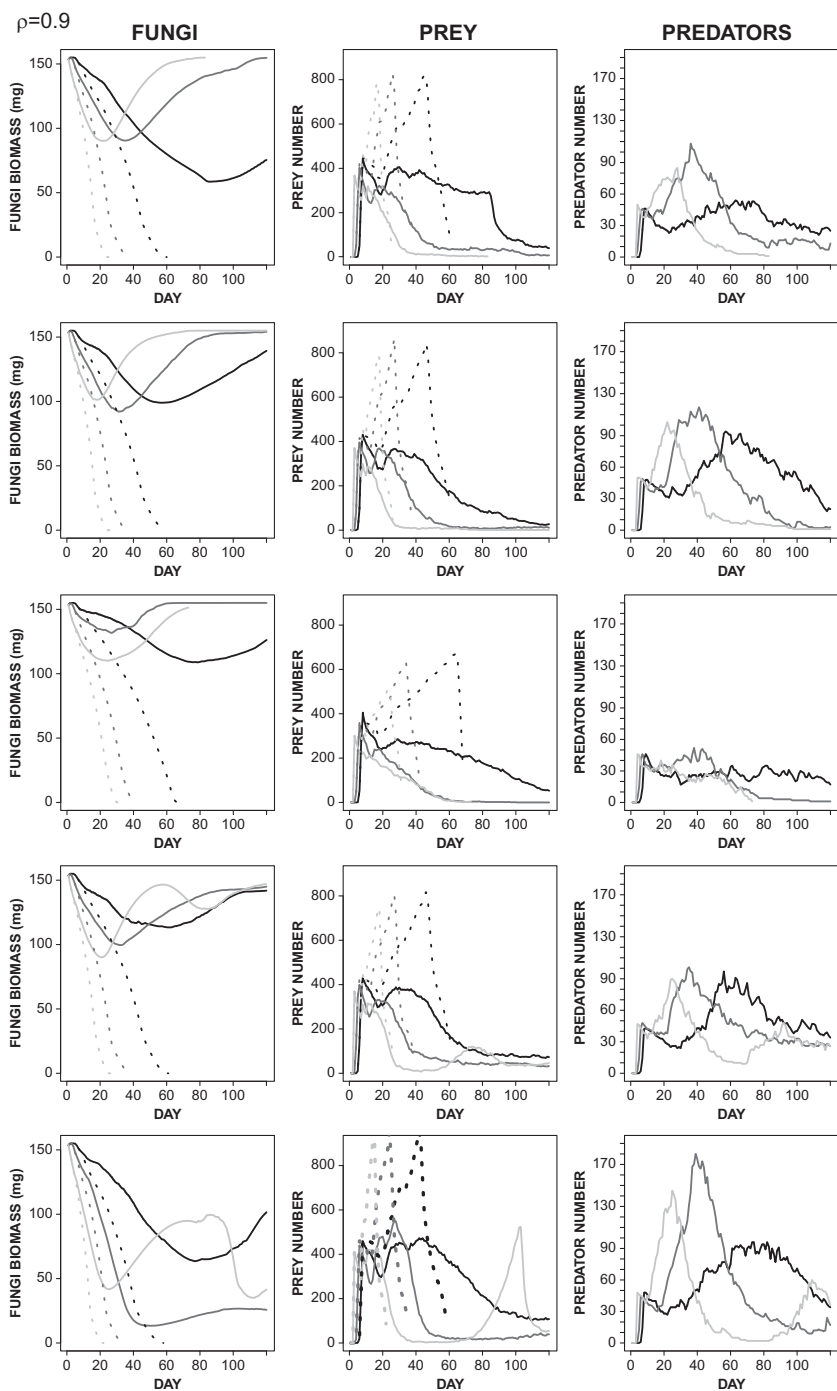
Figure 3 Fungi (basal resource, left column), prey (middle) and predator (right column) population dynamics for the 120 days of simulation. Five replicates for each of two genetic correlation levels among the traits ($\rho = 0.1, 0.9$) are shown. There was a clear predator–prey–fungi cycle in the last replicate ($\rho = 0.9$). Simulations ran for a number of prey generations ranging from 4 to 21 and 4 to 8 predator generations. The maximum number of generations was achieved in the last replicate ($\rho = 0.9$) at the warmer temperature. Dynamics in fungi not leading to actual extinctions are truncated intentionally at the time predators went extinct.

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

3.1.2 Encounter rates

Across replicated simulations, prey tended to encounter more predators *per capita* during their lifetime as temperature increased (Fig. 4). However, this depended on the G-matrix as, although the relationship between temperature and encounter rates was not linear for both levels of trait correlation, there was a clearer peak with higher encounter rates at intermediate temperatures when traits were correlated ($\rho = 0.9$). As expected, lifespan was shorter at warmer temperatures, decreasing by ca. 50% from the lowest to the highest temperatures. After eliminating the effect of lifespan, we detected a linear pattern for the effect of temperature on encounter rates (day^{-1}), which indicates higher predation risk at higher temperatures.

From the point of view of the predator, the pattern was very similar (Fig. 5), with the exception that the trend for lifetime encounters went from non-linear when traits were uncorrelated to linear when they were correlated. Therefore, despite a trend for shorter life spans at warmer temperatures, the number of encounters (not just the rate) was higher.
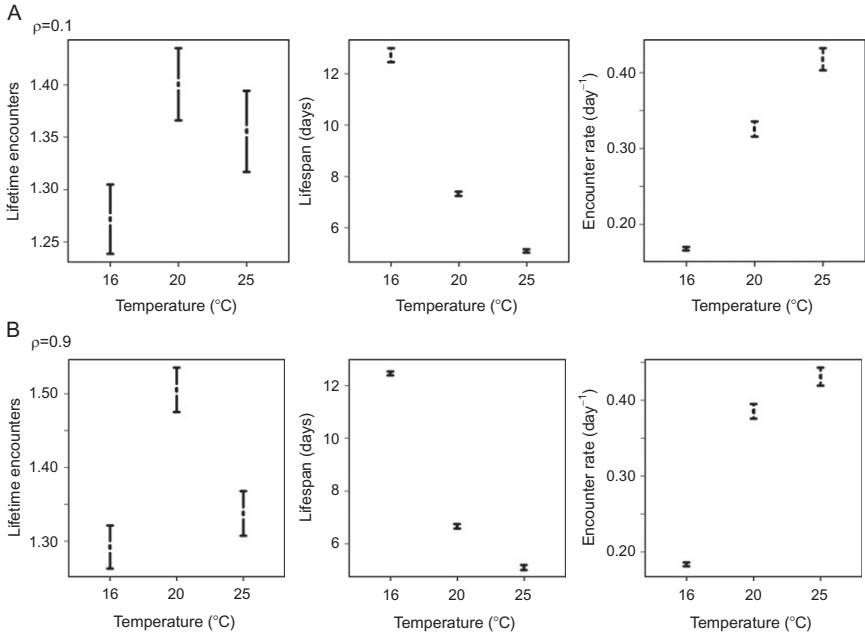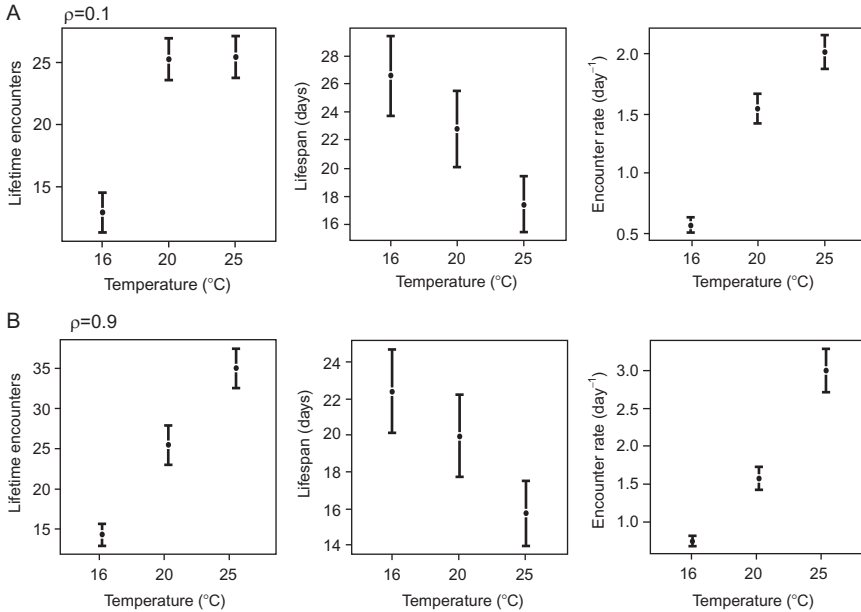
Figure 5 Lifetime number of encounters for predators (left panels), lifespan (mid panels) and encouter rates (day^{-1}, right panels) with prey for two levels of correlation among traits.

3.2. From ecology to evolution

3.2.1 Testing for differences in selection across environments

Differential directional selection across environments occurred in more traits (more three-way highly significant interaction terms entered the final model) when the G-matrix was less constraining ($\rho = 0.1$) than when traits were highly genetically correlated to each other ($\rho = 0.9$). We detected highly significant differences in selection across the two-environment combinations for 10 traits, while only 5 were found for high correlation values (Table A1). Figure 6 shows the three-way interaction (R library "effects"— Fox, 2003) for the trait *growth* (growth ratio). Selection for smaller growth ratios was stronger at cooler temperatures only when predators were absent.

3.2.2 Estimating selection gradients in two contrasting environments

In general, selection gradients were weak ($< |0.1|$, Table A2), although they were stronger ($> |0.1|$) when the traits were strongly correlated to each other ($\rho = 0.9$). Strong ($> |0.5|$) selection gradients were also found in the activation energy for metabolic rate. When genetic correlation was strong, we also

Figure 6 Environment (O matrix) × *Growth* interaction in fitness showing differences in the strength of directional selection for the trait *Growth* ratio across environments. Steeper relationships indicate stronger selection favouring smaller growth ratios.
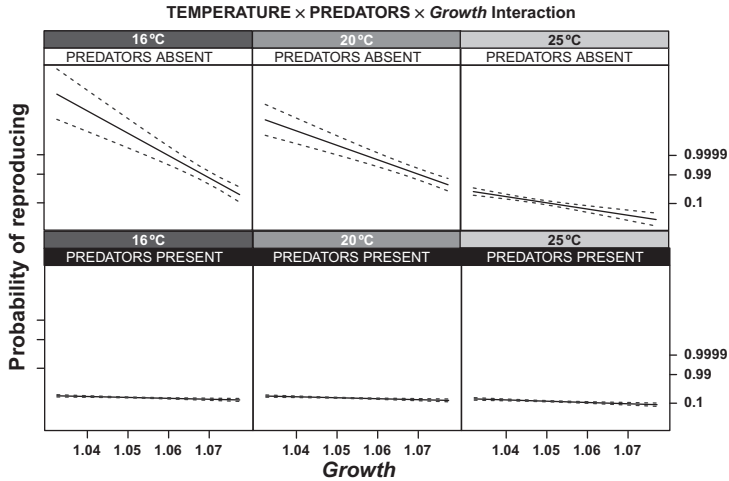
found some emerging trait combinations with sufficiently strong selection gradients $(>|0.1|)$ for traits that were previously uncorrelated, such as for activation energies and several other functional traits (Table A2). Remarkably, in the least stressful environment (low temperatures without predators), we found only 6 examples of sufficiently strong correlational selection $(>|0.1|)$, whereas 15 cases were found in stressful environments, at high temperatures with predators. We mention some of these trait combinations as examples: for instance, at 16 °C without predators, the plastic response for temperature-dependent mobility (srchQ10) interacted with selection on assimilation efficiency (Table A2). Visual inspection of the interaction plot (R library "effects", Fig. 7A) shows how the extreme values for both traits in combination (either both high or both low) lead to the highest relative fitness. Also, at 25 °C with predators present, phenology interacted with the temperature-dependent voracity (vorQ10, Table A2). Again, visual inspection of the interaction plot (Fig. 7B) showed that early birth combined with lower plasticity for voracity or late birth with high plasticity gave the highest fitness combinations. Another example was the interaction of temperature-plasticity for searching area (srchQ10) with growth ratio (Table A2). Selection favoured the extremes, with lowest growth ratios being favoured together with low temperature-plasticity for searching area, and vice versa (Fig. 7C). In general, the combination of traits and the magnitude of the selection gradients were very different for the two environments (Table A2), suggesting a

A   16 °C PREDATORS ABSENT

B   25 °C PREDATORS PRESENT

C   25 °C PREDATORS PRESENT

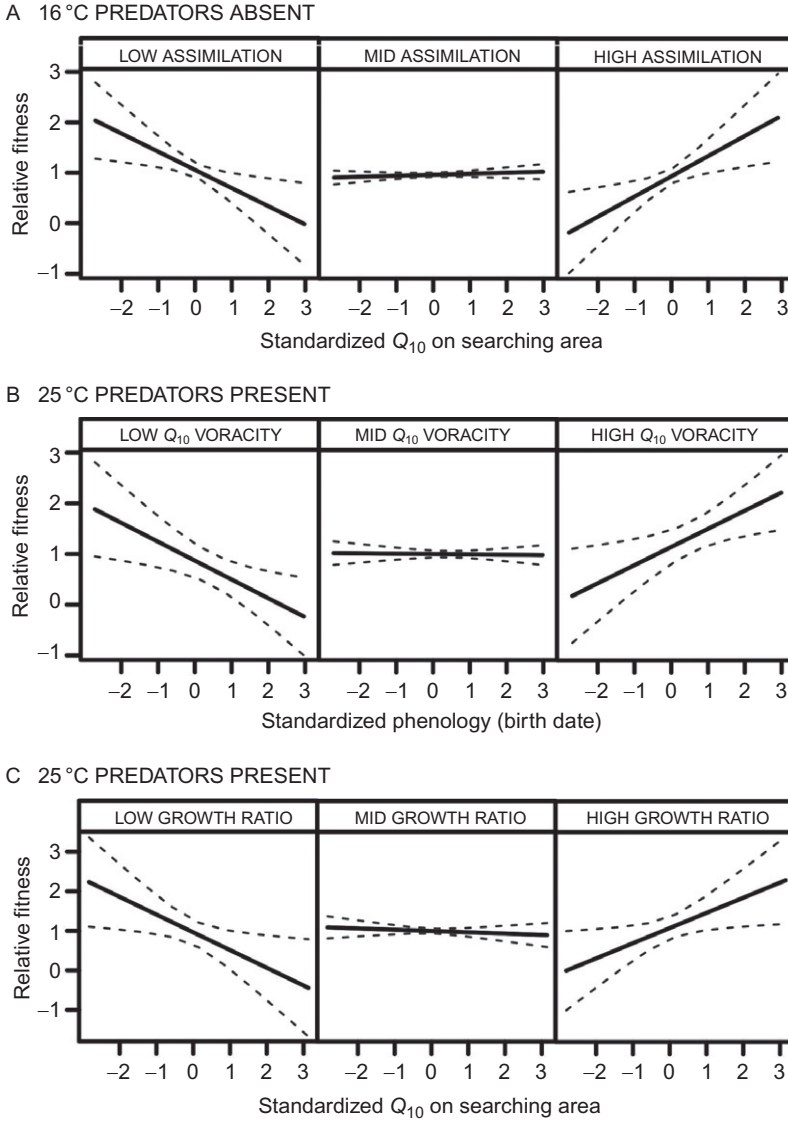**Figure 7** Examples of correlational directional selection on functional traits in two contrasting environments. (A) Assimilation efficiency $\times Q_{10}$ on search area at cooler temperatures with predators absent. (B) Q_{10} on voracity $\times$ phenology (emergence date) at warmer temperatures with predators present. (C) Growth ratio $\times Q_{10}$ on search area at warmer temperature with predators present.

role for both abiotic (temperature) and biotic (predator presence) factors, and the interaction between them. Traits for temperature–adjusted activity were generally more frequently significant (i.e. they were more likely under selection) in the models at warmer temperatures with predators.

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

4. DISCUSSION

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

A   *Phenology* at 16 °C PREDATORS ABSENT

B   *Growth* at 25 °C PREDATORS PRESENT

C   *Voracity* at 25 °C PREDATORS PRESENT
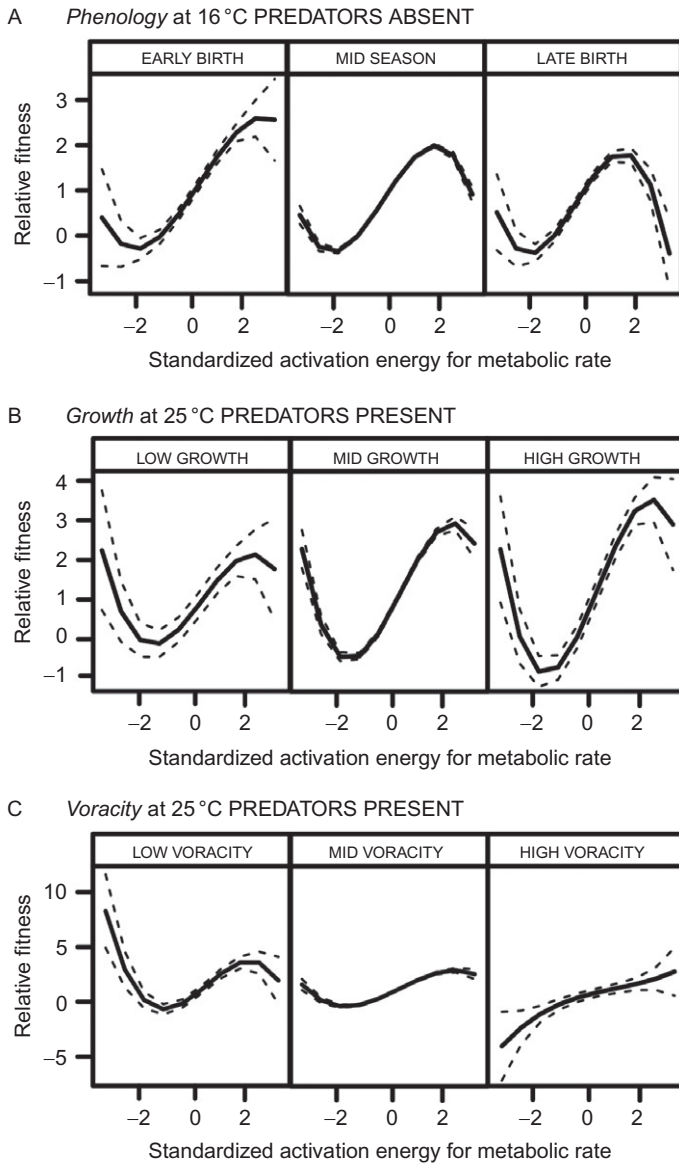
Figure 8 Complex fitness surfaces showing non-linear correlational selection for activation energies of metabolic rate in contrasting environments. (A) At cooler temperatures without predators, and depending on emergence date (phenology) selection on activation energies can go from directional (early emergence, left panel) to (hump-shaped) stabilising (late emergence, right panel). (B) At warmer temperatures with predators, and depending on the magnitude of the growth ratio, the depth of the disruptive selection (U-shaped) valley increases from low growth ratios (left panel) to high growth ratios (right panel) indicating an increase in the strength of disruptive selection on activation energies for metabolism with growth ratio. (C) At warmer temperatures with predators, and depending on the level of voracity, selection on activation energies can go from (U-shaped) disruptive (low voracity coefficient, left panel) to (lineal) directional (high voracity coefficient, right panel). Note that a high coefficient for voracity means lower voracity (see the Appendix).

to increasing our knowledge of how suites of traits evolve and how diver-sification rates change across climatic gradients.

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

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

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

4.2. Correlational selection, diversification and ecosystem resilience

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

Most importantly, by simulating all the combinations for two orthogonal axes of variation in the O matrix (temperature and predator presence/absence), we found that correlational selection was more prevalent (more cases of moderately strong selection) in biotically rich environments: that is, those in which prey had to deal with predators, and at higher temperatures (where encounter rates were higher), as is likely in the tropics. For correlational selection to be a source of new heritable trait combinations to accelerate diversification, however, selection pressures need to be persistent in sign and magnitude for many generations. This reflects the time needed to allow genome reorganisations to occur, as at each generation recombination breaks the linkage disequilibrium achieved by correlational selection (McKinnon and Pierotti, 2010; Sinervo and Svensson, 2002).

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

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

That evolution by natural selection can occur at ecological timescales and that this selection can be diversifying and strong has enormous implications for climate change research. Leaving mutation rates apart, if there is enough multidimensional genetic variability in species embedded in food webs, a gradual increase in temperature from year to year could be buffered by dispersal and range shifts, as well as plastic responses and responses to natural selection from the new selective pressures imposed by warming (Berg et al., 2010; this paper). In addition, if the role of correlational selection increases with temperature and interaction rates, this may stimulate adaptive evolution over ecological timescales. This is of central importance for food webs, as recent work (Rall et al., 2010; Vucic–Pestic et al., 2011) has shown that although predators may increase feeding performance (e.g. ingestion rates, handling time) with temperature metabolic rates do still increase at a rate that is comparatively higher. This can suppress predator survival and may cause extinctions, as recently demonstrated experimentally (Barton and Schmitz, 2009). However, even though on average predator populations would decrease in fitness with rising temperatures,

correlational selection could favour those phenotypes which display a better balance between the traits involved in trophic interactions and metabolic rate, finally rescuing the population exposed to warming. That activation energies for metabolism display correlational selection with few other functional traits and that the fitness surface for activation energies changes depending on the environment and the level of the trait with which it interacts suggest these possibilities are worth further exploration.

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

We illustrated the joint effects of temperature and predator presence/absence upon prey with the example of the growth trait, which measures the linear increase in fixed body size between instars. While there was no clear pattern of temperature affecting growth when predators were present, selection favouring smaller growth ratios was stronger (steeper slopes) at cooler temperatures when predators were absent. This could mean that for the smallest animals, when there is no predation risk, early reproduction at lower temperatures is favoured over the benefit of having larger body sizes. This contrasts with the widespread idea that global warming (higher temperature) leads to smaller body sizes (Daufresne et al., 2009; O'Gorman et al., 2012; Sheridan and Bickford, 2011). However, selection gradients are by definition partial effects on fitness, and when the effects of traits that are directly affected by temperature are considered via multiple regression (including complex correlational selection with activation energy for metabolic rate, Fig. 8B), the net effect of selection and the overall intergenerational response to it will not necessarily favour evolving smaller body sizes at cooler temperatures. Furthermore, developmental rates are more closely dependent on temperature than are growth rates (Forster et al., 2011). Evolution can potentially target either a given body size or an age at maturation both of which can have a quantitative genetic basis and can be genetically correlated to each other (Roff, 2002). For instance, artificial selection experiments show that selecting for small adult body sizes leads to shorter maturation ages (Teuschl et al., 2006). However, selection for larger body sizes, in addition to longer developmental times, leads to higher growth rates (Teuschl et al., 2006). Thus, the combination of genetic variation in several traits is what explains, in turn, the genetic variation of the associated growth and development rates. Therefore, as temperature affects growth and development rates, if evolution targets early development (and timing of maturation), for instance,

in short–lasting environments such as temporal ponds, higher temperatures will lead to adults of smaller body sizes because in that time interval metabolic constraints will allow lower net growth. However, if body size is targeted by natural selection (i.e. larger is better, for instance, by enhancing fecundity), and unless compensated by other traits or if there is predatory pressure (this paper), higher temperatures and higher energetic demand will make maturation times longer for the same targeted body size, leaving population body size eventually unaffected. Distinguishing between the two contrasting targets of selection (maturation timing vs. maturation size) will involve considering moulting time (developmental rate) as an additional evolvable trait. Here, in the absence of predators, our competitive environments were short lasting because populations crashed very quickly (near day 60 Fig. 3). Thus, early reproduction with smaller body sizes would have been favoured more likely in warmer environments, which lasted for shorter. However, as we did not simulate the maturation time trait *per se*, selection in our simulations favoured smaller growth ratios and thus smaller maturation sizes. Why selection for growth ratio was stronger in cooler environments could merely depend on the longer duration of the cool versus the warm environment and the balance between growing more slowly, the duration of the system and selection on other traits. A close look to the patterns of the timing of reproductive events and death dates (not shown) shows that there is a stronger peak of death early in life at warmer versus cooler temperatures when predators are not present, likely suggesting stronger selection on relevant traits other than growth rates at warmer temperatures which could explain the weaker selection in growth ratios.

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

We found strong selection ($\beta > |0.65|$) for the activation energy of metabolism, but not for other traits. When the nature of this correlational selection was disentangled by plotting the fitness surfaces of activation energies for different values of other traits, we found evidence for directional, stabilising or disruptive selection. This is despite the activation energy not being correlated with any other trait in the G-matrix. This contrasts with the empirical evidence and constraints put forward by the MTE, which suggests a value for activation energies for metabolism between 0.6 and 0.7, and high conservatism across the tree of life and different ecosystems (Brown et al., 2004; Yvon–Durocher et al., 2012). Thus, although natural

selection could produce different optima for activation energies far away from the 0.6–0.7 range, biochemical and physiological constraints seem to impede adaptive evolution. A recent study, however, has found abundant variability in activation energies for metabolism, both across and within species (Ehnes et al., 2011), so there may be more scope for adaptive evolution in metabolic activation energies than previously assumed. Artificial selection experiments in which the experimenter selects for higher or lower activation energies at different temperatures would confirm whether the evolution of adaptive activation energies is possible, which would represent a form of adaptive phenotypic plasticity.

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

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

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

predator presence or absence (Table A1), climate change can affect the evolution of plasticity in animal behaviour or "personalities".

4.7. Future directions

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

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

We can define food web engineering (FWE) as an extension of biological pest control that integrates general theory in community ecology and evolutionary biology into specific agricultural systems, where communities are managed as a whole. When applying FWE for pest management, strategies will need to be designed to artificially alter those interactions with potential to influence the wider community (Fig. 9). In agro-ecosystems exposed to rapid climate change, it will be necessary to determine the fitness-related environmentally driven traits that should be artificially selected in predators to maximise trophic cascades (Fig. 9). Combining natural (or quasi-natural) selection experiments, in which food webs are left to evolve (Belliure et al., 2010; Chippindale, 2006; Kassen, 2002), could be used to parameterise the whole eco-evolutionary dynamic process. IBM models could then be used to simulate the eco-evolutionary responses of communities to heat stress, as a possible basis for predicting and managing the effects of warming on pest biological control, when applying FWE to specific agricultural systems (Fig. 9).
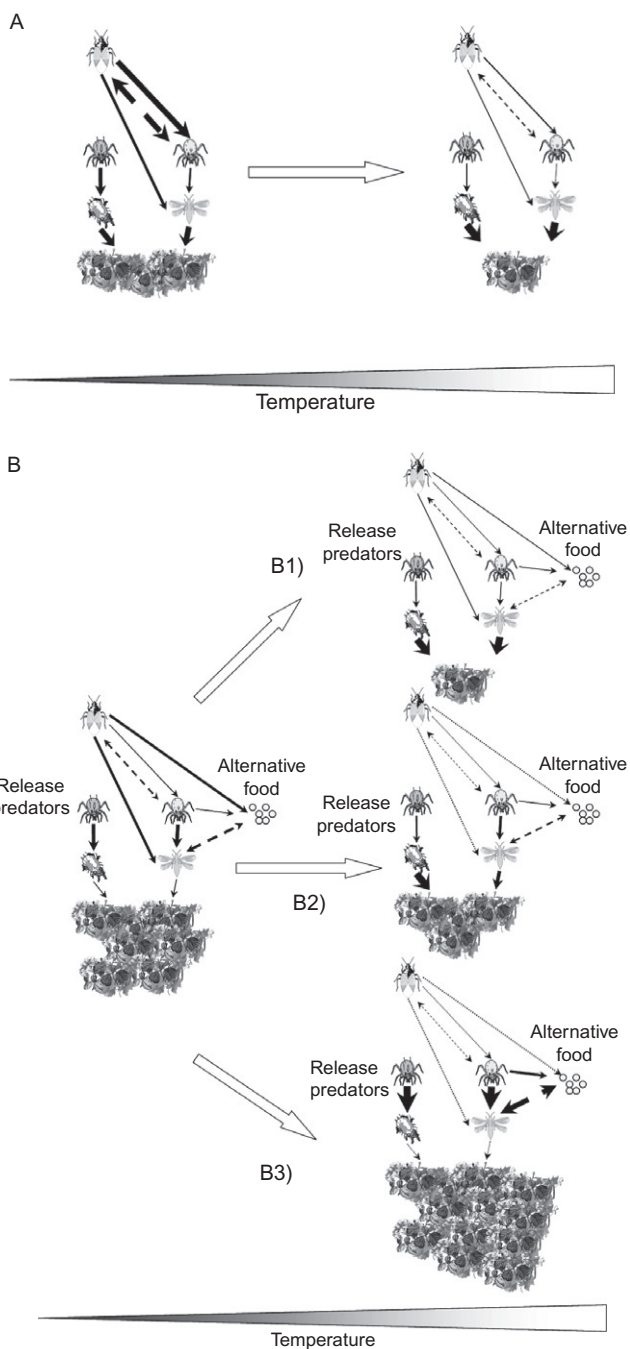
Figure 9 Temperature-dependent eco-evolutionary dynamics of a hypothetical agricultural food web. The food web is composed of two predatory mites, each one preying upon a different pest, spider mites or thrips, and a predatory bug, who is an IG-predator of one of the predatory mites, and is the inferior competitor for the pest they share. (A) Non-engineered biocontrol food web under global warming. (B) Three possible engineered scenarios of biocontrol under global warming. (B1) Engineered food web without previous artificial selection; (B2) Engineered food web with artificial selection

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

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

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

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in one direction (traits down), and only in the predatory bug; and (B3) Engineered food web with bidirectional artificial selection (traits up in predatory mites and down in the predatory bug). Selection and direction of the selection is designed to maximise trophic cascades. As an example, in the figure, the artificial selection could have acted on predation rates and/or on reproductive conversion efficiency. Solid arrows indicate trophic interactions. Dashed arrows indicate indirect predator–predator (competition) or indirect herbivore-alternative food (apparent competition) negative interactions. The strength of the lines indicates the interaction strength.

5. CONCLUSIONS

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

APPENDIX

mA is a semi–spatially explicit IBM implemented in the R language (R Development Core Team, 2012) which aims to simulate eco-evolutionary dynamics in food webs. In its current version (1.01), *mA* includes a single basal resource species (fungus), a single predator species (mesostigmata mite) and one single prey species (springtail or collembolan). Increasing the number of interacting species and allowing for Intraguild predation is merely a question of re-parameterisation and increasing computer time/demand. However, in the present simulations, the level of complexity is already substantial because predators and prey have ontogenies, genetic and phenotypic variability for 13 traits—4 of which are temperature plasticity traits—variable levels of genetically based phenotypic integration (or genotypic integration) and behavioural flexibility. In addition, the rules of movement, predator–prey encounter rates and the outcome of interactions consider both environmental factors and environmentally dependent state variables. Predator individuals are also able to feed on each other (cannibalism). Prey forage adaptively by searching for micro-patches with the lowest predator/resource ratio and predators also behave adaptively by searching for micro-patches with the lowest predator/prey ratio. Each loop through the program equals one day of simulated time. Figure 2 shows the flaw diagram describing the algorithm. The present simulations were run for up to 120 simulated days and stopped when this "time" elapsed or when either the predators or the fungi went extinct. This lasted in real time ca. 48 h when running 10 parallel sessions (replicates) in an Intel Workstation (Intel Core i7 990 Extreme Edition processor and 24GB DDR3 of RAM). A copy of the code used and the input files can be found at http://www.eeza.csic.es/eeza/documentos/mini–Akira_1.01.zip.

A.1. Space and basal resources

The model is semi–spatially explicit, with animals moving only in two alternative directions. The spatial scale is arbitrary and determined by the body size of individuals, their mobility and the productivity of the system. However, given the small body size of the animals simulated, the maximum distance between soil micro-sites in a real-World scenario would be in the order of a few centimetres. In the present simulations, the space of each micro-site is represented by 100 micro-patches which are located in a circle, thus animals that are located in micro-patch number 100 can go to micro-patch 1 and vice versa. Productivity of the basal resource can be or cannot be

spatially autocorrelated. When spatial autocorrelation is included, productivity peaks at the central patch (50) and decreases linearly towards the "edges" (patches 1 and 100). In all our simulations, there was spatial autocorrelation across micro-patches within the micro-site which included a gradient of carrying capacities going from 0.1 to 3 mg (peak of fungi biomass production at patch 50). Thus, K increased from patch to patch in steps of 0.06 mg. In each patch, the basal resource (fungi) grows according to a conventional logistic growth function, and its dynamics is updated following the following algorithm:

$$M_t = M_{t-1} + r_T M_{t-1}\left(1 - \frac{M_{t-1}}{K}\right) \qquad [A1]$$

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

$$r_T = \frac{e^{b - E(1/kT)}}{M_{t-1}^{1/4}} \qquad [A2]$$

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

A.2. Predator and prey traits with quantitative genetic basis

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

established genetically based trait variability within these limits. Thus, for each trait X, we describe the limits and the range used as follows:

$$l_X = L_X + \varphi\left(\frac{U_X - L_X}{2}\right) \tag{A3}$$

$$u_X = U_X - \varphi\left(\frac{U_X - L_X}{2}\right) \tag{A4}$$

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

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

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

energy tank at birth and after molting (tank_ini, ε_o): percentage of mass devoted to maintenance and future growth (L_X, U_X: 25–50% of body size which is added to make the total individual mass; Π_X, K_X: 0–100%). Individual body mass (M) is thus the sum of body size and the energy tank, both of which are also state variables.

voracity (v): maximal consumption rate per day (implemented as a scaling coefficient v which makes voracity to scale with body mass as $0.1\, M^v$). Source: Yodzis and Innes, 1992, DeRoos *unpublished notes*, which provide a fixed maximal consumption rate coefficient of 0.75; see also Englund et al., 2012 for variation around this value). For predators in the simulation, this parameter constrains the number of days in which they are actively searching for prey. If a predator catches a prey which surpasses the predator maximal consumption allowed per day, this predator will remain inactive as many days as necessary to digest this relatively large prey. L_X, U_X: 0.6–0.7; Π_X, K_X: 0.55–0.75.

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

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

$$\ln I = \ln I_0 + a \ln M - E\left(\frac{1}{kT}\right) \qquad [A5]$$

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

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

growth (g): Growth is a trait that determines how much an individual grows in each moulting event. Note that we are simulating arthropods which grow by moulting. Thus, this trait is not truly growth rate but growth ratio at moulting independently of the rate (t^{-1}) at which moulting occurs. Therefore, this trait determines how much of the available energy storage is allocated to fixed body parts in the next developmental stage (instar). As a fraction of the energy tank at moulting should be also allocated to the post-moulting energy

tank (see ε_o above), these two traits basically decide when an individual will moult. Growth is merely included as a ratio of the linear dimension of fixed (structural) body parts of the new (target) instar relative to the previous instar. We use relatively low ratios within the range of extensions of Dyar's rule for arthropod growth (Hutchinson et al., 1997). We fixed the number of instars in both predators and prey to be 4. Although some collembolans have indeterminate growth (i.e. they continue growing and moulting after maturation— Hopkin, 1997) for simplicity, we have not considered this trait here. L_X, U_X: predators, 1.01–1.2; prey, 1.01–1.1; Π_X, K_X: 1.01–1.2.

search area (search_area, m): Importantly, we distinguish between speed and mobility. Speed reflects sprint speed when trying to escape from a predator or trying to catch a prey. However, we consider mobility (search area) as how much one individual is able to move to search for resources or for safe patches. Lacking better information, the entire area covered in 1 day (m), scales with body size in a similar way as sprint speed: M^m. L_X, U_X: predators, 0.1–0.3; prey, 0.2–0.4; Π_X, K_X: 0.05–0.5. As we set body mass to be < 1 mg in the entire simulation, higher m coefficients mean lower mobility for the same body mass. Thus, in order to include efficient predators in the simulations, prey move less than predators. For translating mobility into actual search area in the simulation (see Section A.1), we used linear interpolation, translating the minimum M^m into moving one patch each day and the maximum possible (i.e. largest adult predators at the highest temperatures) into moving up to eight patches each day.

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

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

activation energy for metabolic rate (E_{met}, E in (Eq. A5)): To simulate the effect of climate change on eco–evolutionary dynamics, we also included, in addition to simulations at different temperatures, variability around E, which

will serve to study adaptive evolution around thermal sensitivity of metabolic rate, a form of thermal adaptation. Ranges were set around published coefficients for mesostigmata mites (predators) and springtails (Ehnes et al., 2011). L_X, U_X: predators, 0.3–0.5; prey, 0.55–0.75; Π_X, K_X: 0.3–0.75.

We further included three additional traits that represented variability in plasticity to temperature (Q_{10}) for three activity traits: voracity, speed and search area (vorQ_{10}, spdQ_{10} and srchQ_{10}, respectively). We used recent published accounts from a thorough review on temperature-dependent ecological traits in predator–prey interactions (Dell et al., 2011). For activity traits, we used Q_{10} (i.e. how many times a given trait increases for a 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. (A5) (Ehnes et al., 2011). In addition, Q_{10} values are more easily interpretable and converted to reaction norms. However, E can be easily approximated from Q_{10} by using equation 3 in Vasseur and McCann (2005). Jointly, this fourth module represents thermal plastic adaptation for mobility. For simplicity, we used for simulations a maximum temperature of 25 °C in simulations, which allowed us to use trait temperature dependences below optimal (the rises in the temperature performance curve, which shows an optimum at around 25 °C—Dell et al., 2011). Although animals would ideally benefit from being more active, this could also be detrimental because the potential increase in exposure to predators (e.g. Norrdahl and Korpimaki, 1998). Therefore, we expected this plasticity module to evolve differently in risky versus safe environments.

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

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

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

To estimate the effect of Q_{10} values in the simulation for all traits that involved temperature sensitivity, we used linear interpolation between the minimum and maximum temperatures used for all simulations (15–25 °C). Thus, real Q_{10} was used when a simulation was performed at 25 °C, and for simulations at intermediate temperatures, we estimated the value of Q (e.g. Q_7 at 22 °C) by interpolation between the two temperatures, which assumes linearity of Q across temperatures. As 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.3. Trait modularity and phenotypic integration

Phenotypic integration and phenotypic modularity explain how quantitative traits are inter-related among individuals in a population (Magwene, 2001; Pigliucci, 2003). Highly integrated organisms could be those in which their traits (both genetically and functionally) are strongly correlated to each other across individuals. The opposite would be to say that a highly integrated organism is an organism with low modularity, in which all traits are uncorrelated across individuals. For instance, if animals that are genetically aggressive also have high growth rates, we will say that animals are phenotypically integrated for the aggressive and growth rate traits. However, if these two traits show no correlation across individuals, the animals will have low integration of these traits. A module can be defined as a set of intercorrelated traits (across individuals) which is independent of another set of intercorrelated traits, being the latter a different module. The above 13 traits were initially (i.e. before evolution at time t_0) included in 5 modules, 4 modules with 3 traits each and a 5th module with a single trait (E_{met}). Each of the four three-trait modules included either all positive genetic correlations or two negative and one positive correlation among traits, reflecting genetic trade-offs. However, we would like to stress that trait correlations are implemented as an example to introduce our eco-evolutionary framework, but that such modules do not necessarily need to be arranged in this way in nature. In the future, we need to measure trait modularity and its genetic basis in animals embedded in food webs (e.g. Santos and Cannatella, 2011), and we hope that our approach encourages pursuing this line of research. Through the chapter, three-trait modules will be represented by trait names and two signs, one referring to the direction of correlation with the first trait (as read from left to right) and the other referring to the correlation with the second trait. For instance, in module 1, we have: tank_ini($-$,$-$), growth($-$,$+$) and pheno($-$,$+$), which means that animals which are born with more reserves invest less in growing; that is, they grow to a smaller size and increase their growth rate, and also are born earlier (or develop faster); and thus, animals that have a higher growth ratio do develop later. We stress that the latter pattern is also an ecological constraint, as everything else being equal, growing larger takes more time.

Therefore, here, the genetic constraint (negative correlation) parallels the ecological constraint. The other three three-trait modules were arranged as follows: Module 2, speed(+,+), met_rate(+,+), search_area(+,+); Module 3, size_ini(−,−), assim(−,+), voracity(−,+); Module 4, vorQ10(−,−), spdQ10(−,+), srchQ10(−,+). Therefore, a negative relationship between propagule size and voracity means that larger animals tend to be proportionally more voracious beyond body size constraints, as smaller voracity coefficients mean higher voracity. Similarly, higher assimilation efficiencies positively correlated with voracity coefficients mean that the more voracious animals are the least efficient at assimilating food, reflecting a potential trade-off between voracity and assimilation efficiencies. Finally, module 4 reflects trade-offs on thermal adaptation for mobility, as plastically responding to an increase in temperature by increasing voracity trades-off with increasing other mobility traits (either sprint speed or search area), therefore reflecting genetic constraints in plasticity. This allows us to first approach adaptive evolution of quantitative traits in the context of biotic interactions and climate change. However, despite previous believe, it has been recently shown that the sign and magnitude of genetic correlations can change depending on the environment, which suggests that they may constraint adaptive evolution in a lesser degree than previously thought (Sgró and Hoffmann, 2004). Once the underlying mechanisms are well understood (McKinnon and Pierotti, 2010; Roff and Fairbairn, 2007), this unconstrained form of plasticity integration will be easily incorporated in the present framework. However, for now, we adapt the more classic view of genetic correlations and G-matrices, which have been found to be stable under climate change in at least one study (Garant et al., 2008).

A.4. Quantitative Genetics and G-matrices

To assign a quantitative genetic basis to the traits, we assumed one chromosome per trait. Thus, each individual has 13 chromosome pairs. For simplicity, all animals are hermaphrodites and chromosomes are thus all autosomal. Each trait is determined by 20 loci with 10 possible alleles whose frequency is drawn from a uniform distribution. To induce genetic correlations among traits from pleiotropic effects, a number of loci were allowed to have effects on more than one trait (up to three within the same module). Stronger genetic correlations were achieved by increasing the number of loci shared by traits within a module. We defined the parameter ρ to set the number of common loci for pleiotropic effects as: $\rho = S_L/N_L$, where N_L is the total number of loci involved in the trait, and S_L is the number of pleiotropic loci (i.e. those shared with another trait). Thus, a higher ρ value means that the

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

A.5. State variables and the environmental component of phenotypic variation

Apart from switches and counters which denote, for instance, the age (instar) or the state (alive, dead, reproductive) of the animal, we include phenotypic state variables such as body size (animals grow) and energy tank (energy

stored for maintenance, growth or reproduction). Other traits do also change phenotypically with ontogeny and experience of individuals. Furthermore, all traits that are dependent on body size are state variables which get updated to their new value every day.

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

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

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

environmental component of voracity (voracity_tuned, V): each day, environmental effects add to the genetic component of voracity to determine the actual value of the trait. Relevant indirect environmental effects (e.g. the effect of temperature on metabolic rate) are those that affect overall body mass and its two components (*B* and ε). Fixed (structural) body size will then affect voracity following the scaling dependence of voracity on body mass. However, ε—in

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

$$V = 0.1M^{v}ceQ_{VT} \qquad [A6]$$

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

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

$$A \propto M^{m}ceQ_{AT} \qquad [A7]$$

where m is the genetically driven mobility scaling coefficient, and Q_{AT} is now the interpolated Q value at temperature T for search_area. Here, we do not include a normalisation coefficient accompanying M, as body mass

is transformed into number of patches moved per day by linear interpolation. The value of A is rounded to become an integer number of visited patches.

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

$$S = 4M^s c Q_{ST} \qquad \text{[A8]}$$

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

environmental component of assimilation efficiency (assim): Here, we incorporate recent evidence that predator–induced stress compromises the efficiency with which prey assimilate food (Hawlena and Schmitz, 2010a; Trussell et al., 2006). We used the maximum reduction documented from predatory stress (76%) and interpolated this value between 0 and the maximum number of encounters with predators per day (4). Thus, animals that encounter four predators in 1 day and successfully escape from them will have a 76% reduction in assimilation efficiency for the food ingested that day, animals that experience three encounters will have a 57% reduction, etc.

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

$$t = M^{1/4} e^{\{\beta[T(1+T/273)]+\alpha\}} \qquad \text{[A9]}$$

where β and α are the average slope (-0.12) and the intercept (6) of the original relationship, respectively (Fig. 1 in Gillooly et al., 2002), as calculated by least-squares regression across organisms, and M is total body mass in grams (Gillooly et al., 2002). This resulted in an average Q_{10} for developmental rate (t^{-1}) of 2.84, giving a decrease in developmental time by a factor of 0.35 for each increase of 10 °C in temperature (Q10pheno). To finally calculate birth dates, we multiplied the trait "pheno" by the above factor (for 25 °C), using linear interpolation for temperatures in the middle of the range (15–25 °C). We decided not to include the exact equation ap8 in the model because it would have lead to developmental rates being too short (less than 1 day for the highest temperature), thus impeding

variability in birth dates. Shorter timeframes (e.g. hours instead of days) would be necessary for the inclusion of the above equation to be meaningful for such small animals. Thus, we are assuming that birth dates are not only driven by temperature and mass but also by other factors (e.g. genetic).

temperature-dependent digestion time (Q10digest): When a prey is caught by a predator and this prey is larger than the daily maximal ingestion rate for the predator, digestion will take more than 1 day. The number of days for digesting a prey item equals the ratio between the mass of the prey and the maximal ingestion rate. During this period, the predator is inactive and cannot encounter any other predator or prey in the simulation. Temperature-dependent digestion times are included by multiplying the number of days by a 0.25 factor at $25\,^{\circ}C$ and interpolated between 1 and 0.25 for the range of 15–$25^{\circ}C$ otherwise. This shortening in digestion times with temperature have been obtained for a Q_{10} value on digestion rates of 4 (Dell et al., 2011).

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

A.6. Moving algorithm: Adaptive movement and previous experience

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

A.7. Moulting algorithm

The growth trait is a fixed value for each individual and sets the linear increment in fixed (structural) body size at each moult. Growth is a ratio between the linear structural size after moulting and the linear structural size

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

A.8. Reproductive algorithm

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

A.9. Descriptions of functions or submodels according to the ODD protocol (Grimm et al., 2006)

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

   crea_module: This function assigns genetic values to each of the three-trait modules for each individual, for which it uses the standard chromosome generated in crea_loci. Each individual gets 1 of the 10 uniformly distributed alleles at random for each locus and for each of the 3 chromosomes involved

in the module. The phenotypic values of all these traits, which have been assigned 0–1 values in crea_loci, are summed to estimate a naïve pseudo-phenotypic value which is then transformed to ecological phenotypic values by linear interpolation.

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

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

prey_move—version without predators: This function controls the adaptive movement of prey when predators are not present in the simulation. For each individual and movement, the three cells (current, left and right) are first screened for overall fungi biomass. Then the individual moves to (or remains in) the patch with highest biomass. When resources have been depleted from the three cells, the individual performs a jump across patches in random direction and which equals the number of patches of the trait A (searched area tuned by the environment, see main text) plus 2. This last number is added to avoid negative numbers in the function.

prey_move—version with predators: This function controls the adaptive movement of prey when predators are present in the simulation. For each individual and movement, the three cells (current, left and right) are first screened for overall fungi biomass and predator number. Then, values are interpolated to vary between 0 and 1 and the ratio P/B_f (predator abundance divided by fungi biomass) is used to move adaptively. The individual moves to (or remains in) the patch with the lowest P/B_f ratio. Again, when fungi resources have been depleted from the three cells, the individual performs a jump across patches in random direction and which equals the number of patches of the trait A plus 2. During this movement, we assume that prey do not encounter any predators other than in the arrival patch. For simplicity, we assume that prey are able to assess predator abundance with perfect precision but cannot assess neither predator identity nor the trait values of the predators.

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

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

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

$$P_t = w_A \cdot \left(\frac{W}{A_{max}} \right) + (1 - w_A) \cdot \left(\frac{V}{V_{max}} \right) \quad [\text{A10}]$$

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

4 day^{-1} at the highest temperature (25 °C) and for the maximum simulated predator/prey abundance ratio of 200/500. We then interpolated 0–3 predatory encounters to get the amount of induced stress to the new scale of 0–47% and added the resulting percentage to the energetic losses.

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

$$0.9(B_t + \varepsilon_t) \geq g^3 B_t + \varepsilon_0 g^3 B_t \qquad [\text{A11}]$$

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

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

$$0.9(B_t + \varepsilon_t) \geq \lambda\left(g^3 B_t + \varepsilon_0 g^3 B_t\right) \qquad [\text{A12}]$$

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

tunea_traits and *tunea_traits2:* These functions merely apply the equations to calculate the environmental contributions to V, A, S and the stress effect on "assim" (equations A6–A8).

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

predation_prey_move: This function includes the rules to decide when a predator and a prey interact provided that a prey moves to a new patch. Firstly, it calculates the probabilities that a prey entering a new path encounters each of the predators present in that cell (one probability for the

encounter with each of the predators). Secondly, if encounter occurs with a given predator, it calculates the probability that predation occurs. To decide the final outcome of the interaction, these two probabilities are contrasted with a random number (0–1) drawn from a uniform distribution. The probability of encounter (P_e) for a given predator–prey pair is calculated according to the following logistic function:

$$P_e = 1 \Big/ \left[1 + e^{-\left(\alpha + \beta V_{Pd} + \gamma V_{Py} + \delta V_{Pd} V_{Py} + \varepsilon B_{Pd} + \zeta B_{Py} + \eta B_{Pd} B_{Py}\right)} \right] \qquad [A13]$$

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

$$P_p = 1 \Big/ \left[1 + e^{-\left(\alpha + \beta V_{Pd} + \gamma R_B + \delta R_S\right)} \right] \qquad [A14]$$

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

   pred_assim: This algorithm converts the ingested prey into own predator mass.

pred_move: This function controls the adaptive movement of predators. For each individual and movement, the three cells (current, left and right) are first screened for prey and for predators and the total number of each recorded. Then, these values are interpolated to vary between 0 and 1 and the ratio P_d/P_y (predator abundance divided by prey abundance) is used to move adaptively. The individual moves to (or remains in) the patch with the lowest P_d/P_y. When prey have been depleted from the three cells, the individual performs a jump across patches in random direction and which equals the number of patches of the trait S (searched area tuned by the environment, see main text) plus 2. This last number is added to avoid negative numbers in the function. During this movement, we assume that predators do not interact with either prey or other predators. We assume that predators have perfect assessment of prey and predator abundance but that they cannot assess neither predator or prey identities nor the trait values of either prey or predators.

for_interaction_x1: This function is like "for_interaction" but from the point of view of predators behaving as the cannibal prey, thus counts how many other predators are in a cell.

for_interaction2_x1: This function is like for_interaction but from the predator point of view behaving as predator on shared prey and as the cannibal predator.

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

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

$$P_b = \tau \left\{ 1 \middle/ \left[1 + e^{-(\alpha + \beta V_{Pd} - \gamma B_{Pd} + \delta A - \varepsilon S)} \right] \right\} \qquad \text{[A15]}$$

where τ is a parameter that tunes the rate of background predation to set it to reasonably values for the simulation to run for a few generations (here, $\tau = 0.025$). This function was intended as a proxy of predation by larger predators and included all the traits that could explain predation if larger predatory species would be present. Hence, this probability depends positively on the voracity and the area searched, both of which increase the probability of encounter with predators, and negatively on body size and sprint speed, both of which decrease the probability of predation by predators. Again, the coefficients ($\alpha...\varepsilon$: a random number (0–1) drawn from a

uniform distribution) are naïve and give approximately equal weight to each trait according to its range of values. Also, to decide the outcome, P_b was compared with a random 0–1 number drawn from a uniform distribution.

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

$$N = \frac{E_r}{(B_0 + \varepsilon_0 B_0)} \qquad [A16]$$

$$E_r = \varepsilon_t - \lambda \varepsilon_{min} \qquad [A17]$$

$$\varepsilon_{min} = 0.1 B_t \qquad [A18]$$

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

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

Table A1 Results of GLMs showing trait × environment (O-matrix) interactions in fitness reflecting differences in directional selection for two levels of genetic correlation across 13 traits spread in 5 phenotypic modules

Trait/environment	ρ=0.1			ρ=0.9		
	LR-Chisq	df	*p*-Value	LR-Chisq	df	*p*-Value
PREDATORS	477.8	1	<0.0001	305.9	1	<0.0001
TEMP	32.5	2	<0.0001	75.9	2	<0.0001
assim	66	1	<0.0001	38.1	1	<0.0001
met_rate	99.4	1	<0.0001	60.7	1	<0.0001
size_ini	7.4	1	0.0064	5.3	1	0.0213
tank_ini	92	1	<0.0001	15.2	1	<0.0001
voracity	192.3	1	<0.0001	56.1	1	<0.0001

Table A1 Results of GLMs showing trait × environment (O-matrix) interactions in fitness reflecting differences in directional selection for two levels of genetic correlation across 13 traits spread in 5 phenotypic modules—cont'd

Trait/environment	ρ=0.1			ρ=0.9		
	LR-Chisq	df	*p*-Value	LR-Chisq	df	*p*-Value
pheno	2.7	1	0.1	3.8	1	0.0513
search_area	32.6	1	<0.0001			
growth	149.2	1	<0.0001	53.3	1	<0.0001
speed	0.1	1	<0.8182	7.5	1	0.0062
actE_met	4749.8	1	<0.0001	5071.4	1	<0.0001
vorQ10	20	1	<0.0001	68.9	1	<0.0001
spdQ10	2.6	1	0.1059	6.8	1	0.009
srchQ10	8.4	1	0.0037	6.6	1	0.0099
PREDATORS × TEMP	32.9	2	<0.0001	74.2	2	<0.0001
PREDATORS × assim	56.3	1	<0.0001	41.6	1	<0.0001
PREDATORS × met_rate	88.5	1	<0.0001	56.1	1	<0.0001
PREDATORS × size_ini	8.2	1	0.0041			
PREDATORS × tank_ini	80.7	1	<0.0001	13.1	1	0.0003
PREDATORS × voracity	156.8	1	<0.0001	46.8	1	<0.0001
PREDATORS × pheno	2.6	1	0.1048	5.1	1	0.0237
PREDATORS × search_area	22.9	1	<0.0001			
PREDATORS × growth	123.3	1	<0.0001	46	1	<0.0001
PREDATORS × speed	0	1	0.8641	5.6	1	0.0183
PREDATORS × actE_met	1205.3	1	<0.0001	1367.9	1	<0.0001
PREDATORS × vorQ10	16.5	1	<0.0001	47.6	1	<0.0001
PREDATORS × spdQ10	4.3	1	0.0381	8.2	1	0.0041
PREDATORS × srchQ10	10	1	0.0015	5.7	1	0.0169
TEMP × assim	15	2	0.0006	14.7	2	0.0006
TEMP × met_rate	24.7	2	<0.0001	18.8	2	<0.0001
TEMP × size_ini				17.2	2	0.0002

Continued

Table A1 Results of GLMs showing trait × environment (O-matrix) interactions in fitness reflecting differences in directional selection for two levels of genetic correlation across 13 traits spread in 5 phenotypic modules—cont'd

Trait/environment	$\rho=0.1$			$\rho=0.9$		
	LR-Chisq	df	*p*-Value	LR-Chisq	df	*p*-Value
TEMP × tank_ini	35.1	2	<0.0001	6.5	2	0.0385
TEMP × voracity	34.8	2	<0.0001			
TEMP × pheno	13	2	0.0015			
TEMP × growth	41.3	2	<0.0001	21.5	2	<0.0001
TEMP × speed	5.7	2	0.0566			
TEMP × actE_met	44.1	2	<0.0001	104	2	<0.0001
TEMP × vorQ10	12.6	2	0.0019			
TEMP × srchQ10	27.8	2	<0.0001	31.8	2	<0.0001
PREDATORS × TEMP × assim	12.5	2	0.002			
PREDATORS × TEMP × met_rate	23.8	2	<0.0001	17.8	2	0.0001
PREDATORS × TEMP × tank_ini	31.2	2	<0.0001	6.1	2	0.0477
PREDATORS × TEMP × voracity	33.2	2	<0.0001			
PREDATORS × TEMP × pheno	11	2	0.0041			
PREDATORS × TEMP × growth	42.2	2	<0.0001	21.4	2	<0.0001
PREDATORS × TEMP × speed	7.9	2	0.0193			
PREDATORS × TEMP × actE_met	44.9	2	<0.0001	106.2	2	<0.0001
PREDATORS × TEMP × vorQ10	13.4	2	0.0012			
PREDATORS × TEMP × srchQ10	19.9	2	<0.0001	34.1	2	<0.0001

The models were selected by stepwise AIC ($N=15{,}000$ individuals pooled from five replications of each environmental combination).

Table A2 Selection gradients of prey in two contrasting environments and for two levels of genetic correlation among traits

	16 °C Predators absent				25 °C Predators present			
	β/γ	SE	*t*	*p*-Value	β/γ	SE	*t*	*p*-Value
(a) $\rho = 0.1$								
(Intercept)	1.01	0.01	70.1	<0.0001	0.82	0.03	31.6	<0.0001
actE_met	0.69	0.01	68.4	<0.0001	0.99	0.02	47.8	<0.0001
srchQ10	0.00	0.01	0.0	0.9659	0.01	0.02	0.5	0.5973
growth	−0.01	0.01	−0.9	0.3823	0.02	0.02	0.8	0.4092
assim	0.02	0.01	2.4	0.0180	0.03	0.02	1.4	0.1687
met_rate	0.02	0.01	1.9	0.0568	0.04	0.02	1.8	0.0691
size_ini	0.01	0.01	1.2	0.2301	−0.01	0.02	−0.4	0.6808
tank_ini	0.00	0.01	−0.3	0.7378	0.01	0.02	0.7	0.4750
voracity	−0.02	0.01	−1.9	0.0614	−0.04	0.02	−1.9	0.0580
pheno	0.01	0.01	1.0	0.3187	0.03	0.02	1.4	0.1604
search_area	0.01	0.04	0.6	0.5528	0.02	0.02	1.1	0.2610
speed					0.02	0.02	0.9	0.3841
vorQ10	0.02	0.01	1.7	0.0989	0.10	0.02	4.9	<0.0001
spdQ10	0.01	0.01	1.3	0.1830	0.10	0.02	0.9	0.3573

Continued

Table A2 Selection gradients of prey in two contrasting environments and for two levels of genetic correlation among traits—cont'd

	16 °C Predators absent				25 °C Predators present			
	β/γ	SE	t	p-Value	β/γ	SE	t	p-Value
I(growth$^\wedge$2)	0.08	0.02	5.7	<0.0001				
I(actE_met$^\wedge$2)	−0.10	0.02	−6.6	<0.0001	0.38	0.04	12.2	<0.0001
actE_met × srchQ10	0.02	0.01	2.4	0.0176	0.03	0.02	1.7	0.0957
actE_met × growth	0.04	0.01	3.9	0.0001	0.08	0.02	3.6	0.0004
actE_met × met_rate	−0.02	0.01	−2.1	0.0366				
actE_met × voracity					−0.03	0.02	−1.4	0.1576
actE_met × pheno					0.04	0.02	1.7	0.0834
actE_met × vorQ10					0.07	0.02	3.2	0.0013
srchQ10 × search_area					0.05	0.02	2.4	0.0168
srchQ10 × spdQ10					−0.04	0.02	−1.9	0.0628
srchQ10 × voracity	0.02	0.01	2.4	0.0146				
growth × size_ini	0.01	0.01	0.8	0.4170				
growth × voracity	0.01	0.01	1.4	0.1583				
growth × vorQ10	−0.02	0.01	−2.1	0.0393				
assim × tank_ini	−0.02	0.01	−1.7	0.0806				

assim × met_rate					−0.03	0.02	−1.4	0.1590
assim × pheno					0.03	0.02	1.3	0.2090
assim × search_area	−0.02	0.01	−1.9	0.0623	0.03	0.02	1.3	0.2060
assim × vorQ10	0.02	0.01	2.0	0.0459				
met_rate × tank_ini	−0.02	0.01	−1.8	0.0681				
size_ini × spdQ10	−0.02	0.01	−1.6	0.1085				
size_ini × voracity					−0.03	0.02	−1.3	0.1825
size_ini × speed					0.04	0.02	1.9	0.0555
tank_ini × voracity					−0.04	0.02	−2.0	0.0480
tank_ini × pheno	−0.02	0.01	−2.0	0.0438	−0.05	0.02	−2.3	0.0227
tank_ini × vorQ10					0.04	0.02	2.1	0.0403
voracity × speed					0.04	0.02	2.0	0.0510
voracity × vorQ10					−0.04	0.02	−1.7	0.0964
voracity × spdQ10					−0.03	0.02	−1.2	0.2335
pheno × search_area	−0.02	0.01	−2.1	0.0344				

Continued

Table A2 Selection gradients of prey in two contrasting environments and for two levels of genetic correlation among traits—cont'd

	16 °C Predators absent				25 °C Predators present			
	β/γ	SE	*t*	*p*-Value	*β/γ*	SE	*t*	*p*-Value
(b) *ρ*=0.9								
(Intercept)	1.00	0.02	56.9	<0.0001	0.86	0.03	25.962	<0.0001
actE_met	0.67	0.01	70.1	<0.0001	0.95	0.02	48.216	<0.0001
srchQ10	0.01	0.02	0.3	0.7441	−0.01	0.05	−0.179	0.8577
growth	0.02	0.02	1.3	0.1839	0.02	0.05	0.409	0.6826
assim	−0.03	0.02	−1.2	0.2380	0.06	0.05	1.28	0.2006
met_rate	0.05	0.02	2.5	0.0110	0.04	0.04	0.892	0.3722
Size_ini	−0.03	0.02	−1.4	0.1706	0.02	0.05	0.361	0.7184
tank_ini					−0.07	0.05	−1.403	0.1607
voracity	−0.01	0.03	−0.3	0.7305	−0.08	0.05	−1.441	0.1498
pheno	0.02	0.02	1.3	0.2087	0.00	0.04	−0.041	0.9671
search_area	−0.04	0.02	−1.6	0.1200	−0.09	0.05	−1.96	0.0501
speed	0.02	0.02	1.0	0.3173	0.11	0.04	2.468	0.0136
vorQ10	−0.03	0.02	−1.1	0.2913	0.10	0.05	1.908	0.0565
spdQ10	−0.06	0.02	−2.6	0.0085	−0.02	0.05	−0.335	0.7375

l(growth^2)	0.04	0.02	1.5	0.1224				
l(actE_met^2)	−0.08	0.01	−6.1	<0.0001	0.26	0.01	9.642	<0.0001
actE_met × srchQ10	−0.05	0.02	−2.3	0.0198	−0.07	0.02	−3.458	0.0006
actE_met × growth	0.13	0.02	7.3	<0.0001	0.11	0.02	5.509	<0.0001
actE_met × assim					0.08	0.04	1.794	0.0730
actE_met × met_rate	−0.03	0.01	−2.7	0.0076				
actE_met × size_ini	−0.04	0.02	−1.9	0.0582				
actE_met × voracity	−0.06	0.02	−2.9	0.0033	−0.14	0.04	−3.121	0.0018
actE_met × pheno	−0.04	0.02	−2.2	0.0290				
actE_met × vorQ10	−0.05	0.02	−2.3	0.0237				
srchQ10 × growth	0.03	0.02	1.6	0.1044	0.14	0.06	2.337	0.0195
srchQ10 × tank_ini					0.07	0.05	1.518	0.1291
srchQ10 × assim	0.13	0.05	2.7	0.0071				
srchQ10 × voracity	−0.11	0.05	−2.2	0.0305				
srchQ10 × pheno	−0.03	0.02	−1.5	0.1403				
srchQ10 × search_area	0.05	0.02	2.2	0.0286	0.12	0.05	2.104	0.0355
srchQ10 × speed					−0.04	0.04	−1.025	0.3053

Continued

Table A2 Selection gradients of prey in two contrasting environments and for two levels of genetic correlation among traits—cont'd

	16 °C Predators absent				25 °C Predators present			
	β/γ	SE	t	p-Value	β/γ	SE	t	p-Value
srchQ10 × spdQ10	0.01	0.01	1.7	0.0968				
growth × size_ini					0.07	0.05	1.516	0.1298
growth × search_area					0.12	0.07	1.691	0.0910
growth × speed					−0.11	0.07	−1.599	0.1101
growth × spdQ10					−0.10	0.05	−1.787	0.0741
growth × met_rate	0.01	0.01	1.4	0.1652				
growth × phenol	0.01	0.02	0.6	0.5715				
assim × met_rate	−0.02	0.02	−1.3	0.1855				
assim × size_ini	0.04	0.02	2.0	0.0455	0.02	0.01	1.406	0.1598
assim × voracity	0.05	0.02	2.2	0.0264				
assim × search_area	0.12	0.05	2.7	0.0072				
assim × tank_ini					0.12	0.05	2.275	0.0230
assim × pheno					0.07	0.04	2.015	0.0440
assim × speed	−0.07	0.04	−1.7	0.0893	−0.06	0.03	−1.734	0.0830
assim × vorQ10	0.12	0.05	2.4	0.0186				

Term	Est	SE	t	p	Est	SE	t	p
met_rate × size_ini					0.18	0.09	1.989	0.0469
met_rate × voracity					0.17	0.09	1.923	0.0546
met_rate × pheno					0.07	0.04	1.719	0.0857
met_rate × search_area	−0.03	0.02	−1.6	0.1041				
met_rate × speed	0.03	0.02	1.6	0.1111				
met_rate × search_area					0.04	0.03	1.205	0.2284
size_ini × tank_ini					0.12	0.06	2.073	0.0383
size_ini × search_area					−0.20	0.08	−2.371	0.0178
size_ini × spdQ10					0.04	0.02	2.047	0.0407
tank_ini × phenol					−0.03	0.02	−1.808	0.0708
voracity × search_area					−0.17	0.08	−2.027	0.0428
pheno × search_area					−0.14	0.07	−1.865	0.0624
pheno × speed					0.09	0.07	1.322	0.1864
pheno × vorQ10					0.13	0.05	2.696	0.0071
pheno × spdQ10					0.11	0.05	2.07	0.0386
search_area × speed					−0.04	0.03	−1.339	0.1808
search_area × spdQ10					−0.09	0.04	−2.213	0.0270
voracity × search_area	−0.12	0.04	−2.8	0.0060				
voracity × speed	0.07	0.04	−1.7	0.0979				
voracity × vorQ10	−0.10	0.05	−2.0	0.0457				
search_area × vorQ10	0.04	0.02	1.7	0.0855				

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

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

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